

MARSUPIATE TERTIARY ECHINOIDS FROM SOUTH-EASTERN AUSTRALIA AND THEIR ZOOGEOGRAPHIC SIGNIFICANCE

by G. M. PHILIP and R. J. FOSTER

ABSTRACT. A review of brooding and sexual dimorphism in living and fossil sea urchins reveals the wide variety of marsupia that can be developed. In living sea urchins, brooding, in some species with the concomitant development of marsupia, is an outcome of direct development. In fossil echinoids the presence of marsupia probably indicates a similar omission of free larval stages. Marsupia have been reasonably substantiated in five Cretaceous species, eleven Tertiary species (ten from Australia) and twenty-eight living species. Of these latter, twenty-five are from polar waters, which accords well with the interpretation that direct development is an adaptation to cold or deep waters. In Australia the abundance of marsupiate echinoids decreases through the Cainozoic and there is now but one living species. It is suggested that the occurrence of marsupiate species in the Australian Tertiary supports recent suggestions of the late separation of Australia from Antarctica (in the Late Cretaceous or Eocene) and that these marsupiate echinoids had their origin in Antarctic waters.

The following marsupiate species, of Upper Eocene, Oligocene, or Miocene age, are described and figured: the temnopleurids *Paradoxechinus novus* Laube, *P. granulosus* sp. nov., *P. profundus* sp. nov., *P. stellatus* sp. nov., *Pentechinus mirabilis* gen. et sp. nov., the clypeasteroids *Fossulaster halli* Lambert and Thiéry, *F. exiguus* sp. nov., *Willungaster scutellaris* gen. et sp. nov., the spatangids *Peraspatangus brevis* gen. et sp. nov., *P. depressus* gen. et sp. nov. The family Fossulasteridae is erected for Australian Tertiary clypeasterinid echinoids with simple ambulacral plates in the petals.

ALTHOUGH a revision of the prolific Tertiary echinoids of south-eastern Australia is being published elsewhere (Philip 1963a, 1964, 1965b, 1969), it is useful to discuss separately aspects of the fauna of more general interest. This paper is concerned with the marsupiate urchins. Of the ten such species described here, only two have been named previously. As only one marsupiate species of Tertiary age is known from elsewhere, opportunity is taken to review the occurrence and structure of marsupia in echinoids, and to speculate on their significance.

MARSUPIA IN ECHINOIDS

In living echinoids the sexes are separate although hermaphroditic individuals of normally dioecious species occur as rare anomalies (Hyman 1955, p. 478, q.v.). Generally the tests of individuals of different sexes are indistinguishable. Some claims have been made that different test shapes may obtain in the different sexes (e.g. Ikeda 1931, who identified as females the low tested forms of the highly variable temnopleurid species *Temnopleurus toreumaticus* Leske), but such interpretations have been rejected by subsequent workers (cf. Mortensen 1943, p. 79).

Some echinoids, however, are known to brood their young and with such forms sexual dimorphism may obtain. Brooding urchins, in contrast to others, are thought to develop directly with the omission of the echinopluteus (or free swimming larval stage). The few large yolky eggs of the female develop around her peristome or apical system or even in specially produced brood pouches or marsupia.

Brooding is known best in cidaroids and spatangoids from Antarctic waters, where, apparently, a viviparous habit accords some benefit to the urchins. With the sole exception of *Austrocidaris canaliculata* (Agassiz), which bears its young around the apical system, brooding cidaroids carry their offspring around the peristome, protected by primary radioles. In only two cidaroid species (*Rhynchocidaris triplopore* (Mortensen) in which an annular depression is present and *Ctenocidaris geliberti* (Koehler) in which the edge of the peristome is sunken) is the corona of females modified because of this brooding habit. In the former species Mortensen (1909) has reported the relocation of the genital pores at the edge of the peristome in females infested by the parasite *Echinophyces*.

In all species of the Antarctic spatangoid genera *Abatus*, *Amphipneustes* and *Tripylus*, the petalloid ambulacra of the females are deeply sunken to accommodate the young (vide Mortensen 1951).

Apart from cidaroids, undoubted brooding in living regular sea urchins appears to be confined to *Hypsiechinus coronatus* Mortensen. In this Arctic temnopleurid the females possess an elevated apical system in which the plates are strongly inflected to form a prominent knob. The young are carried around this knob on the adapical surface of the test.

In all other living species in which a marsupium is present in the females, it consists of an apical depression containing the apical system (the neolampadids *Anochanus sinensis* (Grove) and *Tropholampas loveni* (H. L. Clark); the clypeasteroid *Fibularia nutriens* H. L. Clark and the meridosternous spatangoid *Plexechinus nordenskjoldi* Mortensen).

Excluding the fossil species described here, marsupia have been suggested previously in a number of fossil species, but many claims lack reasonable substantiation (Kier 1969, gives seven species, including one redescribed here).

Kier (1967a) has described an undoubted marsupium in the middle Eocene clypeasteroid *Pentedium curator* Kier in which the females possess a deep adapical depression which includes the apical system and the petalloid ambulacra. Again, Lambert (1933, p. 27, pl. 4, figs. 6–7) has described and illustrated young in the deeply sunken petals of his Cretaceous species *Tripylus pseudoviviparus* (referred questionably to the genus *Abatus* by Mortensen 1951, p. 276).

Rosenkrantz (in Mortensen 1951, p. 577) reported that in some specimens of *Brissopneustes danicus* Schlüter the apical system is deeply sunken. He suggested that this depression is a marsupium, and Mortensen (loc. cit.) was in agreement.

Among fossil regular echinoids, the reports are by no means as convincing. The Cretaceous species *Goniopygus royo* Lambert and *G. minor* Sorniguet have deep interambulacral depressions originating at the edge of the genital plates. These depressions have been viewed as marsupia by Lambert (1928, p. 156). Similar depressions occurring in some specimens of *Thylechinus said* (Peron and Gauthier 1881, pl. 19, figs. 4, 6) have been given the same interpretation (cf. Mortensen 1935, p. 468). Gregory (1892) regarded the adapical sutural depressions of the British Pliocene species *Temnechinus excavatus* Forbes as 'marsupial pouches' and gave a similar explanation to some obscure adapical interambulacral depressions in '*Echinus*' *henslovi* Forbes.

Examination of British Pliocene sea urchins in the collections of both the British Museum (Nat. Hist.) and the Sedgwick Museum, Cambridge, revealed that no

dimorphism exists in these last two species. Accordingly, Gregory's interpretation is discounted. On the other hand, in *Goniopygus royo*, *G. minor*, and *Thylechinus said* individuals have been reported which lack depressions, so that Kier (1969) concluded that sexual dimorphism existed in these Cretaceous stirodents.

Of the marsupiate species discussed here, two previously have been described and so interpreted. The adapical depression of *Paradoxechinus novus* Laube was seen as a marsupium by Bittner (1892), Mortensen (1943), and Philip (1969) who described specimens lacking the depression and which, accordingly, were identified as males. Hall (1908), Durham (1955), and Kier (1969) have interpreted the deep adoral bilobed depression anterior of the peristome of *Fossulaster halli* as a marsupium, although Mortensen (1951, p. 577) retained doubts, for specimens of the males were unavailable to him for study. Much new information concerning both of these species is provided here.

The other species described not only increase two-fold the number of known marsupiate fossil sea-urchins, but also have marsupia the architecture of which is not known elsewhere in the class. The remarkable interambulacral pouches of *Pentechinus mirabilis* gen. et sp. nov., are particularly noteworthy. Two new clypeasteroid species are described in which the marsupia are depressions on the oral surface anterior of the peristome. Echinoids with a marsupium in this position are known only from Australian Tertiary strata. The marsupia of the species of *Paradoxechinus* find a close analogue in *Hypsiechinus coronatus*, and the apical depression of *Peraspatangus* is similar to those of other irregular echinoids.

From the foregoing discussion it can be seen that marsupia are widespread throughout different echinoid groups and that marsupia different in location and structure may be developed within the one family. This may be seen best in the following table that summarizes the different types of marsupia presently known.

MARSUPIUM ADAPICAL

A. CENTRAL

1. Apical system raised

a. without annular depression

CAMARODONTA

**Hypsiechinus coronatus* Mortensen

b. with annular depression

CAMARODONTA

Paradoxechinus granulatus sp. nov.

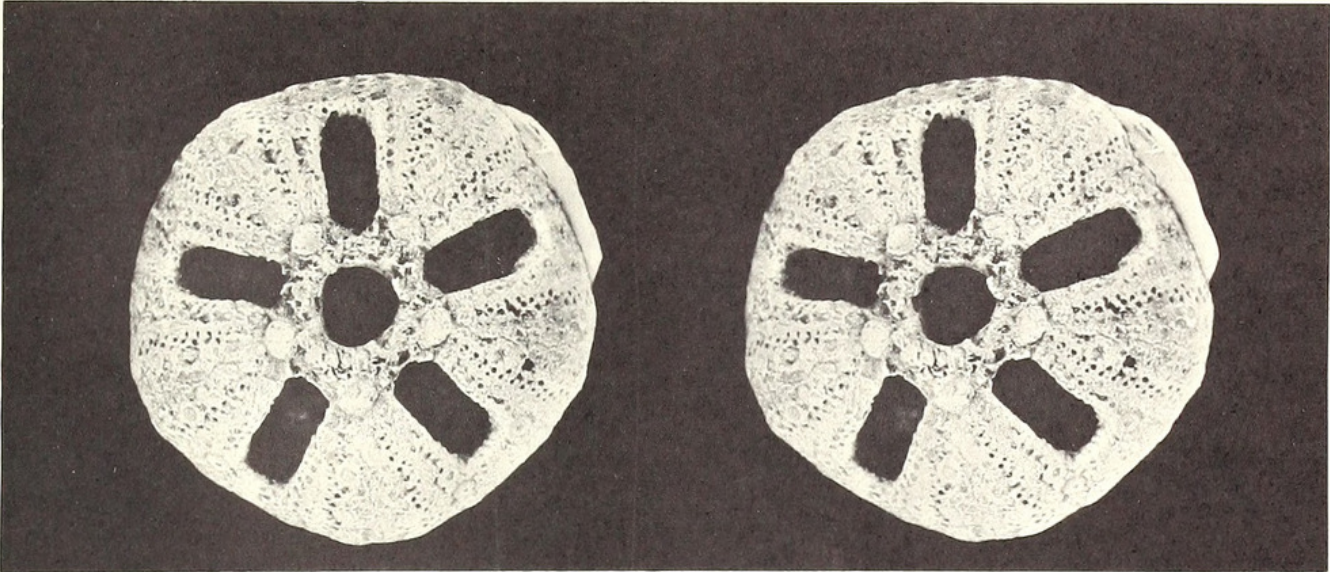
P. novus Laube

P. profundus sp. nov.

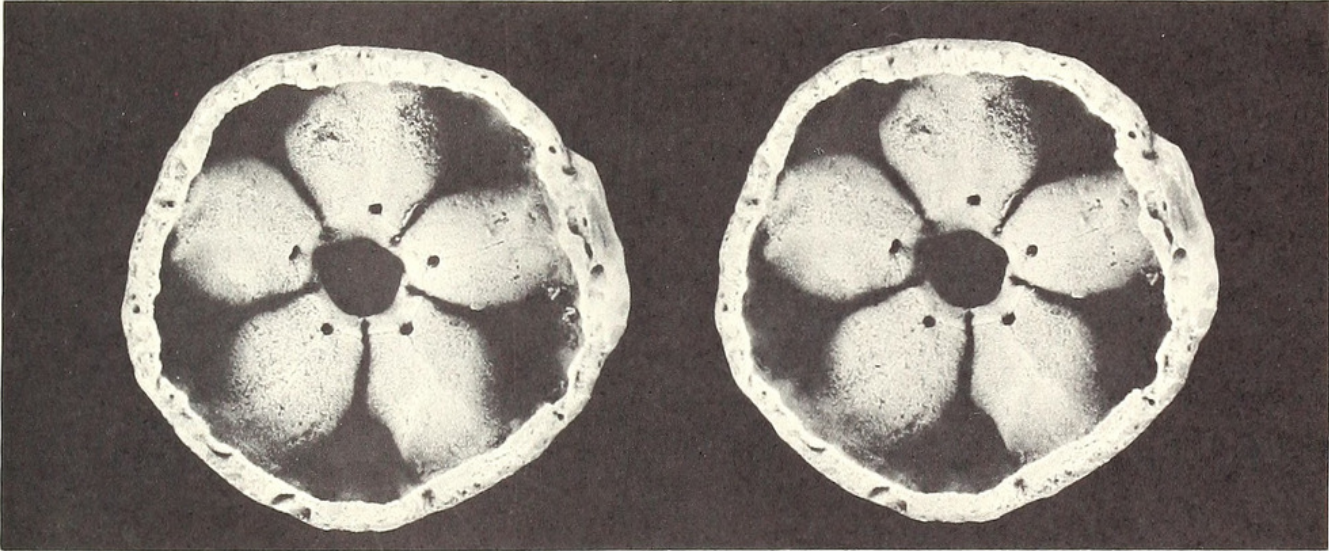
P. stellatus sp. nov.

EXPLANATION OF PLATE 124

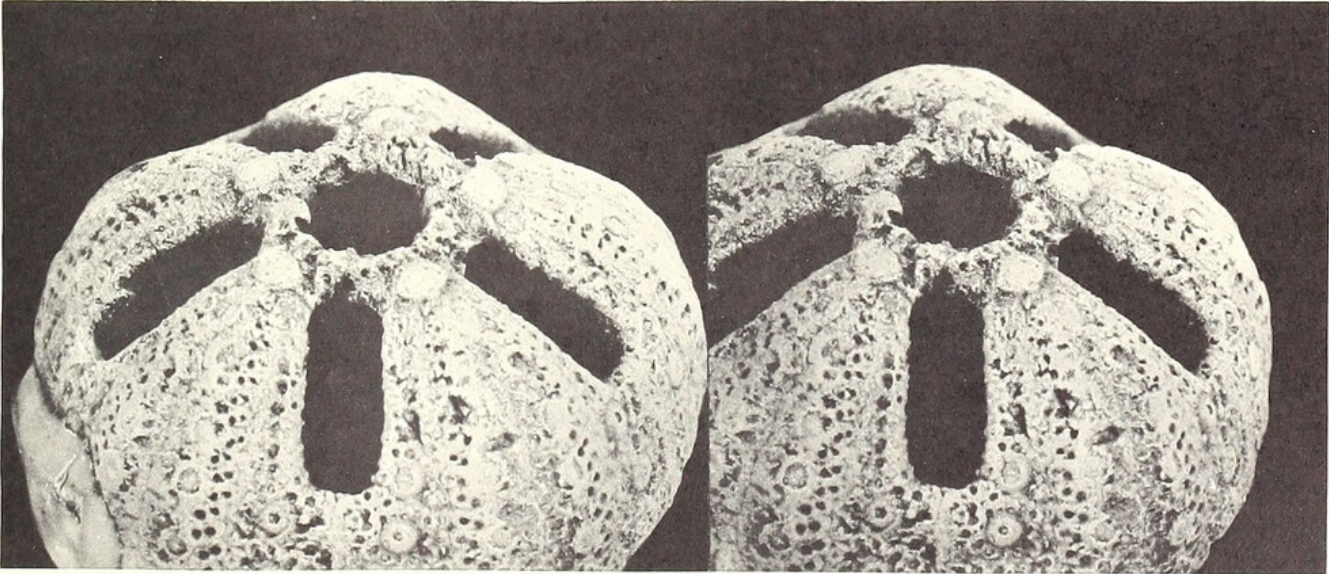
Figs. 1-3. Stereopairs of the holotype (P27942) of *Pentechinus mirabilis* gen. et sp. nov. 1, Adapical view, $\times 5$. 2, Adoral view of the interior of the adapical half of test, showing the five flattened sac-like marsupia, and the genital pores at the extremities of the introverted genital plates, $\times 5$. 3, Oblique adapical view showing the interambulacral marsupial slits, $\times 8$.



1



2



3

2. Apical system sunken

CLYPEASTEROIDA

- **Fibularia nutriens* H. L. Clark
- Pentedium curator* Kier

NEOLAMPADINA

- **Anochanus sinensis* (Grove)
- **Tropholampas loveni* (H. L. Clark)

SPATANGOIDA

- **Plexechinus nordenskjoldi* Mortensen
- Peraspatangus brevis* gen. et sp. nov.
- P. depressus* gen. et sp. nov.
- Brissopneustes danicus* Schlüter

B. LATERAL

1. Ambulacral

SPATANGOIDA

- **Abatus* 9 spp.
- **Amphipneustes* 8 spp.
- **Tripylus* 4 spp. (vide Mortensen 1951)
- '*Tripylus*' *pseudoviviparus* Lambert

2. Interambulacral

CAMARODONTA

- Pentechinus mirabilis* gen. et sp. nov.

STIRODONTA

- Goniopygus royai* Lambert
- G. minor* Sorignet
- Thylechinus said* (Peron and Gauthier)

MARSUPIUM ADORAL

A. CIRCUM ORAL

CIDAROIDA

- **Ctenocidaris geliberti* (Koehler)
- **Rhynchocidaris triplopora* (Mortensen)

B. ANTERIOR

CLYPEASTEROIDA

- Fossulaster halli* Lambert and Thiéry
- F. exiguus* sp. nov.
- Willungaster scutellaris* gen. et sp. nov.

* living species

To date marsupia have been reasonably substantiated in five Cretaceous species, eleven Tertiary species (ten from Australia), and twenty-eight living species.

It is customary to associate direct development and brooding in sea-urchins with cold water or deep water forms (Hyman 1955). Thorson (1950) has pointed out that many groups of marine benthonic organisms that normally have pelagic larval stages tend to lack these in polar seas. He suggested that this is an adaptation to accommodate to slow

larval development at low temperatures and to paucity of phytoplankton for much of the year. In such a situation the greater the size of the individual when it achieves independent existence, then the smaller its relative food requirements and the better its chance of survival (cf. Kier 1969, p. 216).

Of the twenty-eight known living marsupiate species, twenty-three are from Antarctic waters and two inhabit the Arctic Ocean. So striking is the present-day association of marsupiate urchins with cold water conditions, that Fischer (1963, pp. 289–290) took the occurrence of marsupia in the two late Cretaceous spatangoids mentioned above as evidence indicative of cooling during that epoch.

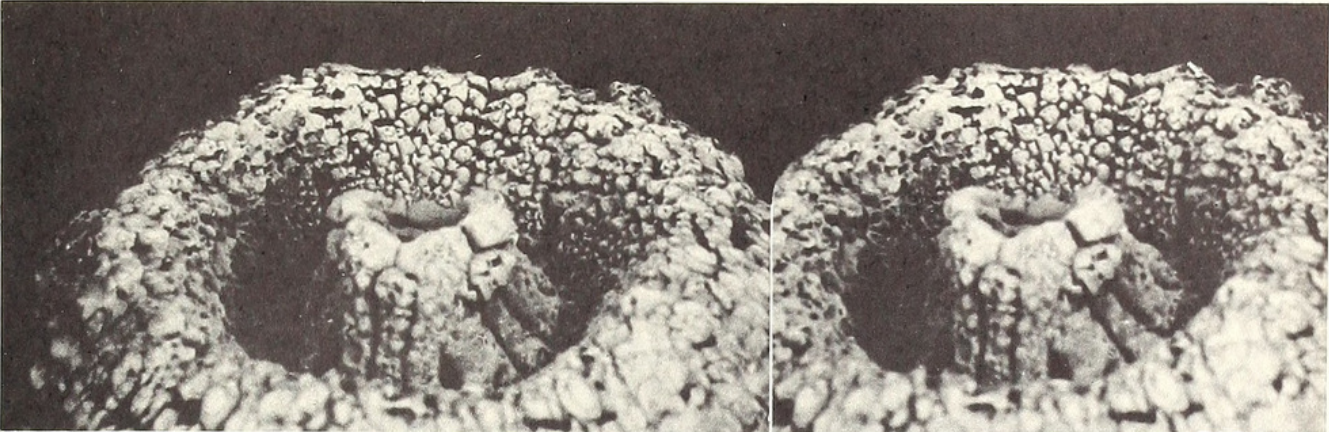
On first consideration, the abundance and diversity of Australian Tertiary marsupiate echinoids would appear to speak against such substantive uniformitarianism. They occur in Upper Eocene to Miocene sediments, which have been thought (at least for the Miocene) to have been deposited in sub-tropical seas. This conclusion was derived from consideration of the diverse and prolific fauna, with its tropical Indo-Pacific elements (David 1950, p. 587) and also oxygen isotope studies (Dorman and Gill 1959).

Yet it now seems probable that the marsupiate echinoids from the Australian Tertiary had their ultimate origin in Antarctic waters. According to present interpretations of magnetic anomalies in the southern Indian Ocean, and reconstructions based on plate tectonics, Australia was not detached from Antarctica until the late Cretaceous (Dietz and Holden 1970). It was not until the late Eocene that the Australian plate began its rapid flight northwards (Le Pichon and Heirtzler 1968) away from the stable Antarctic plate, opening up what are now Antarctic waters. That a brooding habit had been established in southern seas by Cretaceous times is shown in the occurrence in Madagascar of '*Tripylus*' *pseudoviviparus* Lambert (1933), a specimen of which even shows the young still preserved in the sunken petals. If deductions of workers on plate tectonics are accepted, then the oldest of the marsupiate urchins described here in fact inhabited epicontinental seas approximately 20° to the south of where they were collected. Within the Australian Cainozoic record from the Oligocene there is a progressive decrease in the abundance and variety of marsupiate echinoids, until at present only one such living species, *Fibularia nutriens*, inhabits eastern Australian coastal waters. This fact is given new meaning by suggesting that the adaptive advantage of the marsupiate echinoids diminished as their habitat moved northward into more temperate climes.

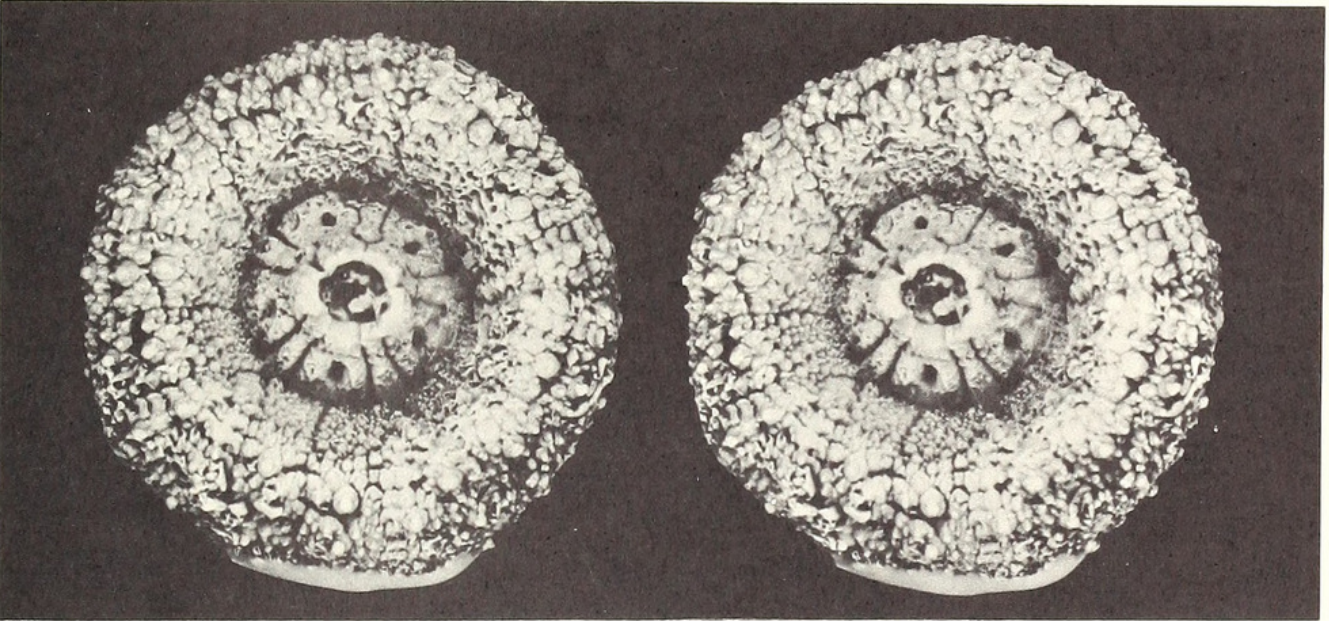
Another aspect of the south-eastern Australian Tertiary echinoid fauna supports current views on continental displacement. Present-day Antarctic and sub-Antarctic seas are inhabited by a specialized group of cidaroids, the ctenocidarines, to the apparent exclusion of all other cidaroids. From the Australian record it has been established that this group evolved from the stereocidarines in the Paleogene (Philip 1964, pp. 452–453).

EXPLANATION OF PLATE 125

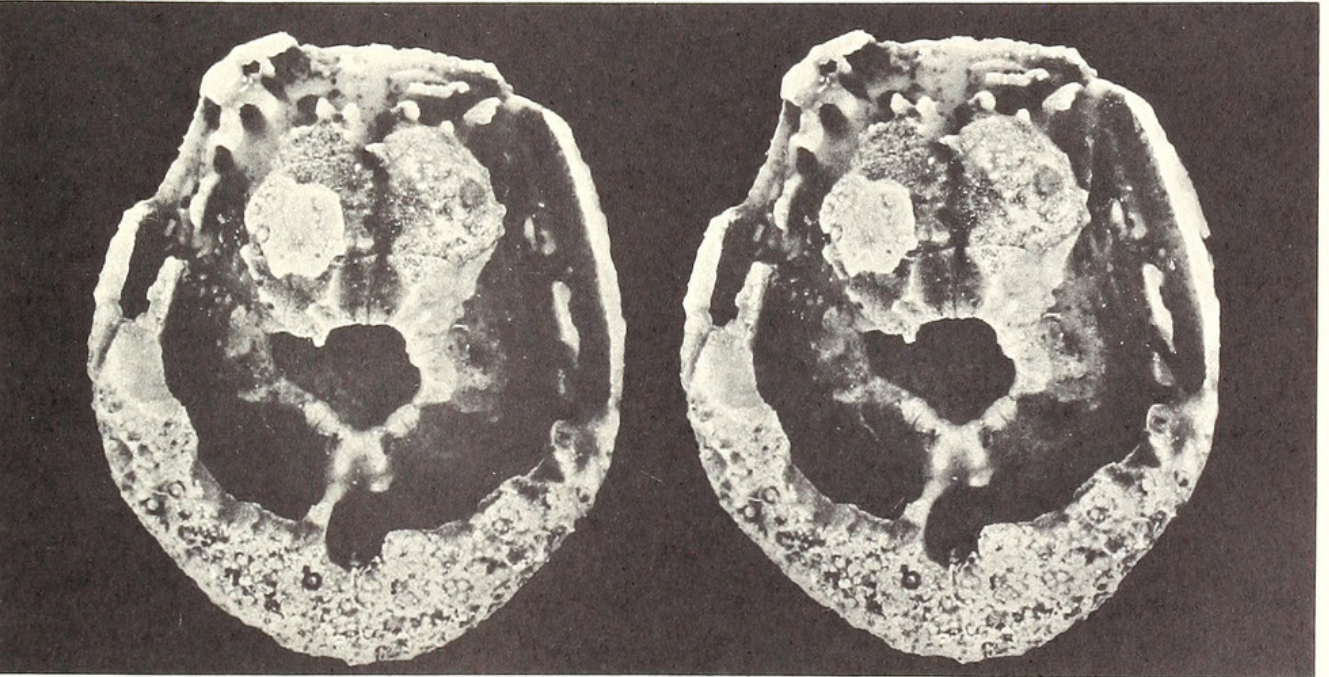
- Figs. 1–2. *Paradoxechinus novus* Laube. 1, Oblique adapical stereopair of apical system of P27943 (♀), × 8. 2, Stereopair of adapical view of same specimen, × 5.
Fig. 3. *Fossulaster halli* Lambert and Thiéry. Stereopair of P27948 (♀), a specimen prepared to show the internal supports of the test. Note portion of adapical surface of test ankylosed to one of the lobes of the marsupium, × 8.



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The group is represented by a typical species of *Austrocidaris* in the Lower Miocene (op. cit., p. 462), but, thereafter, ctenocidarines disappear from the Australian Cainozoic record.

* * *

It may be noted that sexual dimorphism of the apical system is not uncommon in living echinoids. The genital pores of females may be larger, or located differently, or both. The difference in size is particularly conspicuous in urchins thought to have direct development, as the larger pores of the females are necessary for the passage of the larger eggs. However, dimorphism is known in many species which apparently possess echinopluteus larvae. For example, in species of the temnopleurid *Prionechinus*, the genital pores of females are large and rounded, and mounted toward the centre of the genital plates; those of the males are small and slit-like and mounted distally (Mortensen 1943, p. 294). In the echinid *Psammechinus miliaris* the genital pores of males are mounted on short papillae; those of females are not, and in the clypeasteroid *Echinocyamus pusillus* the papillae of males are longer than those of females.

Dimorphism of the apical system attributed to sexual differences has been reported in a number of fossil groups (e.g. neolampadids, Philip 1963*b*; oligopygids, Kier 1967*b*; clypeasteroids, Kier 1967*a*, 1968) and is discussed in detail by Kier (1969).

All specimens with prefix 'P' housed in the fossil collection of the National Museum of Victoria, Melbourne; those with prefix 'UNE' in the collections of the Department of Geology, University of New England, Armidale, N.S.W.

SYSTEMATICS

Subclass REGULARIA

Order CAMARODONTA Jackson

Suborder TEMNOPLEURINA Mortensen

Family TEMNOPLEURIDAE A. Agassiz

Remarks. Philip (1969) divided representatives of this family into two groups; those with sculpture and those with pitted sutures. All Australian Tertiary temnopleurids belong to the former group, including the new genus *Pentechinus*. All known marsupiate temnopleurids are sculptured forms.

Genus PARADOXECHINUS Laube

1869 *Paradoxechinus* Laube, p. 186.

1969 *Paradoxechinus* Laube; Philip, p. 262 (with full synonymy).

Type species. *Paradoxechinus novus* Laube 1869, by monotypy.

Diagnosis. Small to moderate sized sculptured temnopleurids with crenulate tubercles and shallow gill slits. Pore-pairs uniserial or very weakly arcuate within each triad. Sculpture varying from prominent ridges bearing secondary tubercles and granules, to multiple ridges running between primary tubercles. Perignathic girdle of relatively large, spatulate auricles just united above the ambulacra and connected by low apophyses. Test dimorphic, with inferred females possessing a wide, deep adapical depression. Apical system caduceous (known only in one female), dicyclic, with extremely elongate oculars, proximally with all plates strongly inflected upwards to form a prominent knob containing the periproct.

Remarks. The relationship of this genus to similar temnopleurids has been given elsewhere (Philip 1969). At that time topotype material of the type species alone was available for study and the character of the apical system was unknown. In new material from the St. Vincent Basin, S.A., the apical system is preserved in one specimen. Also, material from elsewhere now permits recognition of three other species. The above generic diagnosis accommodates this new information.

Bittner (1892) and Mortensen (1943) have previously interpreted the adapical depression of *P. novus* as a marsupium and this interpretation was enhanced by the recognition of specimens from the type horizon lacking such depressions (Philip 1969). The apical system and marsupium are discussed in detail below.

Paradoxechinus novus Laube

Plate 125, figs. 1, 2; Plate 126, fig. 1; Plate 127, fig. 1;
Plate 129, figs. 7, 12, 13, 17; text-figs. 1, 2.

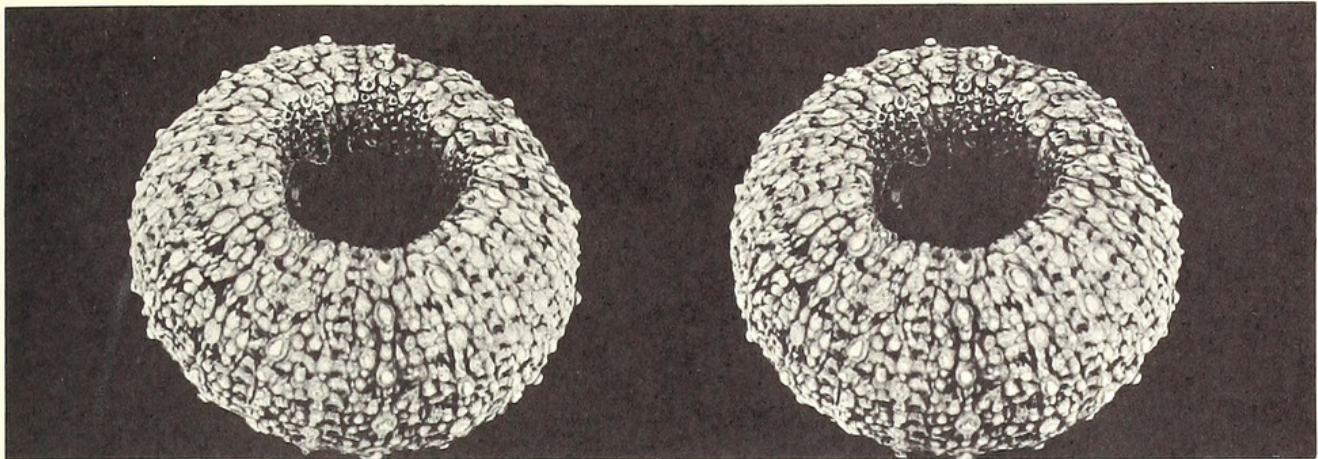
- 1869 *Paradoxechinus novus* Laube, p. 188, fig. 2.
- 1875 *Paradoxechinus novus* Laube; Etheridge, p. 449.
- 1877 *Paradoxechinus novus* Laube; Duncan, p. 65.
- 1878 *Paradoxechinus novus* Laube; Duncan, p. 415.
- 1891 *Paradoxechinus novus* Laube; Tate, p. 274 (in part).
- 1892 *Paradoxechinus novus* Laube; Bittner, pp. 344–345, pl. 4, fig. 5.
- 1892 *Paradoxechinus novus* Laube; Tate, pp. 192–193 (in part).
- 1910 *Paradoxechinus novus* Laube; Lambert and Thiéry, p. 230.
- 1943 *Paradoxechinus novus* Laube; Mortensen, pp. 350–351, fig. 210a.
- 1946 *Paradoxechinus novus* Laube; H. L. Clark, p. 308 (in part).
- 1949 *Brochopleurus australiae* Fell, pp. 18–19 (in part, paratype P4688 only).
- 1966 *Paradoxechinus novus* Laube; Fell and Pawson, fig. 317b (not fig. 317a = *Ortholophus bittneri* Philip).
- 1969 *Paradoxechinus novus* Laube; Philip, pp. 263–266, pl. 11, figs. 1–12; pl. 12, fig. 1; text-fig. 7a–f.

Diagnosis. A small, depressed species of *Paradoxechinus* with prominent sculptural ridges bearing secondary tubercles and granules, and zig-zagging between the primary tubercles. Pore-pairs embedded in the raised 'epistroma' neighbouring the primary ambulacral tubercles.

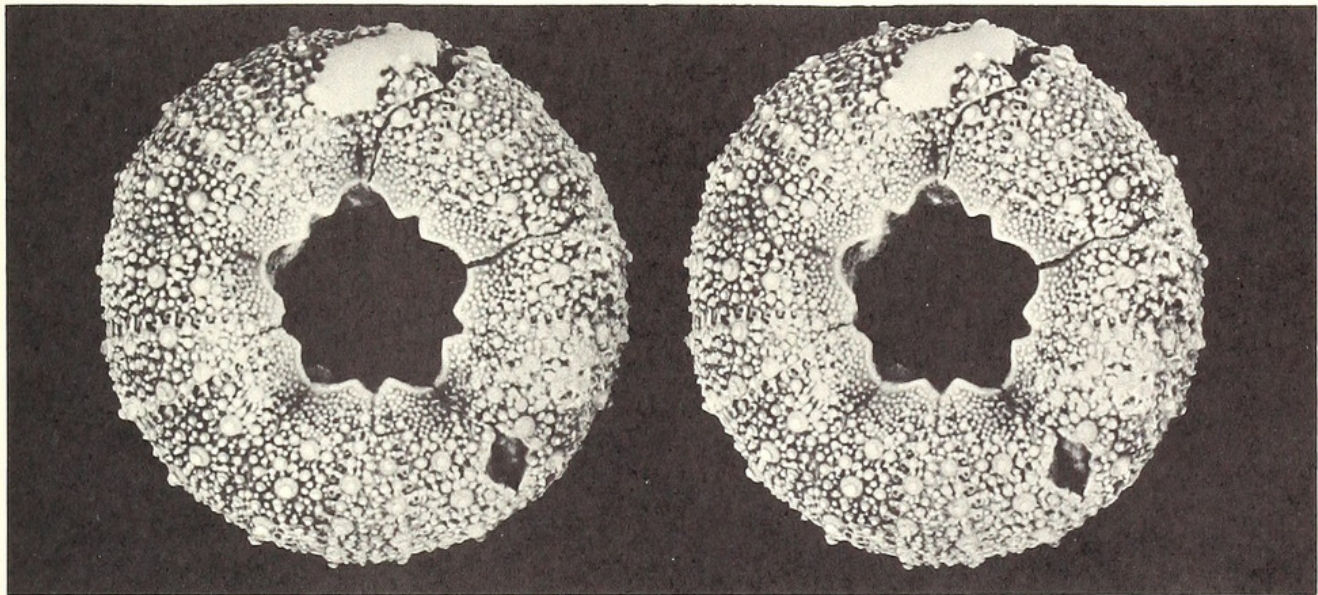
Material. In addition to material described previously from the type horizon (Mannum Formation, South Australia), 54 specimens (26♀; 28♂) from the Adelaide Cement Holdings quarry, 2.5 miles north of Wool Bay, Yorke Peninsula, St. Vincent Basin, S.A. (See McGowran *et al.* 1971 for discussion of Australian Tertiary correlations.) Port Vincent Limestone, *Guembelitra stavensis* zone (Stuart 1970, p. 174) of the Oligocene and Zone p. 21 of Blow (1970).

EXPLANATION OF PLATE 126

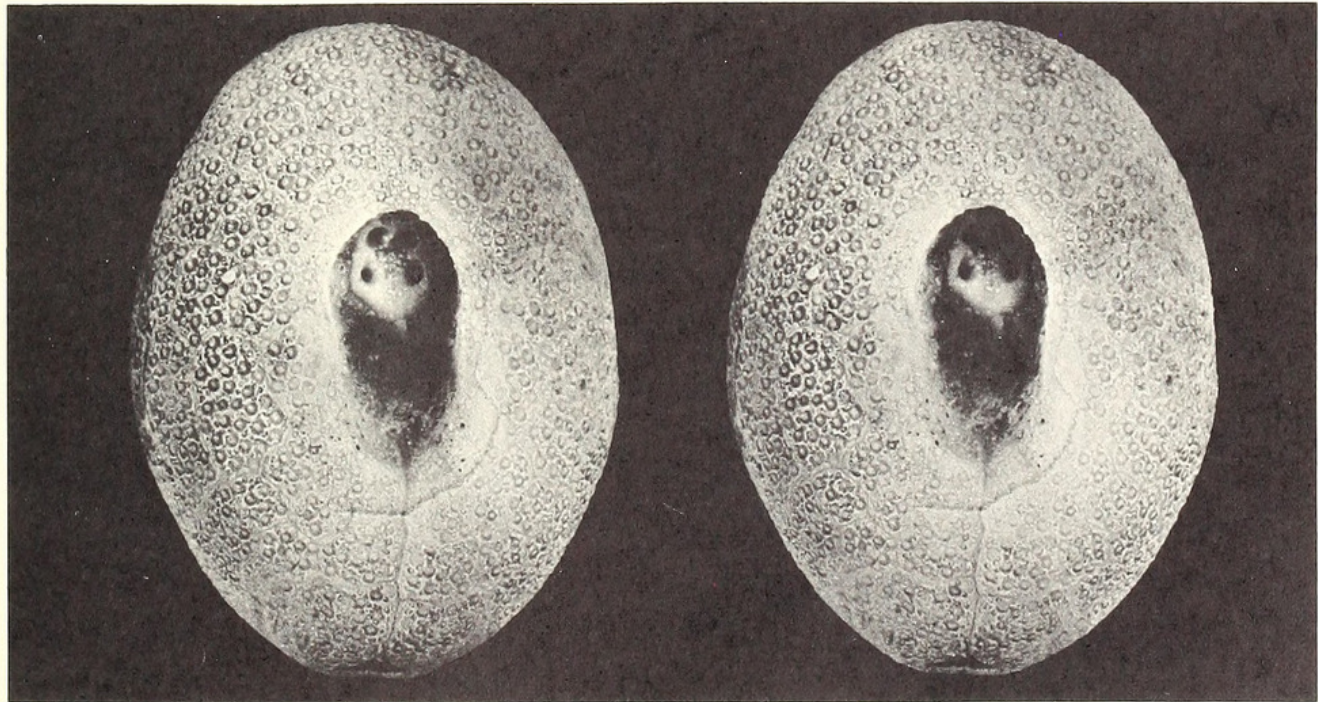
- Fig. 1. *Paradoxechinus novus* Laube. Oblique adapical stereopair of adapical depression of a small specimen, UNE 11522 (♀), ×8 approx.
- Fig. 2. *Paradoxechinus stellatus* sp. nov. Stereopair of adapical view of holotype P27944 (♀), showing pentalobate adapical marsupium, ×5.
- Fig. 3. *Peraspatangus brevis* gen. et sp. nov. Stereopair of adapical view of holotype, P27956 (♀), showing deep adapical marsupium, approx. ×5.



1

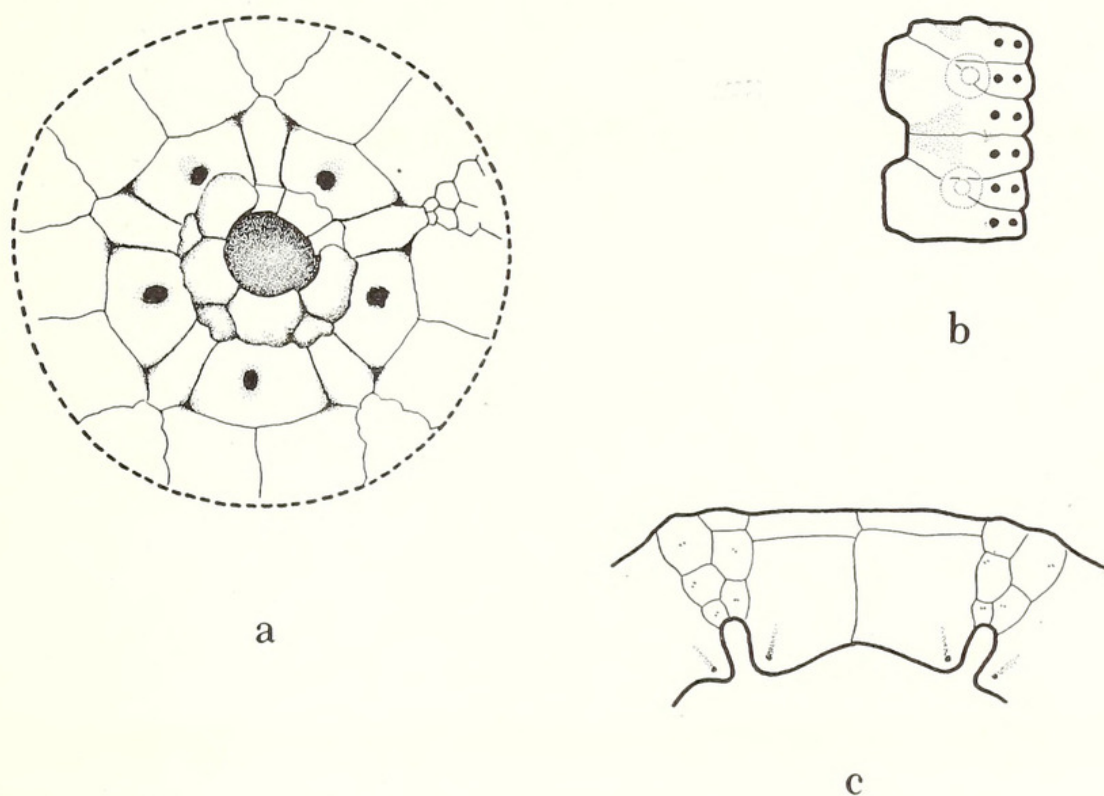


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Remarks. In a female specimen from St. Vincent Basin the apical system (Pl. 125, figs. 1, 2; text-fig. 1a) is dicyclic, with very elongate plates, particularly the oculars. The distal margins of the plates interlock with those of the corona at the deepest part of the adapical depression in a manner which has previously been inferred (cf. Philip 1969, p. 264, text-fig. 7a). However, proximally all of the plates are strongly inflected upwards to give a knob which contains the small periproct. This knob rises well above the level of the outer margin of the adapical depression so that in side view of the test it is clearly visible (Pl. 125, fig. 1). The madreporite cannot be recognized, but this presumably is because the surface of the depression has been overgrown with secondary calcite, obscuring surface detail.



TEXT-FIG. 1. *Paradoxechinus novus* Laube. a, Apical system of P27943 (♀); dashed line marks margin of adapical depression, $\times 8$ approx. b, Analysis of ambulacral plating of P18223 (♂), $\times 10$. c, Oblique view of plating structure within adapical depression of P18243 (♀), $\times 10$.

The structure and profile of the adapical depression is similar in all species of *Paradoxechinus* except *P. stellatus* sp. nov. (q.v.). In *P. novus* it begins developing at a size of about 8 mm horizontal diameter and in large specimens may be over two-thirds of the horizontal diameter (text-fig. 2d). The depression is deep (up to half of the vertical diameter) and sharply bounded by the sudden inflexion of the coronal plates at its borders. The portion of the corona within the depression is slightly concave.

The sculpture and primary tubercles cease abruptly at the margin of the depression and are replaced by granules which become smaller and more distant toward the apical system. In each zone two large interambulacral plates as well as a series of high ambulacral plates are contained in the depression (text-fig. 1c). At the rim of the depression

these simple ambulacral plates pass abruptly into normal echinoid compound plates. At the adradial apex of each of the enlarged interambulacral plate is a small pit which does not pierce the test.

An earlier comparison of the females of *P. novus* and *Hypsiechinus coronatus* Mortensen (Philip 1969) is now seen to be particularly apt. The females of the latter also possess a prominently elevated apical system in which the plates are strongly inflected to form a distinctive knob. The earlier comparison was based on the character of the coronal plates. In both species the upper interambulacral plates are remarkably high, lack primary tubercles, and are covered with small granules. In addition, the upper ambulacral plates (those within the marsupium of *Paradoxechinus*) are simple primaries.

It has previously been suggested that the high interambulacral plates of the females of *P. novus* might afford a barrier to prevent the introduction of new interambulacral plates after the marsupium was initiated. This is born out in text-fig. 2*a*. The females show from 19 to 21 interambulacral plates in each zone independent of size. In contrast the number of plates increases with size to 24 in the males. Other features of growth shown in text-fig. 2 are:

1. Peristome width does not vary significantly between the sexes (text-fig. 2*b*).
2. The males possess a significantly higher test than the females (although no doubt this difference is accentuated by the absence of apical systems in the measured specimens).

Of the 49 specimens it was possible to measure for the purposes of text-fig. 2, the average horizontal diameter of the 26 males was 12.4 mm and that of the 23 females was 10.9 mm.

An analysis of the echinoid ambulacral compounding in *P. novus* previously given by Philip (1969, text-fig. 7*c*), as published, is inverted. A new figure is given here (text-fig. 1*b*).

Paradoxechinus granulatus sp. nov.

Plate 129, figs. 4, 5, 9, 10, 18, 19; Plate 134, fig. 3

Diagnosis. A small species of *Paradoxechinus* with a depressed test and somewhat incised uniserial ambulacra. Surface of test covered with crowded secondary tubercles and granules so that, in large specimens, the zig-zagging sculptural ridges may be obscured.

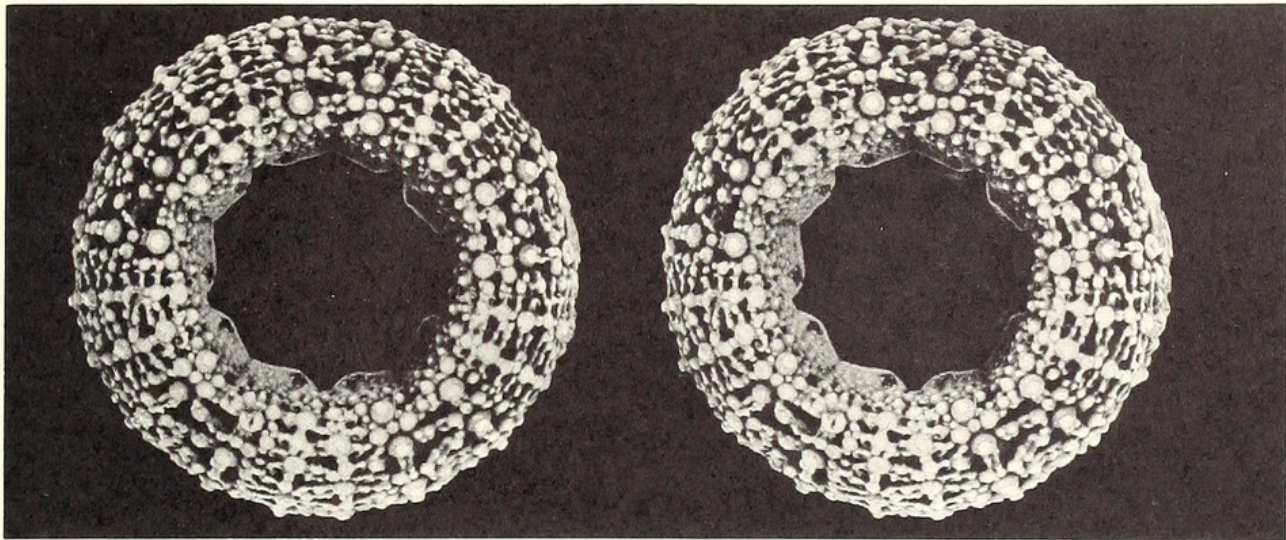
Material. Holotype P27947 (♀) and paratypes UNE 11757 (♀), UNE 11761 (♂) and two other specimens, Airey's Inlet, Anglesea District, Victoria, from the Point Addis Limestone of Junjukian (Upper Oligocene) age and probably Zone p. 22 of Blow. Seven poorly preserved specimens (5♀; 2♂) from Wool Bay, Yorke Peninsula, S.A., from the *Guembelitra stavensis* zone of the Oligocene in the Port Vincent Limestone, are also referred to this species.

EXPLANATION OF PLATE 127

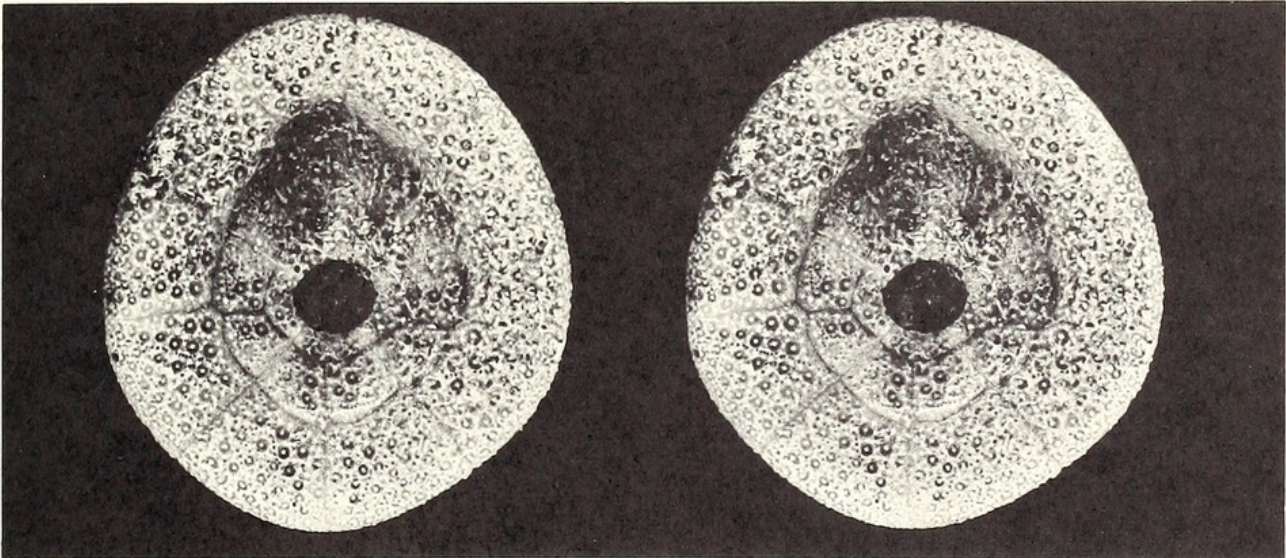
Fig. 1. *Paradoxechinus novus* Laube. Stereopair of adapical view of UNE 11523 (♀), ×5.

Fig. 2. *Willungaster scutellaris* gen. et sp. nov. Stereopair of adoral view of holotype, P27951 (♀), showing marsupial depression to the anterior of the peristome, ×5.

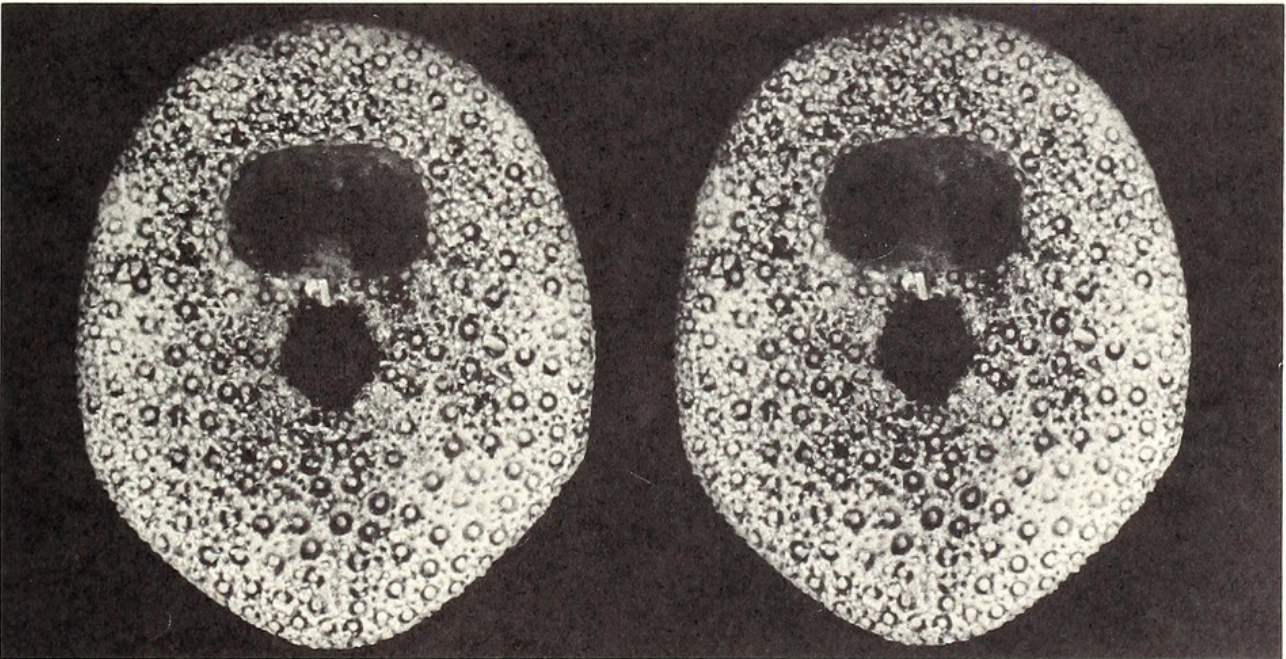
Fig. 3. *Fossulaster halli* Lambert and Thiéry. Stereopair of adoral surface of P19178 (♀), showing bilobed marsupium, ×8.



1

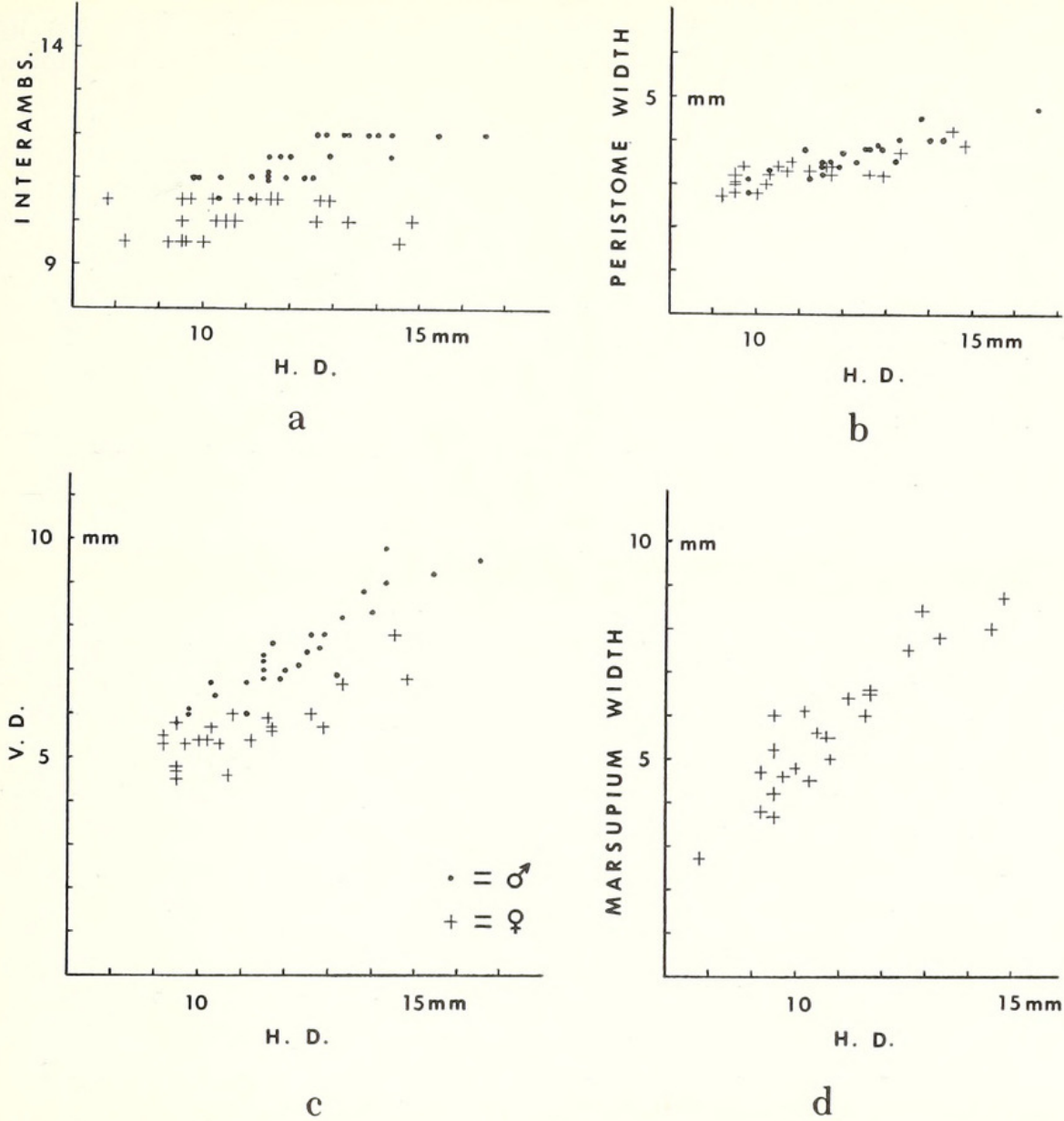


2



3

PHILIP and FOSTER, Marsupiate echinoids



TEXT-FIG. 2. Scatter-diagrams showing relationship of various test measurements in a collection of 49 specimens of *Paradoxechinus novus* Laube from the Adelaide Cement Holdings quarry, Wool Bay, Yorke Peninsula, S.A. *a*, Number of interambulacral plates per column against horizontal test diameter. *b*, Peristome width against horizontal test diameter. *c*, Vertical diameter (test height) against horizontal test diameter. *d*, Marsupium width of females against horizontal test diameter.

Description. Test of females low and depressed with a flattened adoral surface. Gill slits obscure; girdle as in other species of the genus.

Ambulacra about two-thirds of the width of the interambulacra with narrow, incised poriferous tracts. Pore-pairs sunken in transverse 'epi-stromal' ridges. The primary ambulacral tubercles form regular vertical series close to the poriferous tracts and slightly displace outward the median pore-pair of each triad.

Interambulacra with a regular vertical series of primary tubercles which are located somewhat adradially. In moderate sized specimens zig-zagged sculptural ridges are present (Pl. 129, fig. 14), but in larger specimens these are obliterated by coarse

secondary tubercles and granules, although depressions remain along the upper horizontal interambulacral sutures (Pl. 134, fig. 3). Crenulation of the primary tubercles visible in only one specimen.

The adapical depression of this species is as in *P. novus*.

Measurements of different species of Paradoxechinus (in mm)

	Horiz. diam.	Vert. diam.	Diam. apical depress.	Diam. peristome	No. amb.	No. interamb.
<i>P. granulosus</i> :						
P27947	12.7	6.0	8.0	4.1	9 (10)	9 (10)
<i>P. profundus</i> :						
P27945	19.0	—	10.5	5.5	—	—
<i>P. stellatus</i> :						
P27944	15.3	7.3	9.0	6.0	10	10 (11)
UNE 11753	17.0	9.0	9.5	5.5	10 (11)	11

Remarks. This species shows loss of sculpture during growth, a feature of many temno-pleurids (Philip 1969). Such a loss is brought about by rapid development of secondary tubercles and granules, which tend to coalesce, obscuring the ridges. All that remains of the juvenile sculpture on large specimens are irregular pits on the surface of the plates between secondary tubercles or along sutures (although, in *P. granulosus*, traces of sculptural ridges are visible on the adapical interambulacral plates). The coarsely granulated ambital and adoral portions of the test strongly resemble the ornament of the Australian Tertiary species *Ortholophus woodsi* (Laube) (cf. Philip 1969, pl. 8, fig. 11), which shows to a most marked degree loss of sculpture during growth.

Paradoxechinus profundus sp. nov.

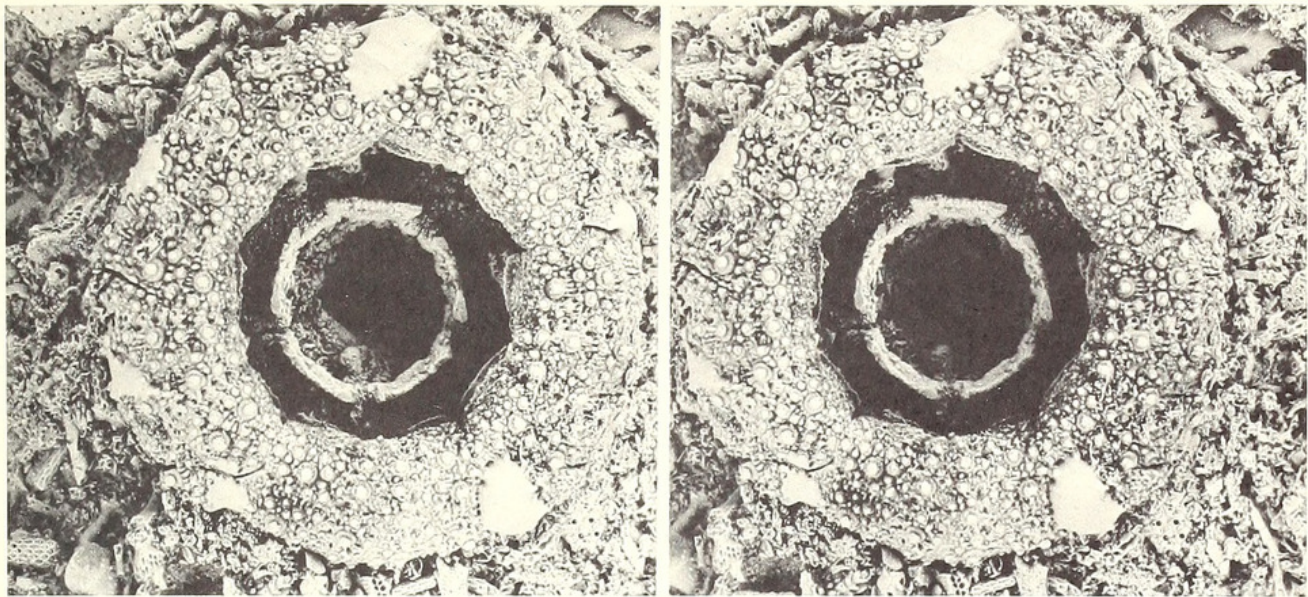
Plate 128, fig. 1; Plate 129, fig. 8; Plate 134, fig. 2

Diagnosis. A moderate sized species of *Paradoxechinus* in which the apical depression of female specimens is extremely wide and deep. Sculpture consisting of delicate, discontinuous multiple ridges which are most prominent between primary tubercles of the one column. Pore-pairs not embedded in 'epistroma', but flush with test.

Material. Holotype P27945 (♀), paratypes P27946 (♂), UNE 11754 (♀) and 6 other specimens (4♀, 2♂), Seaford, south of Port Noarlunga, S.A., from the middle Oligocene near the top of the *Subbotina angiporoides* zone in Zone pp. 19/20 of Blow in the Port Willunga Beds (see Lindsay 1970 for details). Two large specimens from the Mannum Formation (Lower Miocene) at Shell Hill, between Black Hill and Wongulla, River Marne, S.A., are questionably referred to the species.

EXPLANATION OF PLATE 128

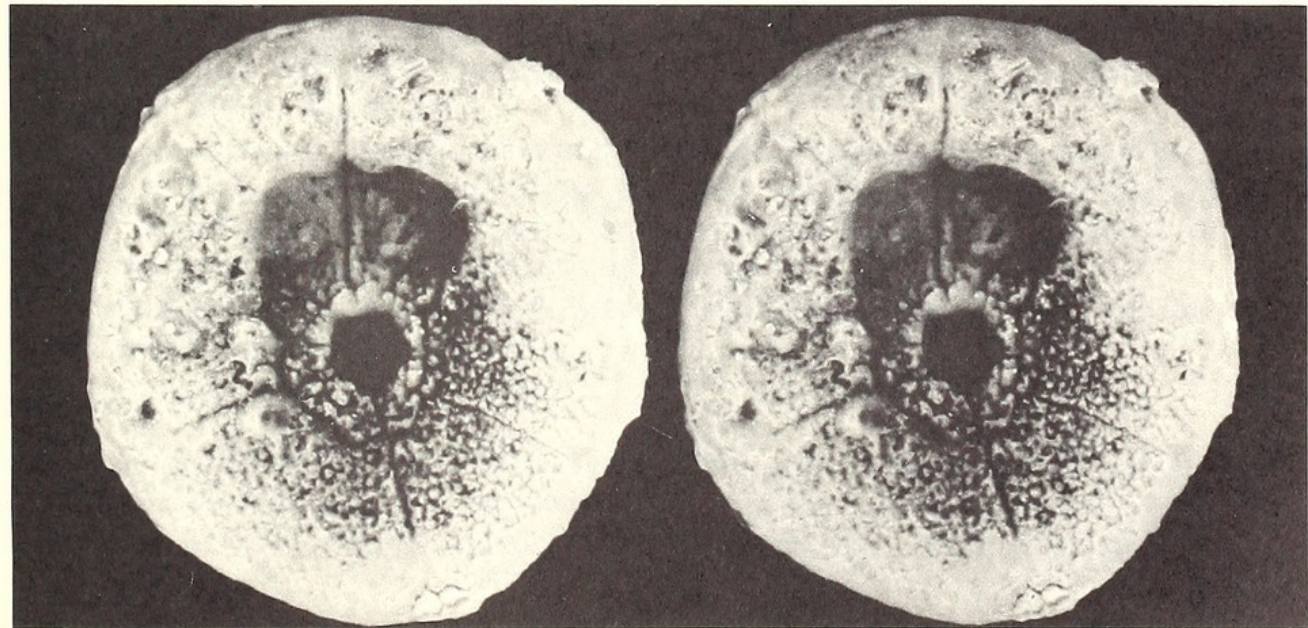
- Fig. 1. *Paradoxechinus profundus* sp. nov. Stereopair of adapical view of holotype, P27945 (♀), × 5.
 Fig. 2. *Peraspatangus depressus* gen. et sp. nov. Stereopair of adapical view of holotype, P27952 (♀), showing the comparatively shallow adapical marsupium, × 3.
 Fig. 3. *Fossulaster exiguus* sp. nov. Stereopair of adoral view of holotype, P27952 (♀), showing marsupial depression to the anterior of the peristome, × 12.



1



2



3

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Description. Test of females low and depressed with a flattened adoral surface. Gill slits very shallow; perignathic girdle of spatulate auricles, united above the ambulacra and connected by low apophyses.

Ambulacra about three-quarters of the width of the interambulacra, with a narrow poriferous tract in which the large pore pairs are flush with the test surface, and arranged in obscure arcs. Primary ambulacral tubercles forming a regular vertical series close to the poriferous tract.

Interambulacra with a regular vertical series of primary tubercles mounted close to the centre of each column. Typically, in large specimens, the sculpture consists of about six irregular, discontinuous vertical strands running between the primary tubercles, with fewer, less pronounced and less regular strands zig-zagging between primary tubercles (Pl. 134, fig. 2). Secondary tubercles and granules are present, either between or mounted on the sculptural ridges. Primary tubercles distinctly crenulate.

Apical depression of females wide and almost vertical sided.

Measurements. See under *P. granulosus*. The measurements are incomplete because the specimens from the type locality were fragile and could not be freed from their matrix.

Paradoxechinus stellatus sp. nov.

Plate 126, fig. 2; Plate 129, figs. 16, 20, 21, 22, 23;
Plate 134, fig. 1

Diagnosis. A large species of *Paradoxechinus* in which females possess a shallow, stellate adapical depression. Test closely tuberculated without obvious sculpture. Primary tubercles coarsely crenulate.

Material. Holotype P27944, paratype UNE 11753 and one other specimen (all ♀), mouth of Onkaparinga River just south of Port Noarlunga, S.A., Port Willunga Beds; high in *Turborotalia aculeata* zone, Zone p. 16 of Blow and Upper Eocene. Two specimens (♀), 1.5 miles north of Port Vincent, Yorke Peninsula, S.A., Rogue Formation, *Turborotalia aculeata* zone (Stuart, p. 169), Upper Eocene or early Oligocene.

Description. Test of females low and depressed with a flattened adoral surface. Peristome notched by shallow, buttressed gill-slits. Perignathic girdle unknown.

Ambulacra about two-thirds of the width of the interambulacra with narrow poriferous tracts in which the oblique pore-pairs are flush with the test, and arranged in obscure arcs within each triad. Primary ambulacral tubercles forming a regular vertical series close to the poriferous tract.

Interambulacra with a regular vertical series of primary tubercles mounted close to the centre of each column. Test lacking sculpture, but covered with closely spaced secondary tubercles and granules, some of which are tear-shaped, and radiate from the primary tubercles. Primary tubercles strongly crenulate.

Apical depression wide and shallow, with the five interambulacra within the depression more sunken than the ambulacra.

Measurements. See under *P. granulosus*.

Remarks. *Paradoxechinus stellatus* is readily separable from other species of the genus by the coarsely crenulate tubercles, the shallow star-shaped adapical depression, the complete lack of sculpture, and the distinct, buttressed gill-slits. These differences, in the

future, may necessitate its separation as a separate genus. At present, no males are known, nor has it been possible to establish the nature of the girdle.

Genus *PENTECHINUS* gen. nov.

Type species. Pentechinus mirabilis sp. nov.

Diagnosis. Small, sculptured temnopleurids with ambulacral pore-pairs arranged in distinct arcs of three. Gill slits shallow; girdle consisting of low styliform auricles, not united above the ambulacra and connected by relatively high apophyses. Adapical surface with five deep, interradian cavities which are floored by the proximal interambulacral plates and the distal extremities of the genital plates. Apical system dicyclic, with the genital pores opening into the interambulacral cavities.

Remarks. Although both of the available specimens are worn, so that the nature of the tubercles cannot be discerned, this genus is referred without question to the family Temnopleuridae. The elongate granules and the shallow pits between these are characteristic of many genera which lack well-defined sculpture in adult growth stages (e.g. *Pseudechinus*, *Genocidaris*, and *Ortholophus*). Indeed, the surface detail of the available specimens of *Pentechinus* is very similar to that of worn specimens of the common Australian Tertiary temnopleurid *Ortholophus woodsi* Laube (cf. Philip 1969, pl. 8, fig. 9).

Pentechinus mirabilis sp. nov.

Plate 124; Plate 129, figs. 1, 2, 3, 11, 15; text-figs. 3, 4.

Material. Holotype P27942, and paratype UNE 11512 both from Airey's Inlet, Anglesea District, Victoria, from the Point Addis Limestone of Janjukian (Late Oligocene) age. The holotype was bisected at the ambitus to reveal the perignathic girdle and internal features of the marsupia.

Description. Test small, somewhat pentagonal in outline, with a flattened adoral surface. Peristome relatively small, with shallow gill-slits. Auricles (Pl. 129, fig. 15) low and styliform, not united above the ambulacra, and connected by high apophyses, the peristomial faces of which are furrowed by continuations of the gill slits.

Apical system regularly dicyclic with raised oculars and with madreporic pores extending over two adjacent genitals. Surface of plates marked by obscure sculpture.

EXPLANATION OF PLATE 129

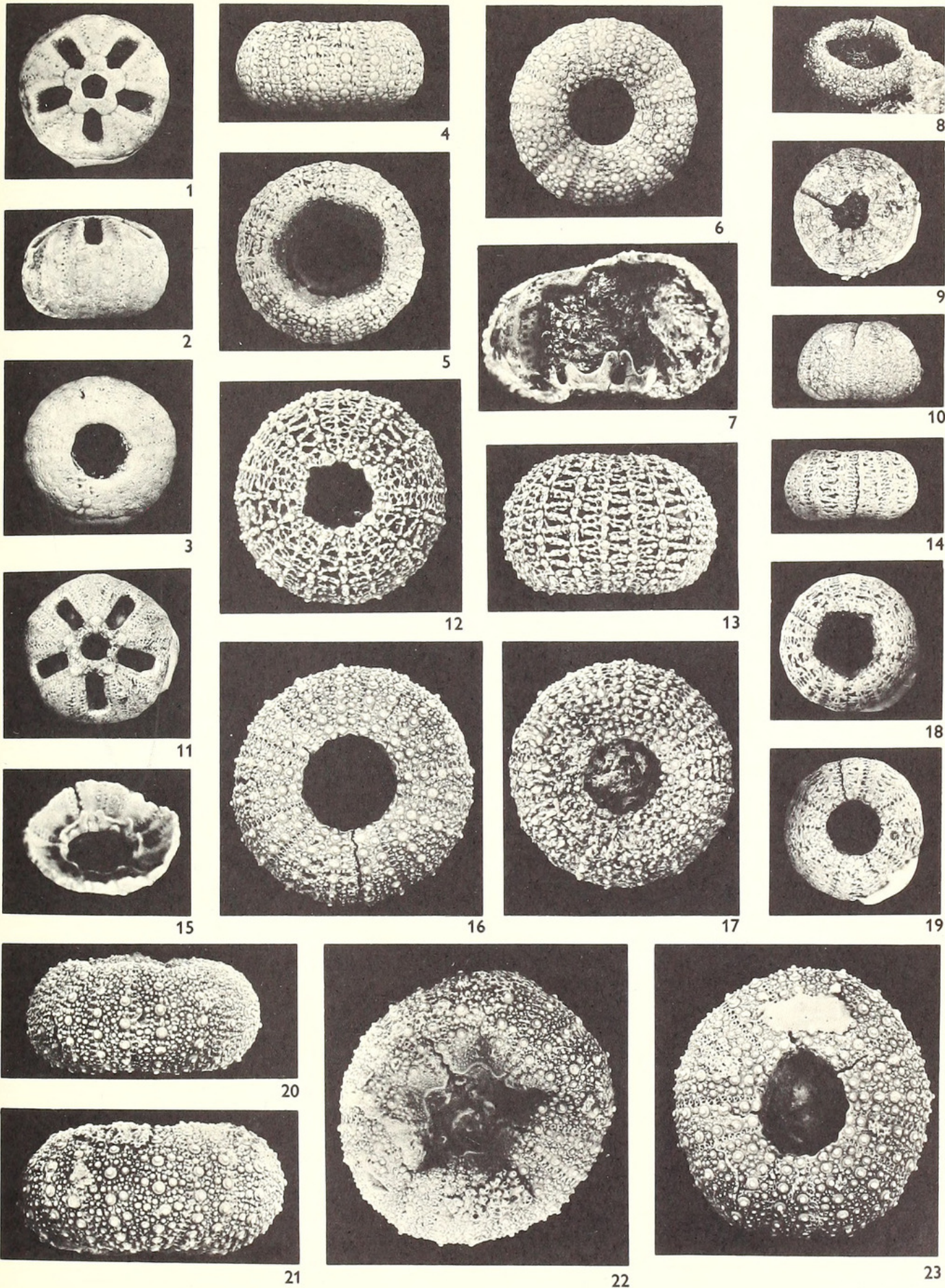
Figures $\times 2.5$ unless otherwise stated.

Figs. 1–3, 11, 15. *Pentechinus mirabilis* gen. et sp. nov. 1, Adapical view. 2, Lateral view. 3, Adoral view of paratype, UNE 11512 (♀). 11, Adapical view. 15, Oblique lateral view of the perignathic girdle of holotype, P27942 (♀).

Figs. 4–6, 9–10, 14, 18–19. *Paradoxechinus granulosus* sp. nov. 4, Lateral view. 5, Adapical view. 6, Adoral view of holotype, P27947 (♀). 9, Adapical view. 10, Lateral view of paratype, UNE 11761 (♂). 14, Lateral view. 18, Adapical view. 19, Adoral view of paratype UNE 11757 (♀).

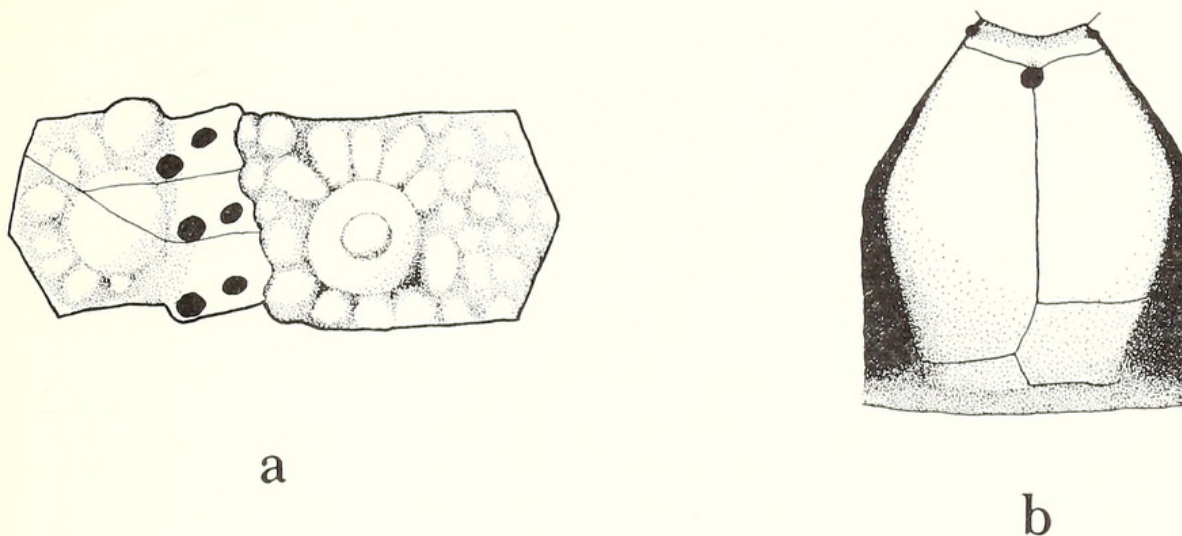
Figs. 7, 12, 13, 17. *Paradoxechinus novus* Laube. 7, Lateral view of a broken specimen, showing perignathic girdle, P11755 (♂). 12, Adapical view. 13, Lateral view. 17, Adoral view of UNE 11756 (♂), $\times 3$.

Figs. 16, 20–23. *Paradoxechinus stellatus* sp. nov. 16, Adoral view. 20, Lateral view of holotype, P27944 (♀). 21, Lateral view. 22, Adapical view. 23, Adoral view of paratype, UNE 11753 (♀).



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Distal portions of genitals strongly introverted to form the proximal walls of the marsupia. Genital pores large, and located at the extremity of the genital plates within the marsupia.



TEXT-FIG. 3. *Pentechinus mirabilis* gen. et sp. nov. *a*, Ornament of an ambital ambulacral and interambulacral plate, paratype, UNE 11512 (♀), $\times 20$ approx. *b*, Plating structure of one interambulacral marsupium, seen from the test interior (cf. Pl. 124, fig. 2), holotype, P27942, $\times 10$.

Ambulacra only slightly narrower than interambulacra with poriferous tracts narrow, and the pore pairs in each echinoid triad arranged in obscure arcs. Primary ambulacral tubercles mounted close to the poriferous tract, leaving a wide ambulacral mid-zone.

Interambulacra with regular vertical series of primary tubercles (apart from the adapical plates, which contribute to the marsupia). Test ornamented with closely spaced, often tear-shaped granules between which pits may be developed (text-fig. 3a).

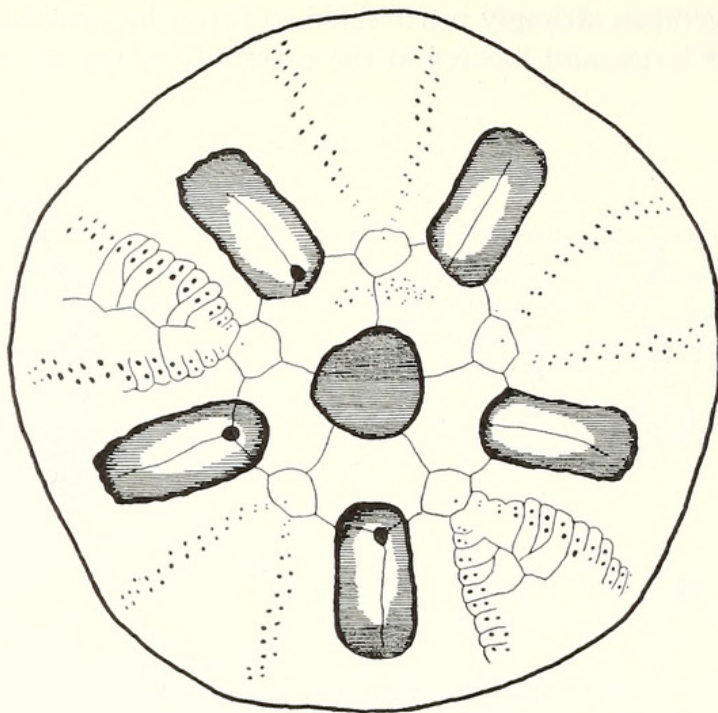
Marsupia with elongate interambulacral openings which extend from the apical system to about two-thirds of the distance to the ambitus. Internally they consist of flattened sac-like structures which extend beneath adjacent ambulacral columns. Much of each marsupium is formed by the proximal pair of interambulacral plates, which are elongated and meet along the floor of the marsupium in a straight median suture. One or two smaller interambulacral plates contribute to the distal portion of each marsupium. The proximal terminations are the distal ends of the introverted genital plates. The interambulacral plates comprising the marsupia all have surface expression, where they are covered by closely spaced granules. The inner surfaces of the marsupia are smooth.

Males unknown.

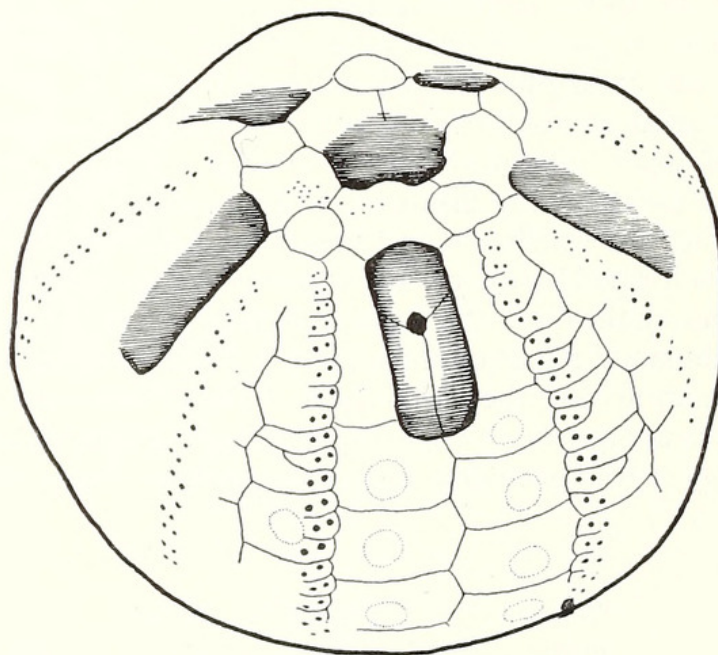
Measurements (in mm).

	Horiz. diam.	Vert. diam.	Peristome diam.	Apical system diam.	No. amb.	No. interamb.
UNE 11512	9.5	6.6	3.2	3.8	11 (12)	9

Remarks. By analogy with other urchins it must be supposed that the remarkable marsupia of *Pentechinus* developed in the growing test at or immediately prior to sexual maturity. It is difficult to envisage how this could take place except through a complex



a



b

TEXT-FIG. 4. *Pentechinus mirabilis* gen. et sp. nov. a, Adapical view of holotype, P27942. Specimen tilted to show genital pores in three of the marsupia. b, Oblique adapical view of same specimen, $\times 10$.

interaction of growth and resorption, or even growth within an ossicle, rather than at its margins.

No further comment would be merited were it not for Durham's (1966*b*, p. 390) recent statement that in echinoids 'Resorption . . . does not occur between adjacent plates'. Yet such resorption is well known. Hawkins (1913) used the term 'plate crushing' to describe the formation of 'plates lessened in height and restricted in width' during growth. The formation of demiplates in the anterior ambulacrum of *Echinocardium cordatum* he ascribed to this process, to the satisfaction of later workers concerned with spatangoid ambulacral morphology (e.g. Chesher 1963, p. 555). Philip (1957) substituted the term 'plate atrophy' when describing the diminution in size with growth of the ambital interambulacral plates of the Miocene spatangoid *Lovenia woodsi*. Among regular echinoids, the very complex aggregation of pores seen in some living diadematids is a secondary development, late in the ontogeny of the urchin, and is brought about by resorption of the median zone (plus tubercles) of the adoral ambulacra (cf. Mortensen 1940, pp. 163-164).

Order CLYPEASTEROIDA A. Agassiz
Suborder CLYPEASTERINA A. Agassiz
Family FOSSULASTERIDAE nov.

Diagnosis. Small, flattened clypeasteroids with separate auricles, and lacking demiplates in the petalloid ambulacra. Ambulacral food grooves simple or absent; apical system with four genital pores. Periproct supramarginal; interambulacra not extending on to the adoral surface.

Included genera. *Fossulaster* Lambert and Thiéry 1925, *Scutellinoides* Durham 1955, *Willungaster* gen. nov.

Remarks. The three genera listed above, all from the Tertiary of south-eastern Australia, stand well apart from other clypeasteroids in possessing separate auricles and simple plates in the petalloid ambulacra.

Mortensen (1948) divided the Clypeasteroida into two suborders, as advocated by Philip (1965*a*) and supported by Kier's (1970, p. 105) study of clypeasteroid lantern supports. All previously described clypeasterinid echinoids have, beside their separate auricles, demi-plates in the petals.

Scutellinoides was referred by Durham (1955, 1966) to the family Arachnoididae on the assumption that the genus possessed demi-plates. However, Durham regarded *Fossulaster* as *incertae sedis* with the suggestion (1955, p. 131) that the ambulacral plates may be simple.

Scutellinoides is based on *Scutellina patella* Tate 1891, but, in reality, has been interpreted through *Scutellina morgani* Cotteau 1891 (e.g. Durham 1966*a*, p. U468) in the belief that these species are the same. The lectotype of *Scutellina patella* Tate is here chosen as Adelaide University Geology Department T27A, the largest of Tate's eleven unfigured syntypes and the specimen that conforms most closely to the first of his measured specimens. Its locality is given as the 'Murray River Cliffs' S.A., where its parent stratum is interpreted as the Morgan Limestone. The lectotype and the abundant material of this species available from the Morgan Limestone indicate that ambulacral petals are lacking.

Scutellina morgani Cotteau is based on a single specimen housed in the École des Mines, Paris, and is from the Gambier Limestone at Mount Gambier, S.A., where the species is common. Examination of the holotype reveals that it is correctly portrayed by Cotteau, i.e. it has well-developed ambulacral petals. *S. morgani* and *S. patella* are similar in possessing separate auricles, and in details of their plating structure. However, because of differences in the ambulacra, here they are not considered to be congeneric. An account of these species, together with closely related forms, will be given elsewhere.

Genus FOSSULASTER Lambert and Thiéry

1925 *Fossulaster* Lambert and Thiéry, p. 577.

1955 *Fossulaster* Lambert and Thiéry; Durham, p. 129.

Type species. Fossulaster halli Lambert and Thiéry.

Diagnosis. Small clypeasterinids with ovate outline; periproct supramarginal, separated from the ambitus by 2 or 3 pairs of interambulacral plates. Ambulacral petals poorly defined, when apparent, open and with small non-conjugate pores. Ambulacral food groove simple and often poorly defined. Apical system with four genital pores. Interambulacral columns narrow and extending only to the ambitus. Girdle of small poorly developed, separate auricles; marginal concentric supports moderately developed; inner supports variable. Females with a marsupium on the adoral surface to the anterior of the peristome.

Fossulaster halli Lambert and Thiéry

Plate 125, fig. 3; Plate 127, fig. 3; Plate 130, figs. 1–10;

Plate 131, fig. 6; Plate 132, fig. 10; text-figs. 5, 6

?1898 *Scutella marsupiata* Tate, p. 196 (*nomen nudum*).

1908 *Scutellina* sp. (? *S. patella* Tate) Hall, pp. 140–142, text-fig.

1916 *Echinocyamus patella* (Tate) Chapman, pp. 182–183, pl. 45, fig. 23.

1925 *Fossulaster halli* Lambert and Thiéry, p. 577.

1946 *Scutellina patella* Tate; H. L. Clark, p. 351 (in part).

1955 *Fossulaster halli* Lambert and Thiéry; Durham, pp. 129–131, figs. 38 a–b.

1966 *Fossulaster halli* Lambert and Thiéry; Durham, p. U468, fig. 3.

1969 *Fossulaster halli* Lambert and Thiéry; Kier, pl. 14, figs. 1–4.

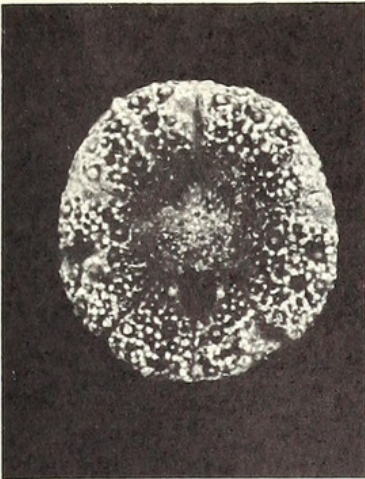
Diagnosis. A moderately large species of *Fossulaster* in which females possess a deep, bilobed marsupium. Ambulacral petals poorly developed.

Material. Hypotypes P19178 (♀), P19179 (♀), P19180 (♂), P19181 (♂), P19182 (♀), P19183 (♀), P19184 (♀), and P19185–P19196 (8♂, 2♀, 2 indet.) from Mt. Gambier, from the Gambier Limestone of Longfordian (Lower Miocene) age. P27942 (♀), P27948 (♀), UNE 11762, UNE 11763, UNE 11764, and 88 other specimens (46♂, 32♀, 10 indet.) from the Gambier Limestone at Nelson, Victoria. Fourteen specimens (9♂, 5♀) from Coobowie, just north of bridge over Salt Creek, Yorke Peninsula, S.A., from the Port Vincent Limestone from the Janjukian or Longfordian (Upper Oligocene or Lower Miocene).

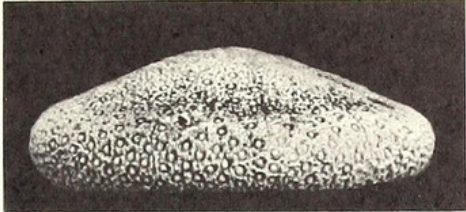
EXPLANATION OF PLATE 130

Figures $\times 5$ unless otherwise stated.

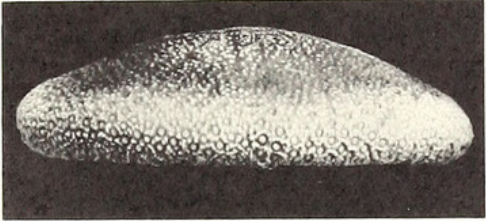
Figs. 1–10. *Fossulaster halli* Lambert and Thiéry. 1, Adapical view of UNE 11762, $\times 10$. 2, Lateral view of UNE 11760 (♂). 3, Lateral view. 4, Adapical view. 8, Adoral view of P19180 (♂). Circular hole in posterior part of test due to some boring organism. 5, Lateral view of P27942 (♀). 6, Lateral view of P19178 (♀). 7, Adapical view of UNE 11763, $\times 10$. 9, Adoral view of P19179 (♀), $\times 10$. 10, Adapical view of P27942 (♀), $\times 10$.



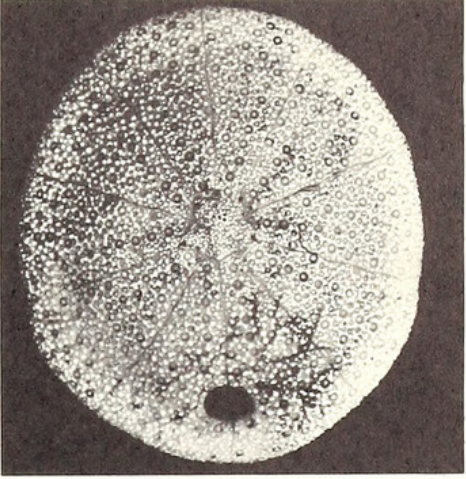
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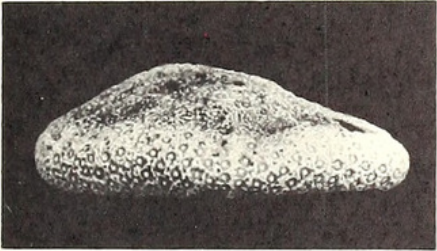
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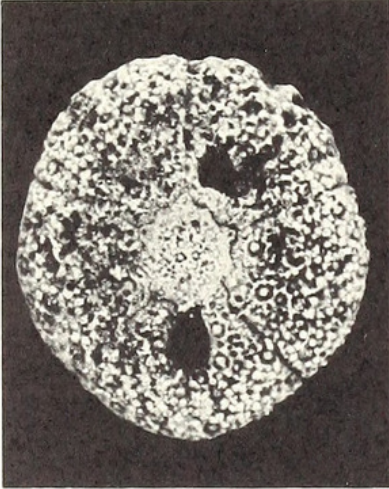
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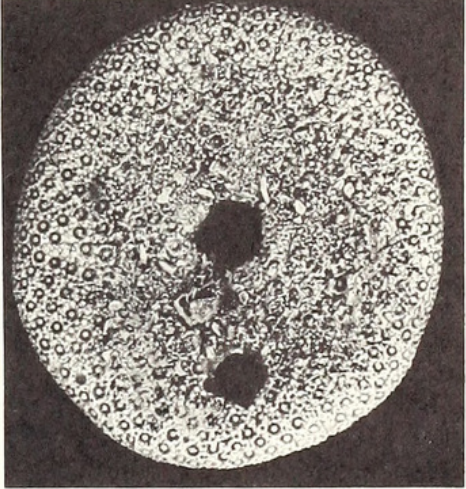
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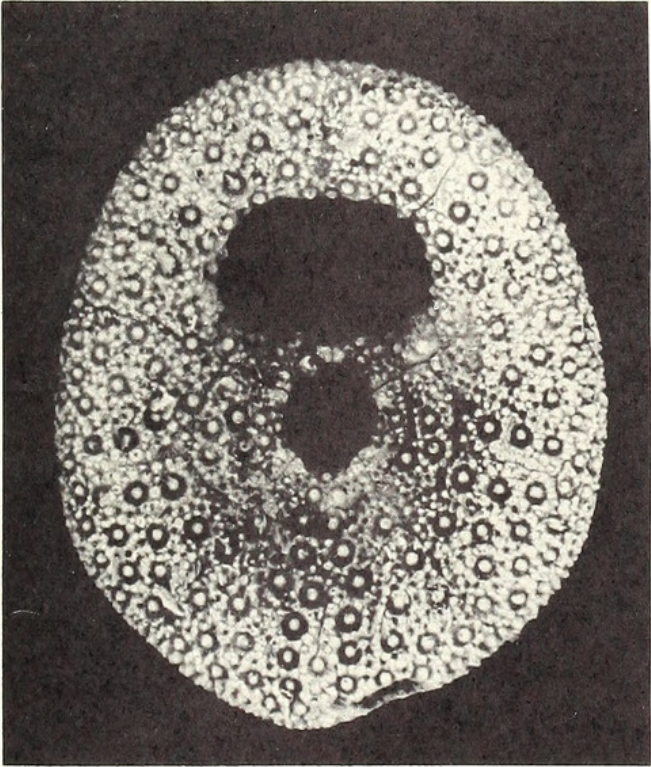
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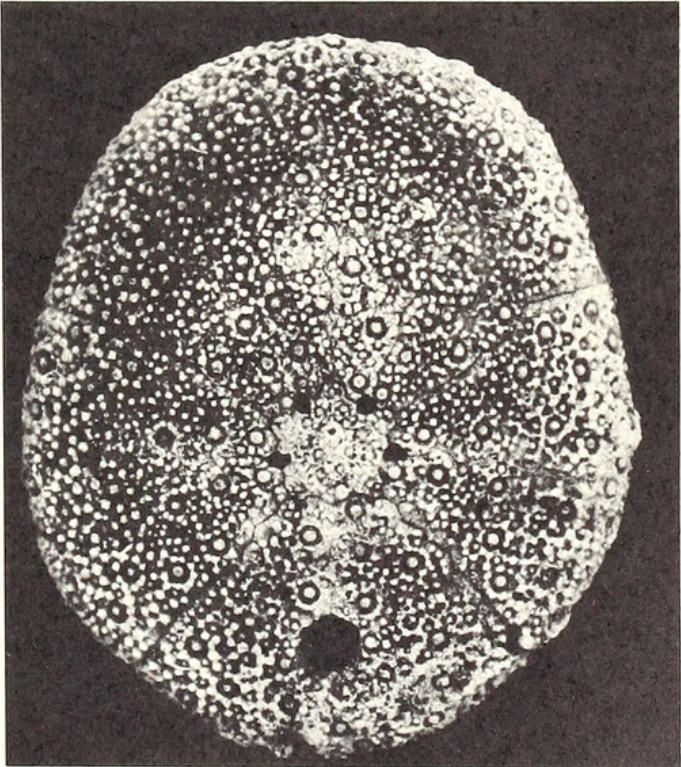
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8



9



10



Philip, G M and Foster, R J. 1971. "Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance." *Palaeontology* 14, 666–695.

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