

## A molecular and morphological review of the asterinid, *Patiriella gunnii* (Gray) (Echinodermata: Asteroidea)

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### Abstract

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The six-rayed species of the asterinid genus *Patiriella* Verrill from the rocky shallows of southern Australia are reviewed. Based on molecular and morphological evidence, it is judged that *Patiriella brevispina* H.L. Clark is a junior synonym of *Patiriella gunnii* (Gray). Three new species are described: *Patiriella medius* sp. nov., *Patiriella occidens* sp. nov. and *Patiriella oriens* sp. nov. A key to the four species of *Patiriella* is provided.

### Keywords

Echinodermata, Asteroidea, *Patiriella*, new species, taxonomy, Australia

### Introduction

Typically, six-rayed asterinid seastars that occur on the rocky coast of southern Australia are currently referred to either the variably-coloured *Patiriella gunnii* (Gray, 1840) or dark-crimson *Patiriella brevispina* H.L. Clark, 1938. Molecular evidence indicated to Hart et al. (1997) and Byrne et al. (1999) that there were genetically divergent eastern and western forms of what is currently referred to as *P. gunnii* in southern Australia, and that a taxonomic revision was necessary.

Gray (1840) described *Asterina gunnii* from material sent to the British Museum (Natural History) (BMNH, now The Natural History Museum, London) from “Van Diemen’s Land” (Tasmania, Australia) by Ronald Gunn. One lot (four specimens, BMNH 40.3.9.10–13) was collected from Sandy Bay, Hobart, in south-eastern Tasmania, and has a note “presumably syntypes, judging from source and Gray’s label.” A second lot (numerous specimens, BMNH 49.11.19) was from George Town, northern Tasmania, and was considered by A.M. Clark (1966) to be “presumably the types.” Dartnall (1970) established one of the Hobart specimens as a lectotype (BMNH 40.3.9.10), and three of the George Town specimens as paralectotypes (BMNH 49.11.19–10, 14, 33). The type locality is thus the Derwent River estuary at Hobart. Verrill (1913) referred *Asterina gunnii* Gray, 1840 to his new genus *Patiriella*.

The lectotype and only one of the paralectotypes (BMNH 49.11.19.33) were present when the BMNH collection was seen by O'Loughlin in April 2002. Two paralectotypes (BMNH 49.11.19.10 and 14) were absent and the remaining individuals from George Town comprised a mixture of *Patiriella* species.

H.L. Clark (1938) correctly distinguished as discrete species variably-coloured and crimson forms of *P. gunnii*. Without reference to the types of *P. gunnii*, he referred the variably-coloured form to *P. gunnii*, and described the crimson form as a new species, *Patiriella brevispina* H.L. Clark, 1938. In this study the taxonomic status of six-rayed species of *Patiriella* is re-assessed after further collecting across southern Australia, and reference to molecular evidence and morphological examination of specimens in the Australian Museum, Sydney (AM), Museum Victoria, Melbourne (NMV), South Australian Museum, Adelaide (SAM), Tasmanian Museum, Hobart (TM), and Western Australian Museum, Perth (WAM). We set out to show by morphological comparison of the lectotype of *P. gunnii* (type locality, Hobart) with the paratypes of *P. brevispina* (type locality, Bunbury in southern Western Australia) that the crimson *P. brevispina* is conspecific with *P. gunnii*, and is thus a junior synonym. The typically six-rayed asterinid seastars which occur in southern Australia are thus the dark crimson *P. gunnii* and three new variably-coloured species described below.

In a few cases it has been possible to assign mentions of “*Patiriella gunnii*” in the literature to one of the species referred to below, and this has been done in the synonymies, but in most cases this has not been possible. Authors who have referred to “*Patiriella gunnii*” are: Lamarck (1816, as *Asterias calcar* variety b; synonymy by Perrier (1876)); Müller and Troschel (1842, as *Asteriscus australis* (part) and *Asteriscus diesingi*; synonymies by Perrier (1876)); Dujardin and Hupé (1862, as *Asteriscus calcar*; synonymy by Perrier (1876)); Perrier (1869,

as *Asteriscus exiguus*; synonymy by Perrier (1876)); Perrier (1876, as *Asterina gunnii*); Sladen (1889, as *A. gunnii*); McCoy (1890, as *A. gunnii*); Farquhar (1895 and 1898, as *A. gunnii*); Verrill (1913, as *Patiriella gunnii*); Fisher (1919); H.L. Clark (1928, 1938, 1946); Cotton and Godfrey (1942); A.M. Clark (1966); Shepherd (1968); Dartnall (1969, 1971, 1980); Rowe and Vail (1982); Zeidler and Shepherd (1982); A.M. Clark (1983); O'Loughlin (1984); A.M. Clark and Downey (1992); Marsh and Pawson (1993); A.M. Clark (1993); Rowe and Gates (1995); Campbell and Rowe (1997); Edgar (1997). The presence of six-rayed specimens of *Patiriella regularis* Verrill, 1867 (normally five-rayed) in New Zealand led to reports by Müller and Troschel (1842 (part), as *Asteriscus australis*), Perrier (1876) and Mortensen (1925) that *Asterina gunnii* occurred in New Zealand. Farquhar (1898) considered the six-rayed material to be *P. regularis*.

## Genetics

**Methods.** Sixty ethanol-preserved specimens provisionally identified as *P. 'gunnii'* (21 locations) and 18 provisionally identified as *P. 'brevispina'* (9 locations), sampled from a broad geographic range, were included in genetic analyses. Genomic DNA was extracted from tube foot tissue using a 5% chelex solution (Walsh et al., 1991) or a CTAB-proteinase K extraction buffer (Saghai-Marooft et al., 1984). A 1580 base pair (bp) portion of the mitochondrial cytochrome oxidase I gene (COI) and the adjacent tRNA-Pro was amplified and sequenced using universal primers F210-COI (5' GGTAATGCCAATTATGATTGG 3') and COII 14098-14078 (5' CCTARTTGGGTTTCARTTTGCC 3') (Hart et al., 1997). Subsequently, an internal 830 bp fragment was amplified and sequenced for all specimens using specific primers GUN COI-L (5' TCCCAAAGCTATCATTCT 3') and GUN COI-R (5' AGAGATCATTCCAAATCC 3').

PCR (polymerase chain reaction) amplifications (25 µl) contained 50 mM KCl, 10 mM Tris-HCl pH 8.3, 0.1% Triton X-100, 0.005% gelatine, 1.5 mM MgCl<sub>2</sub>, 800 µM dNTPs, 0.5 µM of each primer, 0.75 units of Taq DNA polymerase, and 1 µl of extracted DNA. All amplifications were performed in a PTC-100 cycler (MJ Research, Watertown, MA) with 40 cycles of 94°C 1 min, 48°C 30 sec, 72°C 30 sec. PCR products were purified with a High-Pure PCR Product Purification Kit (Roche, Mannheim, Germany) and sequenced using an ABI Prism Big-Dye kit. Completed reactions were purified by ethanol precipitation prior to electrophoresis on an automated DNA sequencer (Perkin Elmer, Foster City, CA).

Phylogenetic analysis of aligned DNA sequence data was performed under maximum parsimony (MP) using PAUP 4.0b10 (Swofford, 1998). Phylogenetic confidence was estimated by bootstrapping (Felsenstein, 1985) with 500 replicate data sets analysed with the "full heuristic" option. Published COI sequences from *P. 'gunnii'* (U50047-48), *P. 'brevispina'* (U50049-50) and *P. calcar* (U50046) (Hart et al., 1997) were also included in analyses. Genetic divergences were calculated using the Kimura (1980) 2-parameter model of sequence evolution.

**Results.** Phylogenetic analysis of DNA sequence data yielded over 1000 equally parsimonious trees (863 steps; Fig. 1). However, bootstrap analysis revealed strong phylogenetic structure among haplotypes, with four well-supported clades (100% bootstrap support). Three of the clades corresponded to the so-called *P. 'gunnii'* samples, and the fourth to the so-called *P. 'brevispina'* (Fig. 1). All four clades were deeply divergent

(7.5–14.1%), and all were supported by strict consensus analysis of 1000 MP trees. By contrast, haplotypes within each clade exhibited small divergences (typically less than 1.0%) and showed little phylogenetic structure.

Strong phylogeographic structure was detected within *P. 'gunnii'*: all eight Western Australian samples were placed in a western clade, whereas all seven sequences from New South Wales were placed in an eastern clade. The eastern clade was also detected in Victoria and Tasmania, and the western clade was also represented in South Australia. Although no geographic overlap was detected between eastern and western clades, a third central clade exhibited an intermediate distribution, encompassing Tasmania, Victoria, and South Australia (Fig. 1). There was moderate bootstrap support (73%) for a sister relationship between central and western clades.

## Morphology

**Methods.** Specimens for which molecular sequences were obtained, and consequent clades established, were used for the selection of morphological diagnostic characters (MOL codes in lists of material, refers to the code of the tissue sample used to obtain sequence data for molecular phylogeny). These morphological characters were then used to identify specimens in Australian museums. Descriptions of species are based on a combination of observations of specimens in wet and dried and cleared condition. Some specimens were cleared of surface spines and spinelets and thin body wall (skin) using commercial bleach, in order to more clearly observe skeletal plate form and size, and the numbers of secondary plates and papulae in papular spaces. Diagnostic characters are most readily observed on dried and cleared specimens. Most diagnostic characters were found to vary and in many cases to overlap amongst the four species. An attempt was made to relate species and size of specimen to numbers of carinal plates on a ray, width of proximal carinal plates, numbers of spinelets on proximal carinal plates, and length of actinal spines, but these characters were found to be so variable that they were unreliable for diagnostic purposes. Morphological characters finally selected for diagnostic purposes all vary within a species and with size. For determination, more than one diagnostic character is most reliable.

Terminology follows that defined in the glossary and illustrated in Clark and Downey (1992, figs 2, 3), except that "papular space" is used for "papular area" ("restricted area with papular pores") and "papulate areas" is used to refer to the parts of the abactinal surface where papulae occur. "Adradial" refers to the series of actinal interradial plates adjacent to the ambulacral plates.

**Results.** The morphological analysis confirmed the existence of four six-rayed species of *Patiriella*, corresponding to the four clades established in the molecular study: *Patiriella gunnii* (Gray, 1840) to the so-called *P. 'brevispina'* clade; *Patiriella medius* sp. nov. to the central clade; *Patiriella occidentalis* sp. nov. to the western clade; and *Patiriella oriens* sp. nov. to the eastern clade (Fig. 1).

## Asterinidae Gray, 1840

### *Patiriella* Verrill, 1913

**Synonymy and remarks.** O'Loughlin et al. (2002) reviewed the status of *Patiriella* Verrill, 1913, and noted that recent molecular phylogenetic analyses of species of Asterinidae (Hart et al., 1997; Byrne et al., 1999; J. M. Waters and M. S. Roy, unpubl.

data) were beginning to provide a basis for a reassessment of asterinid taxonomy. Pending publication of a review of the assignment of species to genera within Asterinidae, the four species treated in this work are retained provisionally in *Patiriella*, most recently diagnosed by Campbell and Rowe (1997).

### Key to six-rayed species of *Patiriella*

1. Subambulacral spines predominantly 1 per plate, up to twice length of adradial actinal spines; actinal interradial spines very short, frequently bulbous; abactinal surface uneven; abactinal spinelets prominently spinous, frequently low to subcapitate; proximal papular spaces large, frequently with more than 10 secondary plates and more than 10 papulae per space when  $R = 30$  mm; abactinal colour of adults consistently uniform crimson to brownish red, tube feet orange . . . . . *Patiriella gunnii* (Gray, 1840)
- Subambulacral spines predominantly 2–3 per plate, not up to twice the length of adradial actinal spines; actinal interradial spines not very short or bulbous; abactinal surface even; abactinal spinelets moderately to minutely spinous, frequently columnar; proximal papular spaces not large, fewer than 10 secondary plates and 10 papulae per space when  $R = 30$  mm; abactinal colour variable, not uniform crimson to brownish red, with orange tube feet . . . . . 2
2. At least a few suboral spines frequently present; adradial actinal spines up to about two-thirds length of subambulacral spines; actinal interradial spines short and fine; carinal plates normally doubly papulate for less than two-thirds ray length, frequently less than half ray length; proximal papular spaces small, frequently up to 3 secondary plates and 3 papulae per space when  $R = 30$  mm; abactinal spinelets relatively small and fine, predominantly narrowing distally, minutely spinous; abactinal colour variable, frequently overall maroon red (not reported with grey or blue, or with black disc); actinal colour off-white, frequently with prominent flecking . . . . . *Patiriella medius* sp. nov.
- Suboral spines rarely present; adradial actinal spines frequently more than two-thirds length of subambulacral spines; actinal interradial spines digitate; carinal plates normally doubly papulate for more than half ray length, frequently more than two-thirds ray length; proximal papular spaces fairly open, frequently with about 6 secondary plates and 6 papulae per space when  $R = 30$  mm; abactinal spinelets relatively coarse, predominantly columnar, slightly narrowing to slightly widening distally, moderately spinous; abactinal colour variable, not overall maroon red . . . . . 3
3. Form variable, commonly distinctive short rays with interradial margin deeply indented; subambulacral spines frequently projecting fairly prominently; abactinal spinelets coarse, columnar, moderately spinous, frequently widened distally; up to about 8 spinelets on inferomarginal plates when  $R = 20$  mm, up to about 11 when  $R = 30$  mm; abactinal colour frequently dark, with grey or brown or blue, infrequently with red . . . *Patiriella occidens* sp. nov.

- Form variable, commonly subhexagonal with interradial margin slightly incurved; subambulacral spines not projecting significantly; abactinal spinelets fairly coarse, columnar, moderately spinous, frequently narrowing distally, up to about 10 spinelets on inferomarginal plates when  $R = 20$  mm, up to about 15 when  $R = 30$  mm; abactinal colour frequently pale, with white or pink or mauve or orange or bright red, disc frequently black (not reported with grey (except in NSW), or blue) . . . . . *Patiriella oriens* sp. nov.

### *Patiriella gunnii* (Gray)

Figures 1 (as *P. 'brevispina'*), 2a–f, 3a–f, 7b

*Asterina gunnii* Gray, 1840: 289–290.—Gray, 1866: 16.—McCoy, 1890: 372, pl. 200 fig. 2 (part).

*Patiriella gunnii*.—Verrill, 1913: 484.—Dartnall, 1970: 74–76, pl. 1.

*Patiriella brevispina* H.L. Clark, 1938: 166–167, pl. 22 figs 2–3.—Cotton and Godfrey, 1942: 202.—H.L. Clark, 1946: 134–135.—A.M. Clark, 1966: 320.—Shepherd, 1968: 745, 747.—Dartnall, 1969: 55.—Dartnall, 1970: 75–76.—Dartnall, 1971: 47, fig. 1.—Dartnall, 1980: 34, 65.—Rowe and Vail, 1982: 222.—Zeidler and Shepherd, 1982: 402, 412; figs 10.7c, d.—O'Loughlin, 1984: 136.—Bennett, 1987: 346–347, fig.—Rowe and Gates, 1995: 39.—Campbell and Rowe, 1997: 130.—Edgar, 1997: 346, fig.—Hart et al., 1997: 1848–1861, figs 1–4, tabs 1, 2.—Byrne et al., 1999: 188–191, figs 1, 3C, 6 (new synonymy).

**Material examined.** *Asterina gunnii* Gray, 1840. Australia, Tasmania, Hobart, Sandy Bay, 2 m, R. Gunn, BMNH 40.3.9.10 (Lectotype: dry; partly cleared; designation by Dartnall, 1970); BMNH 40.3.9.-11, 12, 13 (3 specimens).

*Patiriella brevispina* H.L. Clark, 1938. Western Australia, Koombana Bay, Bunbury, 9–14 m, E.W. Bennett and H.L. Clark, 26 Oct 1949, AM J6181 (2 paratypes, dry).

Other material (selected for molecular confirmation, distribution and depth data). **Vic.** East Gippsland, off Ninety Mile Beach, 38°42' S, 147°53' E, 22 m, NMV F73255 (1); Western Port, Honeysuckle Point, TM H723 (4); Flinders, ocean platforms, NMV F71744 (3) (MOL 54); NMV F93430 (1) (MOL 180); NMV F93429 (1) (MOL 10); NMV F93435 (4) (MOL 130–131); Port Phillip Bay, Altona, NMV F72130 (1) (MOL 53); Geelong, Mackey St jetty, 2 m, NMV F93441 (1) (MOL 51, 56); "Mullet Holes", 10 km NE Apollo Bay, NMV F93433 (3) (MOL 97–99); Port Fairy, Griffith I., rocky shallows, NMV F93432 (1) (MOL 81); Portland, below lighthouse, 2–3 m, NMV F93440 (1). **Tas.** Eaglehawk Neck, rocky shallows, NMV F71873 (1); Bass Strait, Cape Portland, TM H596 (1); Jacobs Boat Harbour, TM H2941 (1). **SA.** Gulf Saint Vincent, Normanville, NMV F74628 (1) (MOL 60); NMV F74629 (1) (MOL 59); NMV F93434 (1) (MOL 111); NMV F93436 (1) (MOL 102); Eyre Peninsula, Point Westall, near Streaky Bay, NMV F93437 (1) (MOL 55); Nuyts Archipelago, Goat I., 29 m, NMV F93446 (1). **WA.** Esperance, Sandy Hook I., WAM Z9471 (1); Busselton, jetty piles, 4 m, WAM Z8948 (3) (MOL 146); Cockburn Sound, TM H1116 (4); Trigg I., WAM Z9539 (2); Yanchep, lagoon, NMV F93443 (2).

**Description (dry and cleared specimens).** Up to  $R = 56$  mm; 5–9 rays, predominantly 6 (102 of 116 AM specimens with 6 rays, 10 with 7 rays, 2 with 5 rays, 1 with 8 rays, 1 with 9 rays); form variable from 6 short rounded to pointed rays with interradial margin incurved, to hexagonal; body thick, flat orally, flattened dome aborally, acute angle at

margin; madreporite conspicuous; lacking pedicellariae; gonopores abactinal.

Abactinal surface uneven; papulate areas more extensive than non-papulate areas; secondary plates abundant, very irregular in size and form; proximal radial and interradial plates openly imbricate; proximal papular spaces large, frequently up to 16–20 secondary plates and 16–20 papulae in proximal papular spaces outside disc when  $R = 30$  mm (5–6 secondary plates and 5–6 papulae when  $R = 20$  mm); abactinal plates thick, raised, prominent, crescentic in papulate areas, carinally with double notch and proximal lobe; carinal series variably regular from close to disc to end or near end of rays, frequently doubly papulate to near end of ray when  $R = 20$  mm and larger; distal interradial non-papulate plates closely imbricate, domed, rounded proximally; disc variably distinct, bordering plates variably regular crescentic radial plates and smaller interradial plates, disc frequently obscured by irregular large plates within and distal to disc; abactinal plates granular, covered by glassy convexities, lacking spine-bearing ridge; abactinal spinelets with variable form, frequently widened distally, some capitate or truncate or columnar or narrowing distally or with swollen base, long spines distally, typically about 0.40 mm long when  $R = 30$  mm (0.32 mm when  $R = 20$  mm), distributed over projecting surface of plates; superomarginal plates aligned longitudinally with inferomarginal plates; lacking internal superambulacral plates between ambulacrals and actinals; distal abactinal and actinal interradial plates with internal tapered vertical contiguous projections.

Projecting inferomarginal plates form margin, up to about 11 spinelets per plate when  $R = 20$ –30 mm; actinal plates in regular series, curving acutely from furrow to margin, some proximal actinal areas not calcified; actinal interradial spines generally thick, very short, columnar to bulbous, distally minutely spinous; actinal interradial proximal plates with 1–2 spines, distally 2–3 (4 rare); adradial row of actinal interradial proximal plates with predominantly 1 short, thick, bulbous to tapered spine, typically up to only half the length of subambulacral spines; adambulacral proximal plates with predominantly 1 (2 rare) thick subambulacral spines, frequently bulbous with waist, form variable from columnar to subspatulate to spatulate, minutely spinous distally; furrow spines 2–3 (4 rare) proximally, fairly thick, form variable from tapered to slightly widened distally; suboral spines rare (7 suboral spines on 1 of 116 AM specimens); oral spines 4–6, predominantly 5.

**Live colour.** Abactinally uniform dark crimson or reddish-brown (a few AM labels refer to “purple” and “indigo blue”), paler actinally; orange tube feet.

**Distribution.** Eastern Vic. (off Ninety Mile Beach) continuous to Abrolhos Islands off WA (Loisette Marsh, pers. comm.); Bass Strait; Tas.; under rocks; 0–29 m (molecular confirmation for Flinders (Vic.) to Busselton (WA)).

**Remarks.** The lectotype of *Asterina gunnii* and the two paratypes of *Patiriella brevispina* seen in this study do not exhibit any significant morphological differences and in

particular have single stout subambulacral spines per plate and very short actinal interradial spines. These two diagnostic characters were used by Clark (1938) to distinguish his new species. Clark (1938) also considered the “consistent deep purple to brownish-crimson colour and orange tube feet” of *P. brevispina* to be diagnostically reliable. This observation is confirmed and specimens with these characteristic colours consistently exhibit the morphological diagnostic characters of *A. gunnii*. Dartnall (1970) followed H.L. Clark (1938) when designating and describing the lectotype of *A. gunnii*, and noted that paired subambulacral spines distinguished *P. gunnii* from *P. brevispina*. Dartnall (1970) then considered the lectotype of *A. gunnii* to be exceptional in having single subambulacral spines. The lectotype of *A. gunnii* ( $R = 24$  mm) and paratypes of *P. brevispina* (up to  $R = 20$  mm) are similar in size, and are small specimens of *A. gunnii* (up to  $R = 56$  mm). On the morphological evidence *P. brevispina* is considered here to be a junior synonym of *A. gunnii*.

Hart et al. (1997) and Byrne et al. (1999) found from molecular evidence that *P. 'brevispina'* specimens from eastern Australia (Mornington Peninsula, Vic.) and Western Australia (Perth) were closely related. Eastern and Western Australian specimens of *P. 'brevispina'* were found to be conspecific in this study. Byrne (1995, 1996), Byrne and Cerra (1996), and Long and Byrne (2001) have reported on the reproductive and developmental biology of *P. gunnii* (as *P. 'brevispina'*).

The combination of characters which distinguishes *P. gunnii* from other six-rayed species of *Patiriella* is: consistent uniform dark crimson to reddish brown colour; orange tube feet; larger maximum size; prominent papular spaces with numerous papulae and secondary plates; noticeably spinous abactinal spinelets; predominantly single thick subambulacral spines per plate; and very short thick actinal interradial spines. No evidence was found to confirm the occurrence of *P. gunnii* in NSW, or the depth of 39 m reported by Rowe and Gates (1995, as *P. 'brevispina'*).

### *Patiriella medius* sp. nov.

Figures 1 (as ‘central’), 4a–f, 7c

**Material examined.** Holotype. Victoria, Port Fairy, Griffith I., rocky shallows, 0–2 m, M. O'Loughlin and M. Mackenzie, 29 Dec 2001, NMV F92986 (MOL 72).

Paratypes. Type locality and date, NMV F92987 (3) (MOL 73, 74, 79); NMV F92988 (2 dry, 2 cleared) (MOL 69, 70, 75, 76).

Other material (selected for molecular confirmation, distribution and depth data). **Vic.** W of Wilsons Promontory, Walkerville South, Bear Gully, NMV F71869 (1); Western Port, McHaffie Point, NMV F93174 (4); Flinders, ocean platform, NMV F93171 (2); Port Phillip Bay, Popes Eye, 5–12 m, NMV F93730 (1); Point Addis, 8–13 m, NMV F93165 (3) (MOL 170, 172); “Mullet Holes”, 10 km NE Apollo Bay, 0–2 m, NMV F92990 (3) (MOL 94–96); Port Fairy, Griffith I., rocky shallows, NMV F83593 (2) (MOL 50); NMV F93164 (1) (MOL 176); NMV F87171 (1) (MOL 177); Portland, Nelson Bay, 24 m, NMV F73193 (2). **Tas.** Port Arthur, below low tide, TM H809 (1); Bass Strait, Waterhouse Passage, rocky shallows, NMV F71872 (1) (MOL 46); Tamar River, Greens Beach, TM H1107 (21); Somerset, near Burnie, under rocks at low tide, WAM Z9394 (5); Rocky Cape, 5 m, NMV F92989 (2) (MOL 211). **SA.** Cape Jaffa, 14–20 m, SAM K1938 (2); Kangaroo I., Western River, 8–10 m, SAM K1917 (1); Gulf

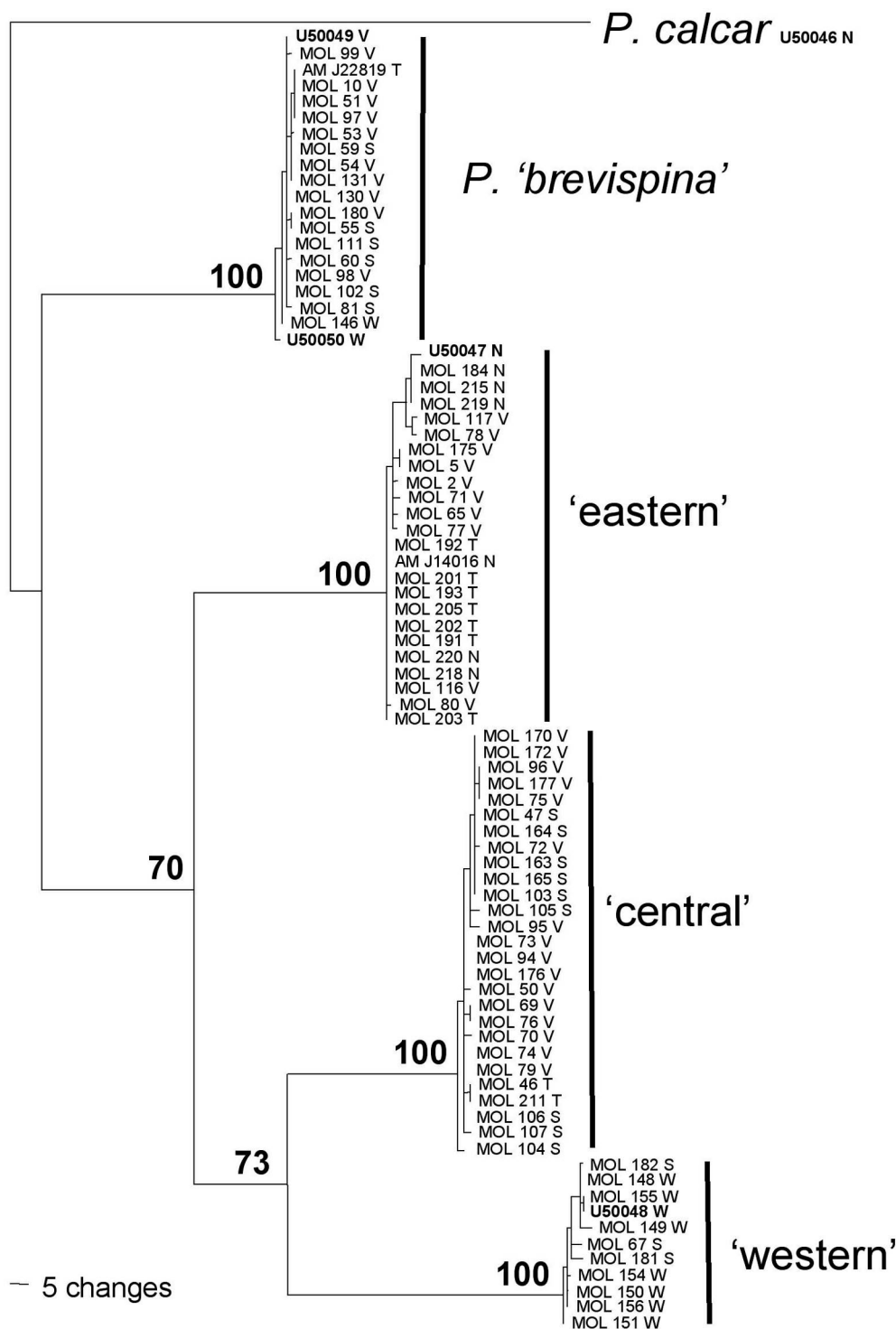


Figure 1. One of 1000+ optimal MP trees (863 steps) derived from analysis of CO1 sequence data. Numbers at nodes are bootstrap percentages based on 500 replicate analyses. MOL codes refer to specimens obtained for the current study. AM codes refer to Australian Museum specimens. Previously published sequences (Hart et al., 1997) are indicated in bold. Geographic origin of samples is indicated: Tasmania (T), Victoria (V), New South Wales (N), South Australia (S), Western Australia (W).

Saint Vincent, Fleurieu Peninsula, Rapid Bay jetty, 8–12 m, NMV F93166 (4) (MOL 163–165); Normanville, rocky shallows, NMV F93163 (4) (MOL 104–107); F93167 (1) (MOL 103); Port Noarlunga, under stones, 1 m, WAM Z9390 (1); Yorke Peninsula, Edithburg, Troubridge Light, 18 m, TM H1359 (1); Sir Joseph Banks Group, 3–14 m, SAM K1923 (3); Investigator Group, 6–8 m, SAM K1901 (1); Eyre Peninsula, near Streaky Bay, Point Westall, rocky shallows, NMV F71856 (1 cleared) (MOL 47, 57); Nuyts Archipelago, 34 m, SAM K1933 (1). **WA.** Hopetoun, east of jetty, rock platform, NMV F73201 (3); Cheyne Bay, intertidal reef, WAM Z9472 (1); Yallingup, under boulders with *P. 'brevispina'* (= *P. gunnii* here) and *P. 'gunnii'* (= *P. occidentis* here), 0–1 m, WAM Z9477 (5); Cape Naturaliste, 9 m, WAM Z9404 (1); Dunsborough, Eagle Bay, under rock, 10 m, NMV F93172 (1); Bunbury, 4 km N, WAM Z9411 (1); Fremantle, Halls Bank, under rock, 8 m, NMV F73178 (1).

**Description (dry and cleared specimens).** Up to  $R = 38$  mm; 5–7 rays, predominantly 6 (134 of 145 SAM, TM and WAM specimens with 6 rays, 9 with 7 rays, 2 with 5 rays); form variable from 6 short predominantly pointed rays with interradial margin incurved, to hexagonal; body flat orally, flattened dome aborally, acute angle at margin; madreporite conspicuous; lacking pedicellariae; gonopores abactinal.

Abactinal surface even; papulate areas slightly more

extensive than non-papulate areas; secondary plates few, very irregular in size and form; proximal radial and interradial plates fairly closely imbricate; proximal papular spaces not large, frequently 1–3 secondary plates and 2–4 papulae in proximal papular spaces outside disc when  $R = 20$ –30 mm; abactinal plates crescentic in papulate areas, carinally with double notch and proximal lobe; carinal series variably regular from close to disc to near end of ray, rarely doubly papulate beyond half ray length; distal interradial non-papulate plates closely imbricate, domed, rounded proximally; disc variably distinct, bordering plates variably regular crescentic radial and smaller interradial plates, frequently obscured by irregular large plates within and distal to disc; abactinal plates granular, covered by glassy convexities, lacking spine-bearing ridge; abactinal spinelets with variable form, subcolumnar to narrowing and rounded distally with swollen base, minutely spinous distally, typically about 0.36 mm long when  $R = 30$  mm (0.30 mm when  $R = 20$  mm), distributed over projecting surface of plates; superomarginal plates aligned distally with inferomarginal plates; lacking internal superambulacral plates between ambulacrals and actinals; distal abactinal and actinal interradial plates with internal tapered vertical contiguous projections.

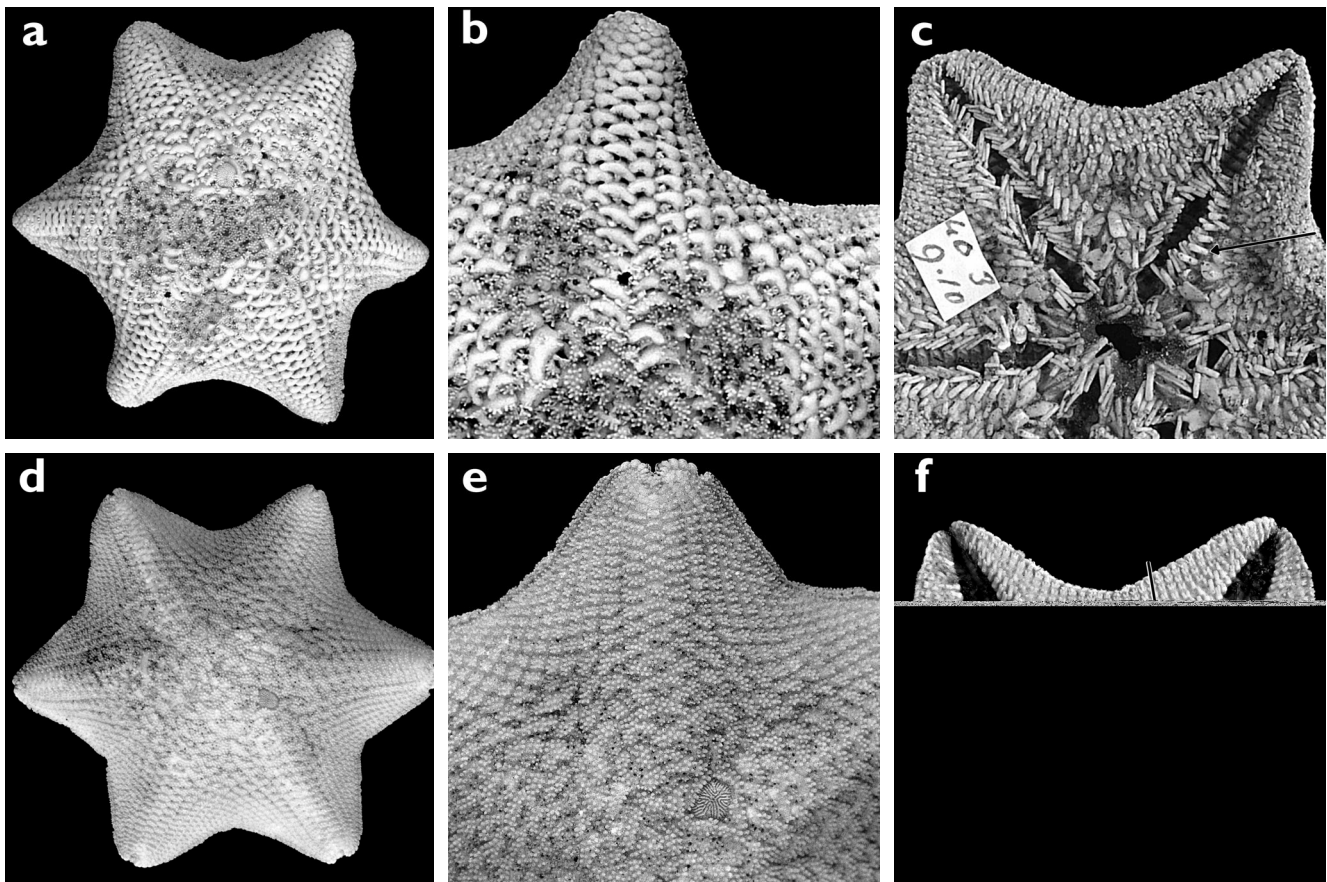


Figure 2. a–c, *Asterina gunnii* Gray, 1840, lectotype,  $R = 24$  mm (BMNH 40.3.9.10, dry). a, abactinal view (extensively cleared); b, abactinal ray (extensively cleared); c, actinal ambulacra and interradia, with single stout subambulacral spines per plate (arrow) and very short interradial spines.

d–f, *Patiriella brevispina* H.L. Clark, 1938, paratype,  $R = 20$  mm (AM J6181, dry). d, abactinal view; e, abactinal ray; f, actinal ambulacra and interradia, with single stout subambulacral spines per plate (arrow) and very short interradial spines.

Projecting inferomarginal plates form margin, widely rounded distally, frequently 10–14 spinelets per plate when  $R = 20\text{--}30\text{ mm}$ ; actinal plates in regular series, curving acutely from furrow to margin; some proximal actinal areas not calcified; actinal interradial spines generally fairly slender, tapered, short; actinal interradial proximal plates with 1–4 spines (predominantly 2–3), distally 2–4 very short tapered spines (frequently 3), minutely spinous distally; adradial row of actinal interradial proximal plates with predominantly 2 tapered spines, minutely spinous distally, significantly shorter than subambulacral spines (about half to two-thirds length); adambulacral proximal plates with frequently 2–3 thick tapered subambulacral spines, minutely spinous distally, frequently unequal, form variable from digitate to spatulate to distally bulbous, commonly slightly longer than furrow spines; furrow spines slender, webbed, tapering, predominantly 3–4 (sometimes 5) per plate proximally when  $R = 20\text{ mm}$  and larger, minutely spinous distally; suboral spines frequently present (at least 1 suboral spine on 68 of 115 AM, SAM and TM specimens examined; 10–12 suboral spines on 42 of 115 specimens); oral spines 5–7, predominantly 6.

**Live colour.** Abactinally very variable; dark-coloured disc not reported; frequently overall maroon red or red or reddish brown appearance, sometimes fairly uniform pale brown or orange or pink, sometimes with red or mauve or orange or brown or cream or white flecks; a few with margin or rays and interradial coloured differently, or with colour patches; some mottled with dark red, red, maroon, mauve, brown, orange, white; actinally typically off-white with prominent maroon flecking.

**Distribution.** Walkerville South (W of Wilsons Promontory, Vic.), Bass Strait, Tas., continuous to Fremantle (WA); under rocks; 0–34 m (molecular confirmation for Point Addis (Vic.) to western Eyre Peninsula (SA)).

**Etymology.** From *medius* (Latin, as a noun in apposition) meaning “between the two”, and referring to a distribution across southern Australia between the most easterly distribution of *Patiriella oriens* sp. nov. (below) and the most westerly distribution of *Patiriella occidentalis* sp. nov. (below).

**Remarks.** The combination of characters which distinguishes *P. medius* from other six-rayed species of *Patiriella* is: rarely doubly papulate carinally for more than half ray length;

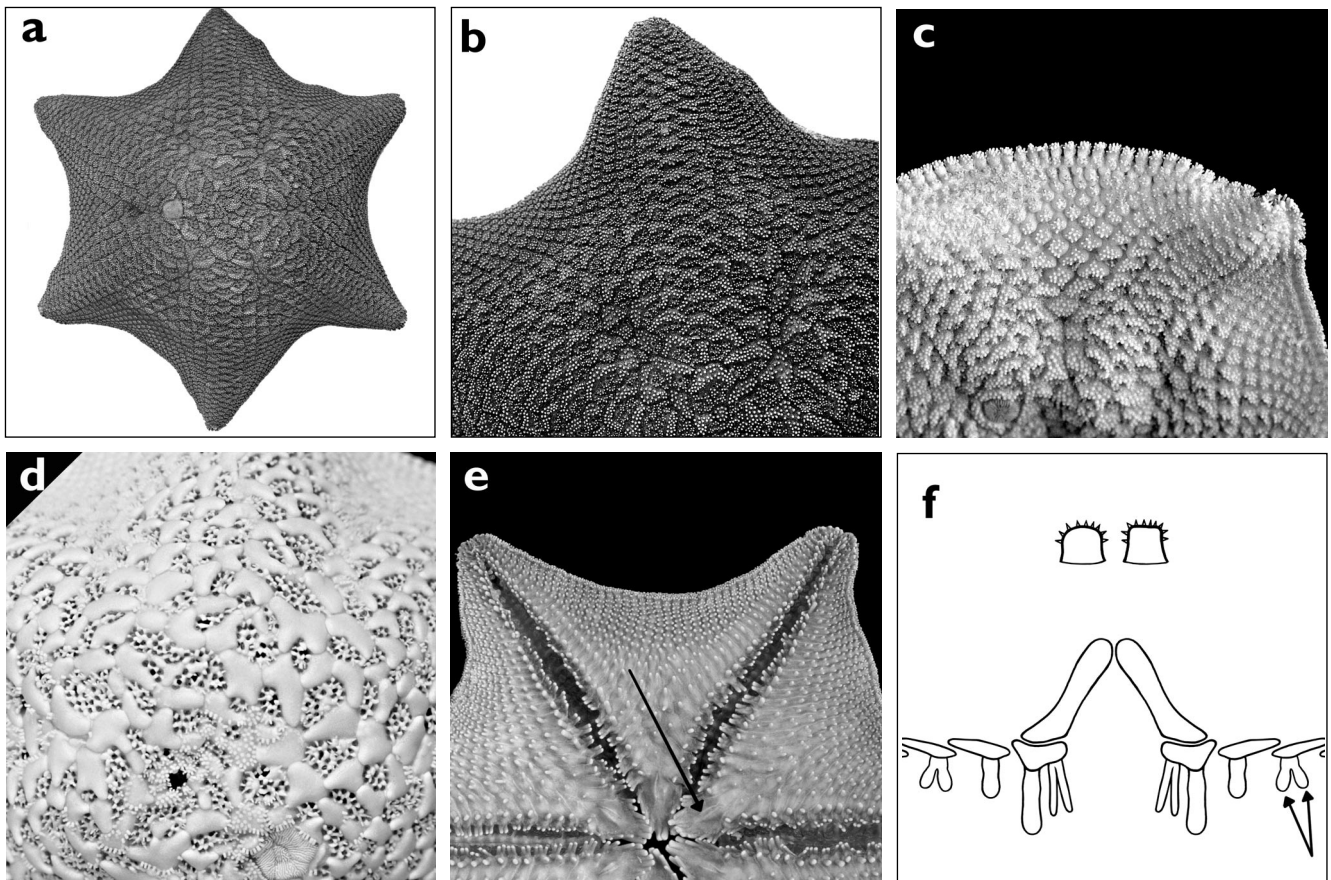


Figure 3. a–f, *Patiriella gunnii* (Gray). a, abactinal view,  $R = 40\text{ mm}$  (NMV F73273); b, abactinal ray, carinally doubly papulate for most of ray,  $R = 40\text{ mm}$  (NMV F73273); c, abactinal interradius with coarse spination and fringe of stout inferomarginal spinelets,  $R = 22\text{ mm}$  (WAM Z8948); d, cleared abactinal view, with numerous papulae and secondary plates,  $R = 35\text{ mm}$  (WAM Z8952); e, actinal ambulacra and interradius, lacking suboral spines (arrow),  $R = 40\text{ mm}$  (NMV F73273); f (above), common forms of abactinal spinelets; f (below), common forms of actinal spines proximal to ambulacrum, with very short interradial spines (arrow).

abactinal spinelets small and fine; frequent presence of some sub-oral spines; adradial row of actinal interradial spines up to about two-thirds the length of subambulacral spines; actinal interradial spines short, thin. The limited live colour data available for confirmed determinations indicates that maroon red is a common abactinal overall colour, with no reports of grey or blue or a black disc.

*Patiriella occidentalis* sp. nov.

Figures 1 (as 'western'), 5a–f, 7d

*Patiriella gunnii* W.—Hart et al., 1997: 1848–1861, figs 1–4, tabs 1, 2.—Byrne et al., 1999: 188–194, figs 1, 3D, 6 (non *Patiriella gunnii* (Gray, 1840)).

**Material examined.** Holotype. Western Australia, Perth, Cottesloe, on reef amongst algae, 1 m, L. Marsh, 29 Dec 2001, WAM Z8951 (MOL 151).

Paratypes. Type locality and date, NMV F92971 (1, cleared) (MOL 150); Albany, Cape Vancouver, Quaranup, amongst boulders, 1 m, L. Marsh, 13 Dec 2001, WAM Z8949 (1) (MOL 148); under boulder, 1 m, WAM Z8950 (1) (MOL 149); Cockburn Sound, Woodman Point, under rocks, 1 m, L. Marsh, 1 Jan 2002, WAM Z8953 (3) (MOL 154–156).

Other material (selected for molecular confirmation, distribution and depth data). **Vic.** Port Fairy, causeway beach, NMV F73149 (1). **SA.** Victor Harbour, The Bluff wharf, NMV F92975 (1) (MOL 67); Cape Jervis, rocky shallows, NMV F74638 (1) (MOL 182); Kangaroo I., Eastern Cove, rocky shallows, NMV F71862 (2) (MOL 181); Gulf Saint Vincent, Glenelg, SAM K1932 (3); Yorke Peninsula, Edithburg, 0–4 m, SAM K1904 (3); Sir Joseph Banks Group, 0–1 m, SAM K1899 (2); Eyre Peninsula, Point Labatt, 0–1 m, SAM K1907 (1); Nuyts Archipelago, 14 m, SAM K1898 (2). **WA.** E of Hopetoun, Mason Bay, East Mason Point, granite/dolerite with algae and seagrass, 0–3 m, WAM Z9470 (1); Cheyne Bay, under stones, WAM Z9479 (6); Two Peoples Bay, WAM Z9576 (2); Albany, Middleton Beach, under rocks, WAM Z9478 (2); Torbay, Mutton Bird I., under boulders, intertidal, WAM Z9474 (2); Kilkarnup, Cape Mentelle, WAM Z9466 (1); Cowaramup Bay, under boulders, 0–1 m, WAM Z9400 (1); Yallingup, limestone reef, under boulders with *P. 'brevispina'* (= *P. gunnii* here), WAM Z9396 (4); Cape Naturaliste, under intertidal granite boulders, WAM Z9405 (2); Geographe Bay, Dunsborough, WAM Z9402 (1); Rockingham, Point Peron, H.L. Clark, Oct

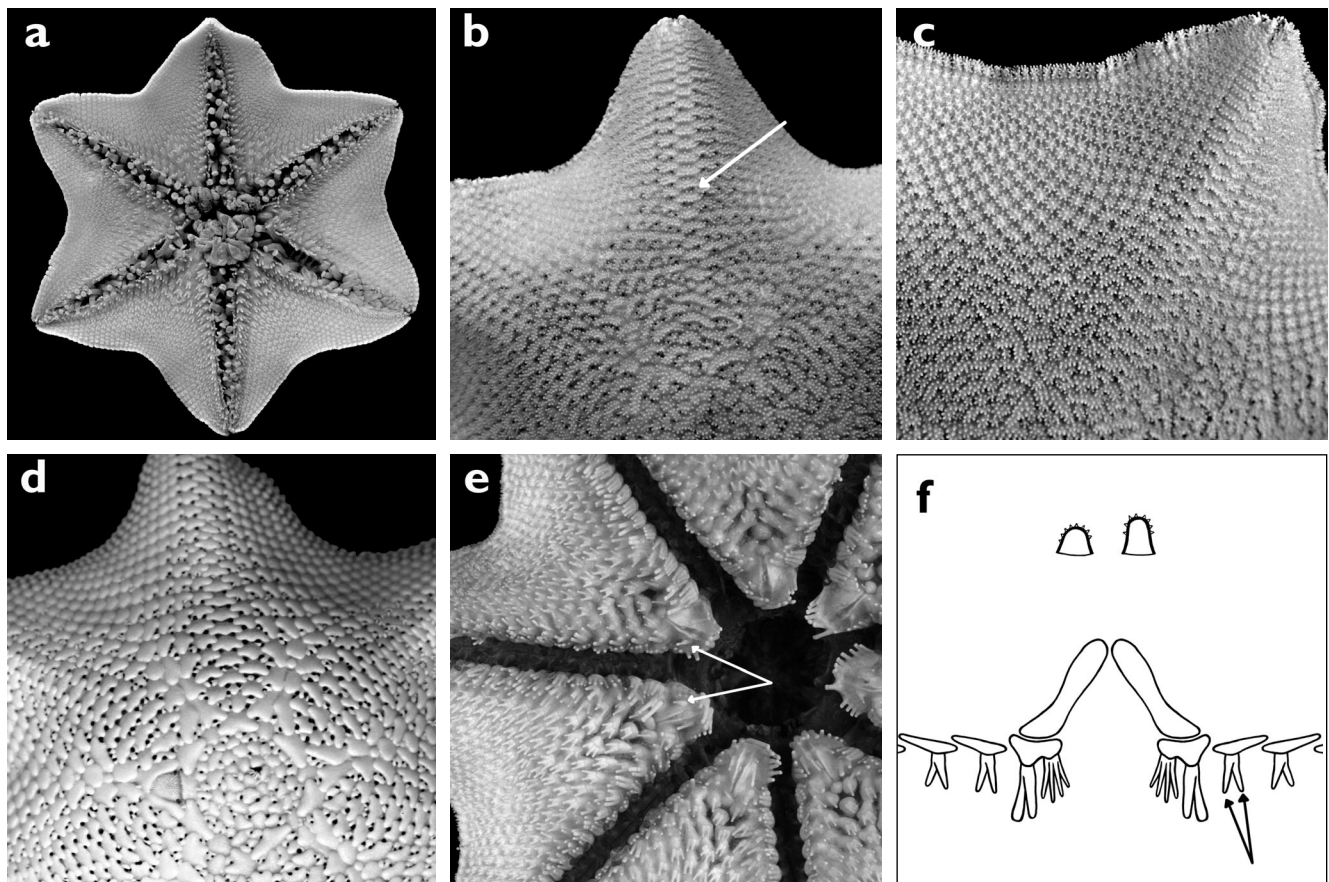


Figure 4. a–f, *Patiriella medius* sp. nov. a, actinal view of holotype, R = 25 mm (NMV F92986); b, abactinal ray of paratype, carinally doubly papulate for about half ray length (ending at arrow), R = 23 mm (NMV F92988); c, abactinal interradius of paratype, with fine spination and fringe of fine inferomarginal spinelets, R = 24 mm (NMV F92988); d, cleared abactinal view of paratype, with few papulae and secondary plates, and carinal plates doubly papulate for about half the ray length, R = 22 mm (NMV F92988); e, actinal ambulacra and interradia of paratype, with suboral spines (arrows), and atypically 7 ambulacra, R = 23 mm (NMV F92988); f (above), common forms of abactinal spinelets; f (below), common forms of actinal spines proximal to ambulacrum, with adradial actinal spines (arrow) much shorter than subambulacral spines.

1929, WAM Z9440-2 (3); SAM K712 (3); Rottneet I., reef, WAM Z9530 (9); Trigg I., reef platform, WAM Z9454 (1); Yanchep, reef, WAM Z9433 (1); Port Gregory, N of Geraldton, top of reef in pool, NMV F73179 (1); Kalbarri (Murchison River), reef top, WAM Z9413 (2).

**Description (dry and cleared specimens).** Up to  $R = 38$  mm; 4–9 rays, predominantly 6 (292 of 331 AM, SAM, TM and WAM specimens with 6 rays, 25 with 7 rays, 9 with 8 rays, 3 with 5 rays, 1 with 4 rays, 1 with 9 rays); form variable from 6 distinct pointed rays with interradial margin deeply incurved (common for larger specimens) to subhexagonal (rare except for smaller specimens); body flat orally, flattened dome aborally, acute angle at margin; madreporite conspicuous; lacking pedicellariae; gonopores abactinal.

Abactinal surface slightly uneven; papulate areas more extensive than non-papulate areas; secondary plates numerous, very irregular in size and form; proximal radial and interradial plates fairly openly imbricate; proximal papular spaces fairly large, frequently 2–6 secondary plates and 6–7 papulae in proximal papular spaces outside disc when  $R = 30$  mm (2–4

secondary plates and 4–6 papulae when  $R = 20$  mm); abactinal plates crescentic in papulate areas, carinally with double notch and proximal lobe; carinal series frequently regular from close to disc to end or near end of rays, doubly papulate for at least three quarters ray length when  $R = 20$  mm and larger; distal interradial non-papulate plates closely imbricate, domed, rounded proximally; disc variably distinct, bordering plates variably regular crescentic radial plates and smaller interradial plates, disc frequently obscured by irregular large plates within and distal to disc; abactinal plates granular, covered by glassy convexities, lacking spine-bearing ridge; abactinal spinelets frequently twice as long as wide, variable form, most frequently columnar, sometimes slightly widened or narrowing distally, sometimes with slight waist, truncate and prominently spinous distally, typically up to 0.48 mm long when  $R = 30$  mm (0.36 mm when  $R = 20$  mm), distributed over projecting surface of plates; superomarginal plates aligned longitudinally with inferomarginal plates; lacking internal superambulacral plates between ambulacra and actinals; distal abactinal and actinal interradial plates with internal tapered vertical contiguous projections.

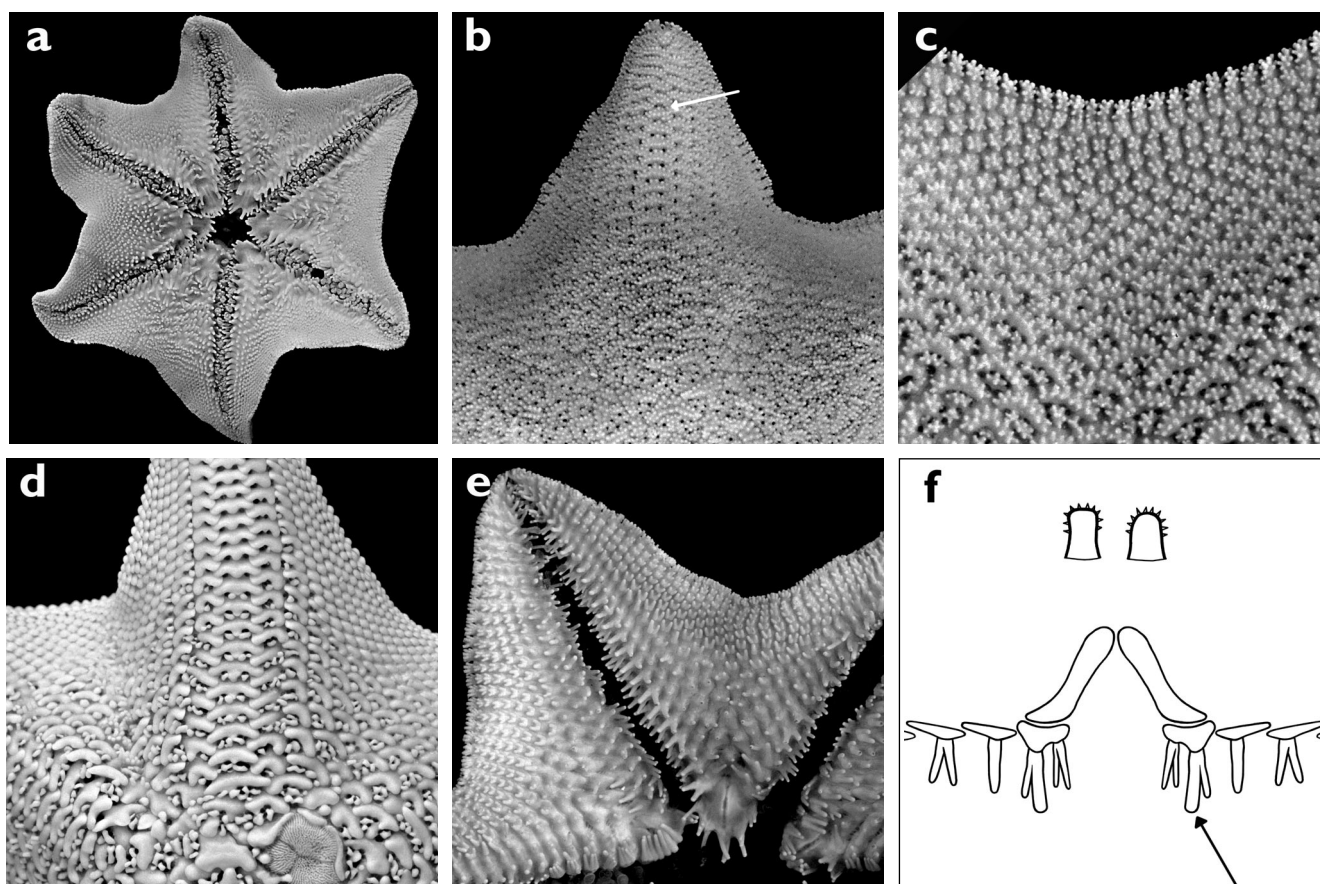


Figure 5. a–f, *Patiriella occidentens* sp. nov. a, actinal view of holotype, with distinctively elongate rays,  $R = 35$  mm (WAM Z8951); b, abactinal ray, carinally doubly papulate for most of ray (ending at arrow), and coarse cover of abactinal spinelets,  $R = 25$  mm (WAM Z9491); c, abactinal interradius with coarse spination and fringe of stout inferomarginal spinelets, up to 10 per plate,  $R = 30$  mm (WAM Z9483); d, cleared abactinal view of paratype, with carinal plates doubly papulate for all of ray shown,  $R = 31$  mm (NMV F92971); e, actinal ambulacra and interradia, with oral plates lacking suboral spines,  $R = 25$  mm (WAM Z9491); f (above), common forms of abactinal spinelets; f (below), common forms of actinal spines proximal to ambulacrum, with projecting subambulacral spines (arrow).

Projecting inferomarginal plates form margin, frequently 8–11 spinelets per plate when  $R = 20\text{--}30$  mm; actinal plates in regular series, curving acutely from furrow to margin, some proximal actinal areas not calcified; actinal interradial spines generally thick, long, digitate, distally spinous; actinal inter-radial proximal plates with 1–2 spines, distally 2 (rarely 3) shorter, digitate to slightly bulbous, distally spinous spines; adradial row of actinal interradial proximal plates with predominantly 1 thick digitate spine, rarely 2, typically about four fifths length of subambulacral spines, some slightly bulbous; adambulacral proximal plates with 1–3, predominantly 2, thick subambulacral spines, frequently unequal, form variable from digitate to slightly bulbous to subcapitate to spatulate to widening distally, minutely spinous distally; furrow spines slender, tapering, webbed, 2–4 per plate proximally, predominantly 3, minutely spinous distally, subequal in length with subambulacral spines; suboral spines rare (at least 1 suboral spine on 23 of 307 AM, SAM, TM and WAM specimens examined; more than 10 suborals on 2 of 307); oral spines 4–6, predominantly 5.

*Live colour.* Very variable abactinally; commonly dark coloured disc, sometimes red; frequently grey appearance; sometimes fairly uniform grey or red or blue-green or grey-blue or blue or brown or orange, sometimes with black or white flecks; some with rays, interradial and margin coloured differently, or with colour patches; frequently mottled with grey, white, green, red, brown, blue, orange, mauve, black.

*Distribution.* Port Fairy (Vic.) continuous to Kalbarri (WA); predominantly on reef flat, sometimes with seagrass; 0–14 m (molecular confirmation for Victor Harbour (SA) to Perth (WA)).

*Etymology.* From *occidens* (Latin, as a noun in apposition) meaning “west” and referring to the westerly distribution in southern Australia.

*Remarks.* Hart et al. (1997) and Byrne et al. (1999) found from molecular evidence that specimens of *Patiriella* ‘*gunnii*’ from eastern and western Australia had divergent lineages. The western material was collected from Margaret River in WA (L. Marsh, pers. comm.). Western Australian specimens are

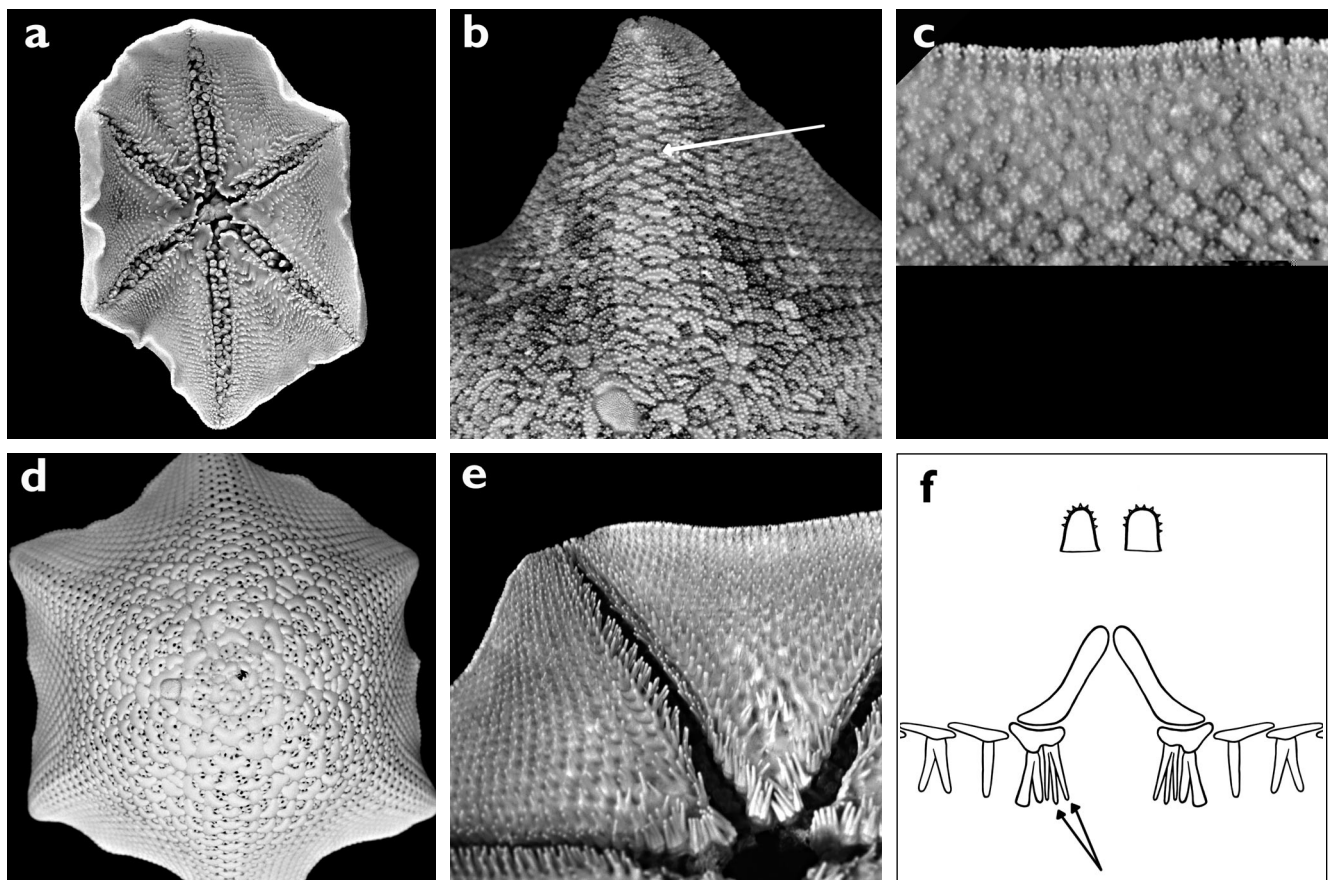


Figure 6. a–f, *Patiriella oriens* sp. nov. a, actinal view of holotype,  $R = 28$  mm (NMV F92983); b, abactinal ray, carinally doubly papulate for about two-thirds of ray length (ending at arrow),  $R = 25$  mm (NMV F73152); c, abactinal interradius with moderately coarse spination and fringe of fairly fine inferomarginal spinelets, up to 15 per plate,  $R = 25$  mm (NMV F73152); d, cleared abactinal view of paratype, with carinal series doubly papulate for most of ray length,  $R = 25$  mm (NMV F92984); e, actinal ambulacra and interradial spines,  $R = 30$  mm (NMV F73155); f (above), common forms of abactinal spinelets; f (below), common forms of actinal spines proximal to ambulacrum, with relatively long furrow spines (arrow).

confirmed by molecular and morphological evidence and described here as *Patiriella occidentalis* sp. nov.

Grice and Lethbridge (1988) reported on the reproductive and developmental biology of *Patiriella 'gunnii'*. Since the research was based on material collected from the region of Perth, it is assumed here that the species was not *P. gunnii* but probably the readily found and collected new species *P. occidentalis* (used hereafter for *P. 'gunnii'* from western Australia). It is improbable that the collections included the cryptic *P. medius*, which is sympatric with *P. occidentalis* in the Perth region. Grice and Lethbridge (1988) found that spawning by *P. occidentalis* occurred in late summer and early autumn. Spawning is thus later than *P. oriens* (see below), a factor which may be significant in the maintenance of genetic identity in these similar species. *P. occidentalis* is found most frequently on intertidal reef platform, a habitat frequently occupied by *P. calcar*. This potential competitive factor may have resulted in the absence of *P. calcar* in most of the distribution range of *P. occidentalis*.

The combination of morphological characters which distinguishes *P. occidentalis* from other six-rayed *Patiriella*

species is: frequently distinct long rays; carinal series of plates frequently doubly papulate for at least three-quarters ray length; abactinal spinelets frequently columnar, distally slightly swollen and spinous, and creating a very coarsely spinous surface appearance; normal absence of suboral spines; subambulacral spines projecting significantly above furrow and actinal interradial spines; actinal interradial spines digitate; up to about 11 spinelets per inferomarginal plate. The limited live colour data available for confirmed determinations indicates that grey or brown or blue are frequently evident abactinally, and red infrequently.

***Patiriella oriens* sp. nov.**

Figures 1 (as 'eastern'), 6a–f, 7e

*Patiriella gunnii* E.—Hart et al., 1997: 1848–1861, figs 1–4, tabs 1, 2.—Byrne et al., 1999: 188–194, figs 1, 3D, 6 (non *Patiriella gunnii* (Gray, 1840)).

**Material examined.** Holotype. Tasmania, Recherche Bay, Black Reef, 8 m, N. Barrett, 6 Jun 2002, NMV F92983 (MOL 193).

Paratypes. Type locality and date, NMV F92984 (1 dry, 1 cleared)

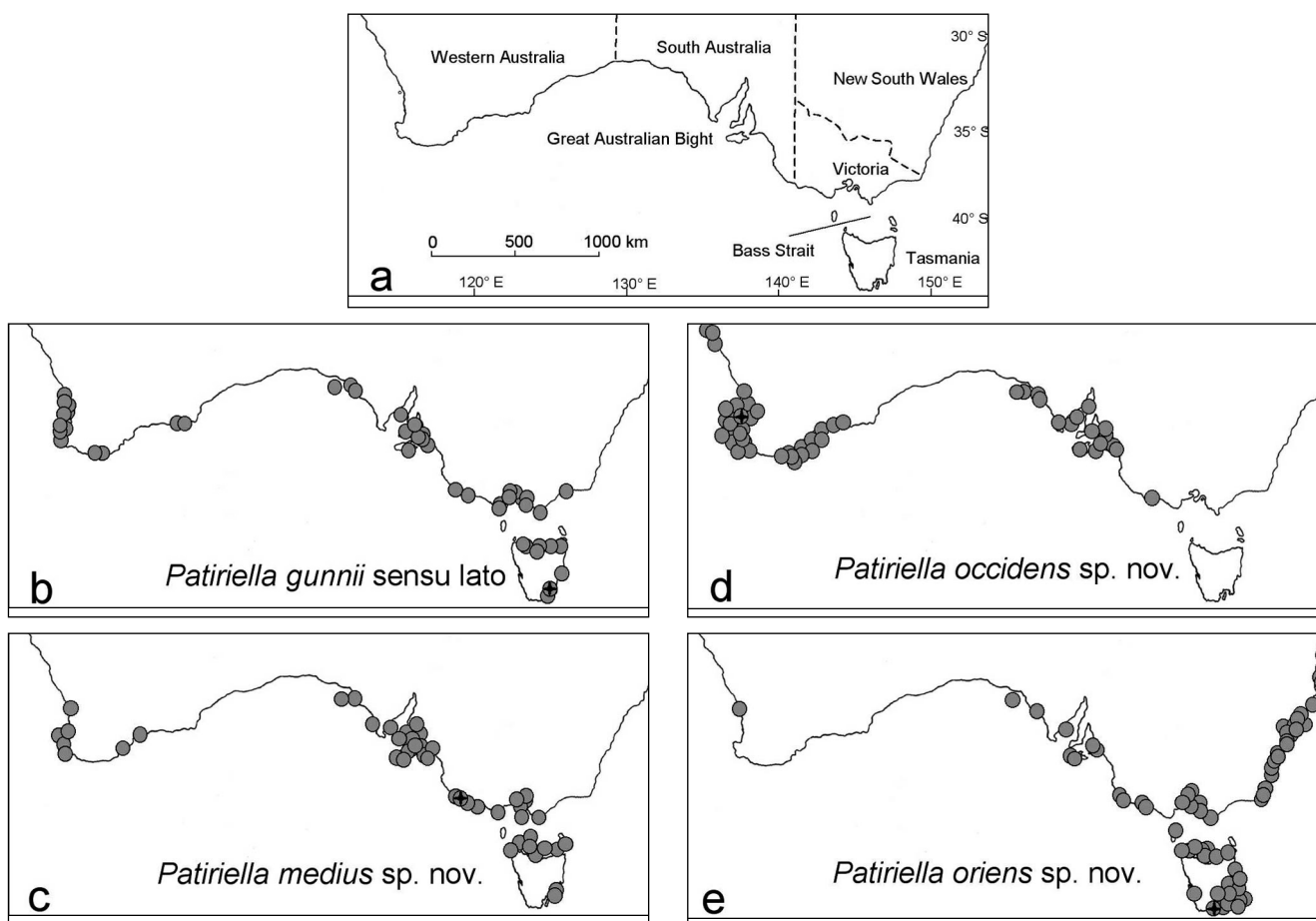


Figure 7. a, the temperate region of southern Australia.

b–e, geographic distributions based on morphological determinations, with type localities for each of the species indicated by crossed symbols; b, *P. gunnii* sensu lato; c, *P. medius* sp. nov.; d, *P. occidentalis* sp. nov.; e, *P. oriens* sp. nov.

(MOL 191, 192); Bicheno, rocky coast, 5 m, N. Barrett, 1 Apr 2002, NMV F92982 (6) (MOL 201–203, 205).

Other material (selected for molecular confirmation, distribution and depth data). Lord Howe I., AM J19339 (1). **Qld.** Rockhampton, Satellite I., 6 m, NMV F73165 (1). **NSW.** Byron Bay, Julian Rocks, 12 m, AM J14869 (1); Minnie Water, AM J12953 (26); Wooli, AM J15570 (6); Woolgoola, North Solitary I., 30 m, AM J14910 (4); Coffs Harbour, Solitary I., 9 m, AM J14942 (13); South Solitary I., 27 m, AM J14899 (1); Broughton I., near Port Stephens, 25 m, AM J12963 (3); Wyong, Nora Head, WAM Z9382 (1); Manly, Long Reef, SAM K1909 (18); Port Jackson, Camp Cove, AM J20059 (1); Swansea Channel, near Heads, 3 m, AM J21893 (4); Clovelly, NMV F93180 (9) (MOL 215, 218, 219, 220); Little Bay, AM J4794 (5); Shellharbour, rock pools, AM J4419 (15); Jervis Bay, under rocks, 25 m, AM J15610 (1); Ulladulla, 24 m, AM J14179 (1); Batemans Bay, 12 km S, Pretty Point Bay, rocky shallows, NMV F71858 (1, cleared) (MOL 184); Montague I., 27–30 m, AM J13972 (1); Merimbula, rocky, 9 m, AM J14651 (2); Eden, Twofold Bay, sublittoral platform, AM J19853 (2). **Vic.** Walkerville South, NMV F93448 (2); Western Port, McHaffie Point, NMV F93175 (1); Flinders, ocean platforms, 0–2 m, NMV F92979 (1) (MOL 175); NMV F92985 (2) (MOL 2); NMV F92980 (1) (MOL 5); NMV F92981 (2) (MOL 116, 117); Port Phillip Bay, Portsea jetty; under rubble, 4–5 m, NMV F73200 (1); Torquay, Point Danger, rocky shallows, NMV F92976 (1, cleared) (MOL 65); Port Fairy, Griffith I., rocky shallows, NMV F92978 (3) (MOL 77, 78, 80); NMV F92977 (1, cleared) (MOL 71); Portland, Nelson Bay, 24 m, NMV F93462 (4). **Tas.** Cape Tourville, rocky shallows, NMV F71870 (3); Maria I., 10 m, TM H1792 (1); Forestier Peninsula, 4–9 m, SAM K1911 (4); Eaglehawk Neck, TM H1109 (2); Hobart, Tinderbox, under rocks, 2 m, NMV F73993 (2); Port Davey, Sarah I., 3 m, TM H1789 (4); Bass Strait, Ringarooma Bay, TM H1114 (5); Tamar River, Low Head, TM H1352 (1); Circular Head, TM H1765 (34); King I., Narracoopa, NMV F93447 (1). **SA.** Encounter Bay, 2–4 m, SAM K1919 (1); Kangaroo I., Western River, 10–12 m, SAM K1915 (1); Spencer Gulf, Gambier Is, Wedge I., under stones, 1–1.5 m, AM J23763 (2); Nuyts Archipelago, 6 m, SAM K1937 (1). **WA.** Perth, Cottesloe, beach after storm, TM H2945 (1).

*Description (dry and cleared specimens).* Up to  $R = 39$  mm; 4–8 rays, predominantly 6 (373 of 396 AM, SAM and TM specimens with 6 rays, 18 with 7 rays, 3 with 5 rays, 1 with 4 rays, 1 with 8 rays); form variable, from 6 short pointed to rounded rays with interradian margin incurved, to sub-hexagonal; body flat orally, flattened dome aborally, acute angle at margin; madreporite conspicuous; lacking pedicellariae; gonopores abactinal.

Abactinal surface even; papulate areas more extensive than non-papulate areas; secondary plates numerous, very irregular in size and form; proximal radial and interradian plates fairly openly imbricate; proximal papular spaces fairly large, frequently 3–5 secondary plates and 4–6 papulae in proximal papular spaces outside disc when  $R = 30$  mm (2–4 secondary plates and 4–5 papulae when  $R = 20$  mm); abactinal plates crescentic in papulate areas, carinally with double notch and proximal lobe; carinal series frequently regular from close to disc to end or near end of rays, doubly papulate for more than half up to three quarters ray length when  $R = 20$  mm and larger; distal interradian non-papulate plates closely imbricate, domed, rounded proximally; disc variably distinct, bordering plates variably regular crescentic radial and smaller interradian plates, disc frequently obscured by irregular large plates within and

distal to disc; abactinal plates granular, covered by glassy convexities, lacking spine-bearing ridge; abactinal spinelets slightly less than twice as long as wide, variable form, not widened distally, most frequently with swollen base and narrowing distally, sometimes columnar, sometimes with slight waist, rounded with small spines distally, typically up to 0.44 mm long when  $R = 30$  mm (0.34 mm long when  $R = 20$  mm), distributed evenly over projecting surface of plates; superomarginal plates aligned distally with inferomarginal plates; lacking internal superambulacral plates between ambulacra and actinals; distal abactinal and actinal interradian plates with internal tapered vertical contiguous projections.

Projecting inferomarginal plates form margin, frequently 10–15 spinelets per plate when  $R = 20$ –30 mm; actinal plates in regular series, curving acutely from furrow to margin; some proximal actinal areas not calcified; actinal interradian spines generally fairly thick, digitate, moderately tall; actinal interradian proximal plates with 1–3 slightly tapered spines, predominantly 1, distally 3–4 short thick spines, columnar to slightly tapered, spinous distally; adradial row of actinal interradian proximal plates with predominantly 1–2 thick spines, minutely spinous distally, slightly shorter than subambulacral spines; adambulacral proximal plates with 1–3, predominantly 2, thick subambulacral spines, frequently unequal, form variable from digitate to spatulate to widening distally, minutely spinous distally, frequently slightly shorter than furrow spines; furrow spines slender, tapering, webbed, minutely spinous distally, 2–4 per plate proximally, frequently slightly longer than subambulacral spines; suboral spines very rare (9 of 273 AM specimens with at least 1 suboral spines, 1 with 7 spines, 1 with 9 spines, 1 with 11 spines); oral spines 4–6, predominantly 5.

*Live colour.* Abactinally very variable; frequently pale or light coloured; commonly dark coloured disc; some fairly uniform white or pink or mauve or orange or bright red, sometimes with dark red or brown or white flecks; some with rays, interradian or margin coloured differently; some finely mottled with brown, red, mauve, pink, orange, yellow, green, white (NSW specimens sometimes with grey); actinally typically off-white with rare to sparse colour flecks.

*Distribution.* Lord Howe I.; Rockhampton (Qld) continuous to Nuyts Archipelago (western SA); Cottesloe, Perth (WA); Bass Strait; Tas.; under rocks; 0–30 m (molecular confirmation for Batemans Bay (NSW) to Port Fairy (Vic.)).

*Etymology.* From *oriens* (Latin, as a noun in apposition) meaning “east”, and referring to the uniquely easterly distribution in Australia.

*Remarks.* Hart et al. (1997) and Byrne et al. (1999) found from molecular evidence that specimens of *Patiriella* ‘gunnii’ from eastern and western Australia had divergent lineages. The eastern material was collected from Clovelly, Sydney (M. Byrne, pers. comm.). Eastern Australian specimens are confirmed by molecular and morphological evidence and described here as *Patiriella oriens* sp. nov. Byrne (1991, 1992, 1995, 1996), Byrne and Anderson (1994), Byrne and Cerra (1996), Cerra and Byrne (2001), and Long and Byrne (2001) reported

extensively on the reproductive and developmental biology of *Patiriella 'gunnii'*. Since this research was based on material collected from Clovelly (M. Byrne, pers. comm.), the species was not *P. gunnii* but the new species *P. oriens* (used hereafter for *P. 'gunnii'* from Clovelly).

Byrne (1992) reported broadcast spawning during spring and summer and some habitat overlap for Clovelly populations of *P. oriens* (typically under subtidal boulders) and *P. calcar* (typically intertidal reef). Byrne and Anderson (1994) subsequently reported viable laboratory hybrids (high frequency of seven rays) of *P. oriens* (typically six rays) and *P. calcar* (typically eight rays). Field and museum specimens of *P. oriens* observed by Byrne and Anderson (1994), and material seen in this study, showed a low frequency of seven rays, suggesting variation of arm number (within the species) or hybridization or both. Relevant to this consideration is the fact that about 10% of specimens of *P. occidentalis* (above) have more than six arms across a distribution range where *P. calcar* is mostly absent. The spawning of *P. oriens* is earlier (spring and summer) than *P. occidentalis* (late summer, discussed above), a factor which may be significant in the maintenance of genetic identity in these similar species.

In this study a single specimen (TM H2945) which was collected on a beach at Cottesloe (Perth) after a storm was identified as *P. oriens*. It is the only specimen in Australian museums, determined as *P. oriens*, which has been collected west of Nuys Archipelago.

The combination of morphological characters which distinguishes *P. oriens* from other species of six-rayed *Patiriella* is: frequently subhexagonal form; carinal series of plates frequently doubly papulate for about two-thirds ray length; abactinal spinelets frequently columnar and moderately spinous distally, creating a fairly coarsely spinous surface appearance; normal absence of suboral spines; furrow spines frequently slightly longer than subambulacral spines; actinal spines continuous in declining height with subambulacral spines; actinal interradial spines digitate; up to about 15 spinelets per inferomarginal plate. The limited live colour data available for confirmed determinations indicates that white or pink or mauve or orange or bright red, with a dark centre, are frequently evident abactinally.

## Discussion

Byrne et al. (1999) concluded that "*P. gunnii* from eastern and western Australia are different species, while *P. brevispina* from eastern and western Australia are the same species". These conclusions were premature as they were based on relative levels of mtDNA divergence rather than any direct assessment of reproductive isolation (biological species concept, Dobzhansky, 1937; Mayr, 1942), or monophyly (phylogenetic species concept, Cracraft, 1983). Nevertheless, Byrne et al. (1999) were correct that multiple species are present: independent morphological and molecular data reveal consistent evidence for three new taxa. The newly recognised taxa are deeply divergent for mtDNA, but exhibit only subtle morphological differences. This discrepancy might reflect the lack of morphological novelty typically associated with the echino-

derm body plan (Janies, 2001), but could also stem from rapid coalescence of mitochondrial genes relative to nuclear genes (Palumbi et al., 2001).

Although the overlapping distributions of these taxa (Fig. 7) provide compelling evidence for some form of reproductive isolation, we cannot rule out the possibility of a small degree of hybridization among some or all of the species in zones of sympatry. Future ecological and genetic studies should help elucidate the strength and nature of reproductive barriers. Parallel analyses of molecular and morphological characters represent a powerful technique for asteroid systematics (Flowers and Foltz, 2001; O'Loughlin et al., 2002).

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## References

- Bennett, I. 1987. *Australian Seashores* (W.J. Dakin 1952). Fully revised and illustrated. 411 pp. Angus and Robertson: Sydney.
- Byrne, M. 1991. Developmental diversity in the starfish genus *Patiriella* (Asteroidea: Asterinidae). Pp. 499–508 in: Yanagisawa, T., Yasumasu, I., Oguro, C., Suzuki, N. and Motokawa, T. (eds), *Biology of Echinodermata. Proceedings of the Seventh International Echinoderm Conference, Atami, 9–14 September, 1990*. Rotterdam: Balkema.
- Byrne, M. 1992. Reproduction of sympatric populations of *Patiriella gunnii*, *P. calcar* and *P. exigua* in New South Wales, asterinid seastars with direct development. *Marine Biology* 114: 297–316.
- Byrne, M. 1995. Changes in larval morphology in the evolution of benthic development by *Patiriella exigua* (Asteroidea: Asterinidae), a comparison with the larvae of *Patiriella* species with planktonic development. *Biological Bulletin* 188: 293–305.
- Byrne, M. 1996. Viviparity and intragonadal cannibalism in the diminutive sea stars *Patiriella vivipara* and *P. parvivipara* (family Asterinidae). *Marine Biology* 125: 551–567.
- Byrne, M., and Anderson, M.J. 1994. Hybridization of sympatric *Patiriella* species (Echinodermata: Asteroidea) in New South Wales. *Evolution* 48(3): 564–576.
- Byrne, M., and Cerra, A. 1996. Evolution of intragonadal development in the diminutive asterinid seastars *Patiriella vivipara* and *P. parvivipara* with an overview of development in the Asterinidae. *Biological Bulletin* 191: 17–26.
- Byrne, M., Cerra, A., Hart, M.W., and Smith, M.J. 1999. Life history diversity and molecular phylogeny in the Australian sea star genus

- Patiriella*. Pp. 188–196 in: Ponder, W. and Lunney, D. (eds), *The other 99%. The conservation and biodiversity of invertebrates*. Transactions of the Royal Zoological Society of New South Wales: Mosman.
- Campbell, A.C., and Rowe, F.W.E. 1997. A new species in the asterinid genus *Patiriella* (Echinodermata, Asteroidea) from Dhofar, southern Oman: a temperate taxon in a tropical locality. *Bulletin of the British Museum, Natural History (Zoology)* 63(2): 129–136.
- Cerra, A., and Byrne, M. 2001. Clade specific cleavage alteration in the genus *Patiriella*. P. 159 in: Barker, M. (ed.), *Echinoderms 2000. Proceedings of the Tenth International Conference, Dunedin*. Swets and Zeitlinger: Lisse.
- Clark, A.M. 1966. Port Phillip Survey, 1957–1963. Echinodermata. *Memoirs of the National Museum of Victoria* 27: 289–384, 10 figs, 4 pls, 1 tab.
- Clark, A.M. 1983. Notes on Atlantic and other Asteroidea. 3. The families Ganeriidae and Asterinidae, with description of a new asterinid genus. *Bulletin of the British Museum (Natural History) (Zoology)* 45(7): 359–380.
- Clark, A.M. 1993. An index of names of recent Asteroidea — Part 2. Valvatida: *Echinoderm Studies* 4: 187–366.
- Clark, A.M., and Downey, M.E. 1992. *Starfishes of the Atlantic*. Chapman and Hall (Natural History Museum Publications): London. 794 pp, 75 figs, 113 pls.
- Clark, H.L. 1928. The sea-lilies, sea-stars, brittle stars and sea-urchins of the South Australian Museum. *Records of the South Australian Museum* 3(4): 361–482, figs 108–142.
- Clark, H.L. 1938. Echinoderms from Australia. An account of collections made in 1929 and 1932. *Memoirs of the Museum of Comparative Zoology at Harvard College* 55: 1–597, 28 pls.
- Clark, H.L. 1946. The echinoderm fauna of Australia. Its composition and its origin. *Carnegie Institution of Washington Publication* 566: 1–567.
- Cotton, B.C., and Godfrey, F.K. 1942. Echinodermata of the Flindersian Region, southern Australia. *Records of the South Australian Museum* 7(2): 193–234, 1 pl.
- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1: 159–187.
- Dartnall, A.J. 1969. New Zealand sea stars in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 103: 53–55.
- Dartnall, A.J. 1970. The asterinid sea stars of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 104: 73–77, 1 pl.
- Dartnall, A.J. 1971. Australian sea stars of the genus *Patiriella* (Asteroidea, Asterinidae). *Proceedings of the Linnean Society of New South Wales* 96 (425): 39–49, pls 3–4.
- Dartnall, A. 1980. *Fauna of Tasmania Handbook* 3. *Tasmanian echinoderms*. University of Tasmania: Hobart. 82 pp., 36 figs, 5 pls, 18 maps.
- Dobzhansky, T. 1937. *Genetics and the origin of species*. Columbia University Press: New York.
- Dujardin, M.F., and Hupé, M.H. 1862. Echinodermes. *Histoire naturelle des Zoophytes*. Paris: Librairie Encyclopedique de Roret. 627 pp.
- Edgar, G.J. 1997. *Australian Marine Life*. Reed Books: Kew. 544 pp.
- Farquhar, H. 1895. Notes on New Zealand echinoderms. *Transactions and Proceedings of the New Zealand Institute* 27(20): 194–208, pls 10, 12, 13.
- Farquhar, H. 1898. On the echinoderm fauna of New Zealand. *Proceedings of the Linnean Society of New South Wales* 23(91): 300–327.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Fisher, W.K. 1919. Starfishes of the Philippine seas and adjacent waters. *Bulletin of the United States National Museum* 100(3): i–xi, 1–712, 156 pls.
- Flowers, J. M., and Foltz, D.W. 2001. Reconciling molecular systematics and traditional taxonomy in a species-rich clade of sea stars (*Leptasterias* subgenus *Hexasterias*). *Marine Biology* 139: 475–483.
- Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma (Asterias Linnaeus). *The Annals and Magazine of Natural History* 1(6)12: 175–184; 275–290.
- Gray, J.E. 1866. *Synopsis of the species of starfish in the British Museum (with figures of some of the new species)*. London: van Voorst. iv + 17 pp., 16 pls.
- Grice, A.J., and Lethbridge, R.C. 1988. Reproductive studies on *Patiriella gunnii* (Asteroidea: Asterinidae) in south-western Australia. *Australian Journal of Marine and Freshwater Research* 39: 399–407.
- Hart, M.W., Byrne, M., and Smith, M.J. 1997. Molecular phylogenetic analysis of life-history evolution in asterinid starfish. *Evolution* 51(6): 1848–1861.
- Janies, D. 2001. Phylogenetic relationships of extant echinoderm classes. *Canadian Journal of Zoology* 79: 1232–1250.
- Kimura, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120.
- Lamarck, J.B.P.A. de 1816. Stellerides. Pp. 522–568 in: *Histoire naturelle des animaux sans vertèbres*. Vol. 1(2). Paris.
- Long, S., and Byrne, M. 2001. Maternal control of development in five *Patiriella* species. P. 185 in: Barker, M. (ed.), *Echinoderms 2000. Proceedings of the Tenth International Conference, Dunedin*. Swets and Zeitlinger: Lisse.
- Marsh, L.M., and Pawson, D.L. 1993. Echinoderms of Rottnest Island. Pp. 279–304 in: Wells, F.E., Walker, D.I., Kirkman, H., and Lethbridge, R. (eds), *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*. Western Australian Museum: Perth.
- Mayr, E. 1942. *Systematics and the origin of species*. (Reprint edn). Columbia University Press: New York.
- McCoy, F. 1878–1890. *Prodromus of the zoology of Victoria. Figures and descriptions of the living species of all classes of the Victorian indigenous animals*. Government Printer: Melbourne.
- Mortensen, T. 1925. Echinoderms of New Zealand and the Auckland-Campbell Islands. III–V. Asteroidea, Holothuriodea, Crinoidea. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kobenhavn* 79(29): 261–420, text figs 1–70, pls 12–14.
- Müller, J., and Troschel, F.H. 1842. *System der Asteriden*. Braunschweig. xx+134 pp., 12 pls.
- O'Loughlin, P.M. 1984. Class Asteroidea. Pp. 130–138 in: Phillips, D.A.B., Handreck, C.P., Bock, P.E., Burn, R., Smith, B.J., and Staples, D.A. (eds), *Coastal invertebrates of Victoria. An atlas of selected species*. Marine Research Group of Victoria in association with the Museum of Victoria: Melbourne.
- O'Loughlin, P.M., Waters, J.M., and Roy, M.S. 2002. Description of a new species of *Patiriella* from New Zealand, and review of *Patiriella regularis* (Echinodermata, Asteroidea) based on morphological and molecular data. *Journal of The Royal Society of New Zealand* 32(4): 697–711.
- Palumbi, S.R., Cipriano, F., and Hare, M. 2001. Predicting nuclear gene coalescence from mitochondrial data: the three times rule. *Evolution* 55: 859–868.
- Perrier, E. 1869. *Recherches sur les pedicellaires et les ambulacres des astéries et des oursins*. Masson: Paris. 188 pp., 2 pls.

- Perrier, E. 1876. Révision de la collection de stellerides du Muséum d'Histoire Naturelle de Paris. *Archives de Zoologie Experimentale et Generale* (1876) 5: 1–104, 209–304.
- Rowe, F.W.E., and Gates, J. 1995. Echinodermata. In: Wells, A. (ed.), *Zoological Catalogue of Australia* Vol. 33. CSIRO: Melbourne. xiii+510 pp.
- Rowe, F.W.E., and Vail, L.L. 1982. The distributions of Tasmanian echinoderms in relation to southern Australian biogeographic provinces. Pp. 219–225, 1 fig. in: Lawrence J.M. (ed.), *Echinoderms: Proceedings of the International Conference, Tampa Bay*. Balkema: Rotterdam.
- Saghai-Maroo, M.A., Soliman, R.A., Jorgensen, R.A., and Allard R.W. 1984. Ribosomal DNA spacer-length polymorphisms in barley: mendelian inheritance, chromosomal location, and population dynamics. *Proceedings of the National Academy of Sciences of the USA* 81: 8014–8018.
- Shepherd, S.A. 1968. The shallow water echinoderm fauna of South Australia. 1. The asteroids. *Records of the South Australian Museum* 15(4): 729–756.
- Sladen, W.P. 1889. Report on the Asteroidea collected during the voyage of H.M.S. *Challenger* during the years 1873–1876. *Report on the scientific results of the voyage of H.M.S. Challenger*, *Zoology* 30: 1–893, 117 pls.
- Swofford, D.L. 1998. *Phylogenetic analysis using parsimony (and other methods)* PAUP\*4.0b10. Sinauer Associates: Sunderland.
- Verrill, A.E. 1867. Notes on the Radiata in the Museum of Yale College, with descriptions of new genera and species. 1. Descriptions of new starfishes from New Zealand. *Transactions of the Connecticut Academy of Arts and Sciences* 1(2)5: 247–251. (Also in: *Transactions and Proceedings of the New Zealand Institute* (1880) 12(34): 278–283)
- Verrill, A.E. 1913. Revision of the genera of starfishes of the sub-family Asterininae. *American Journal of Science* (4) 35 (209): 477–485.
- Zeidler, W., and Shepherd, S.A. 1982. Sea-stars (class Asteroidea). Pp. 400–418, figs 10.3–10.9, pl. 30(2) in: Shepherd, S.A., and Thomas, I.M. (eds), *Marine Invertebrates of Southern Australia*. Part 1. South Australian Government Printer: Adelaide.