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Middle Eocene echinoids from the western Eucla Basin, Western Australia

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ABSTRACT – The oldest carbonate sediments in the western Eucla Basin in south-western Australia are a series of cool-water bryozoan-dominated bioclastic grainstones, packstones and marls that represent deposition during the Tortachilla Transgression during the Bartonian (middle Eocene) planktonic foraminiferal zones 14–15. The two principal units are the Nanarup Limestone and a unit reported here for the first time and named, informally, the Manypeaks limestone. These units contain rich invertebrate faunas dominated by bryozoans, echinoids, bivalves and brachiopods. Herein we document fourteen echinoid species that occur in these limestones. They comprise one cidaroid, one camarodont, one salenioid, two cassiduloids, one echinolampadoid, one clypeasteroid and seven spatangoids. Four new species are described, the cassiduloid *Eurhodia westaustraliae* sp. nov., the clypeasteroid *Fossulaster susae* sp. nov., and the spatangoids *Cyclaster jamiei* sp. nov. and *Gillechinus kaitae* sp. nov. The species of *Fossulaster* represents the earliest known member of the Fossulasteridae and the earliest known record of a marsupiate echinoid in Australia. Analysis of the middle and late Eocene echinoids faunas of the western Eucla Basin establishes that the Nanarup Limestone echinoid fauna represents the cassiduloid biofacies, while the Manypeaks limestone is a mixed cassiduloid and spatangoid biofacies.

KEYWORDS: Echinoidea, Eocene, taxonomy, palaeoecology, Western Australia

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INTRODUCTION

The Eucla Basin in southern Australia represents the largest tract of onshore Cenozoic marine sediments in the world (Clarke et al. 2003). It extends from the south-west corner of the continent near Albany in Western Australia, east for some 2,500 km to the St Vincent Gulf in South Australia. It spreads north about 350 km from the Great Australian Bight, while offshore it extends at least 500 km south of the present day coastline. Including its offshore extension it covers an area of more than one million square km, and as such covers about 15% of the Australian continent. Stratigraphically it is surprisingly uniform across its entire width, consisting of clastic and carbonate units ranging in age from middle Eocene to middle Miocene. These were deposited during a series of major transgressive events across the southern Australian continent, following the final separation of the Australian continent from Antarctica (Clarke et al. 2003; Hou et al. 2008).

This paper concerns the echinoid fauna from the western-most part of the basin. Formerly this area was considered to represent a separate, much smaller basin, the Bremer Basin. However, as Clarke et al. (2003) have argued, the continuous nature of the sedimentation across the entire southern part of the continental shelf at this time suggests they all form part of a single basin of deposition. The oldest Cenozoic rocks preserved in the western part of the Eucla Basin in south-western Australia consist of a sequence of Eocene sedimentary units (Figure 1): the North Royal Formation, overlain by the Nanarup Limestone, Werillup Formation and Pallinup Formation (Clarke et al. 2003). These are predominantly clastic units: sandstones, clays, siliceous spongolites and lignite-rich beds, apart from the Nanarup Limestone. This is one of a number of small, localised bryozoal limestone deposits in the area, within which the echinoids occur, and which may have been deposited as shoals on topographic highs.

These limestones are considered to correlate with the Norseman and Paling formations and the Wilson Bluff Formation in other parts of the Eucla Basin (Clarke et al. 2003), and with the Tortachilla Limestone in the St Vincent Basin in South Australia. These carbonate units were all deposited during planktonic foraminiferal zones P14–15, and are thus late Bartonian (middle Eocene) in age (Li et al. 2003). Their deposition along the southern Australian margin at this time occurred during the Tortachilla transgressive event (Clarke et al. 2003). This marks the initiation of carbonate deposition off the southern margin of Australia and correlates with the acceleration in the divergence of Australia from Antractica.

The limestones of the Eucla Basin contain rich, predominantly invertebrate, faunas but, given the general lack of outcrops, these faunas are relatively poorly known. The Nanarup Limestone is the most westerly outcropping of these limestones and is the most accessible and extensively collected. Like the other Eucla Basin limestones, it is a typical cool-water carbonate (Boreen and James 1995), being dominated by bryozoans and echinoids, but also containing bivalves, gastropods, brachiopods, foraminifers, nautiloids, calcareous algae, asteroids, isocrinid and comatulid crinoids, sponges and crabs (McNamara 1992). Rare shark teeth also occur. Of these groups, only the brachiopods (Craig 1997, 2001; Robinson 2017), the isocrinid crinoids (Whittle et al. 2018), palynomorphs (Hos 1975) and foraminifers (Quilty 1969, 1981) have been described.

Despite being a very common component of these bryozoal limestones, little has been written about any of the Eucla Basin Eocene echinoids. Philip (1970) figured, but did not describe, *Salinida* [sic] *tertiaria* (Tate) (=*Pleurosalenia tertiaria*) (Philip 1970, fig. 56B), *Brissopatagus cudmorei* (Fell) (=*Gillechinus susae* sp. nov.) (Philip 1970, figs 56F, 57D) and *Australanthus longianus* (Gregory) (Philip 1970, fig. 58B, E) from the Wilson Bluff Limestone. McNamara and Philip (1980a) discussed the occurrence of *Echinolampas posterocrassa* in the Nanarup Limestone, pointing out the similarities with penecontemporaneous material from the Tortachilla Limestone, some 2,500 km to the east. McNamara (1994a) recorded the occurrence of the marsupiate echinoid *Fossulaster* in the Nanarup Limestone, noting that it is the earliest record for a marsupiate echinoid in the Australian Cenozoic. Herein we document 14 species of echinoids: one cidaroid; one camarodont; one salenioid; two cassiduloids; one echinolampapoid; one clypeasteroid; and seven spatangoids, describing one new cassiduloid, one new clypeasteroid and two new spatangoid species. In addition to documenting this western Eucla

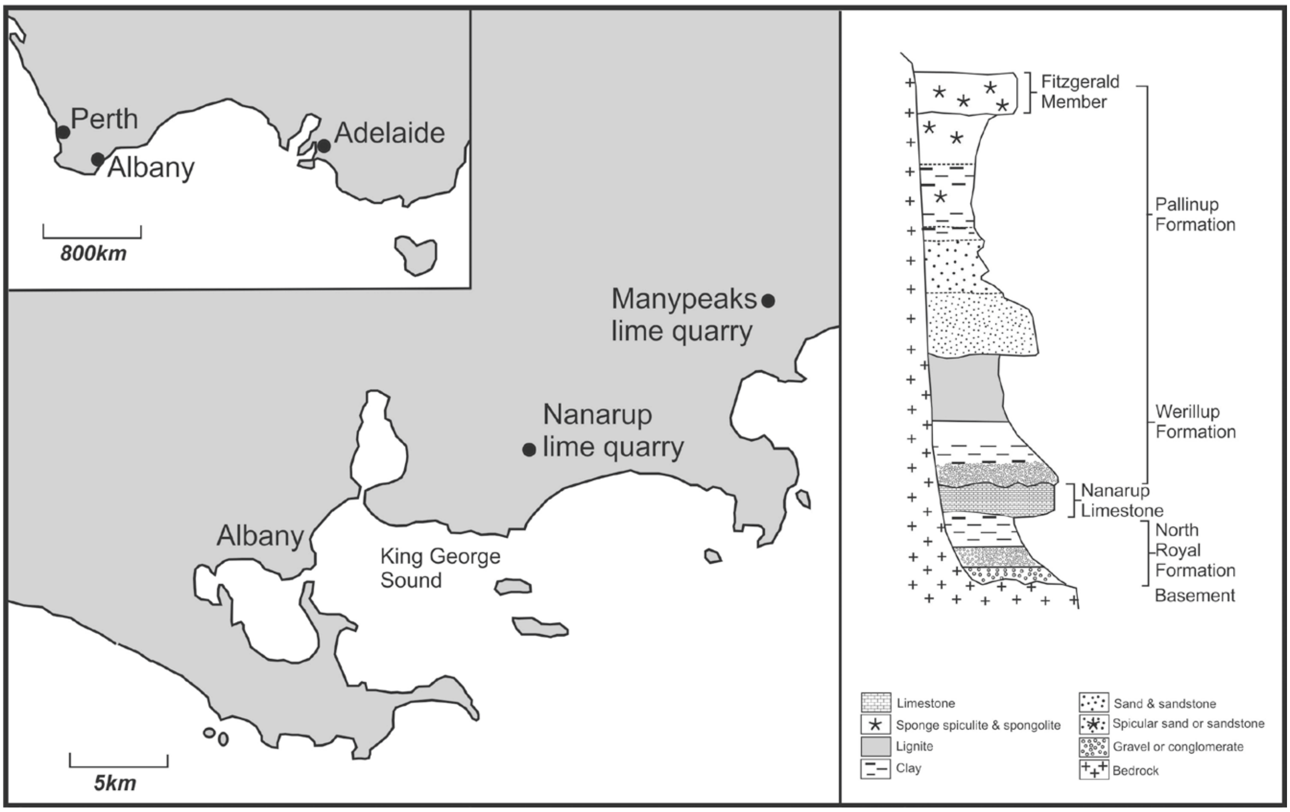

FIGURE 1 Map showing locations of the Nanarup and Manypeaks lime quarries in south-west Western Australia and chart of the middle and late Eocene stratigraphy of the western Eucla Basin (after Clarke et al. 2003). The Manypeaks limestone is contemporaneous with the Nanarup Limestone.

Basin middle Eocene echinoid fauna, we discuss its palaeoecological significance in terms of echinoid biofacies variability within different outcrops of the limestone and also compare it with the echinoid faunas from the younger Pallinup Formation in the western Eucla Basin and the coeval Tortachilla Limestone in the St Vincent Basin in South Australia.

GEOLOGICAL SETTING

This most westerly Eucla Basin echinoid fauna occurs mainly in two discrete limestones: the Nanarup Limestone and a more pelitic facies, informally named the 'Manypeaks limestone', which outcops in a lime quarry 7 km south of Manypeaks townsite. The type Nanarup Limestone is only exposed in the Nanarup lime quarry, 17 km east of Albany, Western Australia at 118°02'45"E, 34°58'35"S (Figure 1). The limestone is about three metres thick in the quarry. A basal one metre of yellow, friable, medium-grained bryozoal grainstone is overlain by a one metre thick layer of white, finer, more silty packstone. The upper metre is similar in character to the lower, coarser-grained bed. The limestone was probably deposited in a shallow-water, open shelf environment.

A previously unrecorded coeval limestone is exposed in a small lime quarry located 20km northeast of Nanarup at Manypeaks, at 118°12'00"E, 34°53'40"S. Here, a basal bed of brown bryozoal grainstone is overlain by a finer-grained pale grey-white packstone, with thin, interbedded green wackestone. This sequence is overall more finer-grained than at Nanarup and was probably deposited in slightly deeper water. It does not appear to be contiguous with the Nanarup Limestone and appears to be one of a series of discrete limestones that occur in the region (Clarke et al. 2003). The limestone unit has not been formally described. Herein we refer to it informally as the 'Manypeaks limestone'. A third, very small and very thin, outcrop occurs 16 km south-east of Manypeaks at Waychinacup Inlet. This bryozoal grainstone is lithologically similar to the Nanarup Limestone. The unit is referred to informally as the 'Waychinacup limestone'. It has only yielded a small number of cidaroid spines.

The Nanarup Limestone overlies a series of middle Eocene clastics and lignite of the North Royal Formation (Clarke et al. 2003) (Figure 1). It is overlain by the Werillup Formation, which Clarke et al. (2003, p. 241) have restricted to late Eocene clastics and lignite deposited in non-marine to marine environments. Formerly, the Nanarup Limestone had been regarded as a member of the Werillup Formation. However as Clarke et al. (2003, p. 240) have pointed out, it is a lateral equivalent to the limestones of the Norseman Formation and with further mapping warrants being elevated to the status of the Nanarup Formation. Herein we simply refer to it as the Nanarup Limestone. As we demonstrate, the close similarity of the echinoid faunas of the Nanarup Limestone and the Manypeaks limestone indicate they are coeval deposits.

MATERIAL EXAMINED

Excluding echinoid spines, 669 specimens were examined in this study, of which 627 were from the Nanarup Limestone, the rest from the Manypeaks limestone (for details see Table 1). 870 spines have been collected from the two limestones. Specimens used in this study are housed in the collections of the Western Australian Museum (WAM) and the Naural History Museum, London (NHM). In species descriptions test length is abbreviated to TL.

SYSTEMATIC PALAEONTOLOGY

Class Echinoidea Leske, 1778

Order Cidaroida Claus, 1880

Family Cidaridae Gray, 1825

Subfamily Cidarinae Gray, 1825

Genus *Temnocidaris* Cotteau, 1863

Subgenus *Stereocidaris* Pomel, 1883

TYPE SPECIES

Cidaris cretosa Mantell, 1835 [=*Cidaris sceptrifera* Mantell, 1822] by subsequent designation of Lambert and Thiéry (1909).

Temnocidaris (*Stereocidaris*) *cudmorei* Philip, 1964

Figure 2

MATERIAL EXAMINED

Australia: ***Western Australia:*** Only incomplete cidaroid tests are known, including infrequent entire interambulacra and conjoined ambulacral plates, along with hundreds of random, single interambulacral plates. No complete specimens are known, nor specimens with attached apical zones. The following specimens from the Nanarup Limestone, Nanarup lime quarry, contain sufficient features to be assigned to this species: WAM 03.23, 03.24, 03.14–03.25, 07.426, 07.442 (36), 72.51[2], 76.87 (2), 76.88 (5), 88.853, 94.845 (8). Specimens from the Manypeaks limestone, Manypeaks lime quarry, include WAM 67.217–67.220, 69.255 (68), 76.90 (2), 76.91 (5), 94.812 (42), 94.813 (5), 94.846 (35), 03.55–03.71. None of the spines from either limestone is associated with coronal fragments.

REMARKS

Cidaroids are a common component of the Nanarup Limestone, less so in the Manypeaks limestone. Specimens are preserved both as incomplete tests and radioles (Figure 2). Test fragments occur commonly, including infrequently entire interambulacra and conjoined ambulacral plates, along with hundreds of random, single interambulacral plates. No complete specimens are known, nor specimens with attached apical zones. Of the many hundreds of cidaroid radioles, none has been found with associated coronal fragments. The coronal specimens are identified as *Temnocidaris (Stereocidaris) cudmorei* Philip, 1964. Philip (1964) described six species of *Stereocidaris* from the Tertiary of south-eastern Australia: *S. australiae* (Duncan, 1877), *S. cudmorei* Philip, 1964, *S. fosteri* Philip, 1964, *S. inermis,* Philip, 1964, *S.* (?) *intricata* Philip, 1964 and *S.* (?) *hispida*. Many specimens from the Nanarup Limestone resemble *T.* (*Stereocidaris*) *cudmorei*, others more closely resemble *T.* (*Stereocidaris*) *fosteri*. Both of these species occur in the middle Eocene Tortachilla Limestone in the St Vincent Basin, South Australia. Variation in the nature of the interambulacral plates in the Nanarup Limestone specimens shows that *T.* (*Stereocidaris*) *fosteri* should be considered a junior synonym of *T.* (*Stereocidaris*) *cudmorei*. Tortachilla Limestone forms of *T.* (*Stereocidaris*) *cudmorei* can possess up to nine interambulacral plates (Philip 1964). Most specimens from the Nanarup Limestone have up to seven, however, large specimens can have nine plates. The very common cidaroid radioles that occur in the Nanarup Limestone can be compared with similar Cenozoic material from other middle Eocene deposits in southern Australia (Philip 1964), particularly *T. (Stereocidaris)* sp. A from the Tortachilla Limestone figured by Philip (1964, pl. LXI, figs 2 and 3).

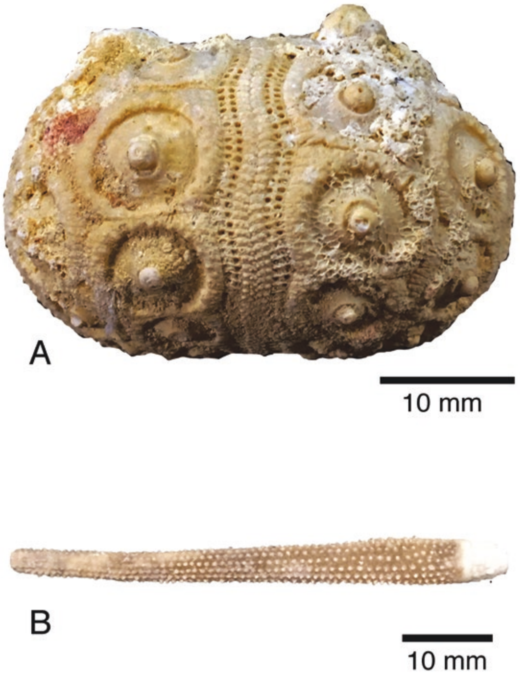

FIGURE 2 A) *Temnocidaris* (*Stereocidaris*) *cudmorei* Philip, 1964, WAM 2022.165 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, incomplete test; B) *Temnocidaris* (*Stereocidaris*) sp., WAM 03.55 from Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone, radiole.

Smith and Wright (1989) referred *T. (Stereocidaris) cudmorei* to the latest Cretaceous to recent genus *Goniocidaris* due to 'test sculpturing identical to that found in *Goniocidaris* and its close relatives' (Smith and Wright, 1989, p. 44), despite preserving a rudimentary upper scrobicule, a feature lacking in *Goniocidaris*. Furthermore, we do not consider that the development of small pits at triple suture points is sufficient to rule out the placement of this species within the subgenus *Stereocidaris*.

Another character that supports this species inclusion in *Stereocidaris*, as Philip (1964) proposed, is the presence of wide pore pairs, and thus wide poriferous zones compared with the overall width of the ambulacra. These are typical *Stereocidaris* traits. In fact, Philip considered that the *Stereocidaris* species generally preserve poriferous zones that are marginally wider or equivalent in width to the interporiferous zones. The possession of wider poriferous than interporiferous zones is present in the Nanarup Limestone specimens — on average the interporiferous zone forms about two-fifths of the ambulacra (range one-third to one-half of ambulacral width).

Smith and Wright (1989) proposed the emplacement of *Stereocidaris* as a subgenus of *Temnocidaris* for all those species in which the uppermost scrobicule is rudimentary, the sculpture mild, and pedicellariae pits confined to the sutures. In addition, the absence of pits scattered amongst the interambulacral miliary tubercles is another characteristic feature of *Stereocidaris.* It should be noted that in their description of the subgenus *Stereocidaris*, Smith and Jeffery (2000, p. 26) consider the ambital and adapical plates need to be 'at least as tall as wide'. This character is present in most plates.

Order Camarodonta Jackson, 1912

Family Trigonocidaridae Mortensen, 1903

Genus *Ortholophus* Duncan, 1887

TYPE SPECIES

Temnechinus lineatus Duncan, 1877, by monotypy.

Ortholophus aff. *bittneri* Philip, 1969

MATERIAL EXAMINED

Fourteen whole or partial tests (WAM 03.26–03.39) from the Nanarup lime quarry, Nanarup Limestone. These are generally well preserved, although all lack the apical system. Two unregistered fragments, which may also belong to this species, are present in the Manypeaks limestone.

REMARKS

Due to the relatively indistinct test sculpturing in the Nanarup Limestone *Ortholophus* specimens, this species can be considered part of Philip's (1969) *O. woodsi* – *O. pulchellus* – *O. lineatus* species group. Philip (1969, p. 253) notes, however, that 'the differences [between species] are based on distinctions in the sculpture, and no fundamental characters permit separation of the species'. In spite of this, the *Ortholophus* species from the Nanarup Limestone differs from the late Miocene *O. lineatus (*Duncan, 1877), the early Miocene *O. venustus* Philip, 1969 and middle Miocene *O. morganensis* Philip, 1969 in possessing narrower ambulacra. It would be expected that the Nanarup Limestone form would be conspecific with the coeval *O. bittneri* Philip, 1969 from the Tortachilla Limestone in South Australia. However, this species often has a pentagonal test and preserves pore pairs sunken within the ornament surrounding the primary ambulacral tubercle. At this stage we prefer to regard the western Eucla Basin form as *Ortholophus* aff. *bittneri*.

Order Salenioida Delage and Hérouard, 1903

Family Saleniidae L. Agassiz, 1838

Genus *Pleurosalenia* Pomel, 1883

TYPE SPECIES

Salenia tertiaria Tate, 1877, by original designation.

Pleurosalenia tertiaria (Tate, 1877)

MATERIAL EXAMINED

Single specimens are known from the Nanarup lime quarry, Nanarup Limestone (WAM 03.29) and the Manypeaks lime quarry, Manypeaks limestone (WAM 94.831).

REMARKS

In addition to its type locality in the Tortachilla Limestone at Aldinga, South Australia (Tate, 1877), this species has also been recorded from the Wilson Bluff Limestone in the eastern Eucla Basin (Philip 1965). Its presence in the Nanarup Limestone and Manypeaks limestone extends its known range to the far western Eucla Basin.

Order Cassiduloida Claus, 1880

Family Cassidulidae L. Agassiz and Desor, 1847

Genus *Eurhodia* Haime
(in d'Archiac and Haime), 1853

TYPE SPECIES

Eurhodia morrisi Haime in d'Archiac and Haime, 1853, by original designation.

Eurhodia westaustraliae sp. nov.

Figure 3

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MATERIAL EXAMINED

Holotype

Australia: *Western Australia*: WAM 07.439 from the middle Eocene (Bartonian) Nanarup Limestone at Nanarup lime quarry.

Paratypes

Australia: *Western Australia*: WAM 07.440 and 07.441 from the same locality and horizon as the holotype.

Other material

Australia: *Western Australia*: One additional, unregistered specimen from the Manypeaks limestone.

DIAGNOSIS

Species of *Eurhodia* with elongate, narrow, low vaulted test; anal furrow narrow, reaching one-third test length and extending to ambitus, indenting ambital outline; periproct dorsal, inclined and longitudinal in furrow; peristome small, narrow, anterior; bourrelets weakly inflated; phyllodes small with eight single pores in each ambulacral column; ventral tubercles coarse; dorsal tubercles uniform and small.

DESCRIPTION

Test elongate, elliptical; maximum length 36.5 mm. Widest part of test at about mid-test, maximum width 66%–68% TL. Anterior two-thirds of test rounded, posterior third tapers and truncated posteriorly. Test not highly inflated; maximum height 35–37% TL at roughly mid-test. No anterior notch. Apical system slightly anterior of mid-test; number of gonopores unknown. Posterior petals relatively long and narrow, not closed distally; anterior petals shorter. Poriferous and interporiferous zones are roughly equal in width; inner pores rounded and outer more elongate. Extra-petal pores present only in anterior ambulacrum. Periproct on aboral surface, set into the test at about 65° to adoral surface; forms an elongate ellipsoid and lies within triangular furrow in test that indents ambitus (Figure 3D); longer than wide (width 43–45% of length); length 10–15% TL.

Peristome small; anterior of mid-test, 37–38% TL from anterior; longer than wide, width being 84–87% of length; length 7–9% TL. Bourrelets weakly swollen, extending slightly across peristome, intruding enough to give peristome a stretched star shape (Figure 3B, E). Phyllodes small, with eight single pores in each row. Plastron extremely reduced and barely raised or distinguishable. Adoral surface concave, both longitudinally and laterally. Aborally, tubercles are developed evenly and uniformly over test surface; small and closely packed; sunken and symmetrical. Adorally,

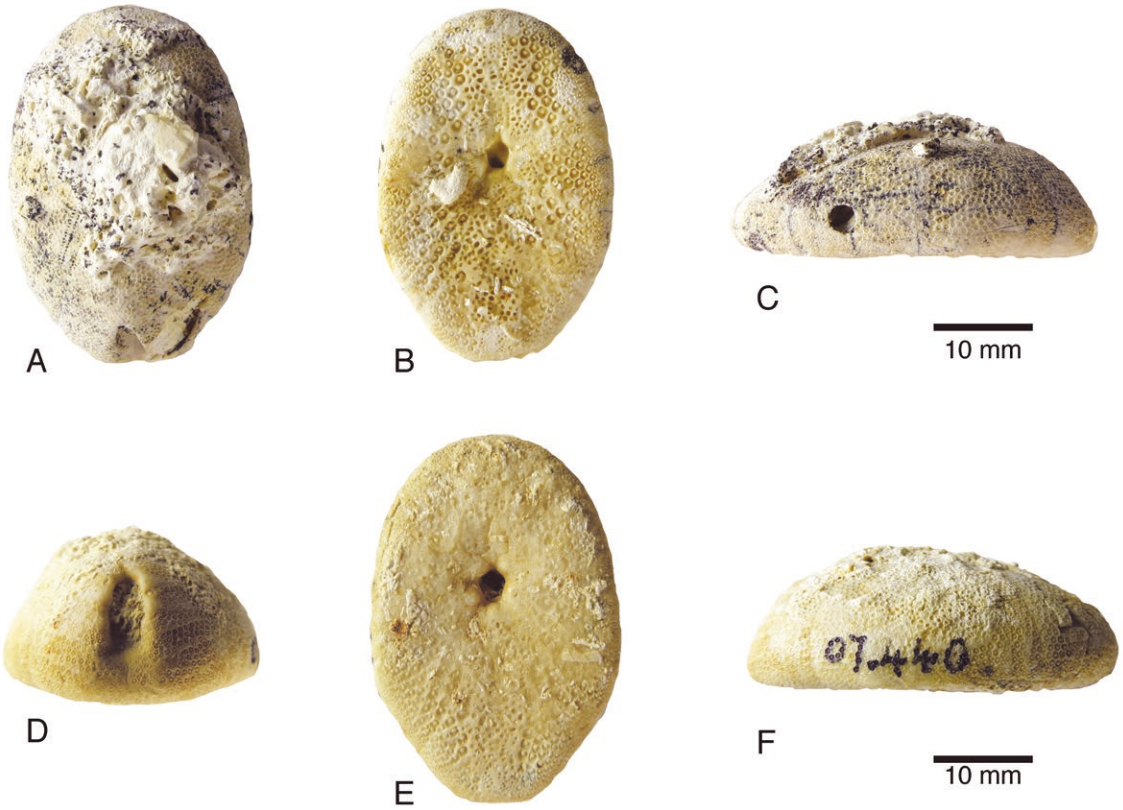

FIGURE 3 *Eurhodia westaustraliae* sp. nov. A–C, holotype WAM 07.439 from the Nanarup lime quarry, middle Eocene (Bartonian) W.A., Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. D–F, paratype WAM 07.440 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: D) posterior; E) adoral; F) right lateral views.

tubercles larger, with aureoles surrounded by a raised rim making them appear inset, and having large boss in relation to areole size (Figure 3B); asymmetrical, indicating a stroke towards posterior of test.

REMARKS

Three morphological features change with increasing test length. The first is a relative decrease in peristome width in relation to its length, and thus a change towards a more equant peristome with increasing test length. The second is a corresponding increase of peristome length in relation to test length, while the last is an increase of periproct length in relation to test length.

Eurhodia westaustraliae differs from *E. australiae* (Duncan, 1877) from the contemporaneous Tortachilla Limestone in a number of features. Most noticeable is the shape of the test, which is much narrower and relatively more elongate in *E. westaustraliae.* On the basis of the measurements given by Duncan (1877, p. 51) for the holotype (NHM GSL 14079), from the Castle Cove Limestone in Cape Otway (Victoria), and two specimens from the Tortachilla Limestone also in the Natural History Museum, London collections (NHM E74558, 74559), the standardised test width for *E. australiae* is 70–75% TL, whereas for *E. westaustraliae* it is 66–68%. Adorally, the peristome is relatively smaller and narrower in *E. westaustraliae*. Similarly, the phyllode is relatively smaller, with only eight single pores in each ambulacral column, compared with 11 in *E. australiae* (http://www.nhm.ac.uk/research-curation/research/projects/echinoid-directory/taxa/specimen.jsp?id=7587).

There are also some differences in the tuberculation. Duncan (1877, p. 51) pointed out that the tuberculation in *Eurhodia* was ‘small everywhere, and smallest in the anal groove’. *E. westaustraliae* has uniform tubercles aborally, but adorally the tubercles are generally much larger and more distinctive. He also described the anal furrow as almost reaching the test vertex, whereas *E. westaustraliae* has an anal furrow that reaches no more than one-third of the way towards the middle of the test. Thirdly, the anal furrow in *Eurhodia australiae*, while reaching below the level of the ambitus, does not affect the ambitus shape. In *E. westaustraliae,* however, the furrow reaches below the ambitus and does affect the shape, creating a small notch.

ETYMOLOGY

With reference to its occurrence on the western side of the Australian continent.

Family Faujasiidae Lambert, 1905

Genus *Australanthus* Bittner, 1892

TYPE SPECIES

Cassidulus longianus Gregory, 1890, by original designation.

EMENDED DIAGNOSIS

Test oval; monobasal apical system with four gonopores; petals open, short, broad with narrow interporiferous tract and widely spaced conjugate poriferous zones with outer pore very elongate, inner rounded. Periproct supramarginal, longitudinal, narrow. Peristome pentagonal. Bourrelets strongly inflated. Phyllodes broad, with few single pores. Interambulacrum V broad and naked adorally.

Australanthus longianus (Gregory, 1890)

Figures 4G–I

Cassidulus longianus Gregory, 1890: 482, plate 13, figures 1–3.

Cassidulus longianus Gregory: Gregory 1892: 275; Tate 1892: 192

Australanthus longianus (Gregory); Bittner 1892: 349–352, plate 3, figure 2; Clark 1946: 375; Mortensen 1948: 222, figure 200a–b; Kier 1962: 151–2, plate 27, figures 1–4; Philip 1970: 183, figures 58B, E.

Procassidulus (Australanthus) longianus (Gregory), Lambert and Thiéry 1921: 363.

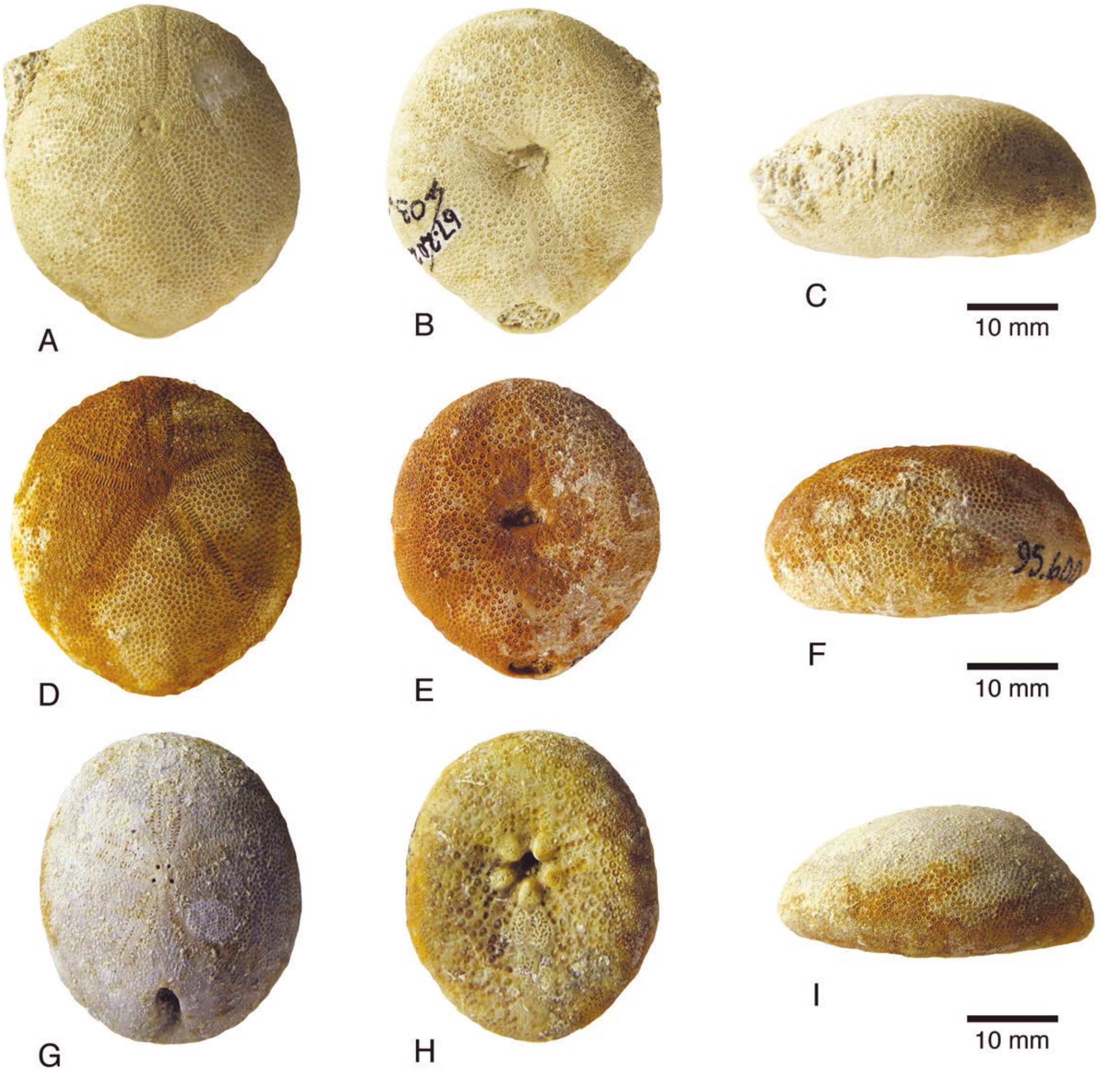

FIGURE 4 *Echinolampas posterocrassa* Gregory (1890). A–C, WAM 03.40 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. D–F, WAM 95.600 from Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone: D) aboral; E) adoral; F) left lateral views. *Australanthus longianus* Gregory (1890). G–I, WAM 03.48 from Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: G) aboral; H) adoral; I) left lateral views.

MATERIAL EXAMINED

Australia: ***Western Australia:*** One whole, 17 partial and four fragmentary specimens (including WAM 03.47–03.49, 07.435–07.438, 72.53 [2]) from the Nanarup lime quarry, Nanarup Limestone. Three incomplete specimens from the Manypeaks lime quarry, Manypeaks limestone (WAM 03.11), none of which preserve dorsal features.

REMARKS

The most common cassiduloid in the Nanarup Limestone is *Australanthus longianus* Gregory, 1890 (Figure 4G–I). Originally described from the Tortachilla Limestone, this species of *Australanthus* possesses a long, narrow, sunken periproct; a strongly demarcated, unornamented strip of plastron; an anal furrow that affects the ambital outline; and a well-developed floscelle (Figure 4H). The bourrelets of the Nanarup Limestone form are slightly less prominent and more rounded than in many topotype specimens, but are still distinct and compare well with Gregory's (1890, pl. 13, fig. 2) figured *A. longianus*.

A lectotype is herein selected for *Australanthus longianus*. The material upon which Gregory based the species was collected in the early 1880s by Harry P. Woodward, then Assistant Government Geologist in South Australia, from 'Willunga', South Australia and sent by him to the then British Museum (Natural History), now the Natural History Museum, where his father, Henry Woodward, was the Keeper of Palaeontology. One of Gregory's described specimens is herein designated as the lectotype of the species, NHM E42428 (Gregory 1890, pl. 13, figs 1, 3) and specimens E42429 (Gregory 1890, pl. 13, fig. 2) and E42430, also used in Gregory's species description, designated as paralectotypes.

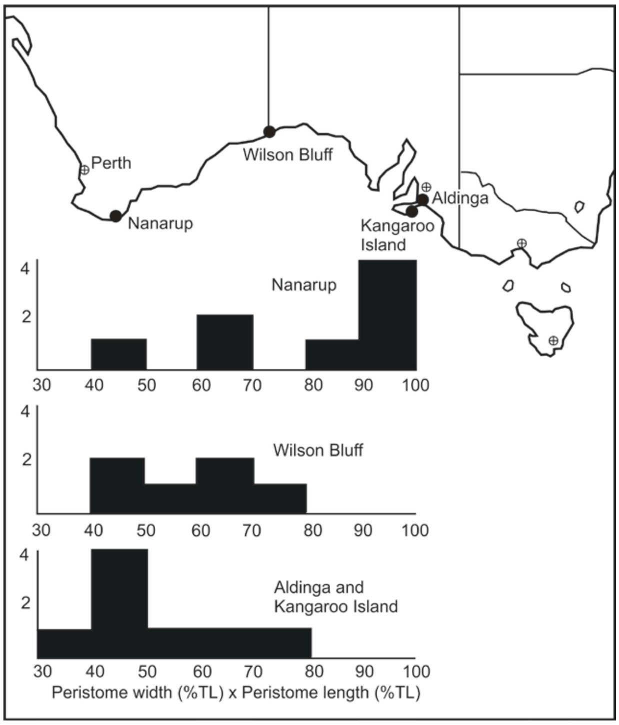

FIGURE 5 Histograms showing peristome shape of *Australanthus longianus* changing along a cline from the western Eucla Basin in Western Australia, east to the St Vincent's Basin in South Australia, showing a progressive widening from east to west.

In addition to occurring in the Tortachilla, Nanarup and Manypeak limestones, *A. longianus* is also present in the contemporaneous Kingscote Limestone on Kangaroo Island, South Australia and in the Wilson Bluff Limestone in Western Australia (Philip 1970, fig. 58B, E). When specimens of the species are compared across its extensive palaeogeographic range of some 2,500 km, there are certain noticeable variations. Specimens are larger in the eastern part of the range. For example, eight specimens from the Kingscote Limestone reach up to 79 mm in test length, compared with 55 mm for the largest from the Nanarup Limestone. There is also a well-developed cline in shape and size of the peristome. In the eastern part of the range the peristome is much narrower, with most specimens having a peristome about half as wide as long. In the geographically intermediate Wilson Bluff Limestone from the Eucla Basin the peristome width is usually more than half the length. However, in the western most part of the range, in the Nanarup and Manypeak limestones, the peristome is almost as wide as long (see Figure 5). Moreover, there is a proportionate increase in peristome size along the cline. However, we consider that it would be unwise to differentiate these forms taxonomically, preferring to regard them as an example of a geographic cline.

Order Echinolampadoida
Kroh and Smith, 2010

Family Echinolampadidae Gray, 1851a

Genus *Echinolampas* Gray, 1825

TYPE SPECIES

Echinanthus ovatus Leske, 1778, by subsequent designation of Pomel (1883).

Echinolampas posterocrassa (Gregory, 1890)

Figures 4A–F

MATERIAL EXAMINED

Australia: ***Western Australia:*** A total of 36 complete and 339 partial specimens from the Nanarup lime quarry, Nanarup Limestone (including WAM 67.202[5], 67.203, 67.204, 67.216[2], 69.256[7], 69.257, 70.184, 70.185, 70.186, 75.44[5], 75.45, 76.89[2], 03.40-03.46, 03.72[18], 03.73[57]). The species also occurs in the Manypeaks limestone in the Manypeaks lime quarry, although it is much rarer, with just one complete (WAM 95.600) and three partial specimens (WAM 95.601, 94.829 and 07.424).

REMARKS

Echinolampas posterocrassa Gregory, 1890 (Figure 4A–F) is by far the most common echinoid in the Nanarup Limestone. This species is also a common component of the Tortachilla Limestone in the St Vincent Basin in South Australia (McNamara and Philip 1980a). Specimens from the Nanarup and Manypeaks limestones compare very closely with the topotype material. As McNamara and Philip (1980a, p. 3) have noted, the only difference between them is that specimens from the Nanarup and Manypeaks limestones have a slightly flatter test. This is not considered sufficient reason to propose yet another species of *Echinolampas*. During its ontogeny the Nanarup Limestone *E. posterocrassa* became less tumid. This is also seen in topotype material, but relative reduction in test height is greater in Nanarup Limestone specimens. Moreover, as the test increases in size the peristome becomes relatively wider, as does the periproct.

Order Clypeasteroida A. Agassiz, 1872

Suborder Clypeasterina A. Agassiz, 1872

Family Fossulasteridae
Philip and Foster, 1971

INCLUDED GENERA

Fossulaster Lambert and Thiéry, 1925 [=*Prowillungaster* Wang, 1994]; *Scutellinoides* Durham, 1955; *Willungaster* Philip and Foster, 1971; *Philipaster* Wang, 1994 [=*Orbispala* Irwin, 1995].

EMENDED DIAGNOSIS

Small, flattened clypeasteroids; apical system with four or five genital pores; periproct supramarginal. Interambulacra discontinuous, not extending onto oral surface; demiplates absent from petaloid ambulacra; petals absent or poorly defined; auricles separate. Oral surface concave; primordial interambulacra greatly reduced; no combed areas; food grooves absent.

REMARKS

When Philip and Foster (1971) first proposed the family Fossulasteridae it was based on three genera: *Fossulaster, Scutellinoides* and *Willungaster*. Since then, three further genera, *Prowillungaster*, *Philipaster* and *Orbispala* have been described (Wang 1994; Irwin 1995). As discussed below, *Prowillungaster* is herein considered to be a junior synonym of *Fossulaster*. *Orbispala* is considered a junior synonym of *Philipaster* (Smith and Kroh 2011). This form, unlike other fossulasterids, does not appear to be marsupiate. Durham (1955, 1966) placed *Scutellinoides* in the Arachnoididae, but Philip and Foster (1971) observed that it lacked pseudocompound plates and so erected the Fossulasteridae to include those genera that possessed separate auricles and simple plates in the petaloid ambulacra.

Irwin (1995) placed *Scutellinoides* in a new family, the Scutellinoididae. He considered that the presence of five gonopores and unique development of radial internal supports, besides the interradial and concentric partitions, formation of multiple minute clustered hydropores and lack of ambulacral petals were grounds for separating *Scutellinoides* from the Fossulasteridae and erecting the Scutellinoididae. However, the differences between *Scutellinoides* and other members of the Fossulasteridae are relatively insignificant and we follow Philip and Foster (1971) in placing it in the Fossulasteridae, considering Scutellinoididae as junior synonym of Fossulasteridae.

Genus *Fossulaster*
Lambert and Thiéry, 1925

Fossulaster Lambert and Thiéry, 1925: 577.

Prowillungaster Wang, 1994: 229. New synonymy.

TYPE SPECIES

Fossulaster halli Lambert and Thiéry, 1925, by original designation.

REMARKS

Wang (1994) was incorrect in saying *Fossulaster* lacks aboral interambulacral plates. They are present and reach the ambitus, as in his *Prowillungaster*. Consequently, there is nothing to justify the retention of *Prowillungaster*. It is herein regarded as a junior subjective synonym of *Fossulaster*.

Fossulaster susae sp. nov.

Figure 6

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM 07.364 from the middle Eocene (Bartonian) Nanarup Limestone at Nanarup lime quarry.

Paratypes

Australia: ***Western Australia:*** WAM 07.330, 07.342, 07.357, 07.358 from the same locality and horizon as the holotype.

Other material

Australia: ***Western Australia:*** WAM 07.320–07.329, 07.331–07.341, 07.343–07.356, 07.359–07.363, 07.365–07.400. In addition to the type material there are eight specimens from the Manypeaks quarry, WAM 94.811[6], 94.833[2]. Of the these, two are essentially complete, while the remaining are partial tests.

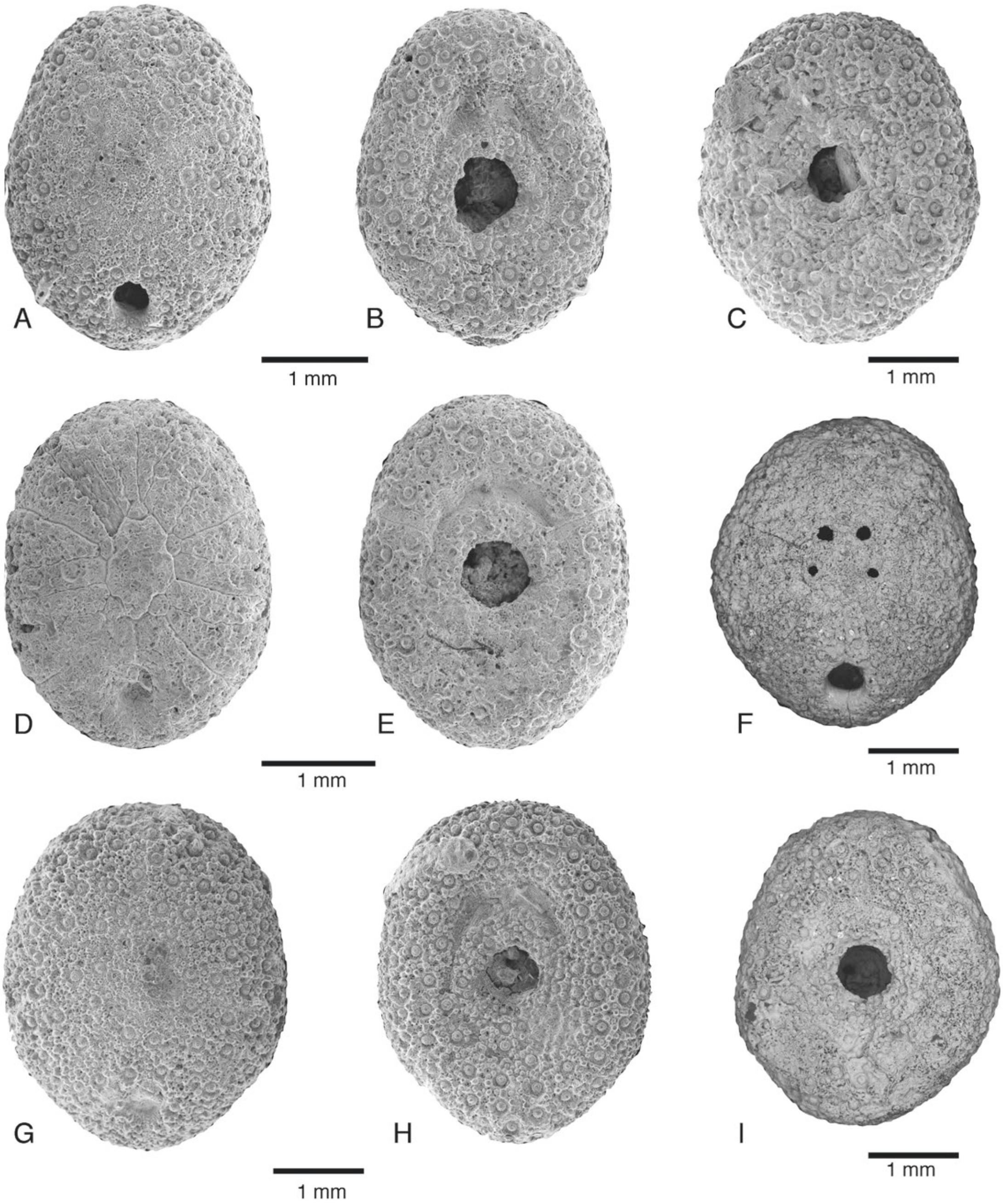

FIGURE 6 *Fossulaster susae* sp. nov. A–B, holotype WAM 07.364 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral views. C, paratype WAM 07.358 from same locality and horizon as holotype: C) adoral view. D–E, paratype WAM 07.342 from same locality and horizon as holotype: D) aboral; E) adoral views. F, I, paratype WAM 07.330 from same locality and horizon as holotype: F) aboral; I) adoral views. G–H, paratype WAM 07.357 from same locality and horizon as holotype: G) aboral; H) adoral views.

DIAGNOSIS

Very small species of *Fossulaster* with elongate, narrow test; shallow, bilobed marsupium; no anterior bulge on aboral surface.

DESCRIPTION

Test very small with a maximum known test length of 5.2 mm; average length 3.19 mm (n=61); rounded to sub-pentagonal in shape. Smallest preserved specimen 1.21 mm long. Test width averaging 82% TL, ranging from 74–92% (n=52); maximum width just posterior of mid-test, averaging 64% TL (n=29); relatively highly vaulted, with the average height just 37% TL, ranging from 39% TL to 54% TL. Aboral surface convex with well-rounded ambitus. Test outline rounded, with posterior slightly narrower than anterior. Aborally, interambulacra tend to be either narrower or equivalent in width to ambulacra (Figure 6D). Apical system on raised, rounded to pentagonal monobasal disc, on which gonopores are situated at edges (Figure 6F); positioned posterior of mid-test, with front of anterior gonopores occurring on average 37% TL from anterior margin. Four gonopores, of which either anterior or posterior pair can be enlarged. However, this enlargement does not occur in all specimens and tends to be more common in larger than smaller individuals. Ambulacral pore pairs not apparent. No visible hydropores are present. Food grooves are lacking.

Peristome anterior of centre of test, averaging 41% TL from anterior (27–50% TL, n=66); generally rounded, but almost pentagonal in some specimens. On average peristome slightly longer than wide, average peristome length being 21% TL (10–49% TL, n=70). Relative size of peristome (both length and width) decreases appreciably as test length increases, with peristome width ranging from 49% TL in small specimens to only 10% TL in larger specimens. Some specimens possess a marsupium (Figure 6B, E, H), which forms around the anterior of rounded peristome, and causes peristome to develop a raised ring. Ventral surface of test concave, with most specimens having an inset peristome.

Periproct on dorsal surface of test near tapered posterior (Figure 6A). Rounded to teardrop shaped, average length and width 11% TL (7–21% TL, n=60). Like peristome, periproct becomes relatively smaller as test length increases. It also migrates closer to test margin with this length increase. On average, periproct lies 27% TL from posterior margin (16–54% TL, n=58). Test covered by a number of tubercles that are very coarse for the test size. These are developed everywhere except on apical disc, including within inset peristome / marsupium.

Sexual dimorphism

Fossulaster susae displays sexual dimorphism, similar to that observed in other species in the genus. As Smith (1984) suggests, it can be assumed that the presence of gonopores in a specimen indicates that the individual had attained sexual maturity. Thus, those well-preserved individuals lacking visible gonopores are considered to be juveniles, whereas those preserving gonopores are adult specimens. Female specimens are generally identified by the presence of a marsupium situated anterior of the peristome. In the largest specimens this marsupium is clearly seen, and develops a low divide, making the depression bilobed, not U-shaped (Figure 6B). In smaller specimens, however, the marsupium is much less developed. There appears to be no fixed size above which juveniles reached maturity, but the transition generally occurred at a test length of between 2.5 mm to 3 mm, with the smallest mature specimen being 2.4 mm, and the largest juvenile 2.8 mm.

Other sexually dimorphic features are apparent in *F. susae.* The width between the anterior gonopores, as a percentage of test length, does differ between genders, as based on the presence or absence of a marsupium, with the anterior gonopores being more widely spaced in forms lacking a marsupium than those with a marsupium. Marsupiate forms generally develop narrower, less rounded tests than non-marsupiate forms. Marsupiate forms also tend to be slightly larger than non-marsupiate forms (average TL of 3.8 mm, compared with 3.5 mm). Non-marsupiate specimens tend to be slightly higher vaulted than marsupiate forms (average test height 33.4% TL, compared with 37.0% TL). Marsupiates are slightly more common than non-marsupiates, 59% compared with 41% male (n=51).

In most sexually dimorphic echinoids, individuals with larger gonopores are considered to be female (Smith, 1984; Néraudeau 1993). Surprisingly, in *F. susae* there appears to be little positive relationship between the size of the anterior gonopores and the presence of a marsupium, as large gonopores can be found on specimens both with and without a marsupium (Figure 6F, I). This could indicate that, if indeed specimens with large gonopores are accepted as being female, then they failed to develop a marsupium. Frequently, individuals with very small gonopores, generally accepted as being males, possess a marsupium (see Figure 6A–B). This raises the intriguing possibility that in some of these earliest known brooding echinoids, the young may actually have been brooded by males.

REMARKS

The nature of preservation at Nanarup, where there has been some recrystallization, does not encourage the preservation of visible plate structure, leading to difficulties in determining some important test features. Although few plating structures are visible, the ambulacra appear to pass the ambitus and continue onto the ventral side, indicating that these specimens belong to *Fossulaster*, not *Willungaster*. The coarse, oversized tubercles and more elongate shape of *Fossulaster* also support this inference. However, the shallow marsupium is more like *Willungaster*, and quite different from the deep, distinctive marsupia seen in the other *Fossulaster* species (see Philip and Foster, 1971).

Of the three known species of *Fossulaster*, *F. exiguus* Philip and Foster 1971, from the early Miocene Melton Limestone of the St Vincent Basin, is the closest in size (less than 8 mm), but develops a U-shaped, not bilobed marsupium. *F. halli* Lambert and Thiéry 1925, from the Oligocene to early Miocene horizons of the Gambier (west Otway Basin) and Port Vincent (St Vincent Basin) Limestones, is the largest of the species with a test length up to 10 mm. Although it develops a bilobed marsupium like the Nanarup *Fossulaster*, the female specimens also develop an anterior dorsal bulge that is not seen in this smaller species. An undescribed form from the Oligocene to early Miocene Gambier Limestone of the west Otway Basin (P. Irwin pers. com.), also has a bilobed marsupium, grew up to 8.7 mm in length and has gonopores occurring peripheral on the apical disc. However, it has juveniles in which the periproct is more marginal than in *F. susae* and it too has an anterior dorsal bulge in the females. The lengths at the onset of maturity for the species are *F. halli* – 6.5 mm, *F. exiguus* – 4.5 mm, *Fossulaster* sp. (Gambier Limestone) – 5.5 mm and *F. susae* – 2.5–3.0 mm. *F. susae* is late middle Eocene in age, whereas the other species range in age from the early Oligocene to Miocene. As such, *Fossulaster susae* represents the earliest known species of *Fossulaster*.

The presence of *Fossulaster susae* was first recorded by McNamara (1994a) who documented the occurrence of this, the first known marsupiate species in the Australian Cenozoic, in the middle Eocene Bartonian Stage (planktonic foraminiferal zones 14–15). Clypeasteroids do not appear in the eastern Australian Cenozoic sedimentary basins until the latest Oligocene/early Miocene, in the form of species of *Monostychia* (Sadler et al. 2016). None occur in the coeval Tortachilla Limestone, with which the Nanarup Limestone shares many species in common. However, one middle Eocene clypeasteroid has been recorded in the Giralia Calcarenite in the Carnarvon Basin in north-west Australia, an undescribed species of *Monostychia* (McNamara 1999). This is of similar age to the middle Eocene new species of *Fossulaster* in the Nararup Limestone and Manypeaks limstone described herein.

Fossulaster susae is one of the smallest known marsupiate echinoids, reaching a maximum known test length of just 5.2 mm, being exceeded only by the living *Fibularia nutriens*, which grows to no more than 3.3 mm in length (Mortensen 1948).

ETYMOLOGY

Named after Sue Radford in recognition of her assistance over many years not only in helping to collect the Nanarup Limestone echinoid fauna, but also in collecting many other fossil specimens now housed in the Western Australian Museum.

Order Spatangoida Claus, 1876

Suborder Micrasterina Fischer in Moore, 1966

Family Micrasteridae Lambert, 1920

Genus *Cyclaster* Cotteau in Leymerie and Cotteau, 1856

TYPE SPECIES

Cyclaster declivus Cotteau in Leymerie and Cotteau, 1856, by original designation.

Cyclaster jamiei sp. nov.

Figure 7

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia:*** WAM 03.12 from the middle Eocene (Bartonian) Manypeaks limestone in the Manypeaks lime quarry.

Paratypes

Australia: ***Western Australia:*** WAM 07.425, 07.432, 07.433 from the middle Eocene (Bartonian) Nanarup Limestone at Nanarup lime quarry.

Other material

Australia: ***Western Australia:*** WAM 89.1235 from the middle Eocene (Bartonian) Giralia Calcarenite, Giralia Range, W.A. WAM 76.16, from the late Eocene (Priabonian) Pallinup Formation.

DIAGNOSIS

Species of *Cyclaster* with elongate, tapering, inflated test; anterior notch absent; no peripetalous fasciole; short, open, weakly bowed petals; elongate pore pairs; small, longitudinal, marginal periproct; anteriorly placed, small, transverse peristome with distinct labrum.

DESCRIPTION

Test up to 41 mm in length, with maximum width about 87% TL; greatest at anterior of test; maximum test height 72% TL developed mid-test, posterior of apical system; rounded anterior, tapering rapidly to an almost truncate posterior. No anterior notch. Well-developed keel runs from behind apical system posteriorly through interambulacrum 5. Apical system slightly sunken; anterior of mid-test, about 40% TL from anterior; three gonopores; ethmophract, with genital plates 1, 3 and 4 meeting mutually; genital plate 2 small and in contact with genital plates 1 and 4. Genital plate 2 with a number of hydropores, sparsely distributed, but lacking gonopore. Petals slightly sunken. Posterior pair slightly shorter than anterior pair, being about 21% TL; open distally; slightly shallower than anterior petals; anterior petals 22% TL. Pore pairs generally elongate. About 20 pore pairs in each anterior row in each petal. Ambulacrum III as sunken as anterior petals (Figure 7A); pore pairs widely spaced, strongly oblique with weak interporal partition. Peripetalous fasciole absent. Distinct subanal fasciole; reniform and relatively narrow, 37% TL; fasciole relatively broad, 3% TL.

Peristome small, wider than long, semicircular; length 68% of width; width about 11% TL; completely encircled by narrow, raised ridge (Figure 7E). Anterior of peristome lies close to test anterior, at around 22% TL. Labrum is extremely long and thin, parallel-sided, about 20% TL. Not anteriorly projecting. Ambulacrum III weakly sunken adorally. Pores in phyllode with prominent interporal partitions. Periproct high on inflated, truncated posterior; small and roughly tear-shaped (Figure 7F). Slightly longer than wide (width 87% of length), length about 10% TL. Plastron weakly developed.

Tubercles on aboral surface uniformly small, but evenly distributed, while adoral interambulacral tubercles are larger and sparser. Small granules surround all larger ‘primary’ tubercles, thus no surfaces densely tuberculated. All areoles symmetrical. Aboral tubercles restricted to interambulacra and are so dense that plating arrangements in these areas generally obscured.

FIGURE 7 *Cyclaster jamiei* sp. nov. A–C, F, holotype WAM 03.12 from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone: A) aboral; B) adoral; C) right lateral; F) posterior views. D) WAM 89.1235 from the middle Eocene Giralia Calcarenite, Giralia Range, W.A., aboral view. E) paratype WAM 07.425 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, adoral view.

Intrapetalous zones clear of primary tubercles. Posterior adoral ambulacra lack primary tubercles and ornamented only by dense granules. Plastron with large, densely packed tubercles, not interspersed with granules, with asymmetrical areoles indicating a sediment movement inwards and towards posterior.

REMARKS

As McNamara (1999) has previously reported, the same species of *Cyclaster* that occurs in the Nanarup and Manypeaks limestones, i.e., *Cyclaster jamiei*, also occurs in the middle Eocene of the Carnarvon Basin, where it is present in the Giralia Calcarenite (Figure 7D). Here it occurs in slightly older strata than the Nanarup Limestone, being, upper Zone P12 in age (Haig et al. 1997). *C. jamiei* has a more elongate, narrower, test than *C. archeri* (Tenison Woods, 1867), which is from the late Oligocene to middle Miocene Morgan Limestone, Gambier Limestone and Port Willunga Formation of the Murray and St Vincent Basins (McNamara *et al.* 1986, fig. 9). Its test width is 87% TL, compared with 89–99% TL in *C. archeri*. More notably, *C. jamiei* lacks a peripetalous fasciole. Smith and Kroh (2011) have noted that this fasciole may be complete, partial or completely absent in *Cyclaster*. *C. jamiei* has less bowed anterior petals than *C. archeri*. While both species possess an ethmophract apical system, *C. archeri* has a more elongate genital plate 2, and has this plate in contact with all other genital plates (genitals 1 and 3 do not touch). In *C. jamiei,* however, genital 2 is only in contact with genital plates 1 and 3, and lies outside the mutual ring formed by the gonopore-bearing plates.

Cyclaster jamiei differs from the type species, *C. declivus* Cotteau, 1856 from the Eocene of France, by its narrower, more tapering test; lack of peripetalous fasciole in adults; more anteriorly positioned apical system; and shorter, shallower petals. *C. jamiei* also shares some similarities to a number of European *Cyclaster* species from the Cretaceous and Paleocene. In particular, it shares its lack of peripetalous fasciole with *C. aturicus* (Seunes, 1888), *C. suecicus* (Schlüter, 1897) and *C. ruegensis* (Kutscher, 1978) (Smith and Jeffery, 2000), but differs from them in lacking a prominent anterior notch and in the form of the petals.

ETYMOLOGY

Named after Jamie McNamara in recognition of his assistance in helping to collect the Nanarup Limestone echinoids and for collecting many specimens now housed in the Western Australian Museum.

Genus ?*Isaster* Desor, 1858

TYPE SPECIES

Isaster aquitanicus Desor, 1858, by original designation.

?*Isaster* sp.

MATERIAL EXAMINED

Australia: ***Western Australia:*** Two incomplete specimens, WAM 94.1340 and 03.52 from the Nanarup lime quarry, Nanarup Limestone.

REMARKS

These two specimens share features reminiscent of *Isaster*, a Maastrichtian to Paleocene micrasterid that has previously been recorded from Kazakhstan, Ukraine, Turkey and Spain. Like *Isaster*, the Nanarup Limestone specimens have an ovate, domed test without an anterior sulcus; short, weakly developed petals; periproct on a truncate posterior margin and no peripetalous or lateroanal fascioles. They differ from described species of *Isaster* in possibly having a subanal fasciole, although this is not completely certain. The presence of *Isaster* in the Eucla Basin, if confirmed, would greatly extend the geographic range of this genus to the eastern Tethys and the stratigraphic range to the Eocene. Superficially the Nanarup Limestone specimens resemble *Prenaster aldingensis* Hall, 1906 from the Tortachilla Limestone and the slightly younger Pallinup Formation. However, unlike ?*Isaster* sp., this species possesses both a peripetalous and lateroanal fasciole (Hall 1906, pl. 13, figs 3–4).

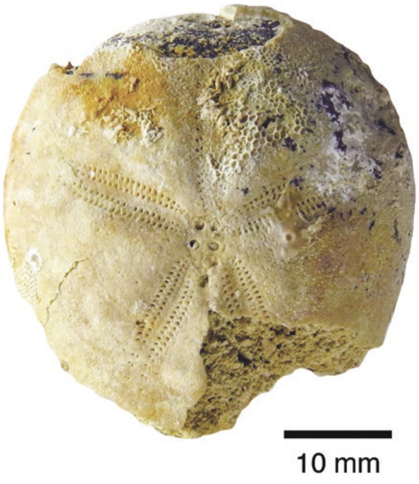

FIGURE 8 Micrasterid indet., WAM 07.431 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view.

Micrasterid indet.

Figure 8

MATERIAL EXAMINED

Australia: ***Western Australia:*** WAM 07.431 from the middle Eocene (Bartonian) Nanarup Limestone, Nanarup lime quarry.

REMARKS

This specimen cannot be assigned to any genus with confidence. Its main characteristics are the possession of four gonopores, an ethmophract apical system, relatively long anterior petals of similar length to the posterior petals, both of which are slightly sunken; it lacks a peripetalous or lateroanal fasciole. It is superficially similar to the Upper Cretaceous to Danian genus *Plesiaster* and also the Paleocene *Pseudogibbaster* and Upper Cretaceous genus *Gibbaster*. Even though it is too incomplete to assign to any of these genera with any degree of certainty, it would seem to be a micrasterid that has lingered deep into the Eocene.

Family Hemiasteridae H.L. Clark, 1917

Genus *Bolbaster* Pomel, 1869

TYPE SPECIES

Spatangus prunella Lamarck, 1816, by original designation.

Bolbaster subidus McNamara, 1987

Figure 9D–F

MATERIAL EXAMINED

Australia: ***Western Australia:*** WAM 03.50 and 03.51 from the Nanarup lime quarry, Nanarup Limestone.

REMARKS

Two relatively well-preserved specimens are both morphologically identical to the type material of the relatively uncommon *Bolbaster subidus* McNamara, 1987 that was described from the contemporaneous Tortachilla Limestone in South Australia. A poorly preserved internal mould of a specimen from the Pallinup Formation in the western Eucla Basin questioningly referred to *Hemiaster* by Martin and McNamara (2004) may also be this species.

Family Schizasteridae Lambert, 1905

Genus *Schizaster* L. Agassiz, 1836

Subgenus *Paraster* Pomel, 1869

TYPE SPECIES

Schizaster gibberulus L. Agassiz, 1847, by original designation.

Schizaster* (*Paraster*) cf. *tatei
McNamara and Philip 1980b

MATERIAL EXAMINED

Australia: ***Western Australia:*** a single, incomplete specimen, WAM 07.430, from the Nanarup lime quarry, Nanarup Limestone.

REMARKS

Schizaster (*Paraster*) *tatei* McNamara and Philip, 1980b is a relatively common spatangoid in the Bartonian Tortachilla Limestone in South Australia. The only known specimen from the Nanarup Limstone has a large amount of bryozoal and foraminiferal debris adhering to the aboral surface of the test surface making it difficult to ascertain morphological details clearly. The adoral surface is not preserved. The position of the apical system, the lengths and the depths of the petals are reminiscent of the contemporaneous Tortachilla Limestone species and thus it is herein regarded as *S.* (*Paraster*) cf. *tatei*. An internal mould of a specimen from the Pallinup Formation has likewise been referred to *S.* (*Paraster*) cf. *tatei* (Martin and McNamara 2004).

Genus *Protenaster* Pomel, 1883

TYPE SPECIES

Desoria australis Gray, 1851b, by original designation.

Protenaster preaustralis
McNamara, 1985a

Figure 9A–C

MATERIAL EXAMINED

Australia: ***Western Australia:*** WAM 03.53 from the Nanarup lime quary, Nanarup Limestone.

REMARKS

This species is the oldest known of the genus. It was described from the Tortachilla Limestone in South Australia on the basis of five specimens (McNamara 1985a). A single specimen is also known from the Wilson Bluff Limestone (McNamara 1985a). The Nanarup Limestone specimen shows slight morphological differences from the previously described material, but this is likely due to ontogenetic differences, as the Nanarup specimen is much smaller than the smallest known topotype specimen, being only 20 mm in length. Topotype material reaches up to 53 mm in length (McNamara 1985a). The anterior notch is particularly faint compared with topotype material (Figure 9A–B), and in this regard is comparable with the living *Protenaster australis* (Gray, 1851b), in which the anterior notch is very faint in juveniles, but deepens significantly during ontogeny (McNamara 1985a). Although very small, the Nanarup specimen of *P. preaustralis* is a young adult, the gonopores being

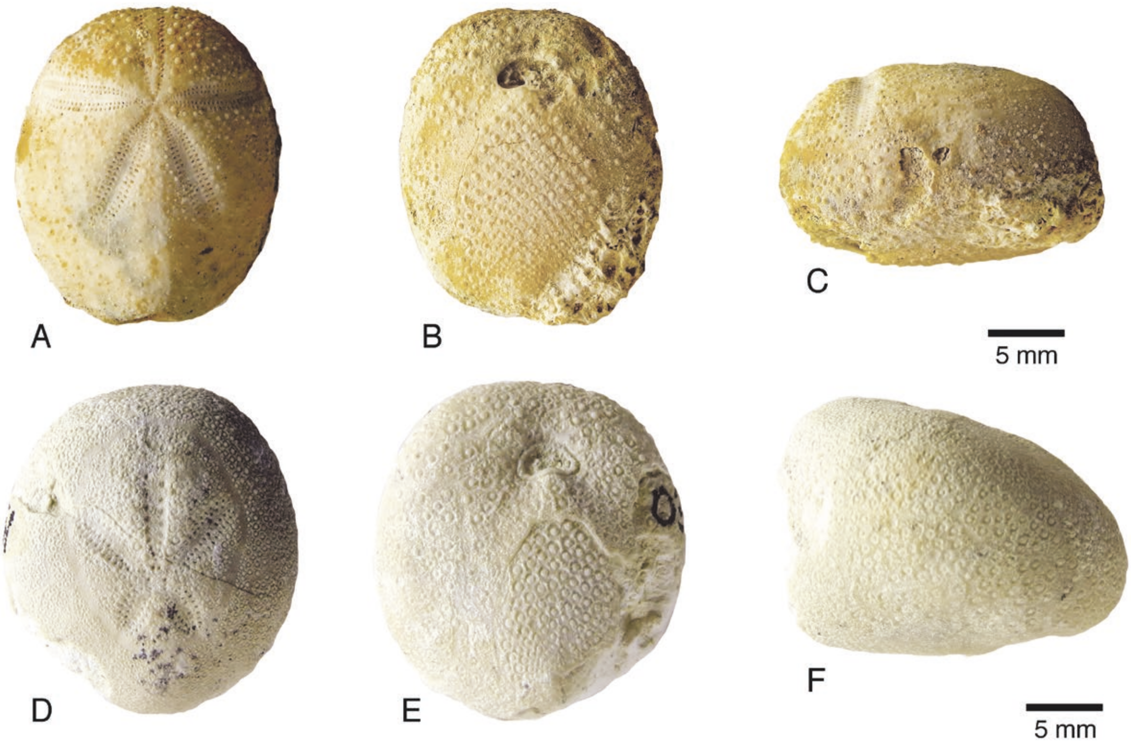

FIGURE 9 *Protenaster preaustralis* McNamara, 1985. A–C, WAM 03.53 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: A) aboral; B) adoral; C) left lateral views. *Bolbaster subidus* McNamara, 1987. D–F, WAM 03.51 from Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone: D) aboral; E) adoral; F) right lateral views.

present. Like the smallest specimen of the living *P. australis* (McNamara 1985a, pl. 32, figs 1–4), the posterior petals are relatively short, being 83% the length of the anterior petals. In the largest specimens of *P. preaustralis* the posterior petals are only slightly smaller than the anterior petals (McNamara 1985a, pl. 33, figs 6–8).

Family Maretiidae Lambert, 1905

REMARKS

Smith and Kroh (2011) suggested that a number of taxa previously included within the Brissidae, and possessing an elongate labral plate and short petals, should not be included within the Brissidae, as genera included within this family typically possess short, wide labral plates. Although they considered that these forms (including *Gillechinus*) could well represent a distinct clade, they prefer to leave them in open nomenclature. Here we consider *Gillechinus* is best placed in the Maretiidae as it possesses reduced pores in anterior ambulacral rows aborally, narrow ambulacra ambitally, relatively elongate wedge-shaped labrum and shield-shaped subanal fasciole.

Genus *Gillechinus* Fell, 1964

TYPE SPECIES

Gillechinus cudmorei Fell, 1964, by original designation.

Gillechinus kaitae sp. nov.

Figure 10

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MATERIAL EXAMINED

Holotype

Australia: Western Australia: WAM, 03.13 from the middle Eocene (Bartonian) Manypeaks limestone, Manypeaks lime quarry.

Paratypes

Australia: Western Australia: WAM 07.422a, 07.422b and 07.423 from the same horizon and locality as the holotype; WAM 68.1357 and 07.444 from the middle Eocene (Bartonian) Nanarup Limestone, Nanarup lime quarry.

Other material

Australia: Western Australia: WAM 68.1357, 92.226, 94.824–94.829, 94.830[4], 07.422, 07.423 from the same horizon and locality as the holotype; WAM 07.434[6] from the Nanarup Limestone, Nanarup lime quarry and WAM 76.16 from the Pallinup Siltstone.

DIAGNOSIS

Paired petals very shallow and short, about one-quarter test length; posterior slightly longer than anterior. Anterior notch very weak. Aboral interambulacra with few primary tubercles. Peristome relatively long and narrow, with labrum not anteriorly protuberant.

DESCRIPTION

Test heart-shaped; up to about 65 mm in length; maximum width varies between 90% and 94% TL at a point roughly 40% from posterior; maximum height varying between 54% and 57% TL, at 35% to 38% TL from posterior. Very weak anterior notch (Figure 10A); posterior of test sharply truncated. Apical system slightly sunken; four gonopores, each ringed by a smooth, raised ridge (Figure 10E). Posterior gonopores tilted and raised to sit above anterior pair. Apical system situated in anterior part of test, at about 35% TL (TL=60.6 mm) and 39% TL (TL=35.5 mm), indicating a shift to anterior with increasing test length. Petals slightly sunken; parallel-sided; open and slightly curved distally; narrow, with very narrow interporiferous zones less than pore pair width; weakly conjugate pores. Posterior petals slightly longer than anterior petals. Anterior petals 26–28% TL; posterior petals 26–32% TL; each with about 20 pore pairs in each row. Ambulacrum III is even less sunken than petals; pore pairs very small, aligned almost exsagittally, with prominent interporal partition. Peripetalous fasciole very thin, thread-like (Figure 11), about 1% TL; not indented between petals; discontinuous across ambulacrum III. Subanal fasciole crescent-shaped, enclosing four or five small pore pairs in ambulacrum I and in ambulacrum V.

Peristome semicircular; wider than long, with length about 60% width; width 13% TL. Periproct lies on truncated posterior surface; almost circular; 13–15% TL. Plastron prominent; triangular, about 30% TL at its widest point above subanal fasciole (28–32% TL). Covered by large tubercles, indicating sediment movement inwards and towards posterior. Labrum broad anteriorly, evenly tapering posteriorly to third adjacent ambulacral plate; 15% TL in length. A keel present extending from behind labrum to posterior, reaching its apex just anterior of subanal fasciole, 58% of distance from posterior of peristome to posterior of test (Figure 10B). Adoral ambulacral zones are extremely wide and featureless, save for a phyllode of single pores, each ambulacrum containing two rows of straight rows of pores.

Aborally, large primary tubercles only occur on posterior series of interambulacral plates and none occur outside peripetalous fasciole. These have bosses that extend well above test surface and aureoles that are not inset and are symmetrical. Numbers vary with size, with the smallest specimen at 35.5 mm TL having about five tubercles in each anterior, and six tubercles in each posterior paired interambulacrum. Largest specimen of about 65 mm TL has no more than 11 tubercles in each interambulacrum. These primary tubercles randomly

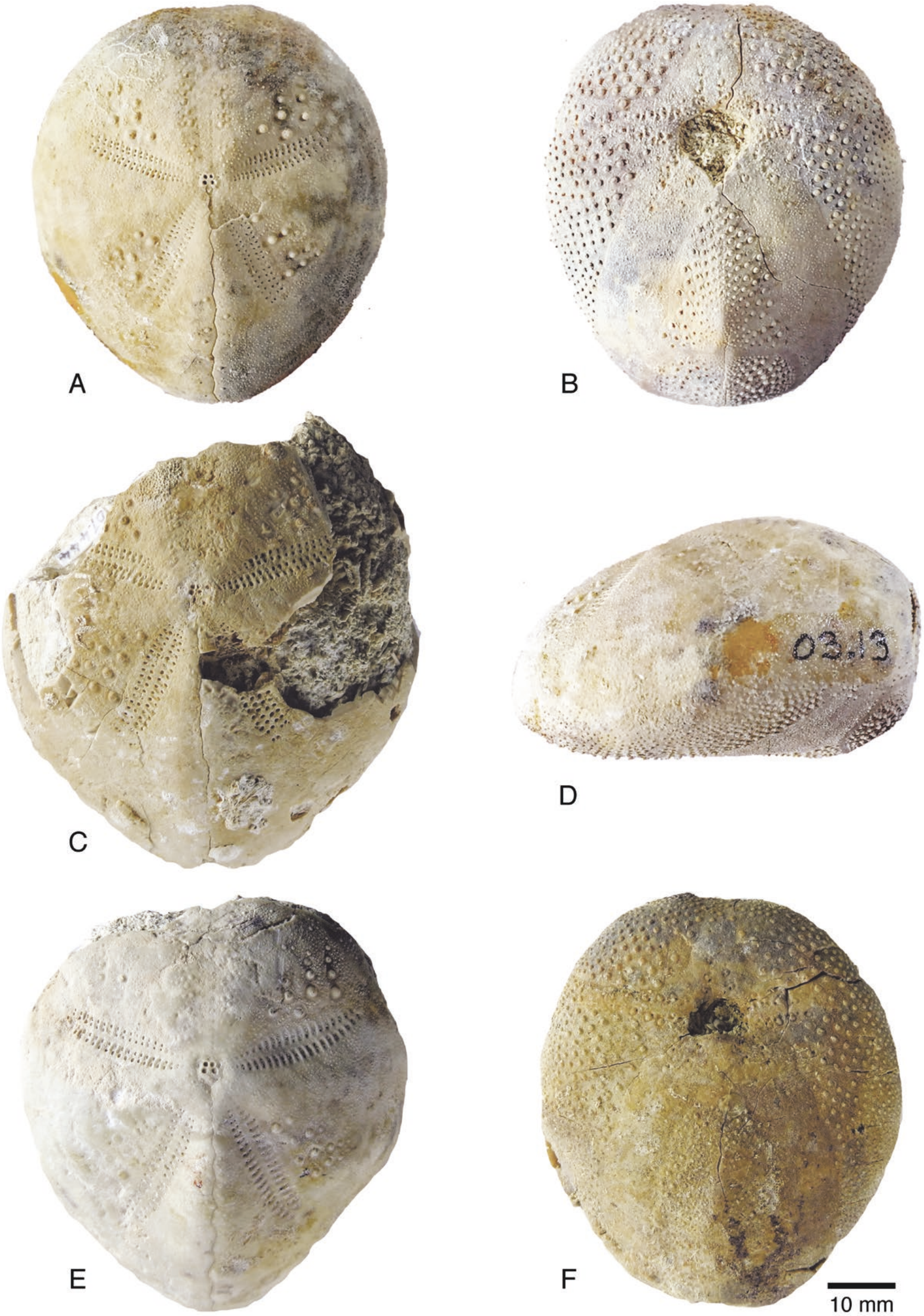

FIGURE 10 *Gillechinus kaitae* sp. nov. A–B, D, holotype WAM 03.13 from the Manypeaks lime quarry, middle Eocene (Bartonian) W.A., Manypeaks limestone: A) aboral; B) adoral; D) left lateral views. C) paratype WAM 07.444 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view. E) paratype WAM 68.1357 from the Nanarup lime quarry, W.A., middle Eocene (Bartonian) Nanarup Limestone, aboral view. F) paratype WAM 07.422a from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone, adoral view.

arranged on obliquely aligned tubercular surface. Smaller tubercles present along dorsal keel. Adorally, tubercles on interambulacral plates are smaller and more densely arranged, similar in arrangement to the plastron. In all interambulacra, asymmetrical aureoles indicate sediment movement away from peristome — that is, posteriorly and laterally for interambulacra 1 and 4, and anteriorly and laterally for interambulacra 2 and 3.

ETYMOLOGY

Named after Kaitie McNamara in recognition of her assistance in helping to collect the Nanarup Limestone echinoids and for collecting many specimens now housed in the Western Australian Museum.

REMARKS

The genus *Gillechinus* was erected by Fell (1964) on the basis of material from the Tortachilla Limestone, which he named *G. cudmorei* Fell, 1964. It has been reported from the middle Eocene Tortachilla and Kingscote limestones of the St. Vincent Basin; middle Eocene Wilson Bluff Limestone and late Oligocene-early Miocene Abrakurrie Limestone of the Eucla Basin; and from the late Eocene Pallinup Formation in the western Eucla Basin (McNamara et al. 1986). However, *Gillechinus kaitae*, described herein from the Nanarup and Manypeaks limestones, differs from *G. cudmorei*, in a number of significant ways.

The most notable difference is the possession of fewer aboral primary interambulacral tubercles in the new species. Small specimens (between 35 and 45 mm in test length) of both species from the Tortachilla, Nanarup and Manypeaks limestones all have a similar number of tubercles (between 1 and 7) in each interambulacrum. However, whereas large specimens (about 60 mm test length) of *G. cudmorei* from the Tortachilla Limestone have up to 36 tubercles (McNamara et al. 1986, fig. 11C), comparable-sized specimens of *G. kaitae* from the Nanarup Limestone have less than a third of this, with a maximum known 11. The Pallinup Formation *Gillechinus* species originally assigned to *G. cudmorei* is herein also considered to be *G. kaitae*.

Gillechinus kaitae can further be distinguished from *G. cudmorei* by its shallower paired petals, which are also significantly shorter, the anterior pair being 26–28% TL in the former species compared with 36–38% TL in the latter. Similarly, the posterior petals are significantly shorter in *G. kaitae*, 28–32% TL, compared with 34–35% TL. Ambulacrum III is extremely shallow in *G. kaitae*, as is the anterior notch, unlike *G. cudmorei*. Moreover, the peristome is longer and narrower, as the labrum does not project anteriorly. The apex of the plastronal keel is also located more anteriorly in *G. kaitae*.

A specimen figured by Smith and Kroh (2011) from the Wilson Bluff Limestone in the eastern Eucla Basin (Museum of Victoria specimen P149924) and called by them *G. cudmorei*, has all the attributes of *G. kaitae*, to which species it should be assigned. This demonstrates that this species was relatively widely distributed across the Eucla Basin during the Bartonian Tortachilla Transgression.

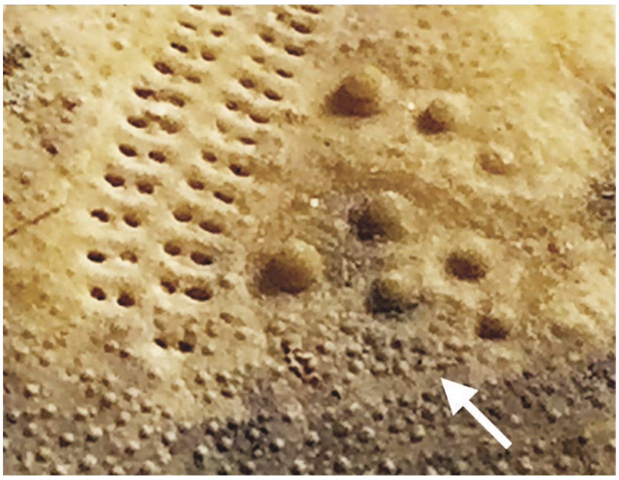

FIGURE 11 *Gillechinus kaitae* sp. nov., WAM 03.13, holotype, from the Manypeaks lime quarry, middle Eocene (Bartonian) W.A., Manypeaks limestone; oblique posterolateral aboral closeup, showing thin peripetalous fasciole (arrowed) skirting interambulacrum 4 and ambulacrum V.

Gillechinus kaitae can be distinguished from *G. sindensis* (Duncan and Sladen, 1884) from the Eocene of the Sind region of Pakistan by its broader test, shallower petals, ambulacrum III and anterior notch and more centrally located apical system. *G. alabamensis* (Cooke, 1942) from the Eocene of the south-eastern USA has even fewer aboral primary interambulacral tubercles, deeper, longer petals and more prominent labrum.

EUCLA BASIN MIDDLE-LATE EOCENE ECHINOID BIOFACIES

NANARUP AND MANYPEAKS LIMESTONES

In terms of numbers of specimens, the echinoid fauna of the Nanarup Limestone is dominated by *Echinolampas, Fossulaster* and *Temnocidaris (Stereocidaris)* (Table 1). The cassiduloid *Echinolampas* is overwhelmingly dominant, comprising almost 70% of the specimens recovered (excluding cidaroids, because of their invariably incomplete preservation). The next most abundant taxon, *Fossulaster*, comprises 17% of the specimens collected. Other taxa comprise less than 10% each (Table 2). In contrast, the Manypeaks limestone is dominated by the spatangoid *Gillechinus*, with *Fossulaster* comprising 20% of the specimens collected (n=40).

The transition from the coarser Nanarup grainstone biofacies to the more silty Manypeaks biofacies probably represents a bathymetric transition from shallower, middle shelf facies to deeper water, outer shelf facies (Boreen and James 1995). The most notable change in the biofacies is the transition from a cassiduloid/clypeasteroid-dominated Nanarup biofacies to a spatangoid-dominated Manypeaks biofacies.

The percentage of the cassiduloid *Echinolampas* in the assemblages differs markedly, from 69% in the Nanarup biofacies to 12% in the Manypeak biofacies, while the spatangoid *Gillechinus* represents just 5% of the Nanarup biofacies, compared with 47.5% of the Manypeaks biofacies (Table 2). However, despite the increase in overall spatangoid numerical diversity in the Manypeaks biofacies, species diversity is different. *Protenaster*, ?*Isaster* and *Bolbaster*, although rare elements in the Nanarup biofacies, are not present in the Manypeaks limestone; while *Gillechinus, Cyclaster, Eurhodia, Pleurosalenia, Ortholophus* and *Australanthus* become relatively a little more common.

McNamara (1993) recorded a similar pattern in late Oligocene limestones in the Torquay Basin. Here the coarse bryozoal grainstones of the Point Addis Limestone are dominated by cassiduloids and clypeasteroids. The finer-grained Waurn Ponds Limestone, however, is dominated by spatangoids (about 70% of species and specimens). The cassiduloid/

TABLE 1 Numbers of specimens of middle Eocene echinoids from the Nanarup Limestone and Manypeaks limestone, western Eucla Basin, W.A., including the nature of preservation, where ‘whole’ specimens are those with more than half the test preserved, ‘partial’ specimens preserve around half the test, and ‘fragments’ preserve less than half the test surface.

A) Nanarup Limestone species	Specimens	Whole	Partial	Fragments
Temnocidaris (*Stereocidaris*) *cudmorei*	72	0	72	??
Ortholophus aff. *bittneri*	14	4	10	0
Pleurosalenia tertiaria	1	1	0	0
Echinolampas posterocrassa	380	37	343	0
Australanthus longianus	22	1	17	4
Eurhodia westaustraliae	3	0	3	0
Fossulaster susae	96	39	53	4
?*Isaster* sp.	1	0	1	0
Protenaster preaustralis	1	1	0	0
Schizaster (*Paraster*) cf. *tatei*	1	1	0	0
Bolbaster subidus	2	1	1	0
Gillechinus kaitae	28	0	14	14
Cyclaster jamiei	3	0	3	0
Micrasterid indet.	1	0	1	0
Total (excluding cidaroid spines)	**627**	**86**	**519**	**22**

B) Manypeaks limestone species	Specimens	Whole	Partial	Fragments
Temnocidaris (*Stereocidaris*) *cudmorei*	2	0	2	0
Ortholophus aff. *bittneri*	2	0	0	2
Pleurosalenia tertiaria	1	1	0	0
Echinolampas posterocrassa	5	2	3	0
Australanthus longianus	3	0	1	2
Eurhodia westaustraliae	1	1	0	0
Fossulaster susae	8	4	4	0
Cyclaster jamiei	1	0	1	0
Gillechinus kaitae	19	4	8	7
Total (excluding cidaroid spines)	**42**	**12**	**19**	**11**

clypeasteroid and spatangoid biofacies form a dominance continuum, paralleling the transition from coarser to finer-grained sediments in shelf transects from the higher hydrodynamic energy of the inner mid-shelf, to the quieter, deeper waters of the outer-shelf. This environmental continuum is reflected in the biofacies seen in the western Eucla Basin. While the Nanarup Limestone represents a near 'complete' cassiduloid/clypeasteroid biofacies (more than 90% of specimens), the Manypeaks marly limestone is more transitional to a 'complete' spatangoid biofacies in that spatangoids comprise 50% of the Manypeaks specimens, the cassiduloids/clypeasteroids just over 40%. A 'complete' spatangoid biofacies is only seen in Cenozoic sediments in southern Australia in the middle Miocene Rutledge Marl, where spatangoids comprise 100% of the echinoid fauna (McNamara 1991) in these muddy sediments. A comparable pattern of cassiduloid/clypeasteroid and spatangoid biofacies has been documented by Challis (1979) in the Miocene of Malta.

The absence of the spatangoids *Protenaster, Bolbaster* and ?*Isaster* from the finer-grained Manypeaks limestone indicates that during the middle Eocene these genera were still adapted to inhabiting a relatively coarse, permeable substrate and had yet to evolve the morphologies to cope with burrowing in fine-grained sediments, despite later species being tolerant of such sediments (McNamara 1985a, 1987). However, the greater proportion of *Gillechinus* in the Manypeaks limestone indicates that this form was already adapted to inhabiting fine-grained sediments and indeed preferred them to sandier substrates. In the case of *Protenaster* (McNamara 1985a) and *Bolbaster* (McNamara 1987) previous assessments of the genera similarly identified these middle Eocene species as sand-tolerant, with later forms becoming gradually adapted to finer substrates. As the changes in the proportions of other cassiduloid and clypeasteroid species are only small, it is assumed that these changes are not real increases or decreases, but are caused by the large change in the amount of *Echinolampas posterocrassa* in the assemblage.

Using biological population statistics, the diversity and dominance of the echinoid assemblages can be assessed. For individual faunas, the species diversity can be calculated using Simpson's α diversity index $D = 1\text{-}\Sigma(n_i/N)^2$, where D is the diversity of the population, n_i is the number of individuals in a species and N is the total number of individuals in the population. Thus, if $D = 0$, there is no diversity, with only one species present (high dominance); while $D = 1$ represents equal amounts of individuals in each species present (low dominance; Knox et al. 2001). Omitting the regular echinoid *Temnocidaris (Stereocidaris)* due to the indeterminate numbers of individuals represented, the

TABLE 2 Proportions of species preserved in the Nanarup Limestone and Manypeaks limestone. *Temnocidaris* (*Stereocidaris*) *cudmorei* is not included because the fragmented nature of these specimens does not allow accurate estimation of the population size.

Species	% of Nanarup	% of Manypeaks
Australanthus longianus	4.0	7.5
Cyclaster jamiei	0.5	2.5
Echinolampas posterocrassa	69.0	12.5
Eurhodia westaustraliae	0.5	2.5
Fossulaster susae	17.4	20.0
Gillechinus kaitae	5.1	47.5
Bolbaster subidus	0.4	-
Ortholophus aff. *bittneri*	2.5	5.0
?*Isaster* sp.	0.2	-
Protenaster preaustralis	0.2	-
Pleurosalenia tertiaria	0.2	2.5
Total	**100.0 (n=551)**	**100.0 (n=40)**

FIGURE 12 Bryozoal and serpulid epibionts on posterior part of aboral surface of a specimen of *Gillechinus kaitae* sp. nov., WAM 07.423, from the Manypeaks lime quarry, W.A., middle Eocene (Bartonian) Manypeaks limestone.

Nanarup Limestone has an α-diversity D of 0.489, with a species richness of 11. In the Manypeaks limestone D = 0.697 and species richness is 8. Thus, while the Nanarup Limestone has a larger number of species, the dominance of the assemblage is high; and although the Manypeaks limestone may have lower dominance, there are fewer species.

Low alpha-diversities, representing high dominance assemblages, are generally considered indicators of environmental disturbance, the cause of which may be external (environmental) or internal (biological). In the case of the Nanarup Limestone, *Echinolampas posterocrassa* appears to have been an opportunistic species, able to deal with conditions better than other species, allowing it to thrive. In the Manypeaks environment, this disturbance was reduced, leading to lower dominance and higher alpha-diversity, suggesting that water depth or substrate were the cause. It has been noted that dominance tends to increase in shallow-water communities due to energy and exposure pressures, but this trend is generally accompanied by lower species richness (Dodd and Stanton 1981), which is not seen in the Nanarup Limestone.

Evidence for instability and sediment disturbance, particularly in the Nanarup Limestone, is provided by the frequency of occurrence of epibionts on the irregular echinoids. Discounting very small, poorly preserved or worn specimens, about two-thirds of specimens from both limestones have some degree of encrustation by epibionts (e.g., Figure 12). The principal epibionts are bryozoans, with a few being serpulids. Boreen and James (1995) have pointed out that many of the bryozoal grainstones of the southern Australian Cenozoic sediments were deposited above storm wave-base. Post-mortem exhumation of the echinoids must have been common, as shown by the frequent presence of epibionts on both the aboral and adoral surfaces. The period of exhumation was probably not that long. Nebelsick et al. (1997) have observed how dead tests of modern species of *Schizaster* can become completely encrusted by epibionts within about a year. While many of the Nanarup specimens are epibiont encrusted, the bryozoal colonies are relatively small (less than 1 cm in diameter), suggesting perhaps short periods of exhumation before being re-covered in the next storm event.

Some specimens from the Manypeaks limestone are heavily iron-stained (e.g. see Figure 4D–F), again indicating reasonably long exposure on the sea floor during periods of little to no sedimentation in the deeper water environment. Some taxa in the Nanarup Limestone, notably *Bolbaster* and *Protenaster*, do not show any evidence of encrustation by epibionts. This could suggest that, as deeper burrowers, they were less prone to post-mortem exhumation, but sample numbers are too small to demonstrate this conclusively.

Marsupiate Echinoids

One interesting aspect of both the Nanarup and Manypeaks limestones is the marsupiate echinoid *Fossulaster susae* described herein. This species is the oldest known marsupiate echinoid in the Australian Cenozoic. Marsupiate echinoids are unknown in the contemporaneous Tortachilla Limestone. This first marsupiate occurrence in the western end of the southern Australian margin during the middle Eocene, with a later occurrence of such echinoids in the east during the late Eocene, reinforces the notion of a progressive easterly spread of marsupiates during the Cenozoic, reflecting the overall, general migration pattern seen in echinoids (Foster and Philip 1978; McNamara 1999).

Although a number of studies have suggested that the occurrence of such brooding echinoids was indicative of cool water conditions (Rowe and Vail 1982; Smith 1984; Néraudeau et al. 2003; Dudicourt et al. 2005), due to their modern ubiquity in high latitude polar waters, McNamara (1994a) has argued that there is no correlation between diversity of marsupiate echinoids in the Cenozoic rock record in southern Australia and palaeotemperatures. Rather, he suggested, as have others (Clarke 1988; Poulin and Féral 1995), that the biodiversity of brooding in echinoids is greatly influenced by environmental seasonality. In the modern environment, marsupiate echinoids are most common in polar regions where the shortened period of sunlight means a short period of phytoplankton bloom, and thus a shortened period for feeding — stressed, but predictable. These conditions favour forms that can coordinate reproduction with these high nutrient conditions, produce small numbers of offspring, and invest considerable energy into reproduction, features which are characteristic of brooding echinoid reproduction (Jeffery and Emlet 2003). Thus, the presence of the marsupiate echinoid *Fossulaster susae* within the middle

Eocene limestones of the western Eucla Basin, suggests a degree of seasonality in the environment of this area during this time. This is supported by arguments that the development of extensive terrestrial silcretes and seasonally adapted vegetation at this time nearby were due to high seasonality (Carpenter et al. 2014).

PALLINUP FORMATION

The Nanarup Limestone is overlain by the clastic and lignitic Werillup Formation (Cockbain 1968; Clarke et al. 2003). This in turn is overlain by the siliceous Pallinup Formation, the upper Fitzgerald Member of which is a fossiliferous spongolite. These rocks extend for about 1000 km, from near Albany in the west, close to Israelite Bay in the east (Gammon and James 2001, fig. 2). The Pallinup Formation contains an echinoid fauna that is essentially undescribed at the species level. The calcareous biota has been leached away and specimens are preserved as internal and external moulds. The unit has been correlated with late Eocene planktonic foraminiferal zones P15 and P16, and represents part of the Tuketja Transgression across southern Australia (Clarke et al. 2003; Hou et al. 2008). The only echinoids previously reported from the Pallinup Formation are the spatangoids *Linthia pulchra* (McNamara 1985b), *Gillechinus kaitae* (as *G. cudmoreii* (McNamara et al. 1986)) and a single specimen of the cassiduloid *Aphanophora*? *bassoris* Holmes, 1995 (Martin and McNamara 2004). The echinoid fauna of the Pallinup Formation, as represented by specimens in the Western Australian Museum (McNamara pers. obs.), is a spatangoid biofacies, being dominated by spatangoids including, in addition to *L. pulchra* and *G. kaitae*, ?*Bolbaster* sp., *Schizaster* (*Paraster*) *tatei*, ?*Isaster* sp., *Cyclaster jamiei* and ?*Pericosmus* sp. The only non-spatangoids, apart from *Aphanophora*? are the holasteroid *Giraliaster bellissae* Foster and Philip, 1978 and the cidaroid ?*Temnocidaris* (*Stereocidaris*) sp.

Whereas the Nanarup Limestone contains a cassiduloid/clypeasteroid, shallow burrowing biofacies and the Manypeaks limestone a mixed spatangoid/cassiduloid biofacies, the Pallinup Formation is dominated by a spatangoid biofacies, containing both shallow and deeper burrowing forms. The Pallinup Formation has been identified as having been deposited in a shallow-water, warm-temperate humid environment (Gammon and James 2003) as opposed to the deep, cool-water environment it was originally considered to be (Gammon et al. 2000, Gammon and James 2001), suggesting that the echinoid faunas of the southern Australian margin may have been strongly influenced by sediment grain size and not just water depth and temperature.

TORTACHILLA LIMESTONE

The Tortachilla Limestone is the South Australian equivalent of the Nanarup Limestone and contains a rich echinoid fauna, comprising cidaroids (*Temnocidaris* (*Stereocidaris*) *cudmorei*, *T.* (*Stereocidaris*) *fosteri*, *T.* (*Stereocidaris*) *inermis*, *T.* (*Stereocidaris*) *hispida*, *T.* (*Stereocidaris*) *intricata*), saleniids (*Pleurosalenia tertiaria*), temnopleurids (*Ortholophus bittneri*, *Tatechinus nudus*), clypeasteroid (*Fibularia gregata*), cassiduloids (*Apatapygus vincentinus*, *Australanthus longianus*, *Eurhodia australiae*), echinolampadoid (*Echinolampas posterocrassa*), holasteroids (*Giraliaster bellisae*, *G. sulcatus*, *G. tertiarus*), neolampadids (*Pisolampas concinna*, *Aphanopora*? *bassoris*) and spatangoids (*Gillechinus cudmorei*, *Bolbaster subidus*, *Linthia pulchra*, *Prenaster aldingensis*, *Protenaster preaustralis*, *Psephoaster lissos* and *Schizaster* (*Paraster*) *tatei*) (Holmes, 1999). Many of the elements present in the Pallinup Formation and in the Nanarup and Manypeaks limestones also occur in the Tortachilla fauna (Table 3).

This Tortachilla assemblage is noticeably richer taxonomically than the western Eucla units. This is unlikely to be a factor of greater collecting of the Tortachilla Limestone, because both the Tortachilla and Nanarup limestones have been extensively collected over many years. This higher species richness at Tortachilla could be related to greater variability in substrate, which has been noted to vary between sandy and marly (Lindsay 1969). Alternatively, if the disturbance that appears to cause the high dominance in the Nanarup Limestone was absent in the Tortachilla Limestone, one would expect this higher species richness, coupled with lower dominance. The fact that there is no evidence for gastropod predation in the Tortachilla Limestone during the middle Eocene (McNamara 1994b) supports the theory that predation pressure was the cause for this disturbance in the Nanarup Limestone, where there is evidence for gastropod predation (e.g. see Figure 3C). For instance, of the 380 specimens of *Echinolampas posterocrassa* collected from the Nanarup Limestone 11%, show evidence of gastropod predation. Interestingly, the middle Eocene marks the time when there was a distinct increase in echinoid predation globally, corresponding to an increase in diversity of cassid gastropods, one of their most common predators (Petsios et al. 2021).

Comparison of the western Eucla and the St Vincent basin assemblages can be undertaken using Jaccard's β diversity constant, $S = a/t$, where S is Jaccard's constant of genus comparison in two areas, a = number of shared genera, and t = total number of genera. Thus, if $S = 0$, the assemblages in the two areas are completely different and share no genera. If $S = 1$, the assemblages are exactly the same and the areas have identical populations (Knox 2001). For Nanarup and Manypeaks $S = 0.75$, while for Pallinup and Manypeaks $S = 0.13$, and comparing Nanarup and Pallinup, $S = 0.24$. These calculations confirm the close comparison between the Manypeaks and Nanarup limestones, and also confirm the lack of similarity between the Nanarup Limestone and Pallinup Formation assemblages. Although the Pallinup fauna seems most like that of the Nanarup Limestone, this may be due to the greater

TABLE 3 Presence and absence of genera from middle and late Eocene units of southern Australia, with a '–' indicating a genus' absence, and a '+' the genus' presence in a unit. Tortachilla assemblage information from Holmes (1999, Appendix 1).

Genus	Nanarup Limestone	Manypeaks limestone	Pallinup Formation	Tortachilla Limestone
Apatopygus	–	–	+	+
Aphanopora?	–	–	+	+
Australanthus	+	+	–	+
Bolbaster	+	+	+	+
Cyclaster	+	+	+	0
Echinolampas	+	+	–	+
Eurhodia	+	+	–	+
Fibularia	–	–	–	+
Fossulaster	+	+	–	–
Gillechinus	+	+	+	+
Giraliaster	–	–	+	+
?*Isaster*	+	–	–	–
Linthia	–	–	+	+
Micrasterid indet.	+	–	–	–
Ortholophus	+	+	–	+
Pericosmus	–	–	+	–
Pisolampas	–	–	–	+
Prenaster	–	–	+	+
Protenaster	+	–	–	+
Psephoaster	–	–	–	+
Pleurosalenia	+	+	–	+
Schizaster (*Paraster*)	+	–	+	+
Temnocidaris (*Stereocidaris*)	+	+	+	+
Tatechinus	–	–	–	+

number of specimens and species at Nanarup than at Manypeaks. As noted, the slight difference between the faunas of Nanarup and Manypeaks appears to be due to a slight difference in sediment type, which in turn may be due to variation in water depth.

When comparing Western Australian and South Australian assemblages, Nanarup and Tortachilla have S = 0.48, for Manypeaks and Tortachilla S = 0.33, and for Pallinup and Tortachilla S = 0.4. Thus neither Nanarup nor Manypeaks is distinctly more like the Tortachilla fauna. As the Tortachilla Limestone has species similar to both the coarse-grained (Nanarup) and fine-grained (Pallinup) units, it appears to contain both these substrates. Therefore, if all three western Eucla units are compared with the Tortachilla Limestone S = 0.64, they are not entirely dissimilar. There are seven genera that are not shared between Western and South Australia — *Cyclaster*, *Fossulaster* and *Pericosmus* occur only in the western Eucla Basin, while *Pisolampas*, *Tatechinus*, *Psephoaster* and *Fibularia* only occur in the Tortachilla Limestone. It is possible that if the deepest water phase of the Nanarup environment was preserved, those forms missing in the Eucla Basin, but found in the Tortachilla Limestone, would be present.

As a number of genera and species are shared between the Eucla and St. Vincent basins during the middle-late Eocene, it appears there was good connectivity between southern Australian echinoid faunas during this period. McNamara (1999) previously noted the similarities between the Nanarup Limestone assemblage and that of the contemporary Giralia Calcarenite of the Southern Carnarvon Basin, revealing that this connectivity extends both down the western and across the southern coast. This he attributed to the action of the proto-Leeuwin Current, activated by the warm climate during the middle and late Eocene. In recent times, the Leeuwin Current is well known for bringing invertebrate larvae from the tropical northwest to higher latitudes, along with warmer water in the process. The current flow would also have encouraged the migration of echinoid species from the Eucla Basin to the St Vincent Basin, enhancing the similarity in faunas.

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