

# TAXONOMY AND EVOLUTION OF THE CAINOZOIC SPATANGOID ECHINOID *PROTENASTER*

by KENNETH J. MCNAMARA

**ABSTRACT.** The spatangoid echinoid *Protenaster* Pomel, 1883, previously known only from the living Australian species *P. australis* (Gray, 1851), is described from the Tertiary for the first time. Three fossil species are recognized from southern Australia: the late Eocene *P. preaustralis* sp. nov.; the late Oligocene *P. philipi* sp. nov.; and the early Miocene *P. antiaustralis* (Tate, 1885), which is fully described and figured for the first time. *P. australis* is redescribed and the ontogenetic development and intraspecific variation documented. *Protenaster* is shown to have been a morphologically conservative genus throughout the Tertiary. The only significant morphological evolution involved the peramorphic evolution of the phyllodal plates, which formed a peramorphocline from the Tertiary to the Recent. This peramorphocline followed an environmental gradient of coarse to fine calcarenites and reflects the adaptation of successive species to feeding on finer-grained sediments.

THE spatangoid echinoid *Protenaster* is uncommon, both as a living species and in the fossil record. Indeed, even though fossil echinoids have been described from the Tertiary rocks of southern Australia since the mid-nineteenth century, and the living species *P. australis* has been known since 1851, the existence of fossil species of this genus has hitherto not been recognized. The rarity of extinct species of *Protenaster* is illustrated by the fact that of the three species described below, two are each known from nine specimens, while the third is known from only two specimens. This latter species was originally described as *Linthia antiaustralis* by Tate (1885). In addition to describing these fossil species, the living *P. australis* is redescribed on the basis of thirty-four Recent and three fossil specimens. Intraspecific and ontogenetic changes are documented in this species for the first time.

Although the genus is shown to range from the late Eocene to Recent, all four species show a remarkable overall morphological similarity to one another. Close examination for distinguishing characters has revealed an interesting evolutionary change in the nature of the phyllodal plates. Phyllodes are broad ambulacral areas surrounding the peristome in which pores are more concentrated and, particularly in spatangoids, larger than other adoral ambulacral pores; the ambulacral plates which bear such pores are termed phyllodal plates. Ontogenetic analysis of *P. australis* has highlighted the close correspondence between both ontogenetic and phylogenetic development of the phyllodal plates; these changes are quite substantial when contrasted to the overall phylogenetic morphological changes, and are analysed here.

Little attention has been paid to the ontogenetic development of the phyllodal pores and their associated periporal areas in echinoids. The phyllodal periporal areas in *Protenaster* undergo appreciable morphological change, during both ontogeny and phylogeny. Four basic states are recognized, and a terminology to describe them is introduced:

1. *Bridged interporal partition.* In this state the interporal partition is arched over the pore, effectively creating a pair of isopores which unite immediately beneath this bridge (text-fig. 5.1).
2. *Breached interporal partition.* The condition where the interporal bridge is breached medially and a unipore thus develops (text-fig. 4.6).
3. *Reniform periporal area.* The two separated interporal segments migrate adaxially and reunite to form a swollen, reniform ridge beneath which, on the adaxial side, the unipore is located (text-fig. 4.1).

4. *Platform periporal area*. The flat, abaxial part of the periporal area swells and forms a raised platform. This may, in the largest specimens, unite with the reniform segment to form one large platform, or more usually the two may be separated by a depression (text-fig. 1A). Occasionally, a minute opening into the test, connecting with the large unipore, may be established in this depression.

#### MATERIALS AND METHODS

This paper is one of a series of revisions (McNamara and Philip 1980, 1984; Kruse and Philip, in press) of the fossil spatangoid echinoids of southern Australia currently being undertaken, largely on the basis of collections made in recent years by R. J. and F. Foster. These collections, and others on which this study is based, are housed in the Tasmanian Museum (TM), Museum of Victoria (NMV), Melbourne University, Geology Department (MUGD), South Australian Museum (SAM), Western Australian Museum (WAM), University of Western Australia (UWA), and British Museum (Natural History) (BMNH).

Measurements were made with a vernier calliper to an accuracy of 0.1 mm. A number of parameters are expressed as percentages of maximum test length (%TL). Where the terms 'adaxial' and 'abaxial' are used, they refer to the axis of the test.

#### SYSTEMATIC PALAEOLOGY

Order SPATANGOIDA Claus, 1876

Family SCHIZASTERIDAE Lambert, 1905

Genus PROTENASTER Pomel, 1883

*Type species*. *Desoria australis* Gray, 1851, pp. 132–133; by original designation.

*Emended diagnosis*. Apical system ethmolytic, with four genital pores; positioned well anterior of centre. Petals sunken; anterior pair transverse, or nearly so. Ambulacrum III sunken, bearing closely spaced pore pairs with prominent interporal partition. Peripetalous fasciole runs close to ambitus anteriorly and is indented between paired petals. Lateroanal fasciole present. Peristome sunken. Pores in phyllode isopores or unipores; periporal area raised. Second plate of interambulacrum I generally abutting both ambulacra I and II adorally.

*Assigned species*. *P. australis* (Gray, 1851), *P. antiaustralis* (Tate, 1885), *P. synapticus* (Henderson, 1975), *P. preaustralis* sp. nov., and *P. philipi* sp. nov.

*Remarks*. Mortensen (1951, p. 224) recognized the similarity of *Protenaster* to *Prenaster* but considered the two taxa to be generically distinct, primarily on account of the course of the peripetalous fasciole. This extends below the ambitus close to the peristome in *Prenaster*, whereas in *Protenaster* it runs close to the ambitus across ambulacrum III. Fischer (1966) preferred to regard *Protenaster* as a subgenus of *Prenaster*. More recently, Henderson (1975, p. 19) placed *Protenaster* in synonymy with *Prenaster*. Henderson's course of action was based in part on his belief that *Protenaster* is only known from a living species, whereas *Prenaster* is restricted to Eocene to Miocene strata; the two taxa, therefore, lying at either end of a morphological-time continuum. However, three fossil species which compare closely with the living species of *Protenaster* are known from the Eocene–Miocene of southern Australia. Furthermore, one of these species (from the late Eocene Tortachilla Limestone) coexists with a species of *Prenaster*. Henderson further considered that a species which he described as *Prenaster synapticus* (from the Eocene of New Zealand) was morphologically intermediate between *Protenaster* and *Prenaster* because it lacked an anterior notch, an attribute of *Protenaster* but not of *Prenaster*. It must be pointed out, however, that the specimens described by Henderson (1975, p. 20) are small, being less than 20 mm test length. Specimens of comparable size of Australian Eocene and Recent species similarly lack an anterior notch or, if present, it is only very weakly developed. During growth, however, the notch deepens to varying degrees in different species as ambulacrum III and the petals deepen (see below). Henderson has observed that *P. synapticus* compares with *Protenaster australis* in the anterior course of the peripetalous fasciole. Consequently, I can see no justification for placing *Protenaster* in synonymy with *Prenaster*.

The two genera were contemporaneous during part of the Tertiary and followed quite separate phylogenetic pathways. *Protenaster* can be distinguished from *Prenaster* by its possession of deeper petals; a deeper ambulacrum III, in which well-developed pore pairs occur; an anterior notch; and a peripetalous fasciole which is indented between the anterior and posterior petals, and which does not extend below the ambitus anteriorly.

In addition to including *Prenaster synapticus* in *Protenaster*, *Linthia antiaustralis* Tate, 1885 is also included. This species is morphologically very similar to the living species *P. australis*. Certainly *Protenaster* is similar to *Linthia* and is likely to have evolved from it in the early Tertiary; indeed, *P. australis* was placed in *Linthia* by Agassiz (1872–1874), Tenison Woods (1878), and Hall (1904). However, *Protenaster* can be distinguished from *Linthia* by its more anteriorly positioned apical system, its broader plastron, and the bisection of the first two plates in interambulacrum 1a by the second plate of interambulacrum 1b adorally.

*Protenaster australis* (Gray, 1851)

Plate 32; Plate 33, figs. 3, 4; text-figs. 1, 2

- 1851 *Desoria australis* Gray, p. 133.  
 1855 *Desoria australis* Gray; Gray, p. 58, pl. 6, fig. 2.  
 1872 *Linthia australis* (Gray); Agassiz, p. 138, pl. 19, figs. 7–9; pl. 21, figs. 5–7.  
 1874 *Desoria australis* Gray; Lovén, pp. 16, 54, 57, 63, pl. 28.  
 1883 *Protenaster australis* (Gray); Pomel, p. 36.  
 1891 *Linthia australis* (Gray); Ramsay, pp. 43, 56.  
 1904 *Linthia australis* (Gray); Hall, p. 73.  
 1914 *Linthia australis* (Gray); Alexander, p. 112.  
 1914 *Linthia australis* (Gray); Clark, p. 169.  
 1917 *Protenaster australis* (Gray); Clark, p. 169.  
 1925 *Protenaster australis* (Gray); Clark, p. 201.  
 1925 *Protenaster australis* (Gray); Lambert and Thiéry, p. 520.  
 1928 *Protenaster australis* (Gray); Clark, p. 479.  
 1938 *Protenaster australis* (Gray); Clark, p. 429.  
 1942 *Protenaster australis* (Gray); Cotton and Godfrey, p. 226.  
 1946 *Protenaster australis* (Gray); Clark, p. 364.  
 1951 *Protenaster australis* (Gray); Mortensen, pp. 208, 224–226.  
 1975 *Protenaster australis* (Gray); Henderson, pp. 19–21.  
 1983 *Protenaster australis* (Gray); McNamara and Bryce, pp. 73–74.

**Diagnosis.** Phyllodal pores unipores; breached periporal area in juvenile; reniform to platform in adults.

**Material.** Gray (1851, p. 133) described this species on the basis of 'several specimens' from Flinder's Island, Tasmania. Only three of these specimens can now be located. Two are numbered BMNH 60.12.17.4, of which that of intermediate size (maximum test length 58.8 mm) is herein chosen as the lectotype, and the third is BMNH 62.1.8.33.

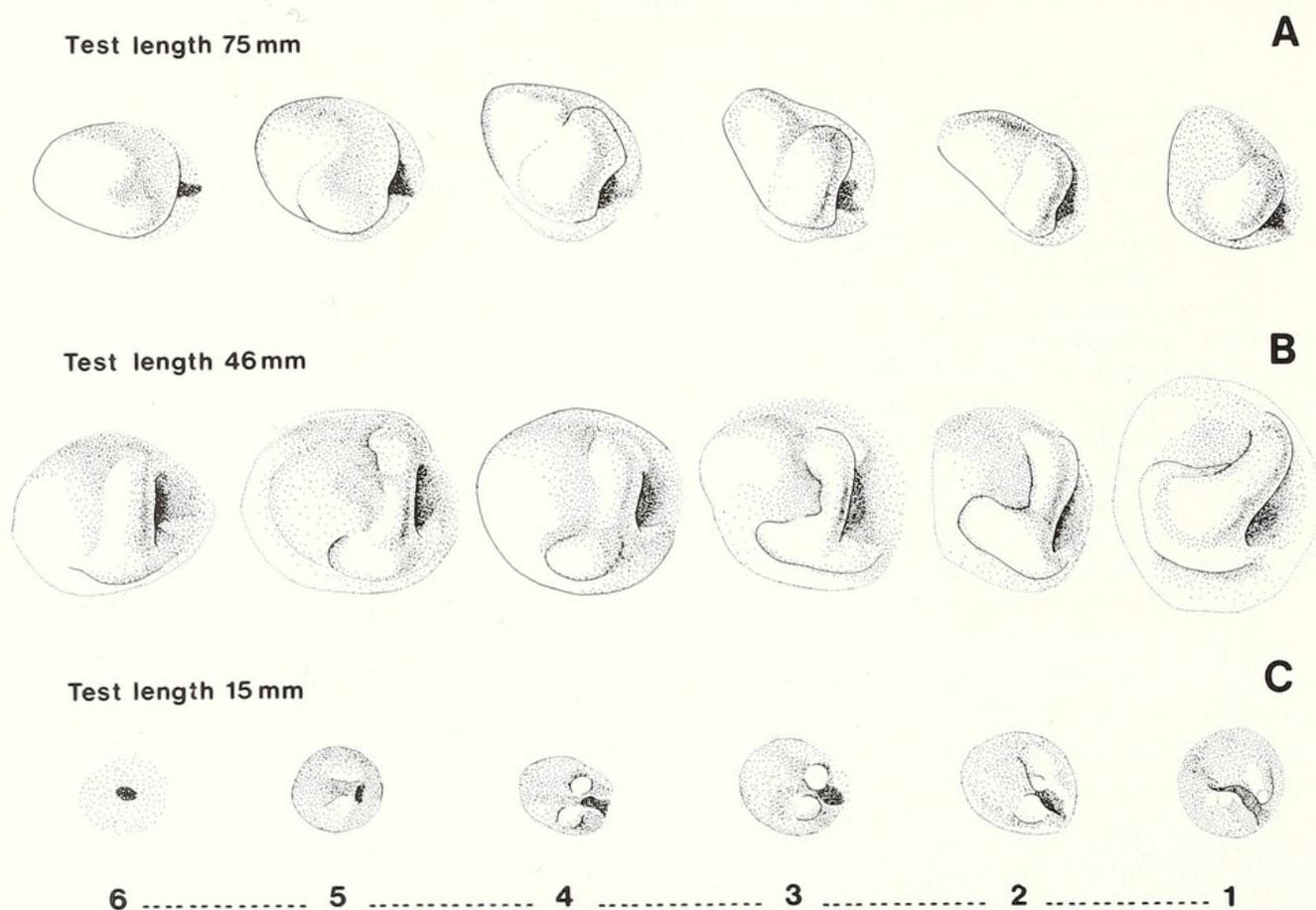
The species is not common in collections. This description is based on eleven BMNH specimens: 72.6.22.25–27, 60.12.17.4 (two specimens), 62.1.8.33, 49.11.19.1, 1953.2.6.311–313, and one unregistered specimen; five TM specimens: H917–920, 15409/H70; sixteen WAM specimens: 397–74, 543–39, 276–74, 331–74 (two specimens), 122–37, 1770–74, 181–37, 41–44, 9491, 151–32, 152–32, 679–71, 740–83, and two unregistered specimens; and three UWA specimens: 41232.

In Tasmania it has been found off Flinder's Island and Cape Barren Island. It ranges as far north as Port Jackson in New South Wales. Clark (1946, p. 364) recorded it from Western Port, Victoria and Cotton and Godfrey (1942) recorded it from waters off South Australia. It occurs in south-western Australia from Hopetoun to as far north as Trigg Beach, Perth. Three specimens (UWA 41232) are known from the late Pleistocene Tamala Limestone, just south of the mouth of the Greenough River.

**Description.** Test ginger-coloured with prominent, large, black pedicellariae on aboral surface; reaches a maximum known length of 94 mm; widest anterior of centre in small specimen (15 mm TL), but widest posterior

of centre in large specimens (75 mm TL); width 81–90% TL. Test highest at about mid-test length in interambulacrum 5; forms a weakly developed keel; height variable, 57–68% TL. Test has broad, shallow anterior notch in adult specimens (Pl. 32, fig. 7). Apical system ethmolytic, slightly depressed, with four genital pores; at 15 mm TL genital pores not open; at 28.5 mm TL genital pores open; situated 25–38% TL from anterior ambitus; migrates anteriorly with growth of test (text-fig. 3A).

Aborally ambulacrum III shallow, deepening abapically; bears isopores which are separated by prominent interporal partition; isopores increase in number from sixteen in juvenile specimen to twenty-seven in adults, and bear extensile tube feet tipped by light sensitive terminal pads (McNamara, 1984b). Anterior petals aligned transversely; anteriorly flexed distally. Petals 37–46% TL long, 6.5% TL wide; relatively shorter in smaller specimens (text-fig. 3D); each row bearing up to forty-one conjugate pore pairs; only twenty present in specimen 15 mm TL; number of pore pairs increases to about thirty-eight to forty-one in adults of about 50 mm TL, thereafter remaining constant in number with growth of test (text-fig. 3C). Rarely, poriferous plates in ambulacrum II or IV may be occluded. Posterior petals slightly shorter than anterior petals, 32–44% TL in

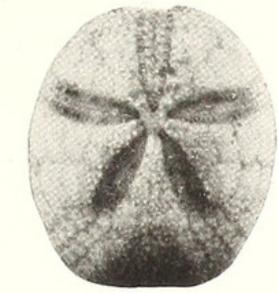


TEXT-FIG. 1. *Protaster australis* (Gray, 1851); camera lucida drawings of phylloidal plates 1 to 6 of ambulacrum Ib. A, WAM 493-84, large adult with platform periporal area,  $\times 15$ . B, WAM 151-32, small adult with reniform periporal area,  $\times 30$ . C, WAM 397-74, juvenile with breached periporal area,  $\times 33$ .

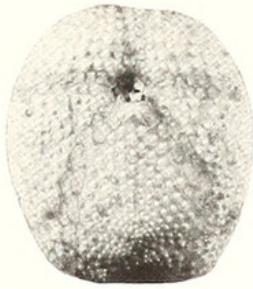
#### EXPLANATION OF PLATE 32

Figs. 1–8. *Protaster australis* (Gray, 1851). 1–4, WAM 397-74, juvenile test, collected from reef platform, Cape Vlaming, Rottnest Island, Western Australia; wet specimen showing plate boundaries,  $\times 2$ . 5, 6, WAM 331-74, from Bunker Bay, Western Australia,  $\times 2$ . 7, 8, WAM 740-83, from sand pocket on limestone reef 30 m off Trigg Beach, Perth, Western Australia, buried 10 cm in 1.8 m of water,  $\times 1$ .

All Recent. Figs. 5–8 whitened with ammonium chloride.



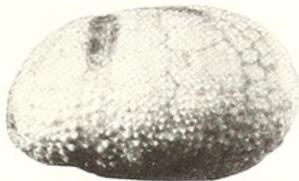
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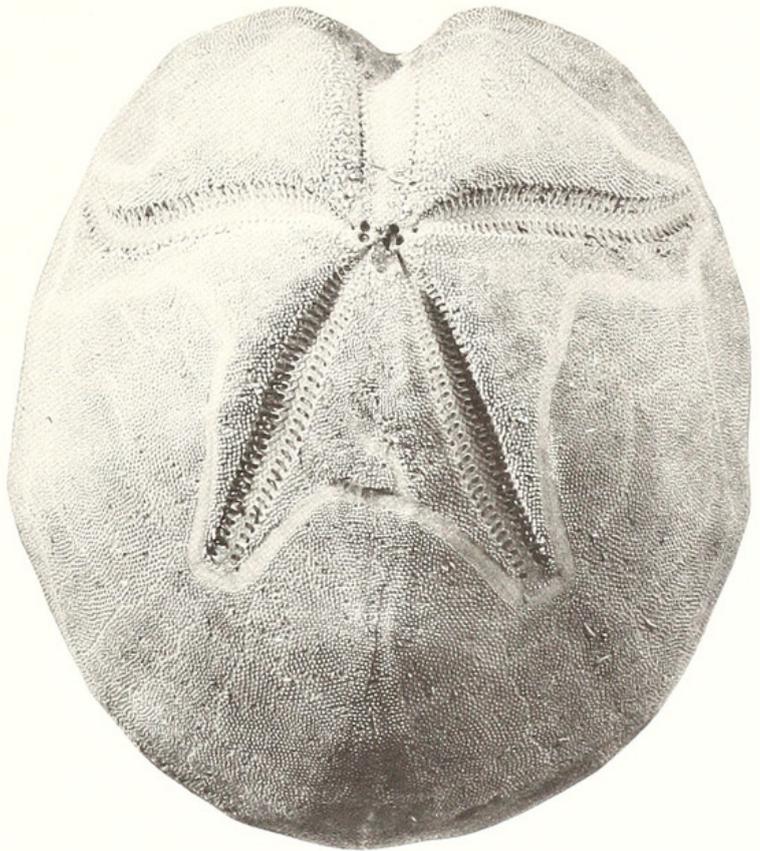
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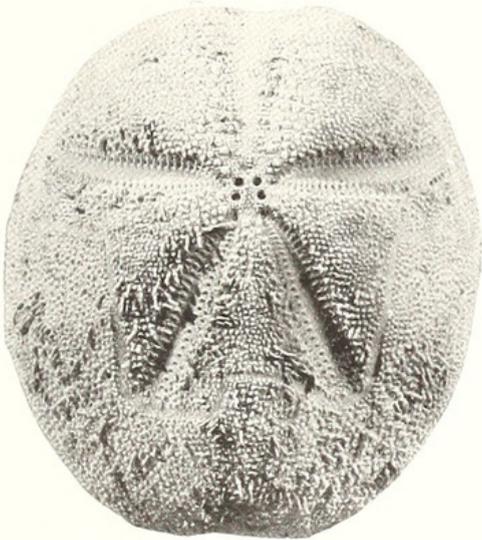
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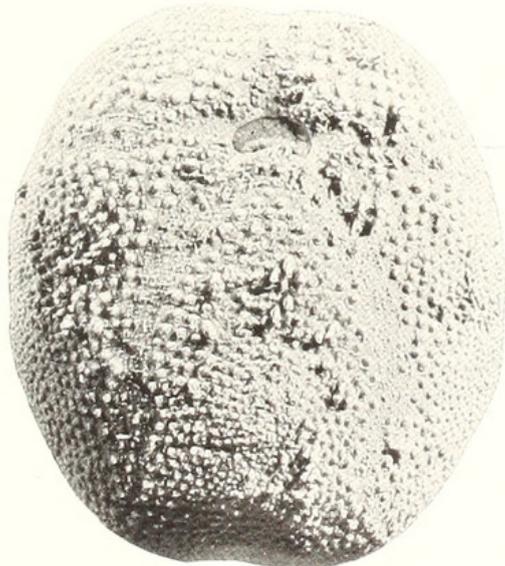
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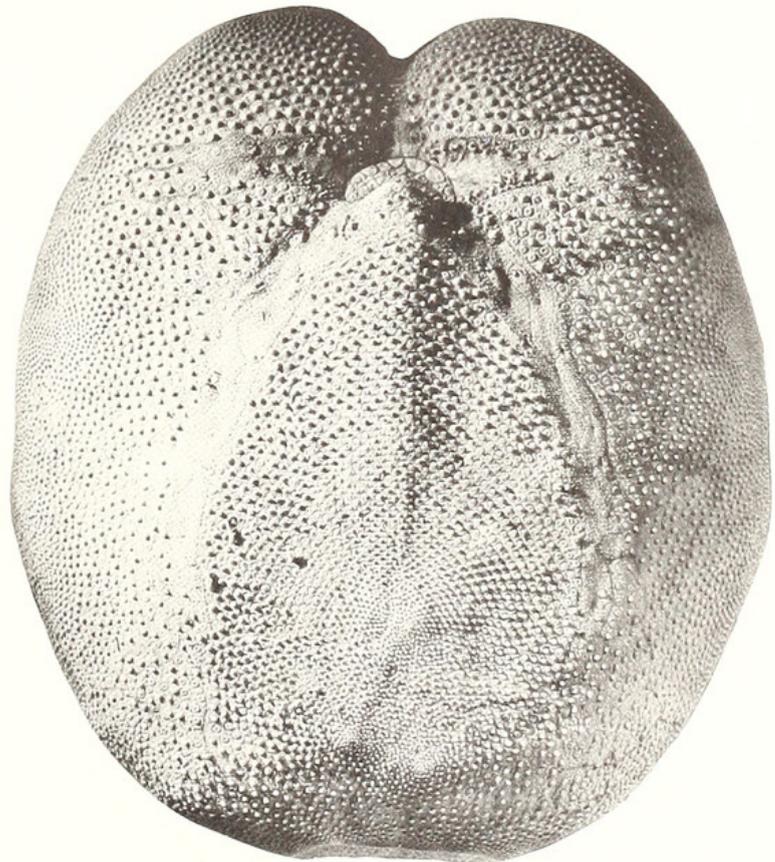
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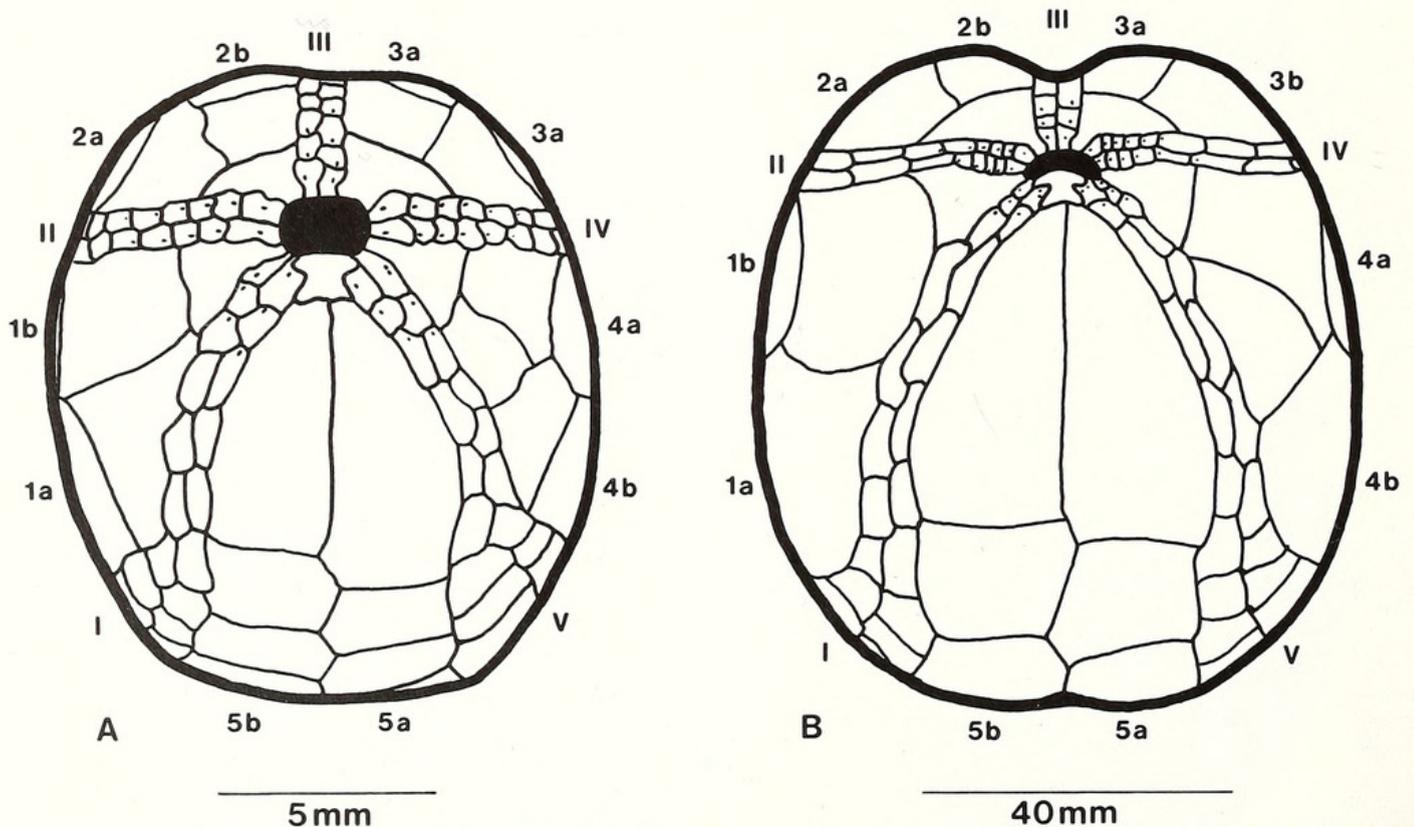
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adults, more so in juvenile; diverge at about  $45-50^\circ$ ; each row bears up to forty-two conjugate pore pairs; rate of increase of number of pore pairs the same as for anterior petals. Peripetalous fasciole indented between petals; crosses interambulacra 1b/4b in plate 6, crosses plates 5-7 in 1a/4a, and plate 4 in 2a/3a and 2b/3b. Lateroanal fasciole one third width of peripetalous; crosses plate 5 of 1b/4b and plate 4 of 1a/4a.

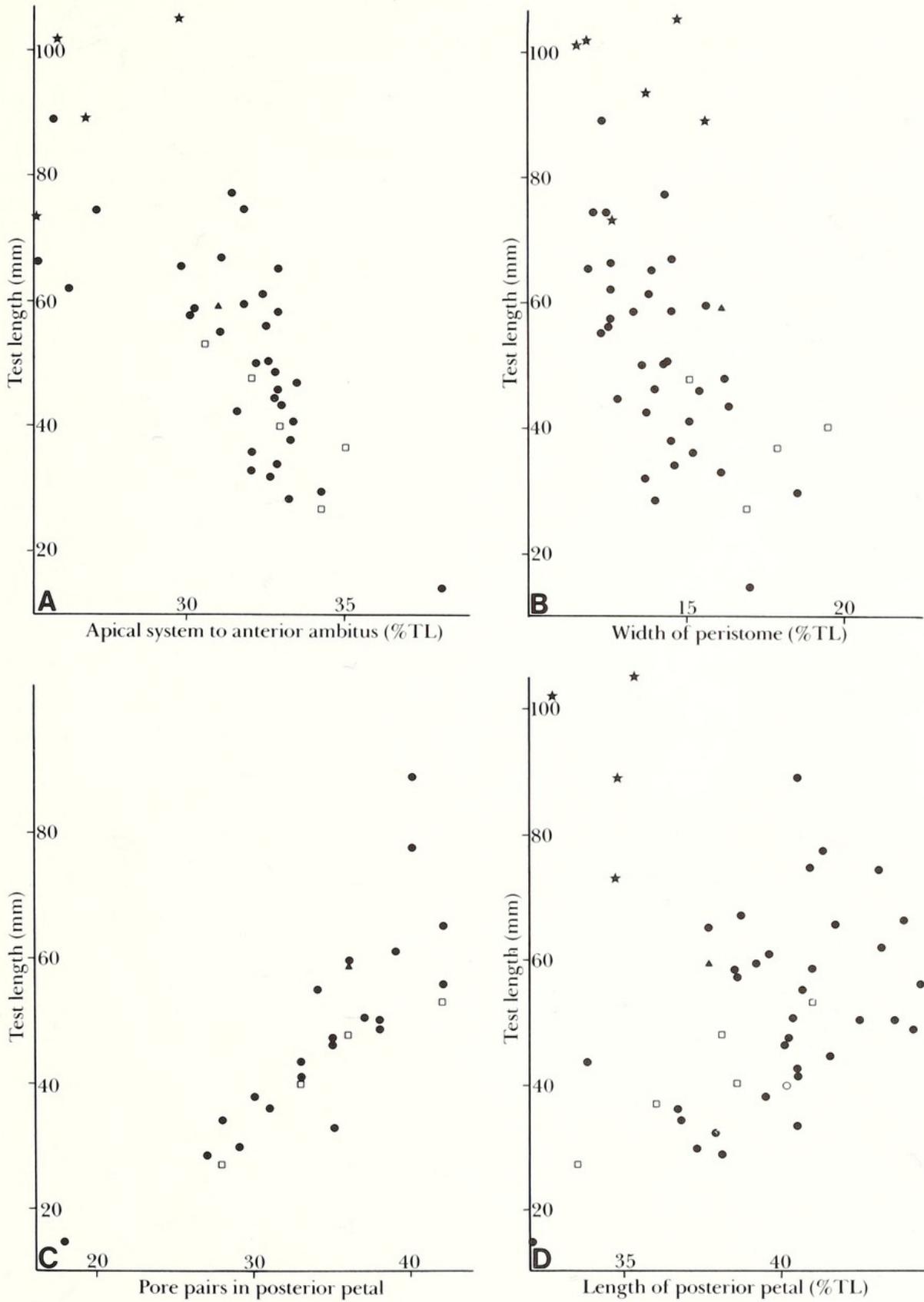
Peristome slightly sunken, lunate, width 12-19% TL, high values in small specimens; relative width progressively decreases with growth of test (text-fig. 3B). Anterior of peristome situated 22% TL from anterior ambitus in juvenile specimen, decreasing to 15% TL in large adults. With test growth labrum increasingly projects across peristome, reaching halfway in largest specimens (Pl. 32, fig. 8). Pores in phyllode generally unipores: eight pores in ambulacra I/V, twelve to fourteen in ambulacra II/IV, and seven or eight in ambulacrum III. With growth of the test, phyllodes pass through breached to platform stages of development. In juvenile specimen (15 mm TL) periporal area in breached condition (text-fig. 1C), apart from one plate which has isopores and a bridged interporal partition. In moderate sized specimens periporal areas have a reniform ridge (text-fig. 1B). In largest tests the abaxial part of the periporal area swells to form a raised platform (text-fig. 1A), which is separated from reniform ridge by a depression in which, rarely, a pore develops connecting to the main unipore.

Plastron broad but variable, 35-50% TL. Adoral plate 2 of interambulacrum 1b bisects plate 1 and plate 2 of interambulacrum 1a (text-fig. 2B) in all specimens examined, except the juvenile, where it fails to bisect and meet ambulacrum I (text-fig. 2A). Periproct oval, width about two-thirds length; length same as peristome width. Twenty-four tubercles per  $5 \text{ mm}^2$  in interambulacrum 2 close to peristome in test 45 mm TL; twenty-one tubercles per  $5 \text{ mm}^2$  in test 58 mm TL. Pedicellariae described in detail by Clark (1938) and Mortensen (1951).

*Habitat.* Hall (1904) recorded *P. australis* from a depth of 6 fathoms. One specimen in the WAM collection records the depth of collection of the live test as 25 fathoms. Recently McNamara and Bryce (1983) have described the habitat of the species off Trigg Beach, Western Australia. Two specimens were collected alive from sand where they were buried to a depth of 10 cm in water only 1.8 m deep, and only some 30 m offshore in a



TEXT-FIG. 2. *Protaster australis* (Gray, 1851); adoral plating. A, WAM 397-74, juvenile, 15 mm TL, showing how the second plate of interambulacrum 1b fails to breach plates 1 and 2 of interambulacrum 1a. B, WAM 740-83, large adult, 90 mm TL, showing breaching of interambulacrum 1a by second plate of interambulacrum 1b.



TEXT-FIG. 3. Morphological changes during ontogeny of *Protaster australis* (Gray, 1851) (●), *P. antiaustralis* (Tate, 1885) (▲), *P. preaustralis* sp. nov. (□), and *P. philipi* sp. nov. (★). Plots of test length against: A, distance of apical system from anterior ambitus (% TL); B, width of peristome (% TL); C, number of pore pairs in each row of the posterior petals; D, length of the posterior petals (% TL).

sheltered sand pocket on a limestone reef. Locality data with museum specimens suggests that this habitat may not be unusual for the species, as many specimens are recorded as having been collected from reef platforms or from beaches off which limestone reefs occur. Three further specimens were collected alive from the same sand pocket in January 1984. The sand is a fine-grained calcarenite (see McNamara and Bryce 1983, table 1, for grain-size analysis).

*Remarks.* Clark (1938) suggested that specimens collected from south-western Australia may belong to a different species from that occurring in Victorian and Tasmanian waters, because there appear to be some colour differences: a few Tasmanian bare tests have a purple tinge, a feature not seen in the south-western Australian specimens. This feature is not consistent and hardly seems a character worthy of specific differentiation. A small number of Tasmanian specimens examined do, however, show a greater degree of variation in certain morphological characters than the south-western Australian specimens. This variation is attributable to the paedomorphic nature of certain characters. For instance, two specimens (TM H918 and H920) both possess relatively shorter petals than other specimens of *P. australis*. However, this slight variation is not sufficient to warrant specific separation of the specimens. They merely lie at the extreme range of variation of the character, resembling juveniles of apaedomorphs.

The late Pleistocene specimens from south of the mouth of the Greenough River, Western Australia compare closely with living specimens in all characters except one: they possess slightly wider tests (90–92% TL, compared with 81.4–90% TL in living specimens). Again, they are merely considered to be variants lying at the extreme range of variation in this one character. The occurrence of these late Pleistocene specimens farther north than the present range of the species (29° latitude, compared with 32°) may indicate a more northward spread of the cold Western Australian current up the coast of Western Australia at some time during the last interglacial.

During the ontogeny of *P. australis* a number of morphological characters change allometrically. The widest part of the test migrates posteriorly during growth; the anterior notch is hardly present in the juvenile, but deepens during ontogeny; pore pairs in the aboral ambulacra increase in number to a test length of about 50 mm (text-fig. 3C); the anterior and posterior petals lengthen relatively during ontogeny (text-fig. 3D); the peristome decreases in relative width and the periproct decreases in relative length (text-fig. 3B); the peristome migrates anteriorly; the labrum lengthens; the pores in the phyllode pass through the breached, reniform, and platform stages; and the second adoral plate of interambulacrum 1b fails to bisect the first and second plates of interambulacrum 1a in the juvenile specimen, although it does in adults.

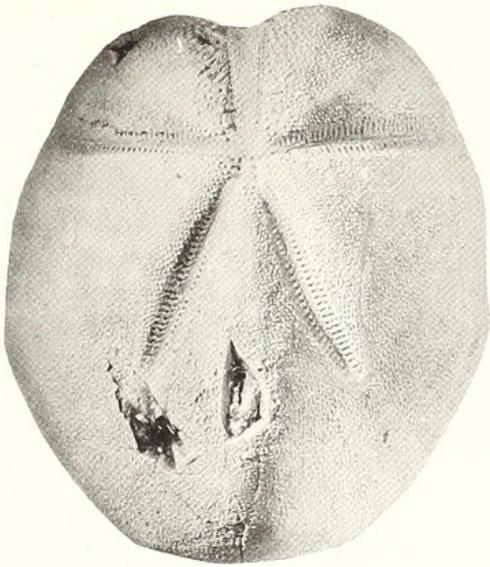
*Protenaster antiaustralis* (Tate, 1885)

Plate 33, figs. 1, 2, 5; text-fig. 4

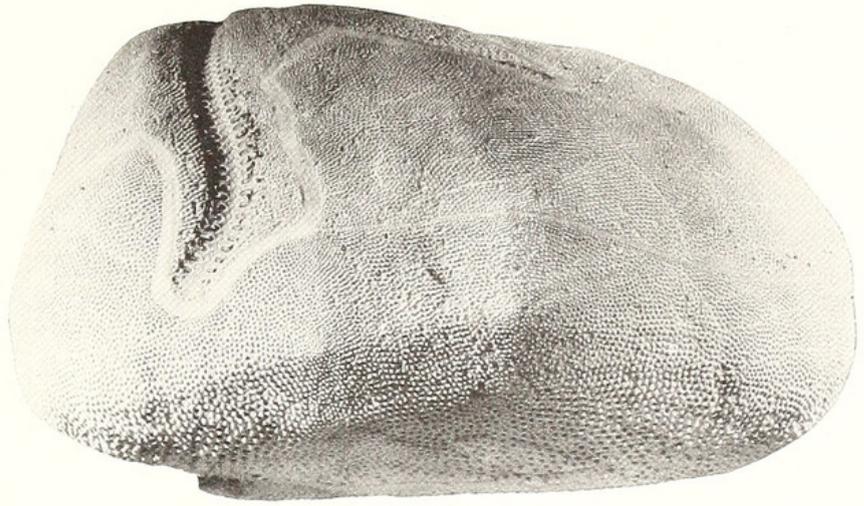
- 1885 *Linthia antiaustralis* Tate, pp. 4–5.  
 1908 *Linthia antiaustralis* Tate; Chapman, pp. 215–216, pl. 19.  
 1908 *Linthia antiaustralis* Tate; Pritchard, pp. 397–398.  
 1946 *Linthia antiaustralis* Tate; Clark, pp. 365–366.

EXPLANATION OF PLATE 33

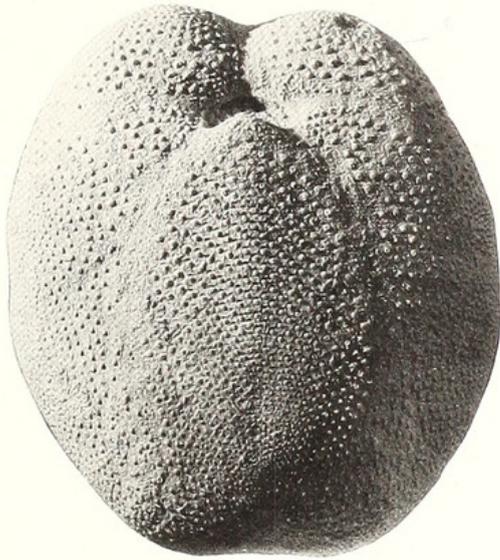
- Figs. 1, 2, 5. *Protenaster antiaustralis* (Tate, 1885). SAM T268, holotype, from River Murray Cliffs, near Morgan, South Australia; Morgan Limestone (early Miocene), × 1.  
 Figs. 3, 4. *Protenaster australis* (Gray, 1851). 3, WAM 397-74, locality as for Plate 32, figs. 7, 8, × 1. 4, WAM 493-84, from Hopetoun, Western Australia, showing detail of the peristome and phyllode, with platform periporal areas, × 2.  
 Figs. 6–8. *Protenaster preaustralis* sp. nov. 6, SAM P24520 from Maslin Beach–Port Willunga district, South Australia; Tortachilla Limestone (late Eocene), × 1. 7, 8, SAM P24519, holotype, from same locality and horizon as fig. 6, × 1.



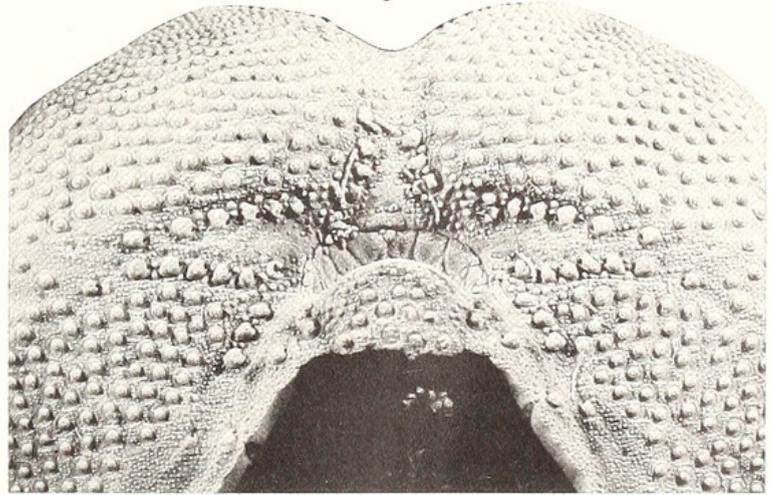
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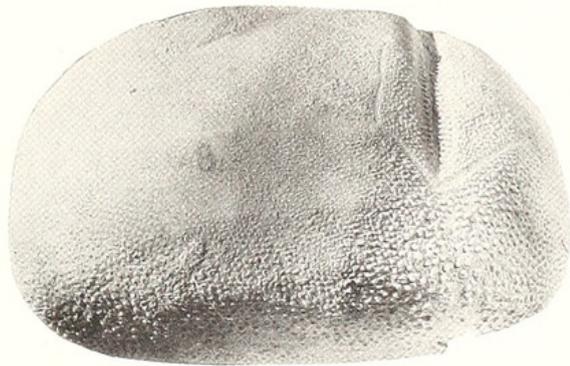
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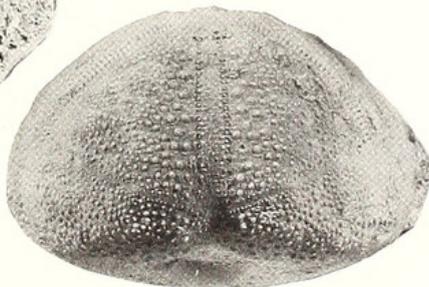
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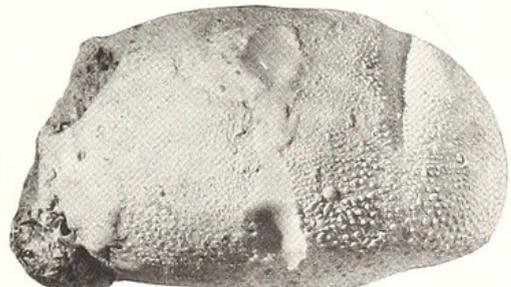
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*Diagnosis.* Phyllodal pores unipores; periporal area breached in most plates, those closest to peristome reniform.

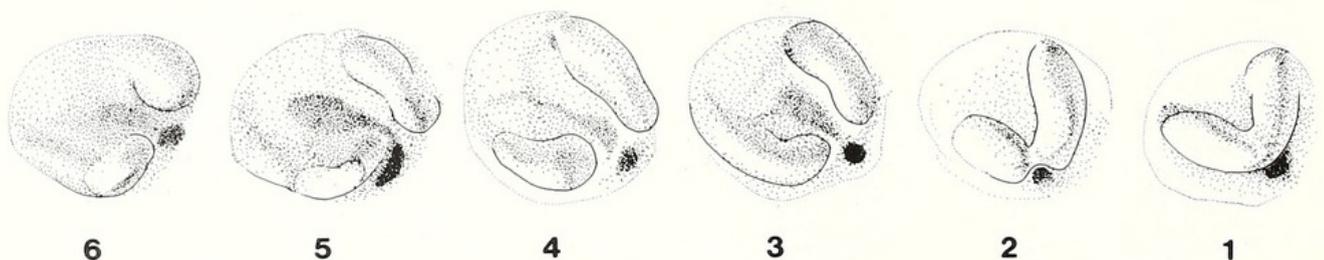
*Material.* The holotype, SAM T268, from the early Miocene 'calciferous sandrock' (probably the Balcombian Morgan Limestone), River Murray Cliffs, near Morgan, South Australia, and NMV P9154, from Balcombian strata at Curlewis, near Geelong, Victoria.

*Description.* Test up to 59 mm in length; widest posterior of centre, width 88% TL; highest at mid-test length in interambulacrum 5, which forms a keel (Pl. 33, fig. 5); height 66% TL; anteriorly a broad, shallow notch is present. Apical system ethmolytic, with four genital pores; situated 31% TL from anterior ambitus. Thirty isopores in ambulacrum III; each pore separated by prominent interporal partition. Anterior petals slightly anteriorly divergent at about 160°; almost straight, shallow, and bearing up to thirty-eight conjugate pore pairs in each row; length 38–43% TL. Posterior petals shorter than anterior pair, 35–38% TL; diverge at about 60°; bear up to thirty-six pore pairs in each row; slightly flexed distally (Pl. 33, fig. 1). Peripetalous and lateroanal fascioles follow same course as those in *P. australis*.

Peristome slightly sunken, lunate, width 16% TL. Anterior of peristome situated 17% TL from anterior ambitus. Labrum projects halfway across peristome (Pl. 33, fig. 2). Pores in phyllode are unipores; eight pores in ambulacra I, III, and V; twelve pores in ambulacrum II, thirteen in IV. Periporal area in plates 1 and 2 in ambulacra II and IV reniform; in plates 3–6 breached, degree of separation decreasing adaxially as raised segments lengthen (text-fig. 4). Similarly, periporal areas in first two plates of ambulacra I, III, and V reniform, others breached. Plastron quite broad, 40% TL. Plates 1 and 2 of interambulacrum 1a bisected by plate 2 of interambulacrum 1b. Periproct oval with long axis sagittal (16.5% TL) and width two-thirds length. Fourteen tubercles per 5 mm<sup>2</sup> in interambulacrum 2 close to peristome.

*Remarks.* Tate (1885, pp. 4–5) considered that *P. antiaustralis* differed significantly from *P. australis* in seven characters. However, analysis of the intraspecific variation of *P. australis* shows that four of these characters cannot be used to distinguish the species, highlighting the overall close morphological similarity between the living *P. australis* and the early Miocene *P. antiaustralis*; those which fall within the range of variation of *P. australis* are test height and width, the form of the adoral surface, and the size and depth of the apical system. However, three of the characters which Tate used to distinguish the two species are valid: *P. antiaustralis* has slightly shallower petals than *P. australis*; the difference in lengths of the anterior and posterior petals is more pronounced in *P. antiaustralis*; and the angle of divergence of the posterior petals is greater in *P. antiaustralis* (60°, not 50° as Tate stated). Furthermore, *P. antiaustralis* can be distinguished from *P. australis* by its relatively broader peristome (text-fig. 3B) and longer periproct; the presence of only breached and reniform periporal areas in the phyllode; and sparser tuberculation in interambulacrum 2 adorally.

Chapman (1908, pp. 215–216, pl. 19) illustrated a specimen which he assigned to *P. antiaustralis*. Pritchard (1908, pp. 397–398) was scathing in his criticism of Chapman's lack of description and poor illustration of the specimen. Furthermore, he doubted whether the two specimens were conspecific. However, examination of the specimen reveals that it does, indeed, belong in *P. antiaustralis*. Its relatively shorter petals are a function of its smaller size.



TEXT-FIG. 4. *Protenaster antiaustralis* (Tate, 1885); camera lucida drawings of phyllodal plates 1 to 6 of ambulacrum Ib. SAM T268, showing reniform periporal area in plates 1 and 2 and breached periporal areas in plates 3 to 6, the degree of breaching increasing away from the peristome,  $\times 25$ .

*Protenaster preaustralis* sp. nov.

Plate 33, figs. 6–8; Plate 34, figs. 1–5; text-figs. 5, 6

**Diagnosis.** Phyllodal pores isopores. Second plate of interambulacrum 1b may or may not bisect plates of 1a adorally. Anterior notch weakly developed.

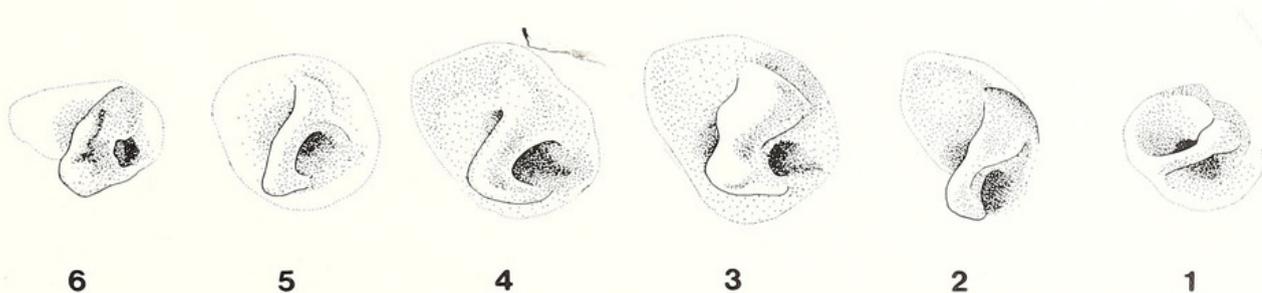
**Material.** Holotype SAM P24519, from the late Eocene Tortachilla Limestone, Maslin Beach–Port Willunga district, south of Adelaide, South Australia. Paratypes SAM P24520–24523 and NMV P71348, P71349, from same horizon and locality as the holotype. Another specimen WAM 66.577, from the Wilson Bluff Limestone (late Eocene), Nurina Cave (N46), Western Australia.

**Description.** Test up to 53 mm in length, widest slightly anterior of centre, width 87–91% TL; highest at mid-test length (Pl. 33, fig. 8); height 62–65% TL; anteriorly a very weak anterior notch is present (Pl. 33, fig. 6). Apical system slightly sunken; ethmolytic, with four genital pores; only just opened in smallest specimen (27 mm TL); situated 31–35% TL from anterior ambitus; closer to anterior in larger specimens (text-fig. 3A). Up to thirty isopores in a slightly sunken ambulacrum III; each pore separated by prominent interporal partition. Anterior petals slightly anteriorly divergent in smallest specimen (Pl. 34, fig. 1); transverse in larger specimens (Pl. 34, fig. 4); shallow and bearing up to forty-three pore pairs in each row; only thirty-three in smallest specimen; length 40–42% TL. Posterior petals shorter than anterior pair, length 34–41% TL; length increases relatively during increase in test length of 27–53 mm; diverge posteriorly at about 60%; pore pairs increase in number from twenty-eight to forty-two during known test growth; slightly flexed distally. Peripetalous fasciole not as indented between petals as in *P. australis*.

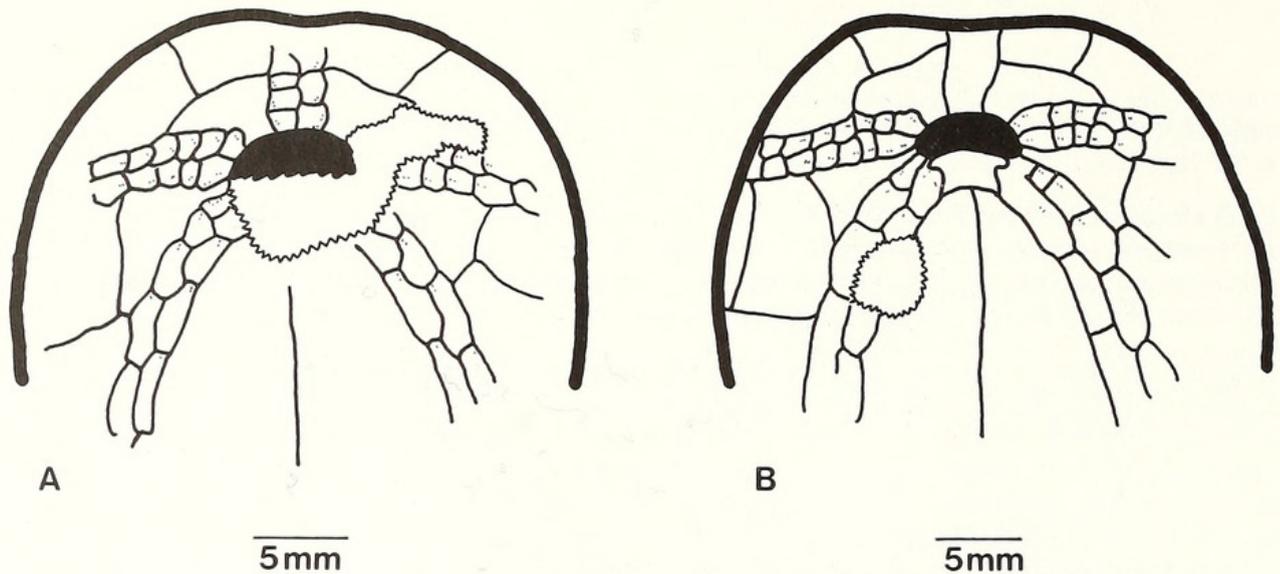
Peristome slightly sunken; width 15–20% TL. Labrum only known in smallest specimens, where it projects slightly across peristome (Pl. 34, fig. 2). Pores in phyllode are isopores, with bridged interporal partition (text-fig. 5): eight pore pairs in ambulacra I, III, V; twelve pairs in ambulacra II and IV. Plastron broad, 37–43% TL. Plates 1 and 2 of interambulacrum 1a bisected by plate 2 of interambulacrum 1b in three specimens (text-fig. 6B). In one specimen (SAM P24521), bisection does not occur (text-fig. 6A). Periproct oval, long axis slightly less than peristome width; periproct width two-thirds length. Sixteen tubercles per 5 mm<sup>2</sup> in interambulacrum 2, close to peristome, at 45 mm TL.

**Remarks.** The late Eocene *P. preaustralis* is very similar to the living species *P. australis*. It can be distinguished, however, by its possession of paired phyllodal pores; shallower anterior notch and ambulacrum III; shallow apical system; peripetalous fasciole which is less indented between the petals; and more sparsely distributed adoral interambulacral tuberculation in the anterior part of the test. Like *P. australis*, certain morphological characters in *P. preaustralis* change with growth of the test: the anterior notch becomes slightly deeper, the apical system moves forward, and the posterior petals lengthen at a greater rate than the anterior pair.

*P. preaustralis* can be distinguished from the early Miocene *P. antiaustralis* by its shallower anterior notch and ambulacrum III, more transverse anterior petals, a shallower apical system, a shallower peristome, and paired phyllodal pores. *P. preaustralis* is similar to *P. synapticus* from the late Eocene (Kaiatan) of New Zealand (Henderson 1975, pp. 20–21, pl. 2, figs. 7, 9–12). *P. preaustralis* can be distinguished, however, by its smaller peristome and less well developed keel in interambulacrum 5 aborally.



TEXT-FIG. 5. *Protenaster preaustralis* sp. nov.; camera lucida drawings of phyllodal plates 1 to 6 of ambulacrum 1b. SAM P24521, showing isopores and bridged periporal areas,  $\times 30$ .



TEXT-FIG. 6. *Protenaster preaustralis* sp. nov.; adoral plating. A, SAM P24521, specimen showing failure of second plate of interambulacrum 1b to breach interambulacrum 1a. B, SAM P24522, specimen showing breaching of interambulacrum 1a by second plate of interambulacrum 1b.

*Protenaster philipi* sp. nov.

Plate 34, figs. 6, 7; text-fig. 7

*Diagnosis.* Moderately large species of *Protenaster* with a shallow anterior notch, and with short, narrow, deeply sunken petals. Phyllodal pores are unipores; raised periporal areas are generally breached.

*Etymology.* Named for Professor G. M. Philip, in honour of his work on Australian Tertiary echinoids.

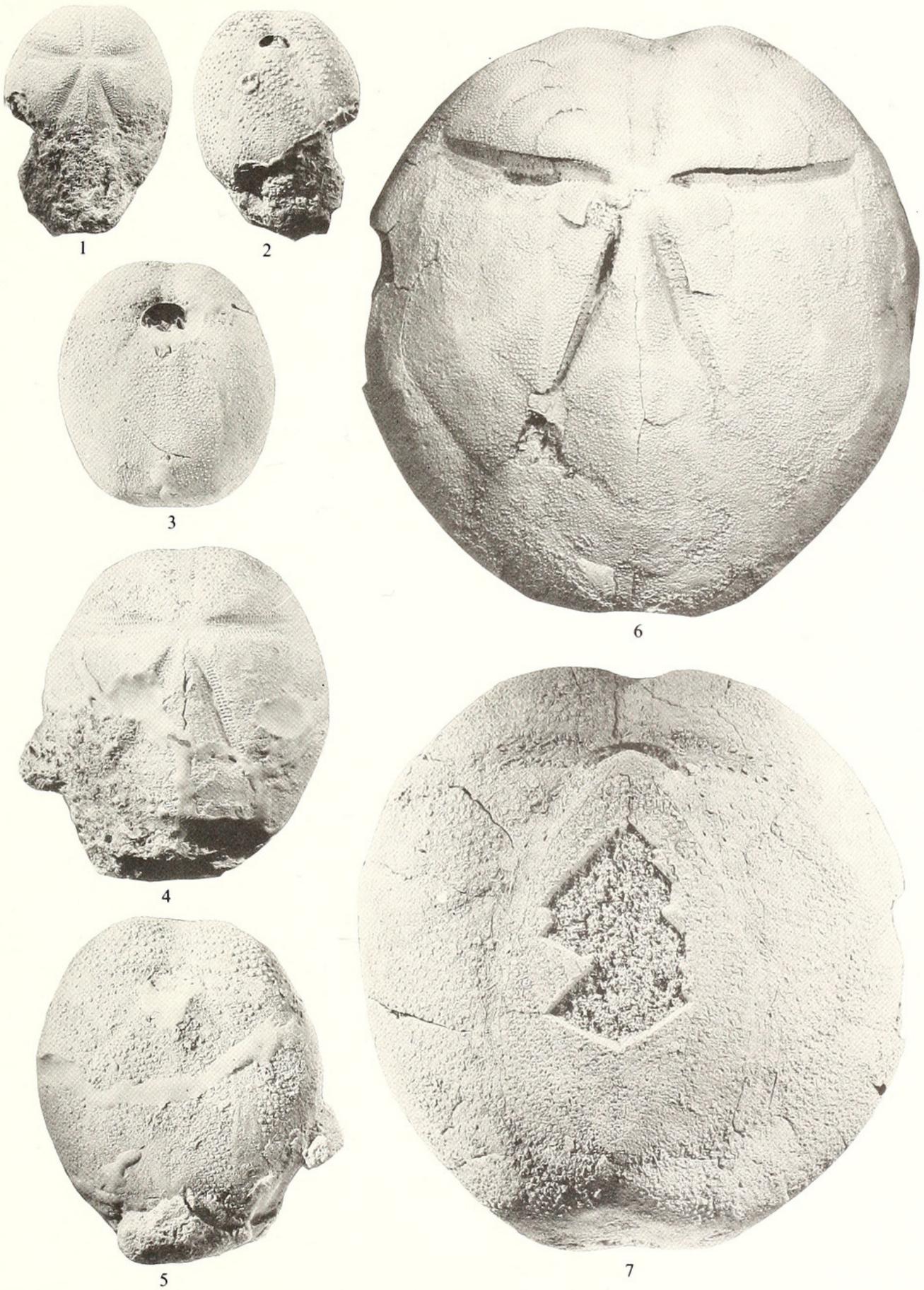
*Material.* Holotype MUGD 1690, from the Janjukian (late Oligocene) Waurn Ponds Limestone, Waurn Ponds, Victoria. Paratypes NMV P4776, P19990, P63040, P63059, and P63064, from the same locality and horizon as the holotype. Other material NMV P19989 and P78064 from the same locality and horizon as the holotype.

*Description.* Test sub-circular, moderately large, length up to 105 mm; widest at mid-length; width 91–97% TL; highest at mid-point in interambulacrum 5 posterior of apical system; height 57–60% TL. Apical system ethmolytic, with four genital pores; slightly sunken; anteriorly eccentric, situated 25–30% TL from anterior ambitus. Ambulacrum III sunken, but shallow; broad; leading to a broad, shallow anterior notch; bearing approximately twenty-seven small pore pairs, with pores in each pair aligned at about 45° and separated by raised interporal partition. Anterior petals diverging anteriorly at about 170°; wider and longer than posterior petals; length 41–43% TL; flexed anteriorly toward distal terminations, where they also shallow; deep adapically where they are overhung by anterior interambulacra; bearing approximately forty-five pore pairs; anterior and posterior rows separated by a distance equal to width of pore pairs, which are not sunken, nor conjugate. Posterior petals shorter than anterior pair (Pl. 34, fig. 6); length 35% TL; narrow, deeply sunken; diverging posteriorly at about 50°; like anterior petals, overhung by lateral interambulacra adapically;

EXPLANATION OF PLATE 34

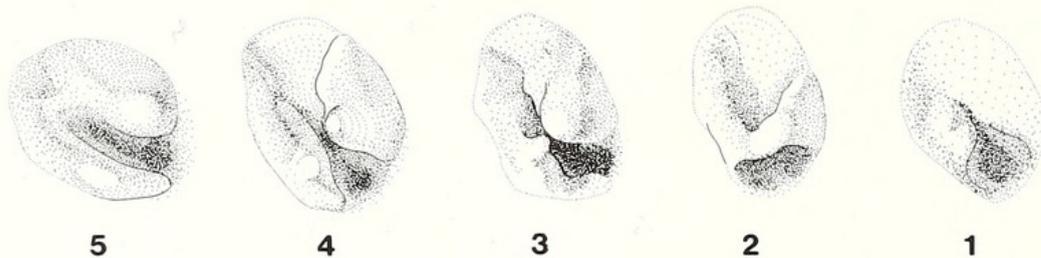
Figs. 1–5. *Protenaster preaustralis* sp. nov. 1, 2, SAM P24522, × 1; 3, SAM P24521, × 1; 4, 5, SAM P24519, holotype, × 1. All from same locality and horizon as Plate 33, fig. 6.

Figs. 6, 7. *Protenaster philipi* sp. nov. MUGD 1690, holotype, from Waurn Ponds, Victoria; Waurn Ponds Limestone (late Oligocene), × 1.



shallowing distally. Peripetalous fasciole follows similar course to that of *P. australis* in lateral and posterior interambulacra; only slightly indented in anterior interambulacra, less so than in *P. australis*. Lateroanal fasciole narrower than peripetalous fasciole; meeting peripetalous fasciole close to distal extremity of anterior petal; extending 14% TL below periproct.

Peristome slightly sunken; situated anteriorly, only 9% TL from anterior ambitus; short and broad (Pl. 34, fig. 7), width 13–15% TL. Paratype NMV P63040 retaining two peristomial plates anteriorly: subrectangular, 3.5 mm in length. Labrum long; projecting almost entirely across peristome (Pl. 34, fig. 7). Phyllode with twelve or thirteen pores in ambulacra II and IV; six or seven in ambulacra I, III, and V; pores are unipores; periporal areas are raised and breached; closer to peristome extent of breaching reduced (text-fig. 7); occasionally plates closest to peristome may be reniform. Ambulacra slightly sunken adorally. Plastron large, width 44–47% TL. Second plate of interambulacrum 1b bisects first and second plates of interambulacrum 1a. Periproct oval, slightly sunken, 10–12% TL.



TEXT-FIG. 7. *Protenaster philipi* sp. nov. NMV P4776, camera lucida drawings of phyllodal plates 1 to 5 of ambulacrum 1b, showing breached periporal areas except for plate 2 in which a reniform plate has developed,  $\times 15$ .

*Remarks.* The Janjukian strata at Waurn Ponds has been renowned for many years for the large spatangoids it has yielded. McCoy (1882) described *Pericosmus nelsoni* from the Waurn Ponds Limestone. This species has been placed in a number of genera by different workers, including *Linthia* and *Prenaster*. McNamara and Philip (1984) have recently placed it in a new genus, *Waurnia*. One of the reasons why *Pericosmus nelsoni* has at times been placed in *Linthia* (Pritchard 1908; Clark 1946; Gill 1952) is probably because of the coexistence, hitherto not recognized, of two species of spatangoids in the Waurn Ponds Limestone. The form described here as *Protenaster philipi* is, indeed, superficially similar to species of *Linthia*, but its near transverse anterior petals and bisected interambulacrum 1a adorally attest to its inclusion in *Protenaster*. It can be distinguished from the coexistent *W. nelsoni* by its deep petals and anterior notch.

*P. philipi* differs from other species of *Protenaster* in the shape of the test, which is less globose in form, and the nature of the interambulacra, which are flat, not convex, aborally. Furthermore, it has deeper, narrower petals than other species of *Protenaster*, and the posterior petals are relatively shorter.

#### EVOLUTION OF *PROTENASTER*

##### *Peramorphic evolution of the phyllode*

The five species of *Protenaster*, *P. preaustralis*, *P. synapticus*, *P. philipi*, *P. antiaustralis*, and *P. australis*, are remarkable for their morphological conservatism, the Eocene species closely resembling the later Tertiary ones, and these the living species. This phylogenetic conservatism is in marked contrast to the wide morphological variability displayed by a number of other Australian Tertiary spatangoids during their evolution, such as *Schizaster* (McNamara and Philip 1980), *Breynia* (McNamara 1982b), *Eupatagus* (Kruse and Philip, in press), and *Pericosmus* (McNamara and Philip 1984). The stable morphology of *Protenaster* is all the more remarkable when it is realized that the living species is such an extremely shallow water inhabitant (McNamara and Bryce 1983). All

of the fossil species are preserved in bioclastic calcarenites (see below), suggesting that *Protenaster* has always been a shallow water inhabitant. *Protenaster* has undergone little change in its geographical distribution throughout the Tertiary, remaining confined essentially to southern Australia.

Selection pressure in genera such as *Schizaster* and *Pericosmus* was primarily centred on changes to the depths and lengths of the petals, anterior notch, size of the labrum, position of the apical system, and overall test shape. These changes have been interpreted as adaptations to the inhabitation of finer grained sediment (McNamara and Philip 1980, 1984). In *Protenaster* slight inter- and intraspecific variations occur in these characters, but much less than in other spatangoid genera. The morphological conservatism in *Protenaster* does not, however, apply to the structure of the phyllodal plates which surround the peristome. The pores and periporal areas undergo a large degree of morphological change during both the evolution of the genus and the ontogeny of later species. I consider that these changes also occurred in response to adaptation to a finer grained sediment (see below).

The tube feet of pores on phyllodal plates are highly specialized feeding structures in spatangoids, such as *Protenaster*. They bear a terminal cap which is covered by numerous, fine, mucous-secreting papillae. Such tube feet are termed penicillate tube feet and have the ability to pick up coarse to fine-grained sediment particles by mucous adhesion and pass them directly into the mouth. Elsewhere (McNamara, 1984b) it is shown that the phyllodal tube feet of *P. australis* are light-sensitive. Like the ambital sensory tube feet, the phyllodal tube feet undergo negative phototaxis at relatively low levels of ambient illumination. This is in contrast to the light-sensitive tube feet in the aboral ambulacrum III which undergo positive phototaxis at the same level of illumination. There is every reason to suppose that the fossil species also possessed this same facility to respond to light.

*Protenaster* compares with a number of Tertiary spatangoids in that during the course of its evolution the pores of the phyllode changed from being double to single pores. Kier (1974) demonstrated this change in species of *Linthia* and considered that in most spatangoids the change occurred during Palaeocene to Eocene times. McNamara and Philip (1980) described a similar change in *Schizaster*, species from the Tertiary of southern Australia demonstrating that the change occurred between the late Oligocene and early Miocene. The same change occurred in *Protenaster*, the late Eocene species *P. preaustralis* and *P. synapticus* having double pores, whereas the late Oligocene *P. philipi*, the early Miocene *P. antiaustralis*, and the Pleistocene to Recent *P. australis* have single pores in adults. As Kier (1974) and Smith (1980a) have pointed out, the double pores in the phyllode join below an interporal partition and only a single canal perforates the tests. The change from double to single pores in *Protenaster* occurred by breaching of the interporal partition sometime during the early to middle Oligocene; subsequently there occurred a sequence of changes to the form of the periporal area both during the ontogenetic and phylogenetic development of subsequent species. These changes may therefore be considered to have occurred by heterochrony. It will be argued that the heterochronic process was acceleration (*sensu* Alberch *et al.* 1979; McNamara, in press).

Increasing degrees of acceleration in the rate of development of the phyllodal plates through successive species in the Tertiary resulted in the development of a peramorphocline. A peramorphocline may be defined as a discontinuous morphological gradient of progressively more peramorphic species through time (McNamara 1982a). Successive species along the peramorphocline will pass through increasingly greater degrees of morphological change during their ontogenetic development. This peramorphic evolution (text-fig. 8) can best be illustrated in *Protenaster* by comparing the extent of phyllodal development in the extinct species with that of the living species; the phyllode of the latter passes through a greater number of morphological stages during its ontogeny than any of its ancestors; while the earliest species in the peramorphocline passed through the fewest.

The smallest specimen of the living species *P. australis* is a juvenile with a test length of 15 mm. Its phyllode possesses mainly unipores with the interporal partition in the breached condition (text-fig. 1c). In this character it therefore most closely resembles large adults of the late Oligocene *P. philipi*. On one plate of the juvenile *P. australis* isopores are present, the interporal partition having

not been breached. This is the most 'primitive' condition and is found in adults of the Eocene species. With test growth, *P. australis* rapidly attains the reniform stage. Following the initial breaching of the interporal partition in the early juvenile stage, the residual stump decreases in size by resorption until the breach is about equal in width to the stumps. There then follows an adaxial migration and elongation of the stumps. Ultimately they rejoin to form a reniform ridge, the convex side of which is adaxially positioned and rises above the unipore (text-fig. 1B). Morphological change in the periporal area as it assumes a reniform shape must be accomplished by resorption of the stereom on the abaxial side of the stump, with subsequent regrowth on the adaxial surface. Various stages of this transformation can be identified in single specimens. This is because the plates closest to the peristome are relatively older than adapical plates. Thus the pore in plate 1 has longer to develop than the pore in plate 2, and so on. With such extensive ontogenetic morphological transformation as occurs in the phyllodal plates, the various stages may therefore be observed 'frozen' in a single specimen.

The reniform stage is attained in *P. australis* at a test length of about 30 mm. There is a certain degree of variation in rate of development of the phyllodal plates, and thus of attainment of the successive stages. This is illustrated by two specimens, each 30 mm in test length. One has all the phyllodal periporal areas in the reniform stage, while the other is more retarded in its development, the outermost plates still being in the breached condition. Between a test length of 30 mm and 50 mm, the rest of the plate, abaxial to the unipore and reniform ridge, swells. Thus by a test length of 60 mm most of the plates are in the platform stage, the whole plate forming a swollen, raised platform (text-fig. 1A). Swelling of the abaxial area continues in large specimens, such that at a test length of about 75 mm the central part of the periporal area may become slightly depressed. Occasionally a narrow channel may run from this depression and connect with the main unipore. Thus anisopores may, rarely, be present in these large specimens.

Whether or not the phyllode passes completely through all four stages of development is not known with certainty, as specimens smaller than 15 mm test length are unknown. There are two possibilities. Either the pores occur as isopores in early juveniles, with a bridged periporal area, or alternatively there has been pre-displacement (Alberch *et al.* 1979; McNamara, in press) and some plates commence development at a slightly more 'advanced' stage than in their ancestral species, perhaps beginning in the breached condition. However, the presence of one plate with bridged isopores in the juvenile specimen suggests that there may have been little or no pre-displacement.

Although it might be argued that the breached stage could be interpreted as a very early ontogenetic 'pre-bridged' phase, this is unlikely to be the case. If it were so the breached stage would be succeeded ontogenetically by the bridged stage. However, in all species the breached stage is succeeded by the reniform stage. This stage is quite distinct from the bridged stage in that the raised interporal partition develops on the periphery of the plate in an adaxial position, and not medially. Furthermore, in both the breached and reniform stages only a single pore perforates the test.

As described above, the late Eocene *P. preaustralis* and *P. synapticus* have phyllodal plates with bridged isopores. The next species, the late Oligocene *P. philipi*, is only known from large specimens, similar in size to the largest known specimens of *P. australis* which, at a similar size, have phyllodal plates in the platform stage. In *P. philipi* the periporal areas are nearly always in the breached condition. The extent of breaching is diminished closer to the peristome as the periporal areas are changing toward the reniform stage. This is only attained in two specimens of *P. philipi* in adoral plates. The early Miocene *P. antiaustralis* is slightly more advanced than *P. philipi* in that, although it is a smaller specimen than any known specimen of *P. philipi*, plates 1 and 2, close to the peristome, have attained the reniform stage. Plates 3 to 6 are breached, the degree of separation of the stumps increasing away from the peristome.

#### *Functional significance of the phyllode peramorphocline*

The phyllodal pores of *P. australis* bear penicillate tube feet. Observations on living specimens (McNamara and Bryce 1983; McNamara 1984b) have revealed that the tube feet in *P. australis*, as in other spatangoids, secrete mucus which allows the echinoid to pick up the fine calcarenite upon which it feeds, and pass it directly into the mouth. Golubic *et al.* (1975) have noted that calcarenite



fragments are generally heavily bored by endoliths, such as algae and fungi. It is most probable that sediment ingesting organisms, such as *P. australis*, obtain much of their nutrition from this source.

McNamara and Bryce (1983) have documented the fine-grained nature of the sediment in which *P. australis* lives, about 75% of the grains being between only 0.125 mm and 0.25 mm in diameter. Examination of the enclosing lithologies of the fossil species has revealed that the earliest species inhabited the coarsest grained sediment, with later species inhabiting progressively finer-grained sediment (text-fig. 8). The late Eocene Tortachilla Limestone, in which *P. preaustralis* is preserved, is a poorly sorted, brown-green bryozoal calcarenite. Most sediment particles lie within the range 0.5–2 mm, with some up to 5 mm in diameter. The late Oligocene Waurin Ponds Limestone, in which *P. philipi* is preserved, is also a coarse bryozoal calcarenite of similar grain size to the Tortachilla Limestone. The calcarenite in which the early Miocene *P. antiaustralis* is preserved is finer grained, the sediment particles mainly lying in the range 0.2–0.5 mm, although some reach 1.5 mm in diameter. Smith (1980b, p. 43, fig. 109b) has observed that there is a general trend for the density of aboral tuberculation in spatangoids to increase with decreasing sediment grain size. His observations are supported by *Protenaster* which shows an increase in tubercle density from sixteen per 5 mm<sup>2</sup> in the earliest species (the late Eocene *P. preaustralis*) to twenty-four per 5 mm<sup>2</sup> in the living *P. australis*.

Although it might be thought that the wide variety of phyllodal pores possessed by spatangoids would bear a wider range of penicillate tube feet, Smith (1980a) has shown that this is not the case. He has observed (Smith 1980a, p. 57) how the structure of phyllodal tube feet are remarkably uniform in holasteroids and spatangoids. Thus the pronounced change in phyllodal morphology in *Protenaster* is unlikely to reflect any change in the structure of the tube feet. However, during the evolution of *Protenaster* there appears to be a reasonably direct correlation between the transformation in the nature of the phyllodal plates and the changing sediment grain size, from coarse to fine calcarenite. This suggests that although there may not have been any great change in the structure of the tube foot, there may have been substantial changes to the mechanical ability of the tube foot to cope with sediments of different grain size.

Smith (1980a, p. 76) has observed that large periporal areas were developed in the phylloides of many spatangoids to allow the stem of the tube foot to be wide enough to support the large papillate terminal disc. However, Smith could see little reason for the development of raised periporal areas, such as those in *P. australis*. He suggested the possibility that a domed periporal area may help to maintain coelomic fluid movement in the lumen by increasing the surface area of the single layer of squamous epithelium which covers the periporal area.

The trend in *Protenaster* is for the surface area of the periporal region to undergo a relative decrease, both ontogenetically and phylogenetically, as it transforms from the bridged to breached to reniform to platform conditions. It is possible that the larger surface area was necessary to allow the penicillate tube foot to pick up larger sediment particles. With a decrease in this surface area the tube foot may well have been restricted in the size of sediment particle which it could pick up. Preferential phylogenetic selection of this character was probably favoured because of the inability of most spatangoids, particularly those inhabiting shallow water, to inhabit fine-grained sediments.

The large morphological change of the phyllodal plates in *P. australis* during ontogeny suggests that juveniles may feed on coarser-grained sediment than adults. Examination of the gut contents of the small 15 mm long juvenile has confirmed this, the sediment being much coarser than sediment upon which the adults feed, lying in the range 0.3–1.0 mm diameter. The occupation by juvenile *P. australis* of coarser sediment than adults is also indirectly indicated by the lower concentration of adoral tuberculation in the 15 mm long specimen. The concentration is about as low as that in the earliest species of *Protenaster*, *P. preaustralis* and *P. synapticus*.

It is also conceivable that the change from isopores to unipores during the Tertiary, which has been recorded in other spatangoids (Kier 1974; McNamara and Philip 1980), also occurred in conjunction with adaptations to the inhabitation of finer-grained sediments. McNamara and Philip (1980) have shown that the morphological changes in the *Paraster-Schizaster* lineage also formed a peramorphocline which followed an environmental gradient of coarse to fine-grained sediment. One of these

changes was the transformation of the phyllodal pores from isopores to unipores. The independent acquisition of phyllodal unipores in a number of spatangoid lineages may therefore be explained by selection of morphotypes capable of inhabiting and feeding upon finer-grained sediments.

*Ontogenetic and phylogenetic development of the adoral plates of interambulacrum I*

One of the characteristics of *Protenaster* is the presence of an enlarged second plate of interambulacrum 1b which separates the first two plates of interambulacrum 1a (text-fig. 2B). This character is present in a number of other genera, including *Pericosmus*, *Paleopneustes*, *Faorina*, and *Plesiozonus*. Largely on the basis of this character Chesher (1968) argued that these four genera should be placed in a single family, the Paleopneustidae. However, McNamara (1984a) and McNamara and Philip (1984) have provided evidence of the strong intraspecific variation in the presence of this character. The analysis of this structure in *Protenaster* provides support for the contention that this character varies both ontogenetically and intraspecifically between adults, and is therefore unsuitable as a major familial character in spatangoids.

Although Chesher (1968) considered the enlarged plate to be a compound plate of the second plates of both 1a and 1b, the ontogenetic transformation of its structure in *P. australis* shows that the plate is not compound, but merely the enlarged second plate of interambulacrum 1b. This can be demonstrated by comparing the adoral plate arrangement of a juvenile and adult *P. australis*. In the juvenile the adoral plates of interambulacrum I are in a 'normal' condition, i.e. the second plate is in contact only with ambulacrum II (text-fig. 2A). In adults this plate abuts both ambulacra I and II. During growth of the test this plate expands to such an extent that it bisects the first and second plates of interambulacrum 1a. The changing nature of such adoral plate boundaries is currently being appraised (McNamara and Philip, in prep.).

Whereas the second plate of interambulacrum 1b is always in the expanded condition in adults of the living species *P. australis*, adults of the earliest species *P. preaustralis* have both conditions (text-fig. 6). Thus later species of *Protenaster* may be considered to have undergone an increase in the rate of allometric growth of this plate, such that only the expanded plate condition occurs in adults.

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