Rec. West. Aust. Mus. 1984, 11 (4): 319-356

A Revision of the Spatangoid Echinoid *Pericosmus* from the Tertiary of Australia

K.J. McNamara* and G.M. Philip†

Abstract

McCoy's (1882) *Pericosmus gigas*, *P. nelsoni* and *P. compressus* are reinvestigated and described. *P. gigas* is referred to *Victoriaster*. *P. nelsoni* is made type species of *Waurnia* gen. nov. and *P. compressus* is redescribed as *P. maccoyi* Gregory, 1890. McCoy's species is a junior homonym of Duncan's (1877) *Megalaster compressus* which is redescribed as *P. compressus*. New species of *Pericosmus* described are the Longfordian *P. celsus*, the Longfordian-Batesfordian *P. torus* and the Bairnsdalian *P. quasimodo*. Two further species of *Pericosmus* are described as new, but left in open nomenclature on account of paucity of material. Evolutionary trends within Australian species of *Pericosmus* are examined in terms of the functional significance of the morphological adaptations.

Introduction

In 1882 Frederick McCoy described three large spatangoid echinoids from the Tertiary rocks of Victoria, *Pericosmus gigas* (said by McCoy to be of Early Miocene age from the Murray River), *Pericosmus nelsoni* (of Late Oligocene Janjukian age from Waurn Ponds) and *Pericosmus compressus* (of Janjukian age from Bird Rock Point, near Torquay).

Pritchard (1908) rightly questioned the correctness of McCoy's placement of *Pericosmus gigas* in *Pericosmus* for, as McCoy himself noted, the marginal fasciole, characteristic of *Pericosmus*, was lacking in the anterior part of the test. Pritchard, in addition to describing a further species, placed them both in *Linthia*. Lambert (1920), however, proposed the genus *Victoriaster* to accommodate *P. gigas*, considering its large size, long petals and anterior disappearance of the 'marginal' fasciole diagnostic. Mortensen (1951) concluded that no satisfactory generic separation of *Victoriaster* from *Pericosmus* could be entertained as absence of the marginal fasciole was not, he believed, definitely established in *P. gigas*. Fischer (1966) adopted a more conciliatory attitude and made *Victoriaster* a subgenus of *Pericosmus*.

Pericosmus nelsoni has likewise suffered from assignment to various genera. Pritchard (1908) considered the species to possess a lateroanal fasciole and not a marginal fasciole, and so placed it in *Linthia*. Lambert (1905) placed it in *Peribrissus*. Lambert and Thiéry (1924),

---

* Department of Palaeontology, Western Australian Museum, Francis Street, Perth, Western Australia 6000.

† Department of Geology, University of Sydney, New South Wales 2006.

however, believed the weakly developed ambulacrum III and anteriorly positioned apical system warranted placement in *Prenaster.* H.L. Clark (1946) also preferred to regard it as a species of *Linthia.*

Since McCoy's original paper, many more specimens of these species have been collected, particularly through the agencies of F. Cudmore and F. and R. Foster. On the basis of these collections housed in the palaeontological collections of the Museum of Victoria (NMV), Department of Geology, University of Melbourne (MUGD), the South Australian Museum (SAM) and the Western Australian Museum (WAM), we redescribe McCoy's species and offer our opinion as to which genera they should be assigned. In addition, we describe three new species of *Pericosmus* and reinterpret the type species of *Victoriaster, V. gigas.* The abbreviation TL is used throughout for test length.

Henderson (1975) has pointed out the confused status of Australian species of *Pericosmus.* This has arisen, we believe, because of the large degree of ontogenetic variation which occurs through growth. We document these changes and suggest possible interrelationships between the species and the functional significance for morphological changes that occur between them.

Systematics

Order Spatangoida Claus, 1876

Family Pericosmidae Lambert, 1905

Remarks

Chesher (1968), followed by Henderson (1975) and Kier (1984), placed *Pericosmus* in the Paleopneustidae as he believed *Pericosmus* belongs in the same family as *Paleopneustes,* and that Paleopneustidae Agassiz has priority over Pericosmidae Lambert. They both consider that these two genera, along with *Plesiozonus, Faorina* and *Antillaster,* share a number of common morphological characteristics, principal among which are a particular place configuration in adoral interambulacrum 1, and paired pores in each phyllodal peripodium. Leaving aside the efficacy of the use of these particular morphological features as familial characteristics, we cannot accept that *Pericosmus* belongs within the Paleopneustidae, principally because many of the extinct species, including the type species *P. latus* (Agassiz) (Henderson 1975, Fig. 11d), do not have the peculiar place configuration attributable to the family. The second interambulacral plate of interambulacrum 1b abutts both ambulacra I and II in *Paleopneustes, Faorina, Plesiozonus* and some modern species attributed to *Pericosmus,* although McNamara (1984) has noted how even within the living species *P. porphyrocardius* McNamara, 1984, the plate configuration is variable. In all Australian fossil species of *Pericosmus* and in *P. latus* the second place is 'normal' in abutting only ambulacrum II (e.g. Figure 12).

We prefer, at present, to retain the family Pericosmidae Lambert, the diagnostic feature being the presence of both a peripetalous and a marginal fasciole. However, we note (below) that the peripetalous and marginal fascioles are not always entirely separate, as in *P. celsus* sp. nov., *P. quasimodo* sp. nov. and *P.* sp. A. In these species the anterior branches of the peripetalous fasciole run exsagittally in interambulacra 2 and 3 to join the marginal fasciole.

Genus *Pericosmus* Agassiz, 1847

Type Species

Micraster latus Agassiz, 1840; by subsequent designation of de Loriol (1875: 115).

Pericosmus compressus (Duncan, 1877)

Figures 1-4

Megalaster compressa Duncan, 1877: 62, Fig. 1; – Duncan 1887: 422-433; – Tate 1891: 271 (pars.).
Pericosmus compressus – Gregory 1890: 485-486, *non* Pl. 14, fig. 1 (*Schizobrissus dicepiens* Tate); – Lambert and Thiéry 1924: 513.
Linthia compressus – H.L. Clark 1946: 366
Pericosmus crawfordi (pars.) – Henderson 1975: 54-57.
non Pericosmus compressus McCoy, 1882: 21-22, Pl. 67, figs 2-2a, Pl. 68.

Holotype

British Museum (Natural History) specimen E296 from the 'Banks of the Murray;' by monotypy; it probably derived from the early Middle Miocene Morgan Limestone of Batesfordian to Balcombian age.

Other Material

This study is also based upon 15 further specimens: NMV P17912, 17913, 18102, 18103, 18364, 55513-55522 from the Morgan Limestone on the banks of the Murray River between Overland Corner and Morgan, South Australia.

Diagnosis

Test low to moderately inflated; interambulacrum 5 most swollen adapically. Apical system situated a little anterior of centre. Ambulacrum III sunken throughout, deep adapically. Paired petals broad and deep with up to 34 pore pairs in anterior pair. Peristome sunken, broad. Labrum projects anteriorly, almost extending across peristome.

Description

Test reaches a maximum known length of 133 mm. Smallest known specimen has a test length of 41 mm. In plan, test almost circular, but slightly longer than broad; with an anterior notch which is shallow and broad in small specimens (Figure 3B), but becoming progressively deeper and relatively narrower with increasing test size (Figure 2). The holotype, however, retains the juvenile broad notch, even though it is 120 mm long (Figure 1). Test of small specimens tumid, with a height up to 64% test length (TL). With growth, test becomes relatively lower as length and width increase at a greater rate than height; in large specimens height ranges from 41 to 50% TL. Anterior and lateral interambulacra gently convex, although becoming flattened to slightly concave adapically. Posterior interambulacrum has a pronounced keel adapically (Figure 4). Test highest at this point in both small and large specimens. Apical system sunken; with three genital pores; ethmolytic and situated between 35 and 44% (TL) from anterior ambitus. This range of values largely reflects a slight relative anterior movement of apical system with growth.

Ambulacrum III depressed, but shallow adapically, becoming deeper abapically, particularly in large specimens; bearing up to 23 sets of very small pore pairs. Anterior paired petals diverge at about 125°; longer than posterior petals in small specimens less than 45 mm TL

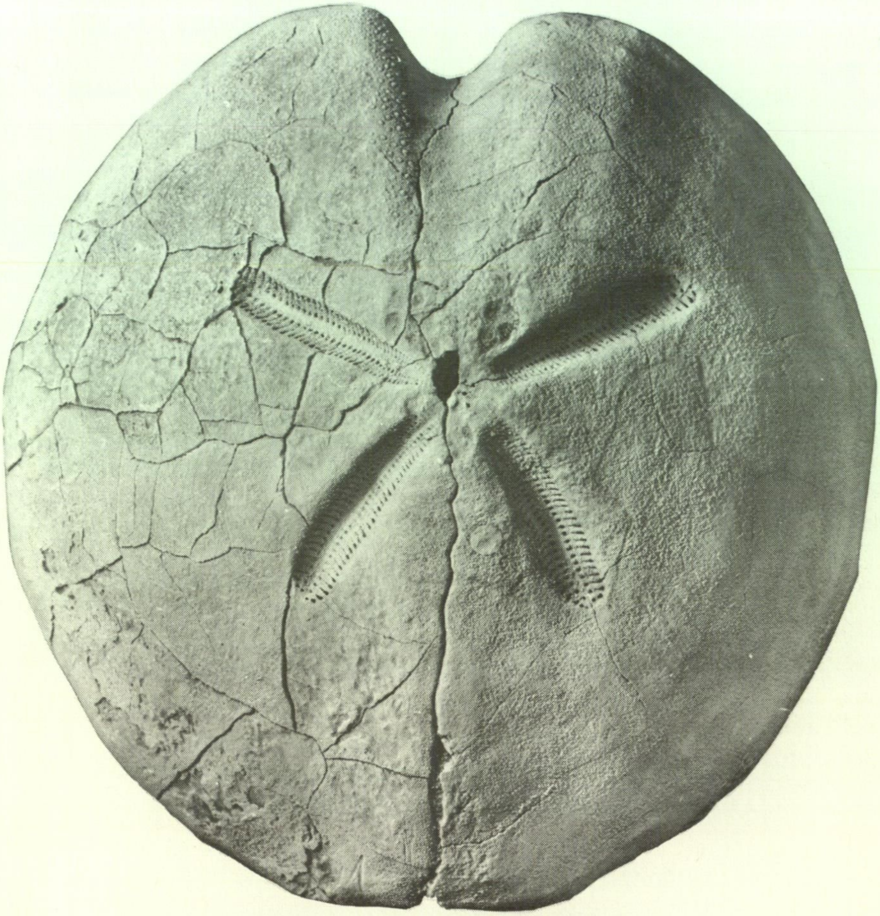


Figure 1 *Pericosmus compressus* (Duncan, 1877); BM E296, holotype, from the 'Banks of the Murray;' probably Morgan Limestone; aboral view; ×1.

(Figure 3B); at 70 mm TL petals of equal length; at 85 mm TL and greater, anterior petals shorter than posterior (Figure 2); 24-30% TL; bearing 20-22 pore pairs in small specimens between 41-45 mm in length, increasing to a maximum of 34 at a test length of about 100 mm. Posterior petals bear up to 38 pore pairs; petals diverge at about 60°; 20% TL in small specimens, increasing to 30% TL in large specimens. Anterior and posterior petals broad in all specimens, but shallow in small specimens and progressively deepening with growth.

Peripetalous fasciole indented to half petal length between petals; anteriorly it runs adambitally through three interambulacral plates of interambulacra 2a and 3b before crossing to 2b and 3a respectively; thence crossing two plates before running transversely across ambulacrum III. Anteriorly it may be ill-defined or missing.

Figure 2 *Pericosmus compressus* (Duncan, 1877); NMV P18364, from the Murray River cliffs, between Overland Corner and Morgan; Morgan Limestone; aboral view; ×1.

Peristome broad, particularly in large specimens, where it reaches up to 18% TL (Figure 3A); situated close to anterior notch; with growth becoming more sunken. Labrum arches strongly forward and almost crosses peristome (Figure 3A). Pores in phyllode paired; 9 pairs in ambulacra II and IV; 6 in ambulacrum III and in ambulacra I and V. Plastron gently convex; width 32-46% TL. Periplastronal width 12-15% TL. Periproct transversely oval, long axis 13% TL; slightly sunken. Subanal area depressed.

Remarks

Duncan (1877) based *Megalaster compressa* on a single specimen from the banks of the Murray River (Figure 1). McCoy (1882) gave *Pericosmus compressus* the same specific name as *Megalaster compressus* Duncan, 1877 as he believed that Duncan's species, said to lack fascioles, was based on a poorly preserved specimen of *Pericosmus* in which the fascioles had

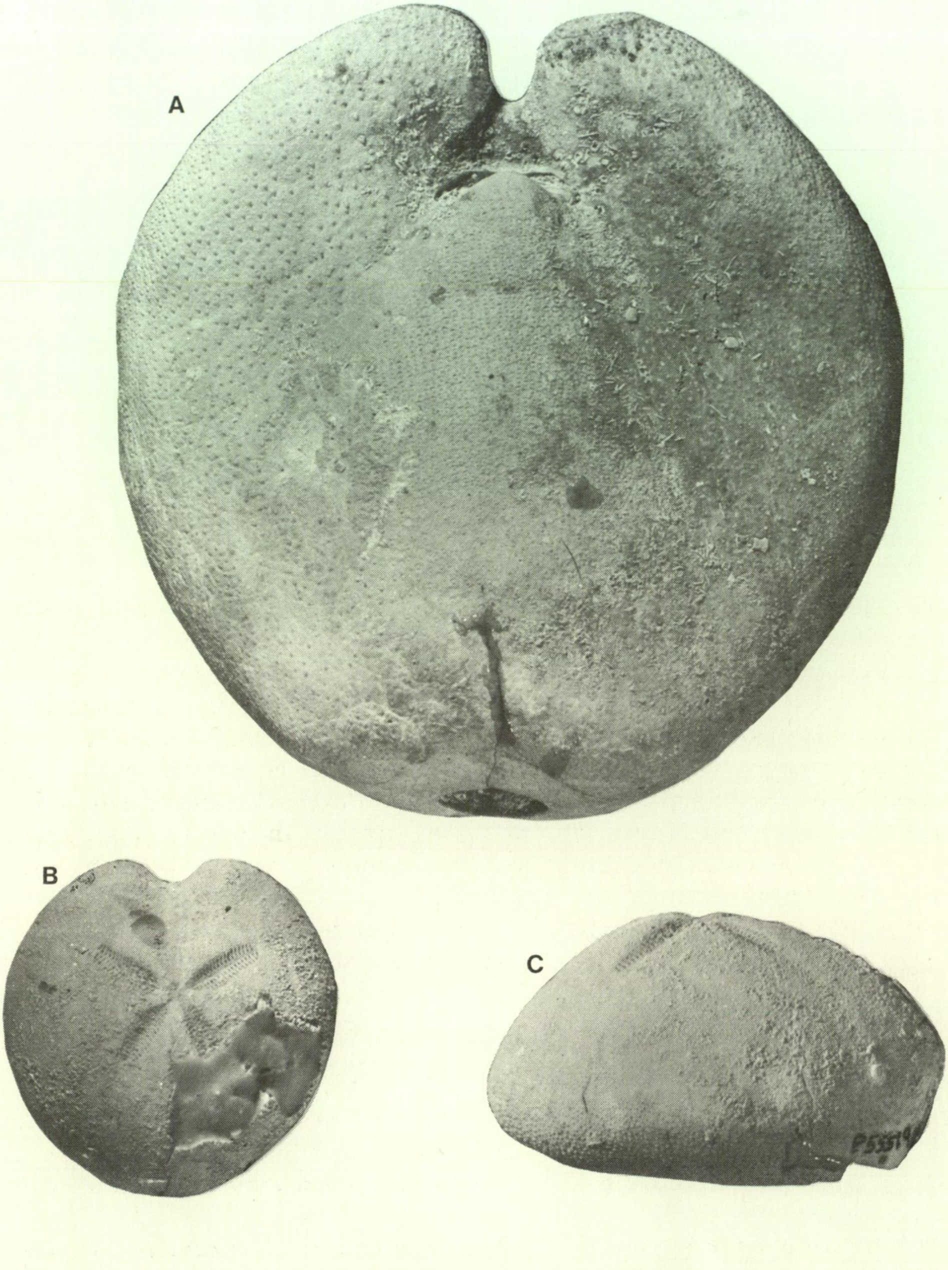


Figure 3 *Pericosmus compressus* (Duncan, 1877); (A) adoral view of NMV P55515; (B) aboral view and (C) lateral view of NMV P55519; all specimens from the Morgan Limestone from the Murray River cliffs, between Overland Corner and Morgan; all ×1, except (C), ×1.5.

Figure 4 *Pericosmus compressus* (Duncan, 1877); NMV P18364, from the Murray River cliffs, between Overland Corner and Morgan; Morgan Limestone; lateral view; × 1.

been obliterated by weathering, and that Duncan's genus would prove synonymous with *Pericosmus*. Duncan (1887) maintained that his specimen in the British Museum (Natural History) (BM E296) lacked all trace of fascioles, a claim reaffirmed by Gregory (1890). However, inspection of the specimen by one of us (G.M.P.) has revealed both peripetalous and marginal fascioles to be clearly visible on the right side of the test. *Megalaster* is thus a junior synonym of *Pericosmus* and, to this extent, McCoy's judgement is vindicated.

McCoy (1882) believed his *Pericosmus compressus* from Bird Rock Point, near the mouth of Spring Creek, 25 km south of Geelong, Victoria, would prove synonymous with Duncan's species, which he considered should be placed in *Pericosmus*. Gregory (1890), however, considered McCoy's specimen to be specifically distinct from Duncan's, naming it *P. maccoyi*. Differences noted by Gregory do not correspond well with the characteristics of McCoy's (1882, Pl. 67, fig. 2, Pl. 68) figure. The apical system is too anterior, the frontal notch and petals are too broad. Examination of McCoy's specimen (NMV P4834) reveals that most of the aboral surface of the test is missing, but sufficient is preserved to show the characteristic short, narrow petals of the species. Further material from Janjukian strata in the vicinity of Bird Rock Point (see below) confirms *P. maccoyi* as being specifically distinct from *P. compressus* (Duncan). Unfortunately, the holotype of *P. compressus* has a much broader anterior notch than is normal for a specimen 118 mm in length. And to compound the problem, the anterior notch of the holotype of *P. maccoyi* is narrower than in topotype specimens.

Much of the confusion regarding the identification of species of *Pericosmus* arises from the degree of morphological distinction between small and large specimens of the same species (contrast Figures 3B, C and Figures 2, 4). Changes with growth include a relative decrease in test height; swelling of adapical interambulacra; increasing length of posterior petals relative to anterior petals; increase in petal depth; increase in depth of anterior notch;

increasingly sunken peristome. Mortensen (1950, 1951), in describing some living adult specimens, noted their characteristic shallow anterior notch; shallow petals; and anterior paired petals which are longer relative to the posterior petals. Larger living species on the other hand, have characteristics in common with large specimens of *P. compressus*. We suspect that the large number of specific names applied to living members of the genus is due to the fact that the extent of morphological changes during ontogeny has not been recognised.

Hutton (1887) and Tate (1894) considered that *Meoma crawfordi* Hutton from Oligo-Miocene strata in New Zealand was a synonym of *P. compressus*. Tate (op. cit.) further added that *Meoma brevipetala* Hutton was based on a crushed specimen of *P. compressus*. Henderson (1975) reiterated Hutton's (1894) view, placing *P. compressus* in synonymy with *P. crawfordi*. *P. compressus* is, however, clearly distinguishable from *P. crawfordi* as it possesses a deeper anterior notch; frequently a more highly vaulted test; a more anteriorly positioned, broader peristome; a labrum that projects further anteriorly; and adapically swollen interambulacrum 5. *P. compressus* differs from the type species, *P. latus* Agassiz, in possessing a deeper anterior notch, a more anteriorly eccentric apical system and in attaining a much larger adult size.

Pericosmus maccoyi Gregory, 1890

Figures 5, 6

Pericosmus compressus McCoy, 1882: 21-22, Pl. 67, figs 2-2a, Pl. 68.
Pericosmus maccoyi Gregory, 1890: 485-486.

Holotype

NMV P4834 from Bird Rock Point, near the mouth of Spring Creek, 25 km south of Geelong, Victoria; Late Oligocene, Janjukian; by monotypy.

Other Material

NMV P18759, 18760, 20141, 20146, 20179 from same locality and horizon as holotype; NMV P20206 from Janjukian or Longfordian (Late Oligocene to Early Miocene) Gambier Limestone at Port MacDonnell, South Australia; NMV P20201 from the Gambier Limestone at Mt Gambier, South Australia.

Diagnosis

A species of *Pericosmus* with low, relatively small test; little adapical swelling of the interambulacra. Ambulacrum III shallow; anterior notch broad. Paired petals short.

Description

Test reaches a maximum known length of 103 mm. In plan, test nearly circular, sometimes wider than narrow. Anterior notch broad, moderately depressed, although being quite narrow in the holotype (NMV P4834). Test low, gently convex, height not exceeding 48% TL. Posterior ambulacrum without pronounced keel (Figure 6B). Test highest apically, with no adapical ambulacral swelling. Apical system situated slightly anterior of centre (37-44% TL from anterior ambitus). Ambulacrum III shallow, not sunken at all adapically. Anterior paired petals diverge at about 125°; short; shallow; of equal length to posterior petals, occupying 21-27% TL: up to 27 pore pairs in anterior petal. Peristome narrow (12% TL)

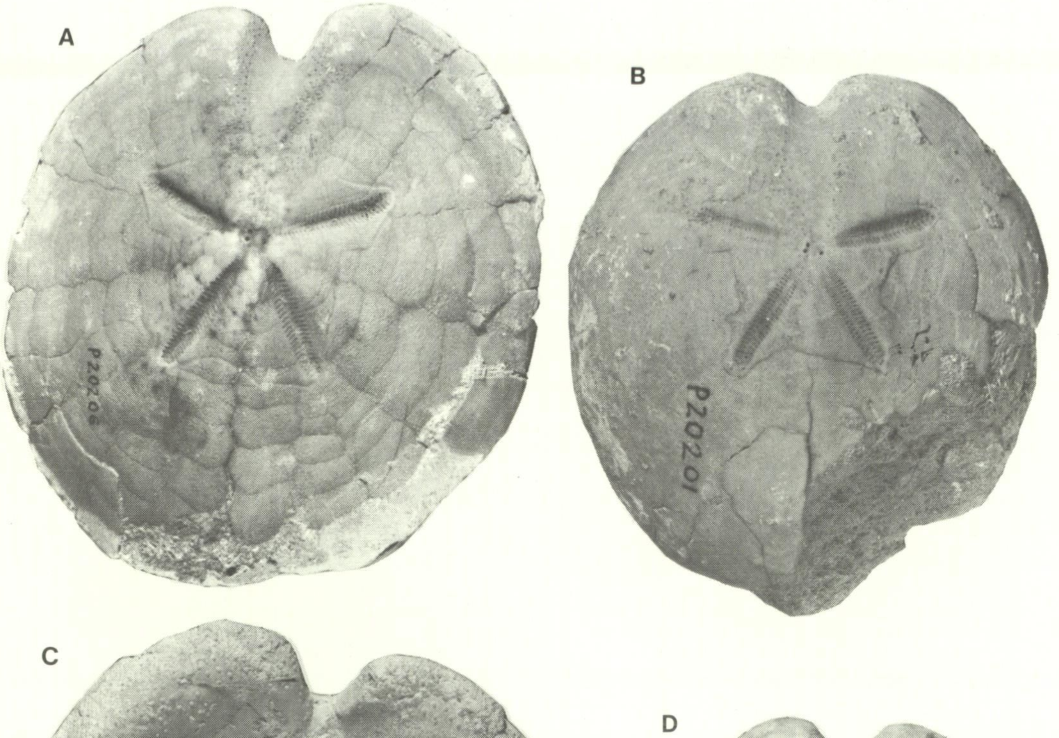


Figure 5 *Pericosmus maccoyi* Gregory, 1890; (A) aboral view and (C) adoral view of NMV P20206, form the Gambier Limestone at Port MacDonnell; (B) aboral view of ANMV P20201, from the Gambier Limestone at Mt Gambier; (D) aboral view of NMV P20141, from Janjukian strata at Bird Rock Point; all ×1.

Figure 6 *Pericosmus maccoyi* Gregory, 1890; (A) aboral view and (B) lateral veiw of NMV P20146, from Janjukian strata at Bird Rock Point; both × 1.

with labrum which does not project appreciably forward. Plastron narrow, width ranging between 33-41% TL.

Remarks

P. maccoyi is the oldest known species of *Pericosmus* in the southern Australian Tertiary, first appearing in the Janjukian Stage and ranging into the Longfordian. It is most similar to *P. compressus* in having a relatively low test and similarly positioned apical system. However, it can be distinguished by its shorter, shallower paired petals, shallower ambulacrum III, broader anterior notch; absence of appreciable swelling in interambulacra adapically; narrower peristome and less anteriorly projecting labrum.

P. maccoyi is also similar to *P. crawfordi* from the Oligo-Miocene of New Zealand, but can be distinguished by its more centrally positioned apical system; its broader anterior notch; its shorter paired petals; and its shallower ambulacrum III aborally. *P. annosus* Henderson, 1975 from the Late Eocene of New Zealand, similarly has a broader anterior notch and broader, shallower paired petals. It differs, however, from *P. maccoyi* in possessing a less deeply indented anterior notch.

Pericosmus celsus sp. nov.

Figures 7-9

Holotype

SAM P23823, from 'Murray River cliffs,' probably from the Early Miocene Longfordian Mannum Formation.

Paratype

NMV P18354 from the Mannum Formation at Mannum, South Australia.

Figure 7 *Pericosmus celsus* sp. nov.; SAM P23823, holotype, from the Murray River cliffs; probably Mannum Formation; aboral view; ×1.

Figure 8 *Pericosmus celsus* sp. nov.; SAM P23823, holotype, from the Murray River cliffs; probably Mannum Formation; adoral view; ×1.

Diagnosis

Large species of *Pericosmus,* with vaulted test; interambulacra 1 and 4 most swollen adapically. Apical system positioned close to anterior ambitus. Petals long, deep and broad. Anterior petals widely divergent. Peristome sunken and relatively narrow. Plastron broad.

Description

Test large, reaching a maximum known length of 135 mm; width less than length; high, 52-56% TL. Anterior notch deep and quite broad (Figure 7). All interambulacra swollen adapically, but interambulacra 1 and 4 are the most tumid. Ambulacrum III moderately depressed. Petals long, deep and broad. Anterior paired petals diverge at about 40°; slightly shorter than posterior pair which occupy up to 34% TL; bear up to 40 pore pairs in each row. Posterior petals diverge at about 65° and possess up to 44 pore pairs in each row. Peripetalous fasciole weakly indented between anterior and posterior petals. Anterior branches plunge down interambulacra 2 and 3 to join marginal fasciole.

Peristome relatively narrow, 13-15% TL and sunken. Labrum projects moderately anteriorly. Plastron broad (Figure 8), 45-48% TL. Plates 1 and 2 of interambulacrum 1a in contact and not separated by second plate of 1b.

Remarks

P. celsus, which occurs in Longfordian strata, can be distinguished from *P. compressus* by its much higher test; its more anteriorly positioned apical system; more swollen lateral and anterior interambulacra (Figure 9), but much less swollen interambulacrum 5; the more steeply inclined anterior of the test; the longer paired petals; the less strongly anteriorly projecting labrum; and the broader plastron.

P. scaevus Henderson, 1975 from the Early Miocene of New Zealand also has a vaulted test and anteriorly positioned apical system, but *P. celsus* can be distinguished by the steeper anterior slope of the test, longer petals and more open anterior notch.

Etymology

Celsus (Latin) – high, lofty.

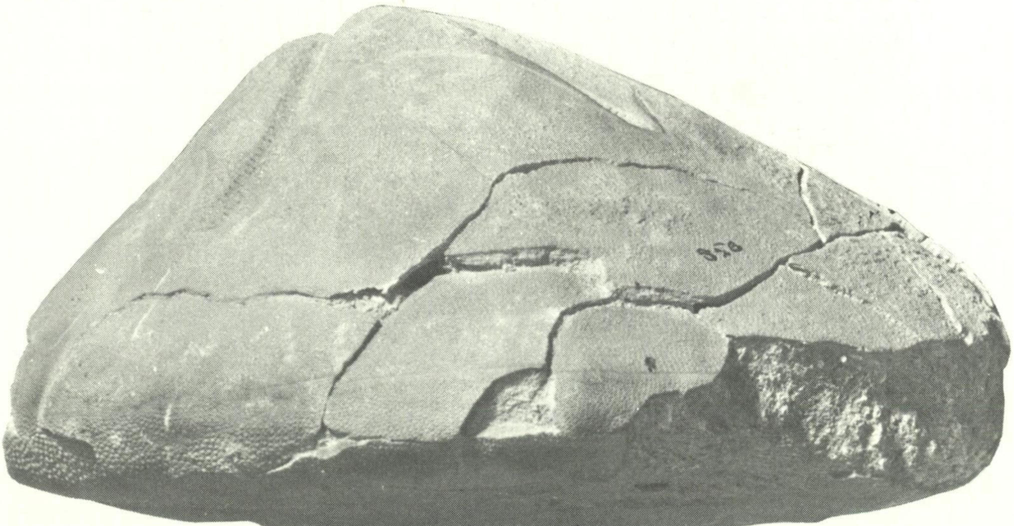


Figure 9 *Pericosmus celsus* sp. nov.; SAM P23823, holotype, from the Murray River cliffs; probably Mannum Formation; lateral view; ×1.

Pericosmus quasimodo **sp. nov.**

Figures 10-13

Holotype

NMV P55512 from 'Marble Arch, Port Campbell', from the Middle Miocene Bairnsdalian Rutledge Marl Member of the Port Campbell Limestone. Specimen collected by Mr George Baker.

Paratypes

NMV P55503, 55504 from the Port Campbell Limestone at the mouth of Ingles Creek, Port Campbell, Victoria.

Diagnosis

Test with very steep anterior slope and apex set anterior of apical system, as interambulacra 2 and 3 and ambulacrum III are very swollen adapically. Anterior notch very deep and narrow. Peristome deeply sunken. Labrum projecting very strongly anteriorly.

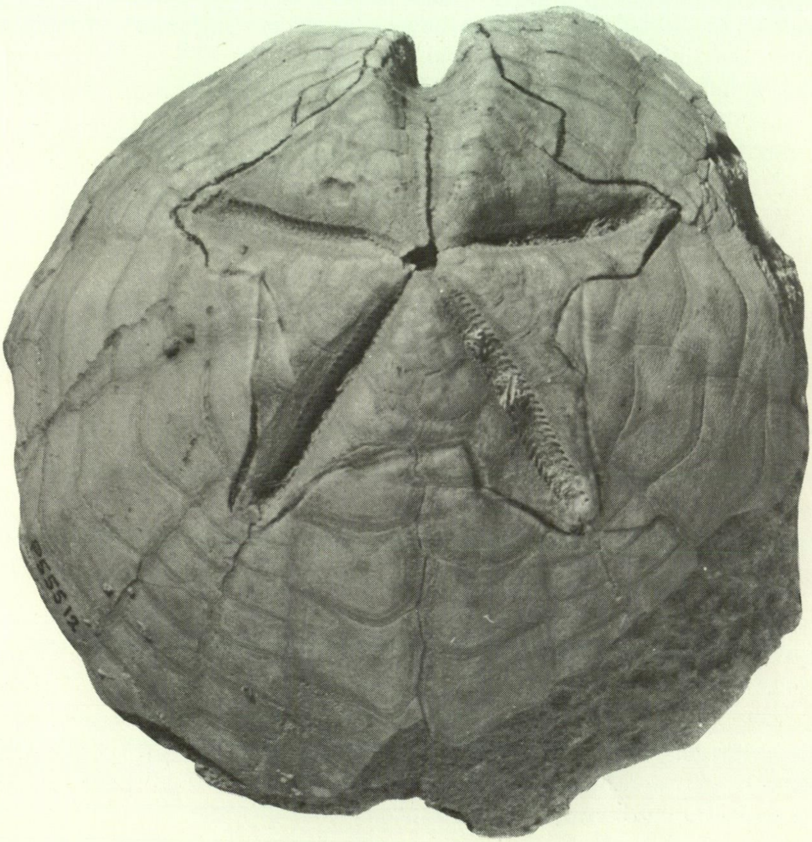


Figure 10 *Pericosmus quasimodo* sp. nov.; NMV P55512, holotype, from the Rutledge Marl Member of the Port Campbell Limestone at Port Campbell; aboral view; ×1.

Figure 11 *Pericosmus quasimodo* sp. nov.; NMV P55512, holotype, from the Rutledge Marl Member of the Port Campbell Limestone at Port Campbell; adoral view; × 1.

Description

Test large, reaching a maximum known length of 130 mm; high, 50-54% TL. Anterior notch very deep and narrow (Figure 11). Interambulacra 2 and 3, and ambulacrum III strongly swollen adapically (Figure 13B). Interambulacrum 5 forms a weak keel. Apical system set posterior of apex, and positioned 22-26% from anterior ambitus. Ambulacrum III shallow adapically, becoming deeply sunken abapically. Petals deep, narrow; relatively short in small specimens of test length 76 mm, occupying 25% TL; in holotype, which has a test length of 130 mm, they occupy up to 32% TL; posterior pair slightly longer. Anterior petals diverge at about 145° and have 25 pore pairs in each row in small specimen, 31 in large specimen. Posterior petals diverge at about 80°.

Peristome deeply sunken and set some distance back from anterior notch (18% TL). Labrum projects strongly forward (Figure 11), passing across peristome and slightly beyond it. Plastron relatively narrow, occupying 43-44% TL.

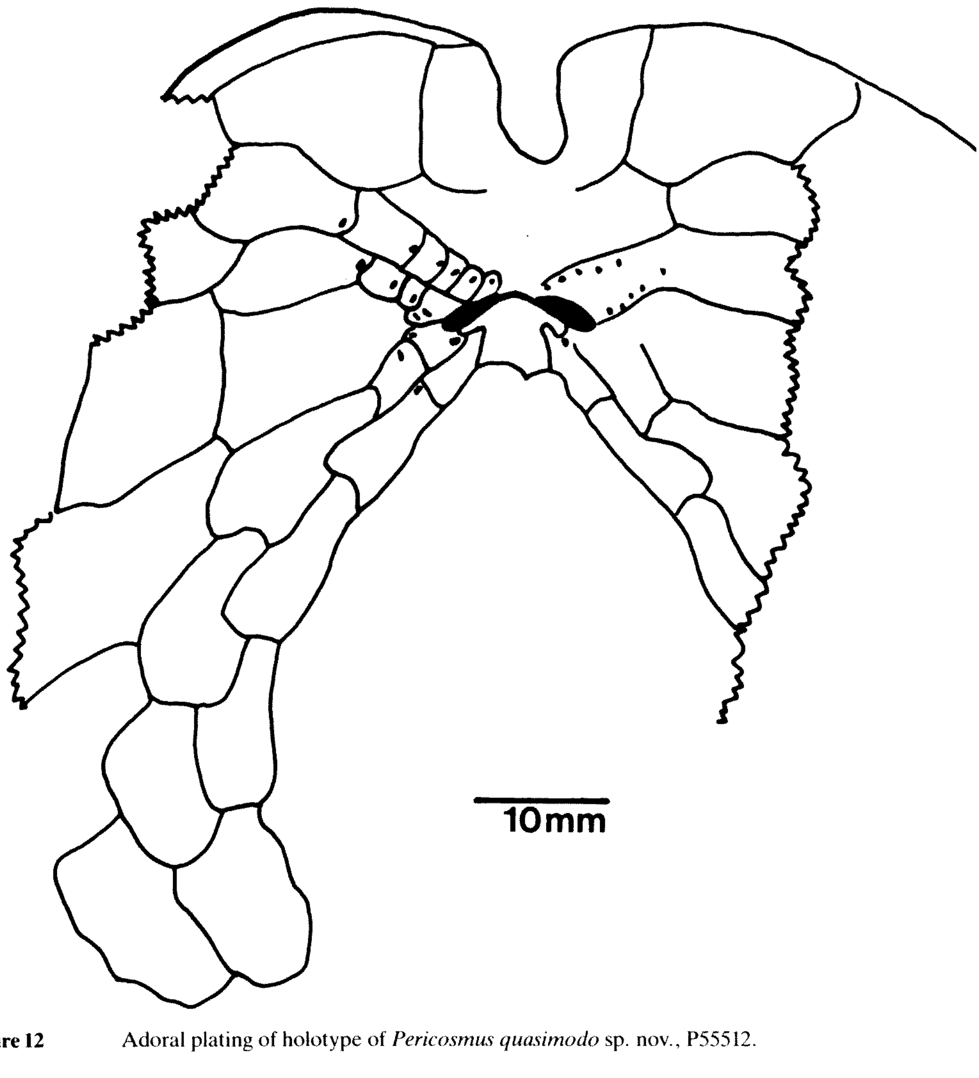


Figure 12 Adoral plating of holotype of *Pericosmus quasimodo* sp. nov., P55512.

Remarks

P. quasimodo is characterised mainly by the presence of a strongly developed 'hump' anterior to the apical system. This distinguishes it from the other vaulted species, *P. celsus,* in which the lateral interambulacra are more swollen adapically. *P. quasimodo* can also be distinguished by its slightly lower test; its shorter, straighter, narrower paired petals; the deeper anterior notch of large specimens; the more anteriorly positioned apical system; the more posteriorly positioned and deeper, more sunken peristome; the more anteriorly projecting labrum and the slightly narrower plastron.

A

B

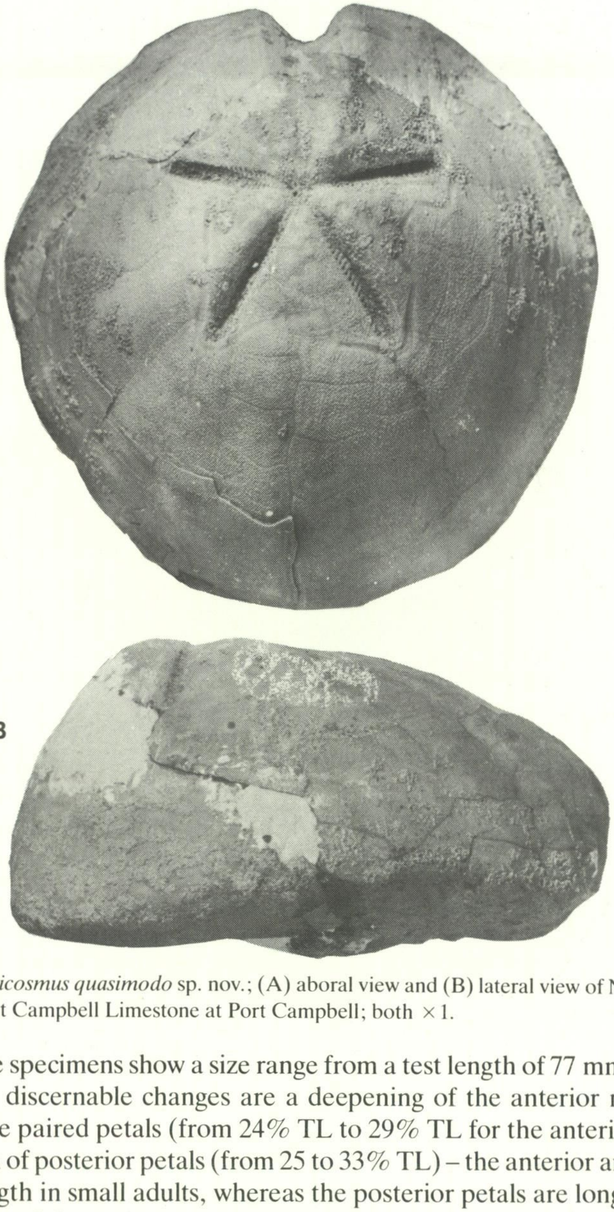


Figure 13 *Pericosmus quasimodo* sp. nov.; (A) aboral view and (B) lateral view of NMV P55504, from the Port Campbell Limestone at Port Campbell; both ×1.

The three type specimens show a size range from a test length of 77 mm to 130 mm. With growth the most discernable changes are a deepening of the anterior notch; the relative lengthening of the paired petals (from 24% TL to 29% TL for the anterior pair); a relative increase in length of posterior petals (from 25 to 33% TL) – the anterior and posterior petals are of similar length in small adults, whereas the posterior petals are longer in large adults; a slight deepening of the peristome and anterior lengthening of the labrum. These changes mirror ontogenetic changes which occurred in *P. compressus*.

Etymology

Quasimodo – the 'Hunchback of Notre Dame', alluding to the prominent hump on the aboral surface of the test.

Pericosmus torus sp. nov.

Figures 14-16

Holotype

NMV P20072 from the Longfordian to Batesfordian (Early to Middle Miocene), Batesford Limestone, Batesford, Victoria.

Paratypes

NMV P20071, 20073, 20074, 55502, 55505 from same horizon and locality as holotype.

Figure 14 *Pericosmus torus* sp. nov.; NMV P20072, holotype, from the Batesford Limestone at Batesford; aboral view; ×1.

Figure 15 *Pericosmus torus* sp. nov.; NMV P20072, holotype, from the Batesford Limestone at Batesford; adoral view; ×1.

Diagnosis

Test highest anterior of apical system, where anterior interambulacra 2 and 3 are slightly more swollen than interambulacra 1 and 4 adapically. Anterior notch deep and broad. Plastron broad, width more than half test length.

Description

Test large, reaching a maximum known length of 140 mm; high, 57% TL. Anterior notch deep and broad (Figure 14). Interambulacra all swollen adapically, interambulacra 2 and 3 being more swollen than 1 and 4; a weak keel present in interambulacrum 5. Apical system

Figure 16 *Pericosmus torus* sp. nov.; NMV P20072, holotype, from the Batesford Limestone at Batesford; lateral view; ×1.

situated at 27% TL from anterior ambitus. Petals straight, deep; relatively longer in larger individuals, being only 20% TL in specimen of 100 mm TL, but 31% in specimen of 135 mm TL; up to 38 pore pairs in each row of posterior petals. Anterior petals diverge at about 145°; posterior at about 65°.

Peristome moderately sunken, width 14% TL. Plastron relatively broad (Figure 15), 52% TL.

Remarks

P. torus is intermediate both in morphology and in stratigraphic position between the older *P. celsus* and *P. quasimodo*. Like *P. celsus* it has long petals in large specimens and a deep, broad anterior notch. It differs from that species in having an anterior 'hump' due to swelling of interambulacra 2 and 3, and a broader plastron. It can be distinguished from *P. quasimodo* in having a less anteriorly eccentric apical system, a shallow ambulacrum III, a less pronounced anterior 'hump,' and a broader plastron. Like other species of *Pericosmus,* smaller adults have relatively shorter petals and the anterior ones are longer, unlike large specimens in whcih the posterior ones are longer.

Etymology

Torus (Latin) – protruberance.

Material, Locality and Horizon

An incomplete specimen (NMV P18037) from the Middle Miocene Morgan Limestone, 6 km below Morgan on the Murray River, South Australia.

Pericosmus sp. A
Figure 17

Description

Test relatively narrow and low (height 34% TL). Apical system anteriorly situated at 30% TL. Paired petals deep and narrow, with 28 pore pairs in anterior and posterior pairs; 25-27% TL. Ambulacrum III shallow adapically, becoming very deep abapically. Anterior notch deep and narrow (Figure 17A). Interambulacra 2 and 3 swollen such that the highest point of test is anterior to apical system. Peripetalous fasciole joining marginal fasciole anteriorly. Peristome moderately sunken; width 14% TL. Labrum gently arched anteriorly to reach half way across peristome (Figure 17B).

Remarks

The low test of this form is reminiscent of *P. compressus* and *P. maccoyi*, but its more anteriorly positioned apical system, deep, narrow anterior notch and swollen interambulacra distinguish it. In these features it compares with *P. quasimodo* but it differs in the much flatter test, the relatively shorter anterior petals and the less anteriorly projecting labrum. It is not unlike *P. crawfordi*, but it has a deeper anterior notch and more swollen anterior interambulacra.

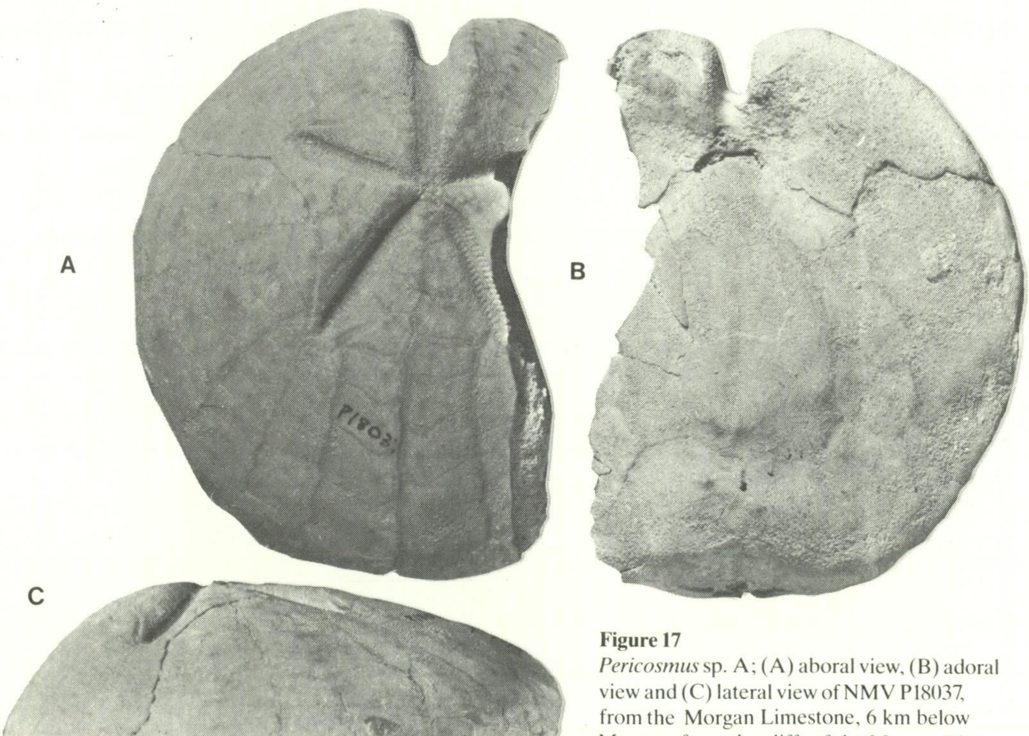


Figure 17
Pericosmus sp. A; (A) aboral view, (B) adoral view and (C) lateral view of NMV P18037, from the Morgan Limestone, 6 km below Morgan, from the cliffs of the Murray River; all ×1.

A

B

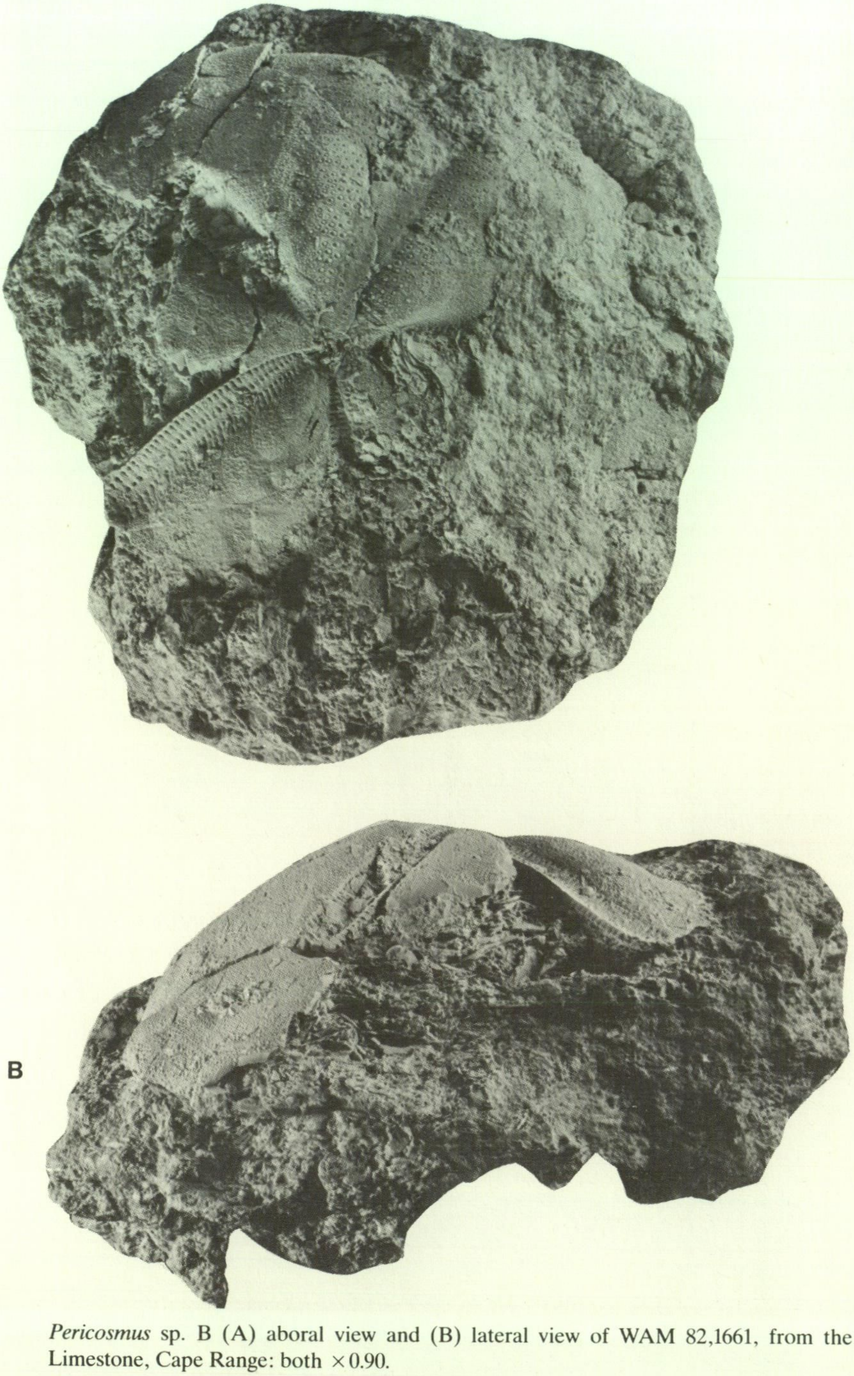


Figure 18 *Pericosmus* sp. B (A) aboral view and (B) lateral view of WAM 82,1661, from the Tulki Limestone, Cape Range: both ×0.90.

Pericosmus sp. B

Figure 18

Material, Locality and Horizon

Two incomplete specimens, WAM 82.1661 and 82.1673, from the Early Miocene Tulki Limestone, from the Cape Range, Western Australia: a ridge 1 km south of Charles Knife Road.

Description

Test large, vaulted; length not known, but probably about 110 mm. All interambulacra swollen adapically to some degree. Interambulacrum 5 most inflated, forming a prominent keel. Interambulacra 2 and 3 more swollen than 1 and 4. Petals short, shallow and broad, posterior petals bearing about 36 pore pairs in each row. Anterior petals diverge at about 130°, posterior at about 70°. Adoral surface unknown.

Remarks

Pericosmus sp. B is closest to the penecontemporaneous *P. compressus*. However, it differs in its possession of a more vaulted test, shallower, broader petals and more swollen interambulacra 2 and 3. In lateral profile *P.* sp. B bears some similarity to *P. torus* but it has a more posteriorly positioned apical system and consequently less divergent anterior petals.

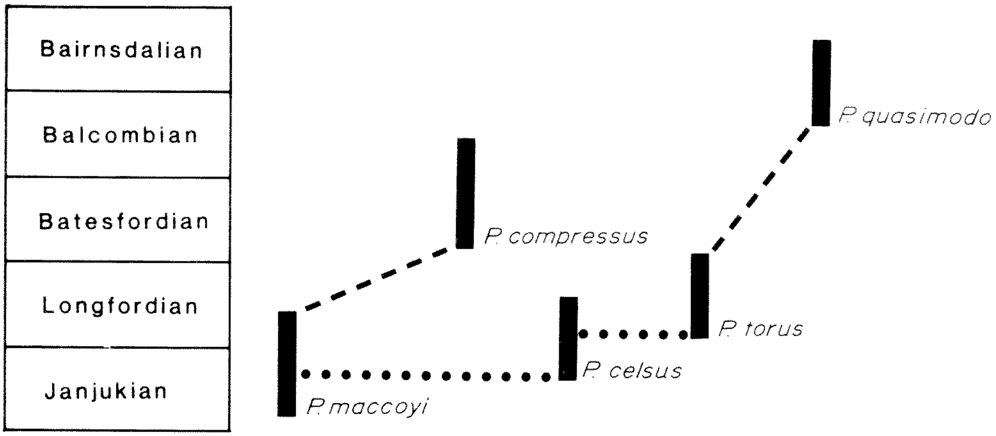


Figure 19 Stratigraphic ranges of the named species of *Pericosmus*, and suggested phylogenetic relationships.

Family Schizasteridae Lambert, 1905

Genus *Waurnia* gen. nov.

Types Species

Pericosmus nelsoni McCoy, 1882: 17.

Diagnosis

Test large, ovoid, with faint anterior notch. Peripetalous and lateroanal fascioles present. Apical system ethmolytic, with four genital pores; anteriorly very eccentric, less than one-fifth test length from anterior. Paired petals almost flush with test. Anterior pair long, extending to ambitus; posterior pair shorter, but pore pairs continuing between peripetalous and lateroanal fascioles, diminishing in size abapically. Labrum short, anteriorly projecting. Periproct longitudinally oval and large.

Remarks

McCoy (1882) originally placed this species in *Pericosmus* because of the nature of the fasciole which has a lateroanal course close to the ambitus, reminiscent of the marginal fasciole in *Pericosmus*. However, junction of the peripetalous fasciole with this lateral fascile in interambulacra 1 and 4 shows that it is a lateroanal fasciole and not a marginal fasciole, as McCoy supposed. Like *Prenaster*, the peripetalous fasciole extends around the anterior of the test below the ambitus. *Waurnia* is similar to *Prenaster* in its possession of paired petals almost flush with the test, and a very anteriorly eccentric apical system. However, *Waurnia* can be distinguished by its much larger size, having pore pairs continue beyond the posterior petals, the anterior paired petals being longer, and the much larger periproct. The size and shape of the test and petal arrangement are reminiscent of *Pseudobrissus*, but in that genus the paired petals are deeply depressed. *Brissomorpha* from the Miocene of Austria, Algeria and Indonesia has a superficial similarity to *Waurnia*, particularly in its large, depressed periproct. Although the question of whether or not *Brissomorpha* has any fascioles other than a peripetalous fasciole is unknown, its more widely spaced pore pairs in the paired petals and the apparent absence of ambulacral pores beyond the petals distinguish the two genera. The only other spatangoid in which pore pairs continue beyond the peripetalous fasciole is the brissid *Gaulteria*. Lambert (1905: 158) considered that *Pericosmus nelsoni* might best be placed in *Peribrissus*. However this genus differs from *Waurnia* in possessing a deep anterior notch and ambulacrum III; deeper, shorter petals; and flatter test.

***Waurnia nelsoni* (McCoy, 1882)**

Figures 20-23

Pericosmus nelsoni McCoy, 1882: 17-19, Pl. 66, Figs 1, 2, Pl. 67, Fig. 1; – Lambert 1905: 158.
Linthia nelsoni – Pritchard 1908: 399; H.L. Clark 1946: 366; Gill 1952: 1-3, Fig. 1.
Prenaster nelsoni – Lambert & Thiéry 1924: 515.

Lectotype

Herein selected: NMV P12211 from the Janjukian (Late Oligocene) Waurn Ponds Limestone at Waurn Ponds, Victoria; Figured by McCoy 1882, Pl. 66, figs 1, 2 and Pl. 67, fig. 1.

Paralectotypes

NMV P12212, 12213 from the same locality and horizon as the lectotype.

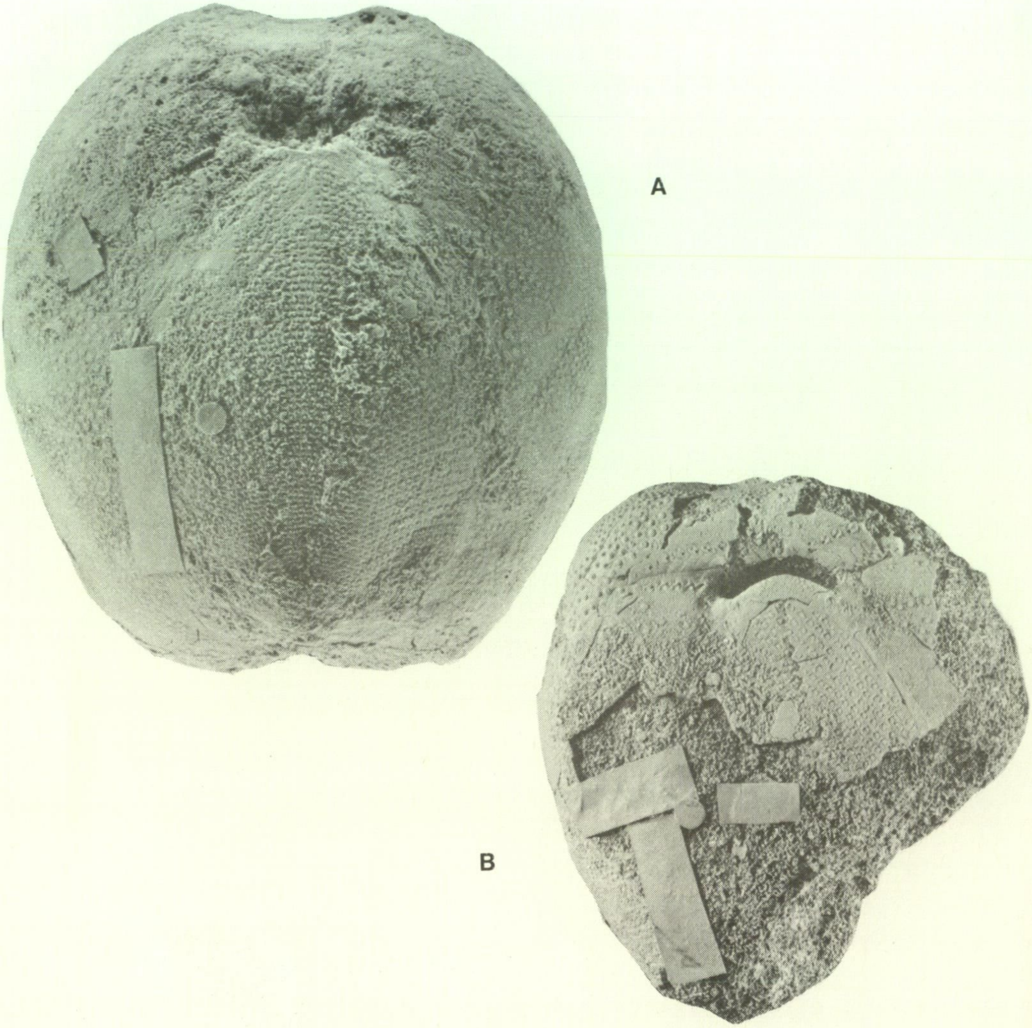
Other Material

Twenty one other specimens from the same horizon and locality as the type material: NMV P4775, 19988, 19990, 19998, 26516, 63058-63063, 63065-63074. The locality at Waurn Ponds is a quarry 'on reserve opposite old "Victoria Inn," Colac Road, 5½ miles from Barwon Bridge' (Gill 1952).

Diagnosis

As for generic diagnosis.

Figure 20 *Waurnia nelsoni* (McCoy, 1882); (A) aboral view and (B) lateral view of NMV P26516, from the Waurn Ponds Limestone at Waurn Ponds; both ×1.



A

B

Figure 21 *Waurnia nelsoni* (McCoy, 1882); adoral views of (A) NMV P12211, lectotype, and (B) NMV P12213, paralectotype; both from the Waurn Ponds Limestone at Waurn Ponds; both × 1.

Description

Test large, reaching a maximum known length of 140 mm; elongate, width 83-86% TL; high (up to 65% TL), highest at mid point, or slightly posterior of centre in interambulacrum 5, which is swollen to form low keel; other interambulacra not swollen aborally. Apical system anteriorly eccentric (Figure 20A) at only one-fifth test length from anterior; flush with test. Ambulacrum III very slightly depressed and forming faint anterior notch; very narrow and bearing extremely small pore pairs, with pores aligned almost exsagittally;

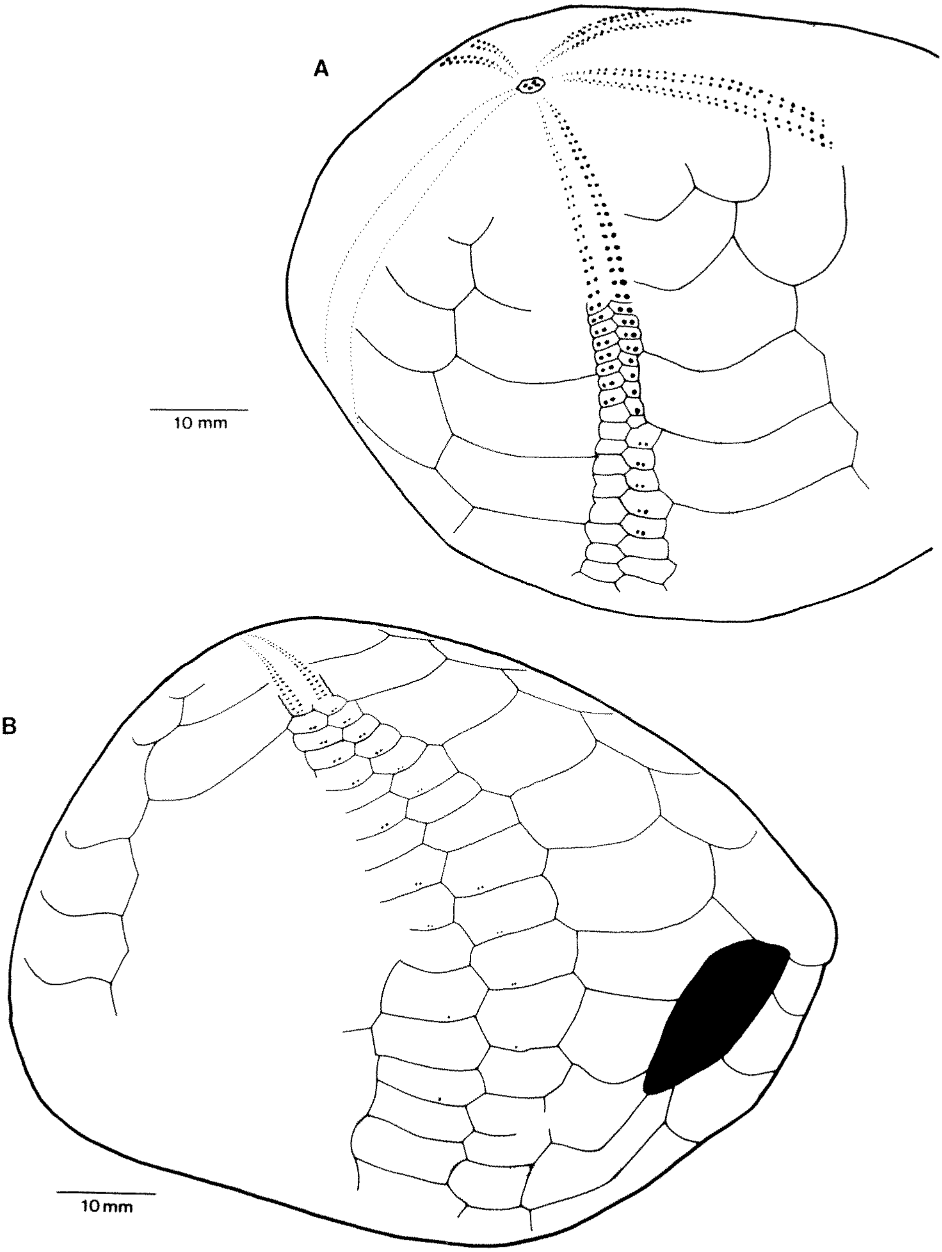


Figure 22 Drawings of plates, course of the fascioles and distribution of pore pairs in *Waurnia nelsoni* (McCoy, 1882); NMV P63072, (A) oblique antero-lateral view of aboral surface and (B) oblique postero-lateral view of aboral surface – note persistence of pore pairs between peripetalous and lateroanal fascioles.

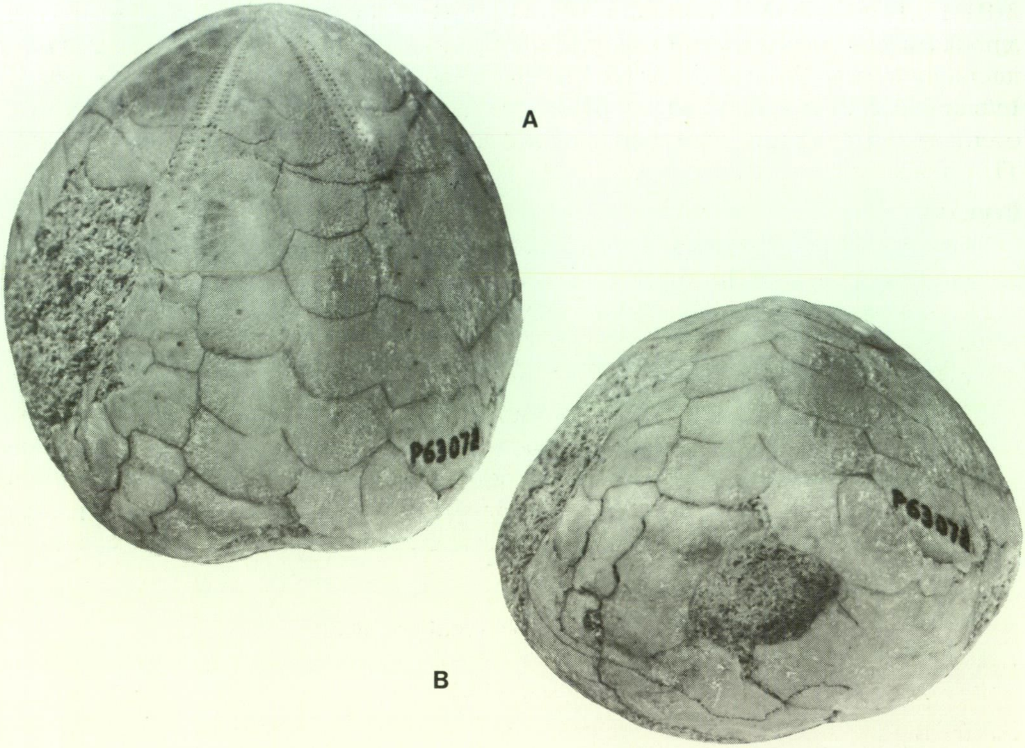


Figure 23 *Waurnia nelsoni* (McCoy, 1882); (A) oblique view of posterior of aboral surface of test and (B) posterior view of test, showing large periproct, of NMV P63072; both ×1.

ambulacral plates bearing much smaller tubercles than occur on adjoining interambulacral plates. Paired petals narrow and flush to slightly impressed. Orientation of anterior pair varies between an angle of a little less to a little more than 180°. Inner pores almost circular to slightly ovoid; outer pores round to tear-shaped; neither sunken nor conjugate. Anterior and posterior rows diverge slightly abapically; about 40 pore pairs in each row, extending to the ambitus. Posterior petals diverge at about 60°. Pore pairs closely spaced between peripetalous fasciole and apical system (Figures 22B, 23A), where they extend for a distance equal to about 33% TL; pore pairs continue between peripetalous and lateroanal fascioles (Figures 22B, 23A) and are more widely spaced and diminish in size toward ambitus, which they reach postero-laterally. About 32 pore pairs up to peripetalous fasciole and a further 12 between the fascioles. Lateroanal fasciole marginal in lateral interambulacra. Met by peripetalous fasciole close to ambitus. Anteriorly peripetalous fasciole runs marginally, just below ambitus.

Anterior of peristome positioned 14-18% TL from anterior ambitus; sunken, lunate, broad, 18% TL. Labrum short, but projecting strongly anteriorly across peristome (Figure

21B). Phyllode with unipores, 8 in ambulacrum III, 12 in ambulacra II and IV, and 8 in ambulacra I and V. Plastron moderately convex; large, width up to 45% TL. Second plate of interambulacrum 1b does not extend to ambulacrum I, only abutting ambulacrum II. Interambulacral areas covered by densely packed, large tubercles. Interambulacrum 5 overhangs periproct posteriorly. Periproct oval, large (Figure 23B), with long axis up to 18% TL. Subanal area slightly depressed.

Remarks

The species description is based largely on topotype material as McCoy's (1882) syntypes are poorly preserved specimens. *W. nelsoni* is well known from Waurn Ponds where it occurs in Janjukian strata. McCoy (1882) records that it occurred in abundance in one particular bed in the old Waurn Ponds quarries, near the base of the section. The specimens occurred in a nodular limestone band, with the lower parts of the test resting on softer marl beneath.

Gill (1952) described a specimen (NMV P15277) of *W. nelsoni* which he believed to be unique in bearing spines. Ten of the specimens studied herein (NMV P4775, 19998, 26516, 63061, 63062, 63065, 63068, 63072-4) bear adoral spines, either on the plastron or on the lateral interambulacra. This, together with their field occurrence, suggests they lived buried in the sediment and died in this position. As the test was not exposed after death, many of the spines remained to be fossilized *in situ*.

Genus *Victoriaster* Lambert, 1920

Type Species

Pericosmus gigas McCoy, 1882: 15; by original designation.

Diagnosis

Test very large size with very deep anterior notch. Pore pairs in ambulacrum III very small. Paired petals long, deep and quite narrow. Peripetalous and lateroanal fascioles present. Peristome deeply sunken with labrum strongly anteriorly projecting.

Remarks

Victoriaster was considered by Mortensen (1951: 169) to be synonymous with *Pericosmus*, and by Fischer (1966) to be a subgenus of *Pericosmus*. Clearly, it is not related to *Pericosmus* as it does not possess a marginal fasciole, but has a lateroanal fasciole. The genus therefore does not belong in the Pericosmidae. *Victoriaster* is most closely related to *Linthia*, in which the type species was placed by Pritchard (1908) and H.L. Clark (1946). However, it can be distinguished by its larger size (specimens attaining a length of 220 mm); its very deep anterior notch; its much reduced pore pairs in ambulacrum III; its long, deep and rather narrow paired petals; and a strongly anteriorly projecting labrum.

Victoriaster gigas (McCoy, 1882)

Figures 24-27

Pericosmus gigas McCoy 1882: 15-16, Pls. 64, 65; Tate 1891: 277; Mortensen 1951: 170-171, Fig. 80.
Linthia gigas – Pritchard 1908: 396; H.L. Clark 1946: 365.
Linthia mooraboolensis Pritchard, 1908: 384, Pls 22,23; H.L. Clark 1946: 366.
Victoriaster gigas – Lambert 1920: 27, Lambert & Thiéry 1924: 573.

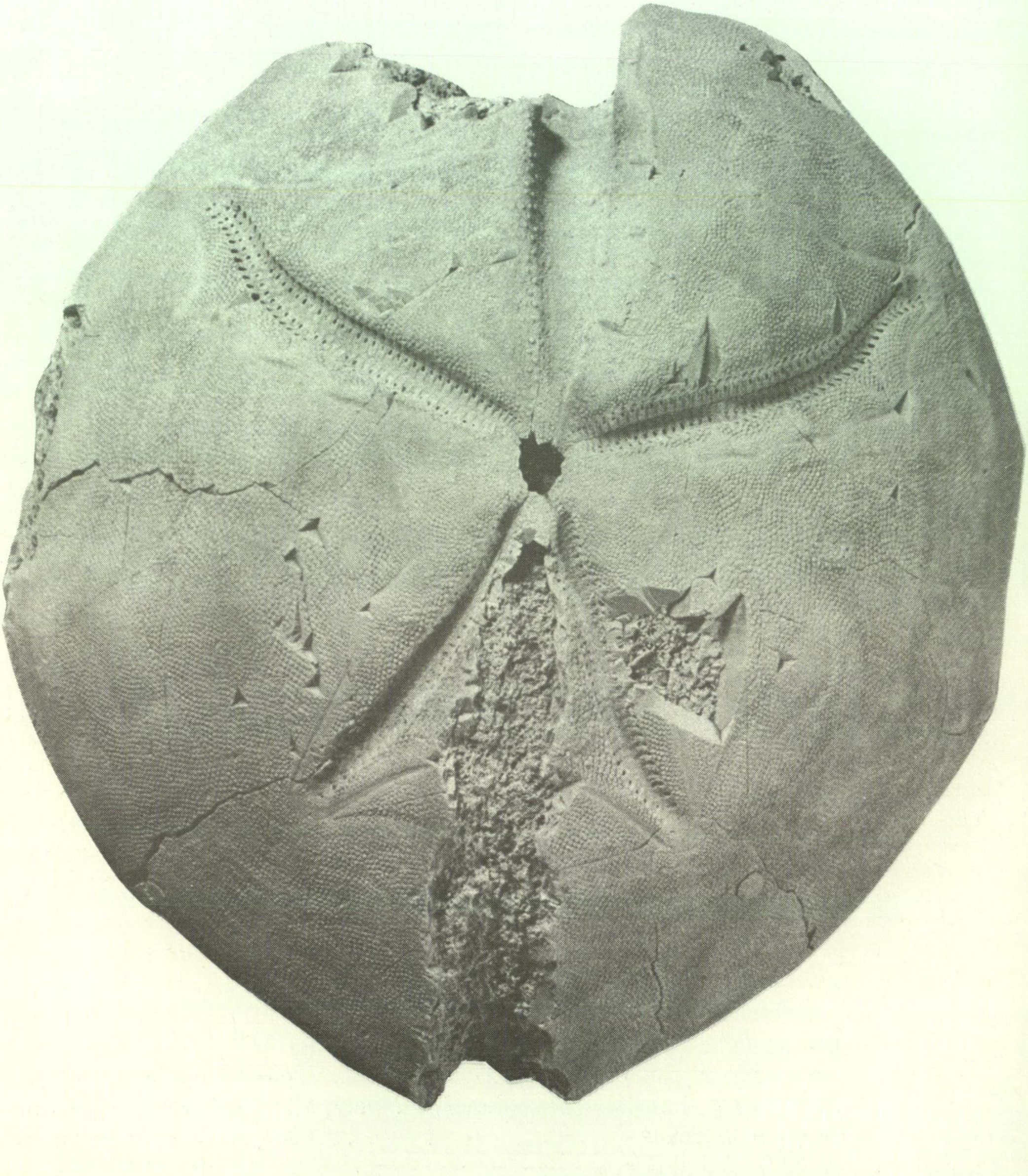


Figure 24 *Victoriaster gigas* (McCoy, 1882); NMV P4833, holotype, from the Batesford Limestone at Batesford; aboral view; ×0.75.

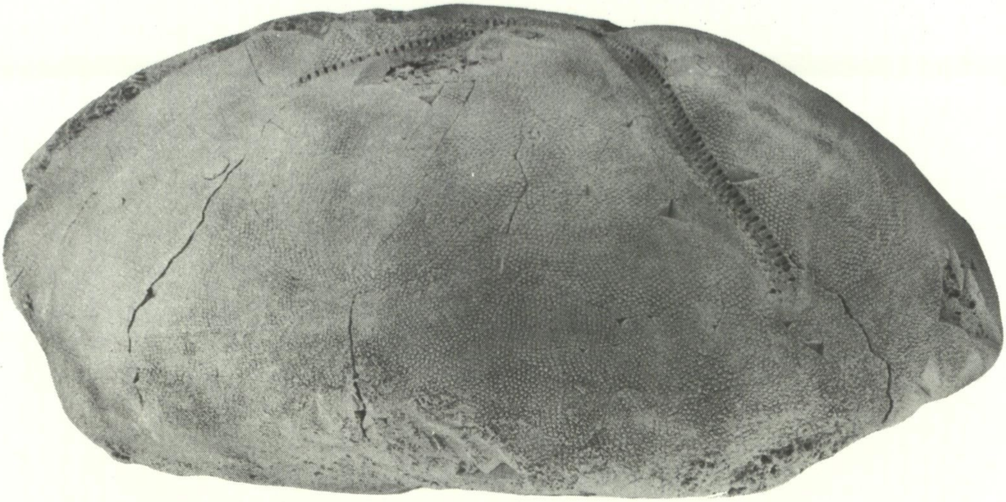


Figure 25 *Victoriaster gigas* (McCoy, 1882); NMV P4833, holotype, from the Batesford Limestone at Batesford; lateral view; ×0.75.

Material and Horizon

The holotype (by monotypy) is NMV P4833. Pritchard (1908) questioned the correctness of the localities originally given by McCoy ('on bank of Murray, near Junction with Darling, and in similar strata of Corio Bay'). He concluded that McCoy's material came from the Batesford Limestone. However, Dr T.A. Darragh of the Museum of Victoria, has recently discovered (Darragh, litt. comm. 26.10.83) that the holotype was given to William Blandowski, Zoologist and Collector of the National Museum of Victoria, when he was leading the Murray-Darling Expedition in 1857. The specimen was collected by Mr T.H. Wigley. It was originally registered as No. 2491 in the list of specimens obtained on the Expedition. A drawing of the specimen by Blandowski has been obtained by Dr Darragh. On it is recorded 'Longit. 140 Lat. 34°', placing the specimen on the Murray River near Waikerie. Therefore although Pritchard (1908) was correct to question the locality given by McCoy (1882), he was in error in believing that the specimen came from the Batesford Limestone. It is almost certainly from the contemporaneous Morgan Limestone.

Apart from the holotype and one incomplete specimen from Grange Burn (i.e. the Hamilton Beds of Balcombian age), the Batesford Limestone is the only horizon from where the species has been collected. Specimens from this horizon are: NMV P20075, 27028, 78027-9, 78031, 78034, 78035, 78039-41, 78060, 78063, MUGD 1080, 1689.

Diagnosis

As for genus.

Description

Test very large, up to 220 mm long; subcircular in plan view, width only slightly less than length. Test high, reaching almost 50% TL (Figure 25); apex in swollen interambulacrum 5 just posterior of apical system. Apical system anteriorly eccentric at 45% TL from anterior ambitus; bearing four genital pores. Anterior notch deep, 11% TL (Figure 26); relatively broad. Ambulacrum III shallow adapically, deepening abruptly at one-third ambulacral length. Pore pairs minute, widely spaced. Floor of ambulacrum covered only by small miliary tubercles; side walls with relatively large (1 mm diameter), scattered tubercles.

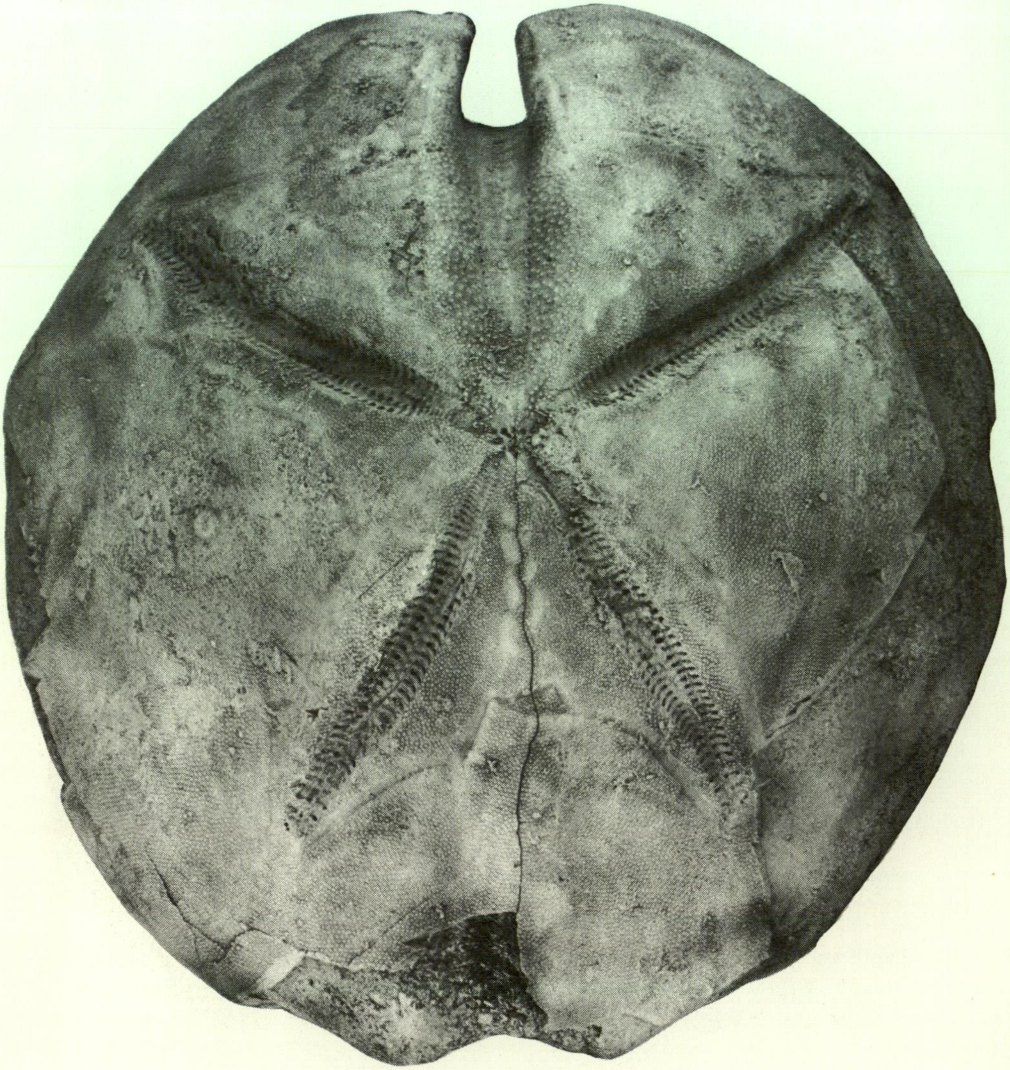


Figure 26 *Victoriaster gigas* (McCoy, 1882); MUGD 1080, from the Batesford Limestone at Batesford; aboral view; ×0.64.

Anterior petals diverge anteriorly at about 135°, almost straight, but flex slightly anteriorly at three-quarters petal length; deep, but relatively broad, width 5% TL; holotype bearing 47 non-conjugate pore pairs. Posterior petals almost straight and diverge at 60°; slightly longer than anterior; about 40% TL; similar width to anterior petals. Peripetalous fasciole following an erratic course, approaching only to within 18% TL of apical system in lateral

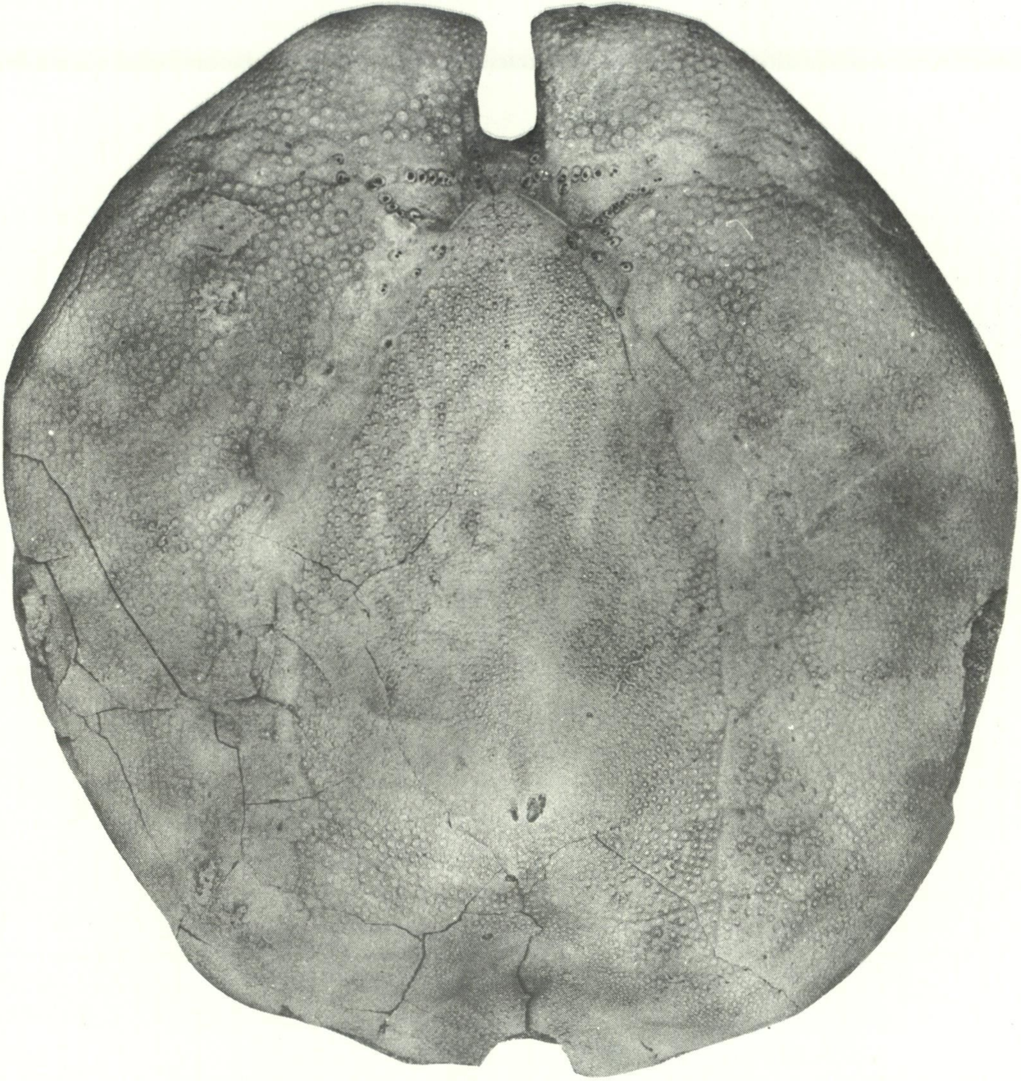


Figure 27 *Victoriaster gigas* (McCoy, 1882); MUGD 1080, from the Batesford Limestone at Batesford; adoral view; ×0.64.

interambulacra. On holotype lateroanal fasciole incomplete: extending posteriorly from peripetalous fasciole for short distance, then disappearing laterally; present posterolaterally. On other specimens (e.g. MUGD 1080 and 1689) it is entire.

Peristome small and sunken; width only 11% TL. Covered entirely by labrum which projects strongly forward (Figure 27). Pores in phyllode both unipores and anisopores; 14 in ambulacra II and IV; 7 in I, III and V. Plastron width 40% TL. Periplastronal width up to 10% TL. Plastron densely tuberculated with relatively small tubercles. Tubercles on other oral interambulacra almost twice as large (up to 30 mm diameter) and more widely spaced.

Remarks

V. gigas is probably the largest of all non-flexible echinoids ever to have lived. The largest known specimen has a length of 220 mm, a width of 205 mm and a height of 110 mm. It thus had twice the bulk of the giant living spatangoid *Plagiobrissus grandis* (Gmelin), the largest of which measured 220 × 165 × 55 mm (Mortensen 1951: 498).

Pritchard (1908) described a single specimen (MUGD 1689), which he called *Linthia mooraboolensis*, also from the Batesford Limestone. The main feature which distinguishes this specimen from the holotype of *V. gigas*, is its much lower test. The broken and dislocated nature of the interambulacral plates around the ambitus indicates that the lower profile is a product of post-depositional compaction. The specimen does possess slightly narrower petals and anterior notch than the holotype of *V. gigas*, but these differences are attributed to intraspecific variation. This is borne out by the character of the largest known specimen of *V. gigas*, MUGD 1080, which differs from the holotype of *V. gigas* in having longer and broader petals. Similar wide intraspecific variation is typical of the larger spatangoid echinoids, occurring also in living species of *Brissus* and *Breynia* (McNamara 1982).

Henderson (1975: 24) preferred to place Pritchard's *Linthia mooraboolensis* in *Lambertona*, but the type species of this genus, *L. lamberti* Sánchez Roig, 1953, is reported as possessing a thin, incomplete marginal fasciole Fischer (1966). *Lambertona lyoni* (Hutton, 1873), which Henderson (1975: 25) redescribed, has only a peripetalous fasciole. Kier (1984) has recently redescribed *L. lamberti*. He reports that this species of *Lambertona*, like *L. lyoni*, has neither a marginal nor a lateroanal fasciole, possessing only a peripetalous fasciole. The holotype of *Linthia mooraboolensis* possesses an entire lateroanal fasciole and, as noted above, is synonymous with *Victoriaster gigas*.

Phylogenetic Relationships of Australian Species of *Pericosmus*

The earliest species of *Pericosmus* to occur in the southern Australian Tertiary, *P. maccoyi*, possesses a relatively low test, subcentral apical system, and shallow to moderately deep petals. The later species, *P. compressus*, *P. celsus*, *P. torus*, *P. quasimodo* (Figure 19) and *P.* sp. B are typified by the possession of more highly vaulted tests (Figure 28); more anteriorly positioned apical systems; deeper petals; more sunken peristomes; more anteriorly projecting labra; and broader plastrons.

The earliest species of *Pericosmus*, such as *P. clarki* Lambert, 1933 from the Paleocene of Madagascar and *P. annosus* from the Eocene of New Zealand, have features more in common with the earliest (Late Oligocene) Australian species. There appears to have been a trend, during the Tertiary, for the periodic development of a smaller number of species which possess a larger test, deeper petals, more anteriorly positioned apical systems, elongate labra, and broad plastrons. However, the ancestral, early Tertiary, morphology appears to have persisted throughout the Tertiary to the present day, while the forms which

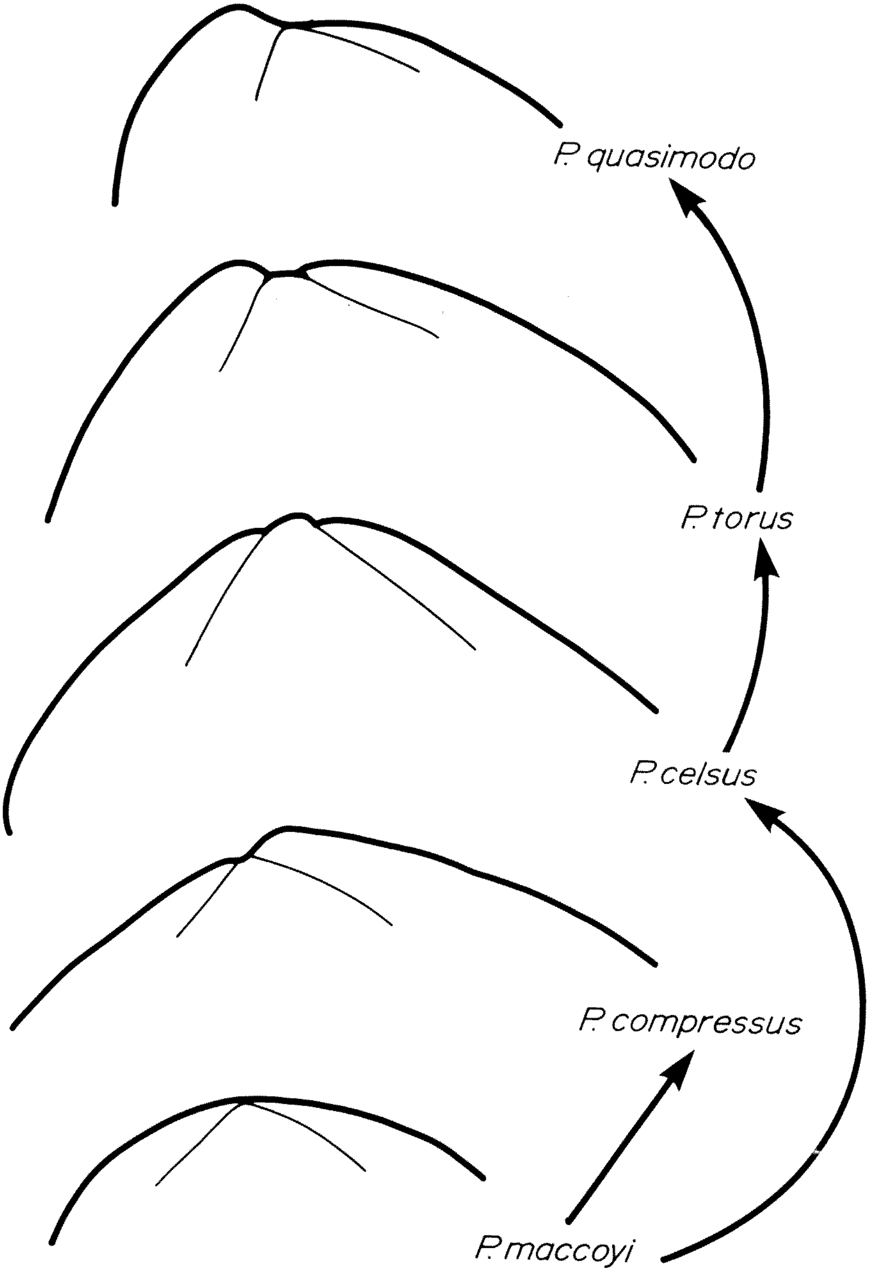


Figure 28 Drawings of lateral profiles of named species of *Pericosmus*, illustrating the general trend of development and anterior progression of adapical interambulacral swelling.

developed a highly vaulted test developed as short-ranging, iterative offshoots from the main *Pericosmus* stock. A recently discovered species, *Pericosmus porphyrocardius* from north-western Australia (McNamara 1984) is morphologically similar to the earliest Australian fossil species, *P. maccoyi.*

The phylogenetically early characters, associated with a low test, occur in small specimens of later species. In other words later species with vaulted tests, undergo greater morphological changes through ontogeny than their ancestors: they may be said to be peramorphic (Alberch *et al.* 1979). Thus, for instance, a small test of *P. compressus* resembles the largest specimens of earlier species in possessing shallow petals and a more open, shallow anterior notch; shorter petals than in large specimens; a more central apical system; a shallower peristome and a less anteriorly protruberent labrum. Growth within these Australian Late Oligocene-Early Miocene species, and later phylogenetic development within the Australian Miocene species, seems to have favoured a deepening of the petals and swelling of the intervening interambulacra; the anterior movement of the apical system and consequent development of a steeper anterior slope of the test; a deepening of the peristome and anterior lengthening of the labrum; and broadening of the plastron. Forms which developed these morphological characteristics are also larger than those species possessing ancestral morphology. These morphological changes may therefore have been brought about by hypermorphosis: delay in onset of maturity allowing continuation of morphological development beyond that of the ancestor. Delay in onset of maturity will also result in attainment of a larger size.

The Australian species show a trend of varying swelling of the aboral interambulacra adapically, from no swelling in the early *P. maccoyi* to swollen posterior interambulacrum in *P. compressus* and *P.* sp. B: swollen lateral interambulacra in the Longfordian *P. celsus;* swollen lateral and slightly swollen anterior interambulacra in the younger Longfordian-Batesfordian *P. torus;* and finally, only a strongly swollen, anterior interambulacrum in the latest species, the Bairnsdalian *P. quasimodo.* This anterior shift of swollen interambulacra accompanies an anterior shift in position of the apical system and increasing angle of declination of anterior of the test.

Functional interpretation of morphological changes.

Some of the evolutionary changes which occur within the spatangoid *Schizaster,* from the subgeneric morphotype *Paraster* to the *Schizaster* morphotype (McNamara and Philip 1980) are comparable to changes which occur between species of *Pericosmus.* Changes in *Schizaster* involve increasing test size; increasing the angle of anterior slope of the test; increase in depth of paired petals and ambulacrum III; increase in depth of anterior notch; anterior lengthening of the labrum; and increase in plastron size. Similar changes have been recorded in *Micraster* (Smith 1984).

The changes also occur between species of *Pericosmus* in the Australian Tertiary. One difference between the two is with respect of the apical system: in *Pericosmus* there is an anterior movement; in *Schizaster* the movement is posterior. The posterior movement in *Schizaster* reflects increase in number of funnel-building tube feet, a facility not possessed by *Pericosmus.* Increase in petal depth in *Schizaster* and concomitant increase in declination of the aboral surface anterior to the apical system, and projection of the labrum, are believed to relate to the occupation of finer sediments, which necessitates optimisation of water flow over the test and to the adoral surface of the test (McNamara and Philip 1980).

The Australian Oligocene-Miocene species of *Pericosmus* all appear to have lived in coarse bioclastic limesands, apart from the youngest species *P. quasimodo.* This species, which has the deepest petals, most arched test, anteriorly positioned apical system and most projecting labrum, is preserved in marly horizons within the Port Campbell Limestone. The development of the morphological adaptations within the Australian Miocene species of *Pericosmus* may, perhaps, reflect adaptation to optimising water flow over the test, either due to occupation of finer sediments, or to living at increased depth in the sediment. Evidence for increased burrowing also comes from the relatively larger plastron possessed by the later species in the lineage; these species would thus bear a relatively greater number of burrowing adoral spines.

All modern described species referred to *Pericosmus* possess the ancestral morphology, suggesting that these more conservative, eurytopic species have persisted from the Eocene to the present day. The more highly vaulted stenotopic species, such as *P. celsus, P. torus* and *P. quasimodo,* were short-lived evolutionary experiments, which probably occupied more restricted niches and possessed particular morphological refinements which allowed their selection and genetic establishment. These refinements may have been made possible by the peramorphosis.

Living species of *Pericosmus* have been obtained from depths between 18 and 486 m, most occuring at about 200 m (Mortensen 1951). What little information is available on the sediment type occupied by these species indicates occurrence in both mud and sand. *Pericosmus porphyrocardius,* recently collected from north-western Australia (McNamara 1984), was obtained from depths between 309 and 420 m. Sediment from within the gut indicates that the species inhabited a foraminiferal-rich muddy substrate. Thus, the living species, all of which possess a basically conservative morphology, live in moderately deep water. Their morphology further suggests that they are ill-adapted to burrowing deeply in the fine substrate they inhabit.

Both the morphological characters of the Australian fossil species and the nature of the sediment in which they are preserved differ from their living and ancestral counterparts. The evolution of a number of short-ranging species during the Late Oligocene and Early Miocene in southern Australia probably reflects the attainment of a distinctive morphology, principally of vaulted test and sunken petals, which allowed occupation of an environment different from that of the ancestral species. Their occurrence in coarse-grained sediments suggests habitation in relatively shallow water in a high hydrodynamic environment.

Consequently, it may be suggested that from the stable, long-ranging, deeper water forms of *Pericosmus,* a series of short-lived species migrated into shallower water and inhabited a coarser sediment than their ancestors. The morphological characteristics developed by these Oligo-Miocene species may reflect the ability of the species to burrow effectively within these coarse sediments. The youngest species, *P. quasimodo,* evolved a morphology which allowed it not only to burrow deeper than its deep water ancestors, but also to inhabit finer sediments than its immediate ancestors which inhabited coarser sediment.

Acknowledgements

We wish to thank Dr P.A. Jell, Mr N. Pledge and Mr G. Quick for loan of specimens in their care, Mr R. Foster for making freely available for our use specimens from his collection, Dr P. Kier for reading the manuscript and offering suggestions for its improvement and Miss E. Ioannidis for typing. This work was supported by a grant from the Australian Research Grants Committee.

References

Alberch, P., Gould, S.J., Oster, G.F. and Wake, D.B. (1979). Size and shape in ontogeny and phylogeny. *Paleobiology*, **5:** 296-317.

Chesher, R.H. (1968). The systematics of sympatric species in West Indian spatangoids: a revision of the genera *Brissopsis*, *Plethotaenia*, *Paleopneustes*, and *Saviniaster*. *Stud. trop. Oceanogr. Miami*, **7:** 1-168.

Clark, H.L. (1946). The echinoderm fauna of Australia. Its composition and its origin. *Publ. Carneg. Instn.* **566:** 1-567.

Duncan, P.M. (1877). On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. *Q. Jl. geol. Soc. Lond.*, **33:** 42-71.

Duncan, P.M. (1887). A revision of the Echinoidea from the Australian Tertiaries. *Q. Jl. geol. Soc. Lond.*, **43:** 411-430.

Fischer, A.G. (1966). *In Treatise on Invertebrate Palaeontology, Pt. V, Echinodermata 3, Asterozoa-Echinozoa.* R.C. Moore ed., (Geol. Soc. Amer.: Univ. Kansas Press.)

Gill, E.D. (1952). Note on the spines of a Tertiary echinoid from Victoria. *Proc. R. Soc. Vict.*, n.s. **64:** 1-3.

Gregory, J.W. (1890). Some additions to the Australian Tertiary Echinoida. *Geol. Mag.* **27:** 481-492.

Henderson, R.A. (1975). Cenozoic spatangoid echinoids from New Zealand. *Palaeont. Bull. N.Z. geol. Surv.*, **46:** 1-90.

Hutton, F.W. (1887). On the geology of the Trelissick or Broken River Basin, Selwyn County. *Trans. N.Z. Inst.* **19:** 392-412.

Kier, P.M. (1984). Fossil spatangoid echinoids of Cuba *Smithson. Contr. Paleobiol.* **55:** 1-336.

Lambert, J. (1905). *In* L. Doncieux, Fossiles nummulitiques de L'Aude et de L'Hérault. *Ann. Univ. Lyon* **17:** 129-164.

Lambert, J. (1920). Sur quelques genres nouveaux d'échinides. *Mém. Soc. acad. Agric. Sci. Dép. Aub.* **83** & **84:** 145-170.

Lambert, J. and Thiéry, P. (1909-1925). *Essai de nomenclature raisonnee des Échinides.* Ferriere, Chaumont.

McCoy, F. (1882). *Prodromus of the palaeontology of Victoria* (Decade VII), Melbourne.

McNamara, K.J. (1982). Taxonomy and evolution of living species of *Breynia* (Echinoidea: Spatangoida) from Australia. *Rec. West. Aust. Mus.*, **10:** 167-197.

McNamara, K.J. (1984). Living Australian species of the echinoid *Pericosmus* (Spatangoida: Pericosmidae). *Rec. West. Aust. Mus.* **11:** 87-100.

McNamara, K.J. and Philip, G.M. (1980). Australian Tertiary schizasterid echinoids. *Alcheringa*, **4:** 47-65.

Mortensen, T. (1950). New echinoidea (Spatangoidea). (Preliminary notice). *Vendensk. Meddr dansk naturh. Foren.*, **112:** 157-163.

Mortensen, T. (1951). *A monograph of the Echinoidea 5(2), Spatangoidea II.* Reitzel, Copenhagen.

Pritchard, G.B. (1908). On the occurrence of the genus *Linthia* in Victoria, with description of a new species. *Proc. R. Soc. Vict.*, n.s. **21:** 392-400.

Smith, A. (1984). *Echinoid palaeobiology.* (George Allen and Unwin: London).

Tate, R. (1891). A bibliography and revised list of the described echinoids of the Australian Eocene, with description of some new species. *Trans. R. Soc. S. Aust.*, **14:** 270-282.

Tate, R. (1894). A critical list of the Tertiary Mollusca and Echinodermata of New Zealand in the collection of the Colonial Museum. *N.Z. geol. Surv. Rep. geol. Explor. 1892-1893*, **22:** 121-127.

Received 28 March 1983 **Accepted 21 July 1983** **Published 22 October 1984**