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# TERTIARY SPECIES OF *ECHINOLAMPAS* (ECHINOIDEA) FROM SOUTHERN AUSTRALIA

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**Abstract**

Representatives of the genus *Echinolampas* are the most widely distributed cassiduloids occurring through the Tertiary rocks of southern Australia. Although some species were named by the turn of the century mostly they remain poorly defined and inadequately illustrated. In three nominal species the type material is lost and so there is need for the names to be stabilised. This paper presents a revision of all known species from southern Australia, including previously described species and three new forms: *E. posterocrassa curtata* subsp. nov., *E. gregoryi* sp. nov. and *E. gregoryi corrugata* subsp. nov. The ontogenetic development of *Echinolampas* is described and discussed.

## Introduction

*Echinolampas* is a most compact, morphologically conservative and widely spread genus which achieved world-wide distribution throughout most of the Tertiary. According to Roman (1965, p. 689) more than 285 species have been recognised. Attempts to subdivide the genus have not found acceptance (Kier, 1962). The Indian Ocean species, *Echinolampas ovata* (Leske), which occurs along the northwest coast of Australia (Clark, 1946), represents the sole living representative occurring in Australian waters.

Material for this study came from collections in the British Museum (Natural History), London (BM); l'École des Mines, Paris; the National Museum of Victoria (NMV); the Western Australian Museum (WAM); Adelaide University, Geology Department (AUGD) and R. J. Foster.

## Systematic Palaeontology

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|---|---|
| Order | CASSIDULOID Claus, 1880 |
| Suborder | CASSIDULINA Claus, 1880 |
| Family | ECHINOLAMPADIDAE Gray, 1851 |
| Genus | **Echinolampas** Gray, 1825 |

*Type species: Echinus oviformis* Gmelin, 1789, by the subsequent designation of Pomel, 1883, p. 62.

### Echinolampas posterocrassa posterocrassa Gregory, 1890
(P1. 1, Figs 1-6)

1890 *Echinolampas posterocrassus* Gregory, pp. 483-484, P1. 13, figs 4.6.
1891 *Echinolampas posterocrassus* Gregory; Tate, p. 276
1892 *Progonolampas Novae-Hollandiae* Bittner, pp. 357-359, P1. 3, fig. 1.
1892 *Echinolampas posterocrassus* Gregory; Tate, p. 193.
1892 *Echinolampas* cf. *posterocrassa* Gregory; Bittner, pp. 356-357.
1921 *Echinolampas* (*Miolampas*) *posterocrassa* Gregory; Lambert & Thiéry, p. 383.
1921 *Echinolampas* (*Progonolampas*) *Novae-Hollandiae* (Bittner); Lambert & Thiéry, p. 387.
1930 *Echinolampas posterocrassus* Gregory; Brighton, p. 569.
1930 *Echinolampas novae-hollandiae* (Bittner); Brighton, p. 569.
1946 *Echinolampas posterocrassa* Gregory; Clark, p. 359.
1948 *Progonolampas Novae-Hollandiae* Bittner; Mortensen, p. 272, figs 260a-c.
1962 *Echinolampas posterocrassus* Gregory; Kier, pp. 113-115, P1. 32, figs 5-7, text fig. 66.
1965 *Echinolampas posterocrassa* Gregory; Roman, p. 295.

*Type specimen*: The holotype is the poorly preserved specimen figured by Gregory (1890, P1. 13, figs 4-6) from 'Willunga, near Adelaide', and is registered in the British Museum (Natural History) as E3381.

*Material, localities and horizons*: Tate (1891, p. 276) recorded *E. posterocrassa* only from the 'glauconitic limestone, Aldinga cliffs', *i.e.* the Tortachilla Limestone (early Late Eocene). The species has been collected from this formation in the Maslin Beach (north of Blanche Point) to Port Willunga district. In all, forty specimens from the Tortachilla Limestone have been studied. In addition twenty specimens have been recovered from an unnamed formation at Kingscote, Kangaroo Island, which is probably early Late Eocene in age, like the Tortachilla Limestone, and a further twenty specimens are known from the Nanarup Limestone member of the Late Eocene Werillup Formation near Nanarup, Western Australia.

*Diagnosis*: Test is low in small individuals, higher in larger individuals; sub-pentagonal in outline; apex set posterior of apical system, in small and medium-sized individuals, but almost coincident with it in largest individuals. Rostrum is well developed. Maximum width of test is posterior to apex. Apical system small and low, set one-third test length from anterior, bearing one to five tubercles. Ocular plates tumid adapically. Petals long and lanceolate, not closing distally. Pore-pairs circular and conjugate. Interporiferous zone narrow, poorly tuberculate, bearing, on average, one tubercle every other ambulacral plate. Poriferous tracts of petals markedly unequal in length. Adoral surface pulvinate with moderately depressed, sub-pentagonal peristome; bourrelets poorly developed. Sparsely tuberculate adorally; broad, non-tuberculate, sagittal tract present adorally on interambulacrum V.

*Discussion:* The collections from the Tortachilla Limestone reveal that only one species of *Echinolampas* is present. Tate (1892, p. 193) was of this opinion when he questioned the validity of Bittner's (1892) new genus and species *Progonolampas Novae-Hollandiae*. Bittner based his taxon on one of three specimens labelled *E. posterocrassa* sent him by Tate. Tate (1891, p. 276) held that *E. posterocrassa* was restricted to the 'glauconitic limestone, Aldinga cliffs', *i.e.,* the Tortachilla Limestone, and (1892, p. 193) asserted that "the specimens forwarded to Vienna are authentic examples of Gregory's species", adding "I most strongly protest against such reckless species-making". Later workers (Kier, 1962, p. 115; Roman, 1965, p. 295) have followed Tate's interpretation. Bittner's (1892, Pl. 3, fig. 1) drawing of his specimen shows it to be very like *E. posterocrassa posterocrassa*, although somewhat unusual in its well-rounded posterior termination. Unfortunately Bittner's specimen is now lost. Although the available specimens of *E. posterocrassa posterocrassa* show little variation in outline, it is here concluded that Bittner based his new species on a specimen of *E. posterocrassa posterocrassa*. Reasons for regarding *Progonolampas* as a synonym of *Echinolampas* have been fully discussed by Mortensen (1948, p. 278) and Kier (1962, p. 115).

In its well rounded shape and petals which are parallel-sided distally, *E. posterocrassa posterocrassa* compares with the younger *E. morgani*. It can be distinguished, however, by its larger size (up to 60mm test length), broader test, more medially positioned apex, smaller apical system with tumid ocular plates, longer poriferous tracts which are more unequal in length, and conjugate pore-pairs. In *E. morgani* (as in *E. gambierensis* and *E. tatei*) interambulacrum V is fully tuberculated adorally; in *E. posterocrassa posterocrassa* a broad sagittal band bare of tubercles is present (Pl. 1, fig.

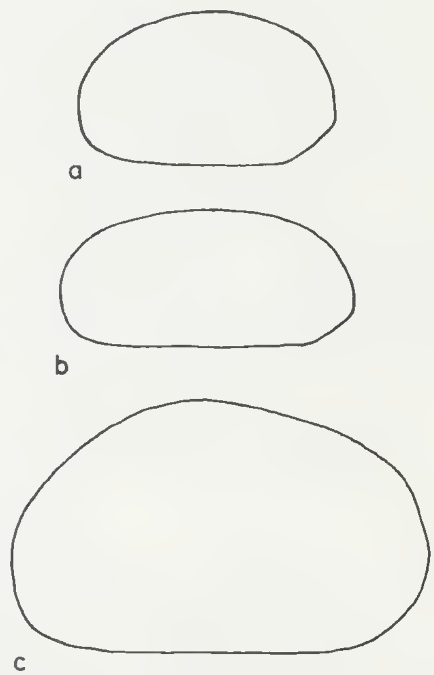


Figure 1—Lateral profiles of *Echinolampas posterocrassa posterocrassa* Gregory, 1890; a, NMV P55448, from the Tortachilla Limestone, Willunga, South Australia; b, WAM 72.52e from the Nanarup Limestone Member of the Werillup Formation of the Plantagenet Group, Nanarup Quarry, Western Australia; c, NMV P55446, from an un-named formation of Late Eocene age at Kingscote, Kangaroo Island, South Australia; all x1.

2); a similar zone exists in *E. ovula*, but it is much narrower.

The difference in lengths of the poriferous tracts of the petals is most marked in *E. posterocrassa posterocrassa*. In a specimen 35 mm in length the number of pore-pairs varies between 6 and 12. Even so, the difference is always greater than in *E. gambierensis, E. ovula, E. morgani* or *E. tatei.*

Specimens from the Late Eocene at Kingscote, Kangaroo Island referable to *E. posterocrassa posterocrassa* differ from topotype material only in the larger size attained. Some specimens from the Nanarup Limestone near Albany, W.A. tend to be slightly flatter than topotype specimens of corresponding test length (Fig. 1b). In all other respects they are identical with *E. posterocrassa posterocrassa* and so identified with the Tortachilla Limestone species. A collection from the younger Oligocene Port Vincent Limestone, however, shows sufficient differences to be distinguished as a separate subspecies of *E. posterocrassa*.

**Echinolampas posterocrassa curtata** subsp. nov.
(Pl. 1, figs 7-9)

*Type specimen*: The holotype of the subspecies is NMV P55451 from the Port Vincent Limestone in the Adelaide Cement Holdings Quarry, 4 km north of Wool Bay, east coast of Yorke Peninsula, South Australia (see McGowran *et al.*, 1971). Paratypes from the same locality are NMV P55452 and P55453.

*Material, locality and horizon*: In addition to the type specimens four other specimens are known from the same locality. This horizon is referred to the *Guembelitria stavensis* Zone (Stuart, 1970, p. 174) of the Oligocene and Zone P. 21 of Blow (1970).

*Diagonsis*: A subspecies of *E. posterocrassa* with short petals and swollen bourrelets; peristome and periproct small.

*Discussion*: The poriferous tracts of ambulacra I and V are shorter than those of *E. posterocrassa posterocrassa*, possessing on average, three-quarters of the number of pores. Although *E. posterocrassa curtata* possesses relatively fewer pore-pairs than *E. posterocrassa posterocrassa*, the difference in length of the poriferous tracts in each petal is similar. The phyllodes of *E. posterocrassa curtata* are more sunken than those of *E. posterocrassa posterocrassa* and so the bourrelets are correspondingly more swollen. With growth of the test, swelling of the bourrelets was largely in a vertical direction so that the outline of the peristome remains oval. In *E. posterocrassa posterocrassa*, however, the swelling of the bourrelets (which occurred at a much later stage of growth than in *E. posterocrassa curtata*) was largely in a horizontal direction so that the peristome developed a pentagonal outline.

The slightly smaller periproct and peristome of *E. posterocrassa curtata* is apparent in comparing Pl. 1, fig. 4, and Pl. 1, fig. 8.

The trivial name for the new subspecies derives from the Latin *curtatus*, meaning "shorten".

**Echinolampas morgani** Cotteau, 1889
(Pl. 1, figs 10-13, Pl. 2, figs 1-3)

1889 *Echinolampas morgani* Cotteau; pp. 546-547, Pl. 12, figs. 13-15.
1891 *Echinolampas morgani* Cotteau; Cotteau, pp. 144-146, Pl. 18, figs. 13-15.
1892 *Echinolampas gambierensis* Tenison Woods: Tate, p. 193 (*pars.*).
1921 *Echinolampas* (*Isolampas*) *morgani* Cotteau; Lambert & Thiéry, p. 380.
1930 *Echinolampas morgani* Cotteau; Brighton, p. 568.
1965 *Echinolampas morgani* Cotteau; Roman, p. 291.

*Type specimen:* The holotype, the single specimen on which Cotteau based this species, is an unnumbered specimen in the Cotteau Collection, École des Mines, Paris. It is from 'Mount Gambier', *i.e.*, the Gambier Limestone of Longfordian (Early Miocene) age.

*Material, localities and horizons:* Twenty-five specimens are known from the Gambier Limestone. In addition to those from Mt. Gambier, specimens have been collected from Peuker's Quarry, 5 km north-east of Mount Gambier, the Glenelg River north of Nelson in Victoria, and a quarry 2 km north of Nelson.

Additional material includes: twenty-two specimens from the Longfordian Mannum Formation from the cliffs of the Murray River between Swan Reach and Mannum; forty-one specimens from the early Early Miocene (probably Longfordian) Port Vincent Limestone from the sea cliffs between Giles Point and Coobowie; fourteen specimens from the same horizon in the Abrakurrie Limestone in the road cut where Highway 1 descends the Hampton Scarp at Madura, Western Australia.

*Diagnosis:* Test small and well-rounded; flat adapically with highest point almost two-thirds of the test length from the anterior end. Rostrum variably developed. Maximum width of test anterior to the apex. Apical system less than one-third test length from the anterior to the apex. Apical system less than one-third test length from the anterior end, well domed, and non-tuberculate. Petals short and lanceolate; not converging distally. Interporiferous zone narrow, flat and sparsely tuberculated, approximately one tubercle every ambulacral plate. Pores circular and not conjugate. Poriferous tracts within each petal differing only slightly in length. Adoral surface pulvinate with a quite deeply sunken, oval peristome. Floscelle small with bourrelets hardly developed; phyllodes small. Periproct at high angle (between 40°-55°) to the adoral surface.

*Discussion:* The only appreciable difference between specimens of *E. morgani* from the Gambier Limestone and those from the Mannum Formation is in the degree of development of the rostrum on the aboral interambulacrum V. It is always present in the Gambier Limestone forms (Pl. 2, fig. 2), but the material from both the Mannum Formation and the Port Vincent Limestone shows much more variation in this feature (Fig. 2). In some specimens, therefore, the rostrum is hardly developed, so that their outline is more circular (Pl. 1, fig. 13).

This species is characterised particularly by its low profile but tumid shape, and its short, lanceolate petals. Compared with other species of *Echinolampas* from the Australian Tertiary, *E. morgani* possesses the shortest petals with

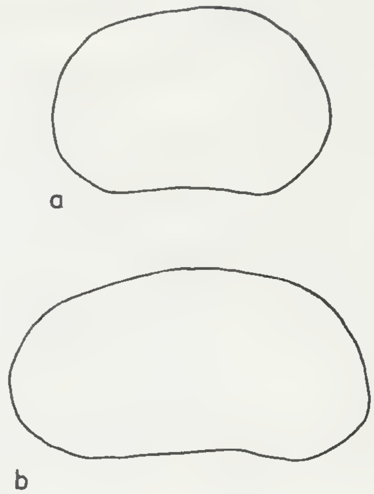


Figure 2—Lateral profiles of *Echinolampas morgani* Cotteau, 1889; a, NMV P55454, from the Mannum Formation, Murray River Cliffs, South Australia; b, NMV P19176, from the Gambier Limestone, Mt. Gambier, South Australia; both x1.

the fewest pore-pairs. The number of pore-pairs present in the longer poriferous tract in ambulacra I or V is somewhat variable, between 22 and 28 in a specimen of *E. morgani* 40 mm in length. By comparison, in specimens of similar size, *E. ovulum* has between 26 and 34, *E. gambierensis* between 32 and 35, and *E. posterocrassa* between 32 and 41 pore pairs (Fig. 5b).

Although *E. morgani* and *E. posterocrassa* have tests of similar size, they differ conspicuously in the apical system which in *E. morgani* is proportionately larger. In addition, whereas the ocular plates in *E. morgani* are depressed (as they are in *E. gambierensis*) they are domed in *E. posterocrassa*.

*E. morgani* is the smallest species of *Echinolampas* so far known from the Australian Tertiary. The largest test has a maximum length of 50 mm.

**Echinolampas ovulum** Laube, 1869
(Pl. 2, figs 4-8)

1869 *Echinolampas ovulum* Laube, pp. 191-192.
1877 *Echinolampas ovulum* Laube; Duncan, pp. 44, 66.
1885 *Echinolampas ovulum* Laube; Tate, p. 37.
1885 *Echinolampas gambierensis* Tenison Woods; Tate, p. 41 (pars.).

1887 *Echinolampas ovulum* Laube; Duncan, p. 420.
1890 *Echinolampas ovulum* Laube; Gregory, p. 483, ?P1. 13, figs 7-8.
1891 *Echinolampas gambierensis* Tenison Woods; Tate, p. 276 (pars.).
1892 *Echinolampas ovulum* Laube; Bittner, p. 357.
1921 *Echinolampas* (*Miolampas*) *ovulum* Laube; Lambert & Thiéry, p. 383.
1930 *Echinolampas ovulum* Laube; Brighton, p. 568.
1965 *Echinolampas gambierensis* Tenison Woods; Roman, p. 281 (pars.).
non 1847 *Echinolampas ovulum* Tallivignes; p. 1141 (*nomen nudum*).

*Type specimen:* The original specimen on which Laube founded this species is no longer in the collections of the Naturhistorisches Museum, Vienna, and must be presumed lost. It is not known for certain whether or not the specimen which Gregory (1890, P1. 13, figs 7, 8) attributed to *E. ovulum* does in fact belong to this species (see below). Consequently for taxonomic stability NMV P55457 (P1. 2, figs 4-7) from the Mannum Formation (Early Miocene) at Blanchetown, Murray River, is here chosen as neotype.

*Material, localities and horizon:* This species is represented in the collections by nine specimens, all from the Mannum Formation from the Murray River at: Swan Reach, Blanchetown, Nildottie, River Marne and Younghusband. It is not known from any other horizon or locality.

*Diagnosis:* Test large and of variable height (see P1. 2, fig 6 and Fig 3b), but is flattened adapically; rostrum moderately developed. Apical system close to mid-length. Petals very wide and confluent distally. Interporiferous zone flat to gently domed; poriferous tracts only slightly unequal in length. Pores well separated, inner smaller and more circular than tear-shaped outer pores; connected by long, narrow canal whose length equals twice the pore diameter. Each ambulacral plate bears 4-5 tubercles. Adoral surface moderately pulvinate. Periproct shallow and pentagonal. Floscelle with weakly tumid bourrelets and narrow phyllodes. Test densely tuberculate; tubercles large. A narrow sagittal band on the adoral surface of interambulacrum V lacks tubercles, but bears fine granules; these commonly occur between the tubercles on the adoral surface.

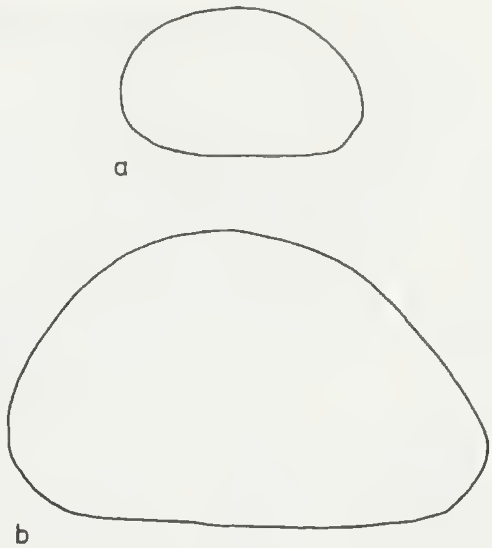


Figure 3—Lateral profiles of *Echinolampas ovulum* Laube, 1869; a, NMV P55459, from the Mannum Formation, River Marne, South Australia; b, NMV P55458, from the Mannum Formation, Nildottie, South Australia; both x1.

*Discussion:* This species has had a rather chequered history. Laube's (1869, p. 191) original description was brief and not accompanied by any illustration of the species. Although Duncan (1877, p. 66; 1887, p. 420) was convinced of the validity of the species, Tate (1885, p. 41) considered it synonymous with *E. gambierensis*. Duncan (1887, p. 420) gave some dimensions of a specimen which he considered to be *E. ovulum*, but provided no details concerning the locality from which it had come. Later, however, Gregory (1890, p. 483) published dimensions of Laube's specimen from the Murray cliffs, along with those of a specimen which he presumed to be that seen by Duncan (BM E1107); this specimen he figured (Gregory 1890, P1. 13, figs 7, 8). The specimen however is not from the Murray cliffs, but from 'Bairnsdale, Victoria'. Consequently it seems probably that this specimen is younger than the early Early Miocene (Longfordian) specimen of Laube. It is 57 mm in length (Gregory, 1890, p. 483), and has ambulacrum II 8 mm in width, and ambulacrum I 9.5 mm in width (Duncan, 1887, p. 420); there is little difference between the lengths of the poriferous tracts (see Gregory, 1890, Pl. 13, fig. 8). A topotype of specimen *E. ovulum* (NMV P55460) of comparable length to the Bairnsdale specimen, has ambulacrum I 8.6 mm in width. Gregory's (1890, Pl. 13, fig. 8) illustration of the lateral view of the Bairnsdale specimen shows a more conical form than seen in topotype material, and has the apical system set posterior of the mid-test length. As the Bairnsdale specimen cannot at present be located at the British Museum (Natural History) (D. N. Lewis, *pers. comm.* 3/5/78) it is considered advisable to identify it as *E.* aff. *ovulum.*

*E. gambierensis,* within which some workers (Tate, 1885, 1891; Roman, 1965) have placed *E. ovulum,* is, indeed, rather similar in the possession of a large (up to 67.8 mm in length), high test and broad, distally narrowing petals. *E. ovulum* can be distinguished, however, by its broader (Fig. 5a), flatter ambulacral interporiferous zone (Pl. 2, fig. 7), more separated pores, flattened aboral surface, more densely tuberculate test, more ovate dorsal outline (on account of the greater development of the rostrum), shallower periproct, less tumid bourrelets and narrower phyllodes. *Echinolampas ovulum* Tallivignes (1847) is merely given in a faunal list, and is apparently a *nomen nudum* which has never been validated.

**Echinolampas gambierensis** Tenison Woods, 1867
(Pl. 3, figs 1-7)

1867 *Echinolampas gambierensis* Tenison Woods, p. 1, figs 1a-c.
1878 *Echinolampas gambierensis* Tenison Woods; Etheridge, p. 139.
1878 *Echinolampas australis* Tenison Woods; Etheridge, p. 139. (*lapsus calami pro E. gambierensis*)
1885 *Echinolampas gambierensis* Tenison Woods; Tate, pp. 37, 41 (*pars.*).
1891 *Echinolampas gambierensis* Tenison Woods; Tate, p. 276 (*pars.*).
1892 *Echinolampas gambierensis* Tenison Woods; Tate, p. 193 (*pars.*).
1921 *Echinolampas gambierensis* Tenison Woods; Lambert & Thiéry, p. 386.
1930 *Echinolampas gambierensis* Tenison Woods; Brighton, p. 568 (*pars.*).
1946 *Echinolampas gambierensis* Tenison Woods; Clark, p. 359 (*pars.*).
1965 *Echinolampas gambierensis* Tenison Woods; Roman, p. 281 (*pars.*).

*Type specimen:* The whereabouts of Tenison Woods' original specimen is not known, and it must be presumed lost. Consequently a neotype is selected (AUGD S35) from the Gambier Limestone of Longfordian (Early Miocene) age, from the quarry at the side of the road to Port Macdonnell, 6.5 km south of Mt. Gambier.

*Material, localities and horizon:* In additon to its occurrence in the Gambier Limestone in the region of Mt. Gambier, this species also occurs in the Gambier Limestone in the banks of the Glenelg River north of Nelson, Victoria. Sixteen specimens are known from the Gambier Limestone. In the penecontemporaneous Mannum Formation this species commonly occurs in the cliffs of the Murray River between Swan Reach and Mannum; twenty-eight specimens have been recovered.

*Diagnosis:* Test large and conical; apex slightly posterior of apical system. Apical system set more than one-third test length from anterior; tuberculate and gently domed. Petals broad, interporiferous zone five times width of poriferous tracts; raised and confluent distally. Poriferous tracts slightly unequal in length in each petal differing between four and seven pore pairs. Inner pores circular, outer tear-shaped; conjugate. Adoral surface is flattened. Periproct is shallow and pentagonal. Floscelle large, and has tumid bourrelets and broad phyllodes.

*Discussion:* Although, as in other species of *Echinolampas,* the height of the test varies intraspecifically, the conical form of the aboral surface, rising to a gently rounded apex at about mid-length in mature specimens (Fig. 4b) is characteristic of this species. *E. gregoryi* sp. nov. has a similar shaped aboral surface, but the apex and apical system are coincident, unlike *E. gambierensis* where the apical system is positioned anterior to the apex.

*E. gambierensis* differs from *E. morgani,* with which it occurs in both the Gambier Limestone and Mannum Formation, in a number of ways. In additon to its larger size (reaching a maximum known test length of 61

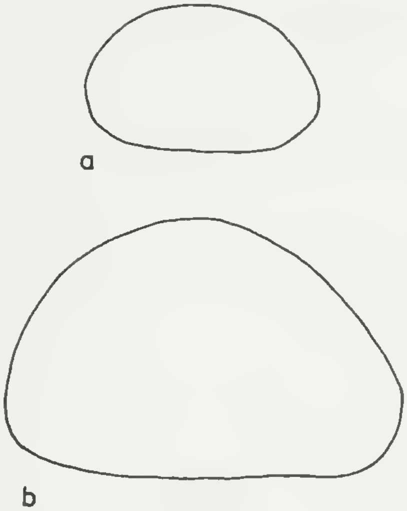


Figure 4—Lateral profiles of *Echinolampas gambierensis* Tenison Woods, 1867; a, from the Mannum Formation, Kroehn's Landing, Murray River, South Australia; b, AUGD S35, from the Gambier Limestone, Mt. Gambier, South Australia; both x1.

mm) and more conical test, *E. gambierensis* has longer and broader petals (Fig. 5a) which close distally and bear conjugate pore pairs; the outer pore is pear-shaped (Pl. 3, fig. 4) whereas in *E. morgani* it is circular. The ambulacral plates of *E. gambierensis* are far more tuberculate than those of *E. morgani,* bearing 3-4 tubercles every plate, whereas those of *E. morgani* bear only one. *E. gambierensis* has a poorly developed rostrum, whereas it is well developed in specimens of *E. morgani* from the Gambier Limestone. The adoral surface of *E. gambierensis* is much flatter than in *E. morgani* with a larger floscelle with more tumid bourrelets.

Comparisons with the morphologically similar *E. ovulum* Laube are made under the discussion of that species.

### **Echinolampas tatei** Lambert, 1898
(Pl. 3, figs 8-11)

1893 *Conoclypeus rostratus* Tate, pp. 194-195, Pl. 13, figs 1a-b. (non Mazetti, 1885).
1898 *Pleisiolampas rostratus* (Tate); Tate, p. 412.
1898 *Echinolampas tatei* Lambert, p. 165.
1921 *Echinolampas* (*Progonolampas*) *tatei* Lambert; Lambert & Thiéry, p. 387.
1943 *Conoclypus rostratus* Tate; Crespin, p. 76.
1946 *Pleisiolampas rostrata* (Tate); Clark, p. 358.
1965 *Echinolampas tatei* Lambert; Roman, p. 302.

*Type specimen:* The holotype (Pl. 3, figs 8-10) is AUGD T358, a specimen from 'Table Cape, Tasmania', figured by Tate 1893 (Pl. 13, figs 1a-b), as *Conoclypeus rostratus* Tate. Preservation of the specimen is characteristic of the 'Upper Beds' (Fossil Bluff Sandstone) at Table Cape. These beds are Janjukian (Late Oligocene) in age (Gill, 1957).

*Material, locality and horizon:* In addition to the holotype, nine specimens are known from the 'Upper Beds' (Fossil Bluff Sandstone) at Table Cape. Preservation of material from Table Cape is poor, particularly that from the 'Upper Beds', from which all specimens are crushed to some extent. Material from the 'Lower Beds' (Freestone Cove Sandstone) has retained better the original shape. The species is not known from elsewhere.

*Diagnosis:* Test of moderate size, low, but conical. Rostrum well-developed; apex conjunct with, or slightly posterior of, apical system, which is set close to mid-length of test; gently domed. Petals broad and parallel-sided for most of their length; poriferous tracts of similar length. Pore pairs circular, conjugate (Pl. 3, fig. 11). Adoral surface flattened, but with impressed ambulacra. Peristome oval and broad. Bourrelets barely developed. Tubercles large and closely spaced.

*Discussion:* Specimens of *Echinolampas* from Table Cape were originally described by Tate (1893) as '*Conoclypeus rostratus*'. Lambert (1898) considered that the species belonged, in fact, to *Echinolampas*. He also proposed a new name, *E. tatei*, as, in his opinion *Echinolampas rostrata* Cotteau 1894 from the Early Eocene of L'Oise had priority. In fact, Tate's *C. rostrata* predates Cotteau's name by one year. However, the name *E. rostrata* had been used earlier, by Mazetti (1885), although the species is considered (Roman, 1965, p. 297) to be synonymous with *E. angulata* Merian. Consequently, Lambert's name *E. tatei* is valid, but

Cotteau's *E. rostrata* is a homonym, requiring a new name.

*E. tatei*, which reaches a maximum test length of 54.1 mm, compares with *E. morgani* and *E. posterocrassa* in the possession of parallel-sided petals which show little distal closure. Like *E. morgani*, it has circular, though conjugate, pore pairs. These two species can further be distinguished by: the more pulvinate adoral surface of *E. morgani;* the broader ambulacral poriferous tracts, both adorally and aborally, in *E. tatei* (Fig. 5a); and the much higher inclination of the periproct in *E. morgani*.

The shape of the test of *E. tatei* bears some resemblance to small forms of *E. gambierensis* in which the test is low. The boader, distally narrowed petals of *E. gambierensis* and the greater rostal development in *E. tatei* serve to distinguish the two species.

In shape of the test, *E. tatei*, also compares with *Echinolampas westraliensis* (Crespin, 1943) from Cape Range, in north-west Western Australia, a species originally referred to *Conoclypus*. This Middle Miocene species, although having a similar test shape to *E. tatei*, has longer, wider and more petaloid ambulacra which possess slit-like outer pores.

### **Echinolampas** aff. **tatei** Lambert, 1898
(Pl. 4, figs 1-3)

*Material, locality and horizon:* A single specimen (NMV P55466) from a marly lens within the Gambier Limestone, from the left bank of the Glenelg River at Nelson, Victoria.

*Discussion:* Of the two species of *Echinolampas* found in the Gambier Limestone this specimen most resembles *E. gambierensis*. However, it does not have the inflated aboral ambulacra, nor does it possess a well-developed floscelle, characteristic of *E. gambierensis*. The specimen more closely resembles *E. tatei* in its low, but conical test, low-angled periproct and flattened oral surface. *E.* aff. *tatei* can be distinguished from the Tasmanian species, however, by its possession of slightly longer poriferous ambulacral tracts, less well-developed floscelle and more centrally situated apical system.

### **Echinolampas gregoryi gregoryi** sp. nov.
(Pl. 4, figs 4-6)

*Type specimen:* The holotype, and only known specimen, is NMV P18379, probably from the Bairnsdale Limestone (Middle Miocene).

*Diagnosis:* Test conical, apex and apical system coincident. Petals long, reaching almost to ambitus; broadening progressively abapically. Inequality in lengths of poriferous tracts in each petal small, about 4 pore pairs in ambulacrum I. Outer pores pear-shaped; weakly conjugate with smaller, rounded inner pores. Interambulacra raised above level of ambulacra. Within this raised area, a narrow, depressed zone extends along junction between interambulacral plates. Interambulacra also raised on oral surface. Peristome quite deeply sunken. Bourrelets weakly developed. Periproct inclined almost horizontally.

*Discussion: E. gregoryi gregoryi* shows a number of similar morphological features to *E. tatei*, in particular the test shape and form of the ambulacra. However, *E. gregoryi gregoryi* can be distinguished by its swollen interambulacra on both the adoral and aboral surfaces; ambulacral poriferous tracts of more equal length; and less well-developed bourrelets. *E.* aff. *tatei*, from the Gambier Limestone, is like *E. gregoryi gregoryi*, but lacks the swollen interambulacra and has a more oval peristome. *E. posterocrassa posterocrassa* has narrower, parallel sided petals, a flatter test, and a more pulvinate oral surface with a shallower peristome.

### **Echinolampas gregoryi corrugata** subsp. nov.
(Pl. 4, figs 7-9)

*Type specimen:* The holotype and only known specimen is NMV P55477 from the Muddy Creek Formation at Clifton Bank, and is Balcombian in age (Middle Miocene).

*Diagnosis:* This subspecies differs from *E. gregoryi s.s.* by having: more swollen interam-

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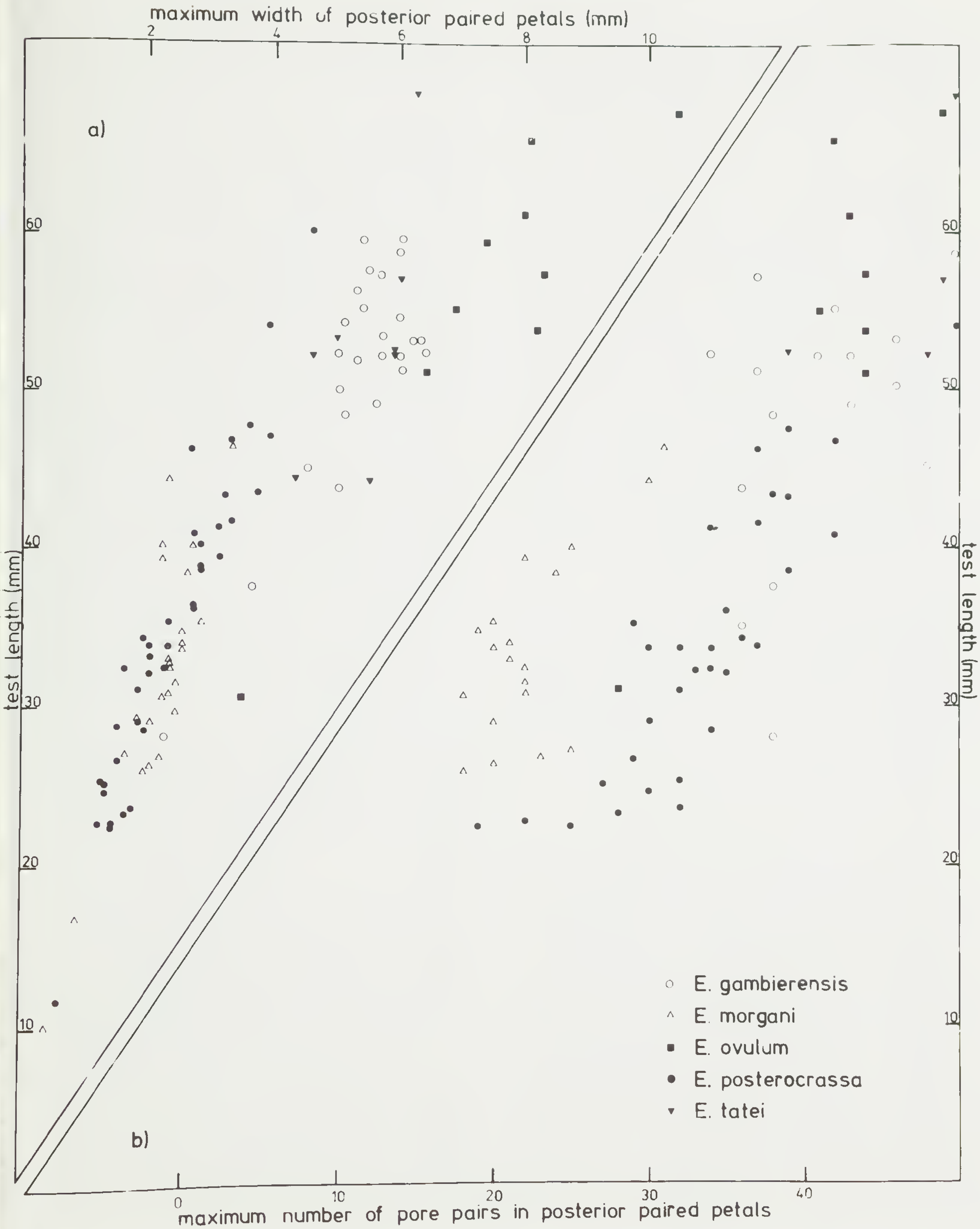
Figure 5 — Plots of test length against, a: maximum width of posterior paired petals, and, b: maximum number of pore pairs in posterior paired petals for five species of *Echinolampas*.


maximum width of posterior paired petals (mm)
2
4
6
8
10
a)
test length (mm)
60
50
40
30
20
10
b)
0
10
20
30
40
maximum number of pore pairs in posterior paired petals
E. gambierensis
E. morgani
E. ovulum
E. posterocrassa
E. tatei

bulacra, which do not possess the median depression; ambulacral poriferous tracts of very unequal lengths, in ambulacrum I difference being 12 pore pairs, in ambulacrum II, 15; oral surface flatter with shallower peristome.

*Discussion:* Of the two subspecies of *E. gregoryi, E. gregoryi corrugata* is the larger, being 68.7 mm in length, *E. gregoryi gregoryi* being 52.1 mm in length. The more highly vaulted test of *E. gregoryi corrugata* is considered to be a function both of the large size of the test (test height increasing at a greater rate than would be expected from normal allometric growth) and of slight dorso-ventral compression of the test of *E. gregoryi gregoryi.* The other large and often highly vaulted species of *Echinolampas* from the Tertiary of Australia is *E. gambierensis.* The two forms can be distinguished, however, by the raised petals of *E. gambierensis*; its distally narrowed petals; more swollen bourrelets; and higher angled periproct. The petals of *E. gregoryi corrugata* are relatively longer than those of *E. gambierensis.*

*E. gregoryi corrugata* compares with large specimens of *E. fraasi* de Loriel from the Middle Eocene of Somalia and Egypt (Kier 1957, p. 848, P1. 103, fig. 12, P1. 104, fig. 1) in shape of test and length and nature of the poriferous tracts. *E. fraasi*, however, has a more well developed floscelle and ambulacral poriferous tracts of more equal length.

## Ontogeny of Echinolampas

In those Australian species of *Echinolampas* in which sufficient juvenile material is known (*E. posterocrassa, E. morgani* and *E. gambierensis*) the ontogenetic development is similar, but varies in the degree of morphological change. Although many features, such as form of the pore-pairs, degree of inequality of poriferous zones, position of the apical system and position of the peristome, remain constant through the growth series available, a number of other morphological features change. As the greatest ontogenetic changes occur in the oldest species, *E. posterocrassa*, most of the following discussion is based on this species, although supplementary information is drawn from other species. Changes include:

(1) With increase in size of the test, the adapical surface changes from being low and flattened to being high and conical (Figs 1a,c,6). This trend has been noted previously by Kier (1957, p. 852) in *E. fraasi* de Loriol from Somalia. It is variable, for the change in height of the test is less in material of *E. posterocrassa* from the Nanarup Limestone, than in topotypes from the Tortachilla Limestone, perhaps suggesting that the feature may be controlled by environmental factors. *E. gambierensis* attains a conical test at an earlier growth stage than does *E. morgani* although there is some degree of intraspecific variation within each.

(2) With increase in size, the "apex" (the highest point of the test when the adoral surface is horizontal) moves forward (Figs 1a,c,3). Thus, in large individuals, the apical system may almost coincide with the "apex". This, in turn, results in a small change in the angle of orientation of the apical system to the plane of the adoral surface.

(3) There is a proportionate increase in length of the petals with growth of the test (Fig. 5b). Thus, in a specimen 22.5 mm in length, the petals of ambulacra I and V extend slightly less than half the length of the ambulacra (measured in a horizontal plane) to the ambitus (P1. 1, fig. 5). In a specimen 38.5 mm in length, they extend four-fifths of the distance (P1. 1, fig. 3) and in the largest known specimen of *E. prosterocrassa* the petals almost reach the ambitus.

The rate of production of pore-pairs shows some important differences between species (Fig. 5b). A regular increase in the number of pore-pairs with growth is seen in *E. posterocrassa.* In *E. gambierensis*, however, the rate of development of pore-pairs is initially much greater so that almost the entire complement is attained when a length of about 30mm is reached, although the species may attain a length greater than 60mm. *E. morgani* is like *E. posterocrassa* for pore-pairs are produced reasonably constantly with growth (although at a reduced rate). The variations in rate of development of pore-pairs are illustrated in Fig.

5b and in the Table below which gives the number of pore-pairs for different sized specimens of the three species.

| | small | | large | |
|---|---|---|---|---|
| | length | pore-pairs | length | pore-pairs |
| *E. posterocrassa* | 27mm | 30 | 53mm | 53 |
| *E. gambierensis* | 28mm | 40 | 52mm | 43 |
| *E. morgani* | 26mm | 19 | 47mm | 32 |

Within each petal, the difference in length of the tracts does not seem to change with growth (cf. Kier, 1957, p. 851), although such a difference appears more marked in small specimens because of the shortness of the petals. Intraspecific variation in equality of the length of the zones may be quite marked (see below).

(4) In *E. posterocrassa* the interporiferous zone is flat in small- and medium-sized individuals, being flush with the interambulacral surface. In specimens approximately 50mm in length, the interporiferous zone becomes slightly raised. This swelling increases with further growth of the individual, so that specimens 60mm in length have prominently swollen interporiferous zones, similar to those of medium-sized specimens of *E. gambierensis* and *E. ovulum*.

(5) The bourrelets become progressively more swollen with growth. In specimens over 40mm in length the bourrelets become gently swollen, whilst in specimens more than 60mm in length they are prominently swollen. As the bourrelets become more tumid, there is an increase in the number of small, densely packed tubercles that cover them.

(6) This swelling of the bourrelets results in a change in outline of 'the peristome. In small specimens it is smoothly oval in outline, but in larger specimens the peristome becomes subpentagonal.

(7) The peristome and periproct decrease in relative size. For instance, in *E. posterocrassa*, a specimen 22.5mm in length, the diameter of the peristome is about one quarter of the test width. For a specimen 47mm in length, however, the diameter is only one-sixth of the test width. An incomplete specimen of width 55mm has a peristome only one-eighth of this dimension.

(8) Small and medium sized specimens of *E. posterocrassa* generally bear only a single large tubercle on the apical system. Large specimens (more than 60mm in length) may have four or five. In *E. gambierensis*, however, the smallest specimens have two or three tubercles, whilst the large ones possess up to ten.

The smallest known specimen of *E. ovulum* has a test length of 30.7mm and had only one genital pore weakly developed, indicating that the specimen had just reached sexual maturity. At a similar size, specimens of *E. gambierensis, E. morgani* Cotteau and *E. posterocrassa* Gregory all have well developed genital pores. Specimens of *E. posterocrassa* as small as 22mm in length possess genital pores, and so were presumably sexually mature. A specimen 12mm in length, however, has no genital pores developed. *E. ovulum* attained a larger size before the onset of maturity than did other Australian species of *Echinolampas*.

*Discussion:* It is possible to interpret some of the morpholgical changes which occurred with growth in terms of change in life habit. Kier (1962, p 2) has conjectured that cassiduloids lived partially buried in sediment to the base of the ambulacral petals. This interpretation was influenced by Agassiz's (1873, p 555) observation on the life habits of *Rhyncholampas pacificus* (Agassiz). Higgins (1974) has shown that the cassiduloid *Apatopygus recens* (Milne Edwards) burrows completely, which throws some doubt on Kier's generalization. Unfortunately data is lacking on the life habits of living species of *Echinolampas*. Several dead tests of *Echinolampas ovata* from Roebuck Bay, Western Australia which have been examined by one of us (K.J.M.) clearly show staining of the test above the level of the tips of the petals. This staining appears to have been made by algal growth on that part of the test projecting above the sediment. It would seem that at the time of death of the test at least, it was buried in the sediment only below the level of the distal tips of the petals. If, indeed, *Echinolampas* is oriented in the sediment like *Rhyncholampas* (buried only below the petals) then the different lengths of the anterior and posterior petals means that the oral surface would have been inclined to the sediment/water interface (Fig. 6). The effect of this orientation would be to position the apical system at the highest point above the sediment, and directly above the peristome. Such tilting would also mean that the periproct and peristome would be at the same level beneath the surface of the sediment.

Thum and Allen (1976) have reported that in a very course shelly sediment, *Echinolampas crassa* (Bell) often burrows completely under laboratory conditions. However, the burrowing behaviour of echinoids is notoriously variable, depth of burrowing within a species varying with time of day, size, gonadal condition, rate of movement, nature of sediment, wave action and water temperature (Chesher 1969).

Species of *Echinolampas* are characterised by the irregular lengths of the poriferous tracts of the ambulacra. It is conceivable that at periods when individuals were only partly buried, say at night or at times of spawning, the echinoid would not have been orientated with its oval surface horizontal, but with the ends of the poriferous tracts of the ambulacra lying along the sediment/water interface (Fig. 6).

In fact, during growth the adoral surface becomes more domed, but the adoral part of the test maintains its profile, so that the peristome remains buried to about the same depth in their natural habitat.

As mentioned above, there is considerable variation in the height of the test within some species. Specimens of *E. posterocrassa* from the Nanarup Limestone are flatter and specimens from Kangaroo Island more conical than those from the Tortachilla Limestone. Likewise specimens of *E. morgani* from the Mannum Formation may be more conical than topotypes from Mt. Gambier. A consistent correlation does exist, however, between the length of the petal and the height of the test, for those specimens with a lower test have shorter petals.

Figure 6 — Suggested possible life orientations of juvenile and adult *Echinolampas posterocrassa posterocrassa* Gregory, x1.

## Acknowledgements

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## Explanation of plates

PLATE 1

Figs 1-6 — *Echinolampas posterocrassa posterocrassa* Gregory, 1890, from the Tortachilla Limestone (Late Eocene) Port Willunga, South Australia; 1, enlargement, x10, of apical system of NMV P55448; 2, enlargement, x5, of peristome and floscelle of NMV P55450; 3, 4 and 6, NMV P55447; 5, NMV P55449.

Figs 7-9 — *Echinolampas posterocrassa curtata* subsp. nov. from the Port Vincent Limestone (Late Oligocene), 4km north of Wool Bay, Yorke Peninsula, South Australia; NMV P55451, holotype; 9, enlargement, x5, of peristome and floscelle.

Figs 10-13 — *Echinolampas morgani* Cotteau, 1889, NMV P55455, from the Mannum Formation (Early Miocene), Murray River cliffs; 10, enlargement, x6, of apical system.

Except where otherwise stated, figures are x1.

PLATE 2

Figs 1-3—*Echinolampas morgani* Cotteau, 1889; 1, enlargement, x5, of petal of ambulacrum V of NMV P55455, from the Mannum Formation (Early Miocene), Murray River cliffs; 2-3 NMV P19176 from the Gambier Limestone (Early Miocene), Mt. Gambier, South Australia; 3, enlargement, x4, of peristome and floscelle.

Figs 4-8—*Echinolampas ovulum* Laube, 1869, NMV P55457, neotype, from the Mannum Formation (Early Miocene), Blanchetown, South Australia; 7, enlargement, x5, of part of petal of ambulacrum I; 8, enlargement, x6, of peristome and floscelle.

Except where otherwise stated, figures are x1.

PLATE 3

Figs 1-7—*Echinolampas gambierensis* Tenison Woods, 1867; 1-3 AUGD S35, neotype, from the Gambier Limestone, Mt. Gambier, South Australia; 4, enlargement, x6, of apical system; 4-5 NMV P55463 from the Mannum Formation (Early Miocene), Murray River Cliffs; 6, enlargement x3.5, of peristome and floscelle of NMV P55461 from the Gambier Limestone, 1.5km north of Nelson, Victoria.

Figs 8-11—*Echinolampas tatei* Lambert, 1898 from the Fossil Bluff Sandstone (Longfordian, Early Miocene) at Table Cape, Tasmania; 8-10 AUGD T358, holotype; 11, enlargement, x8, of part of petal of ambulacrum I of NMV P55464.

Except where otherwise stated, figures are x1.

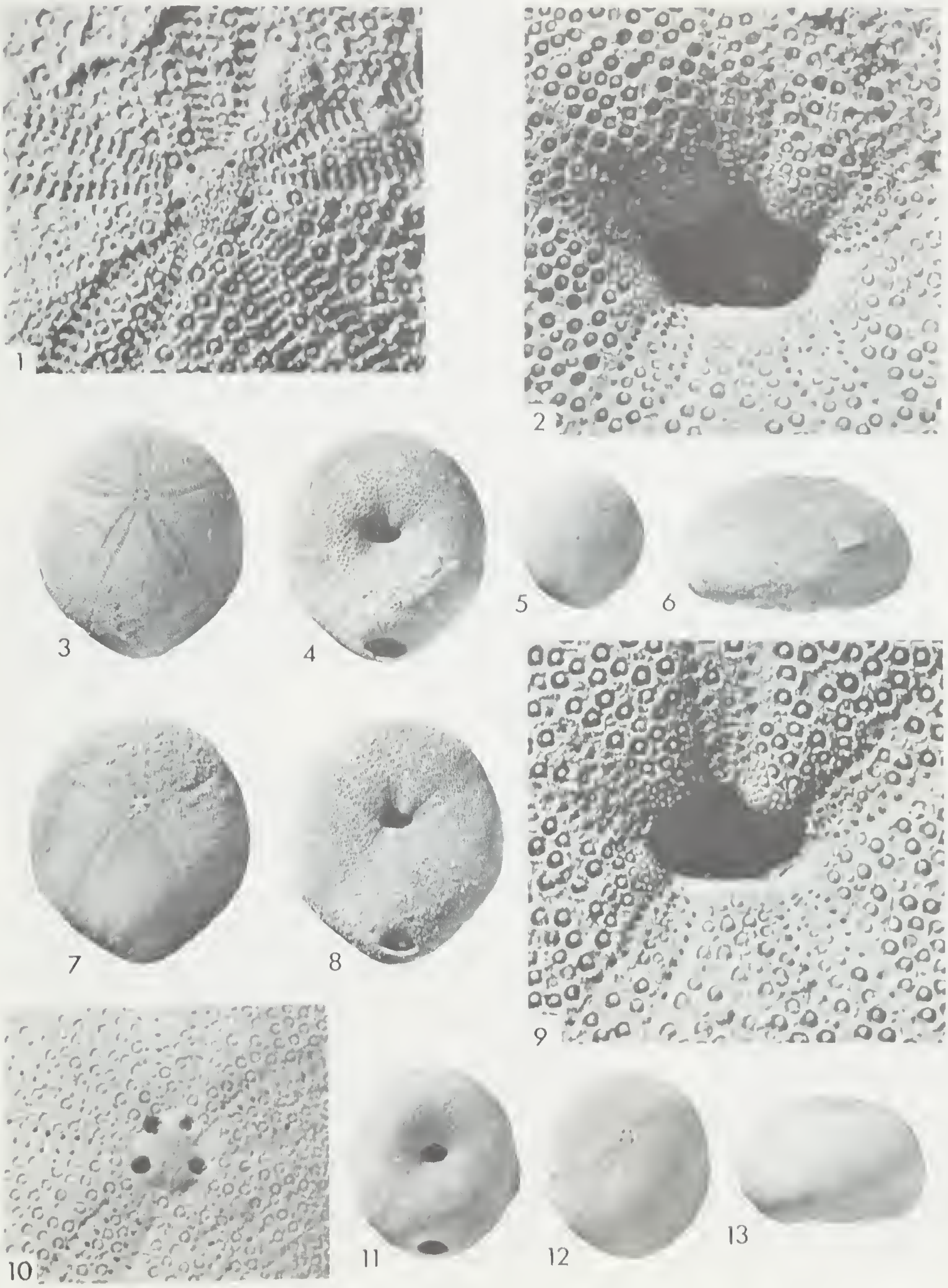
PLATE 4

Figs 1-3—*Echinolampas* aff. *tatei* Lambert, 1898, NMV P55466, from the Gambier Limestone, left bank of Glenelg River, Nelson, Victoria.

Figs 4-6—*Echinolampas gregoryi gregoryi* sp. nov. NMV P18379, holotype from Orbost Victoria, probably Bairnsdale Limestone (Middle Miocene).

Figs 7-9—*Echinolampas gregoryi corrugata* subsp. nov. NMV P55477, from the Balcombian, Muddy Creek Formation (Middle Miocene) at Clifton Bank, Victoria.

All figures x1.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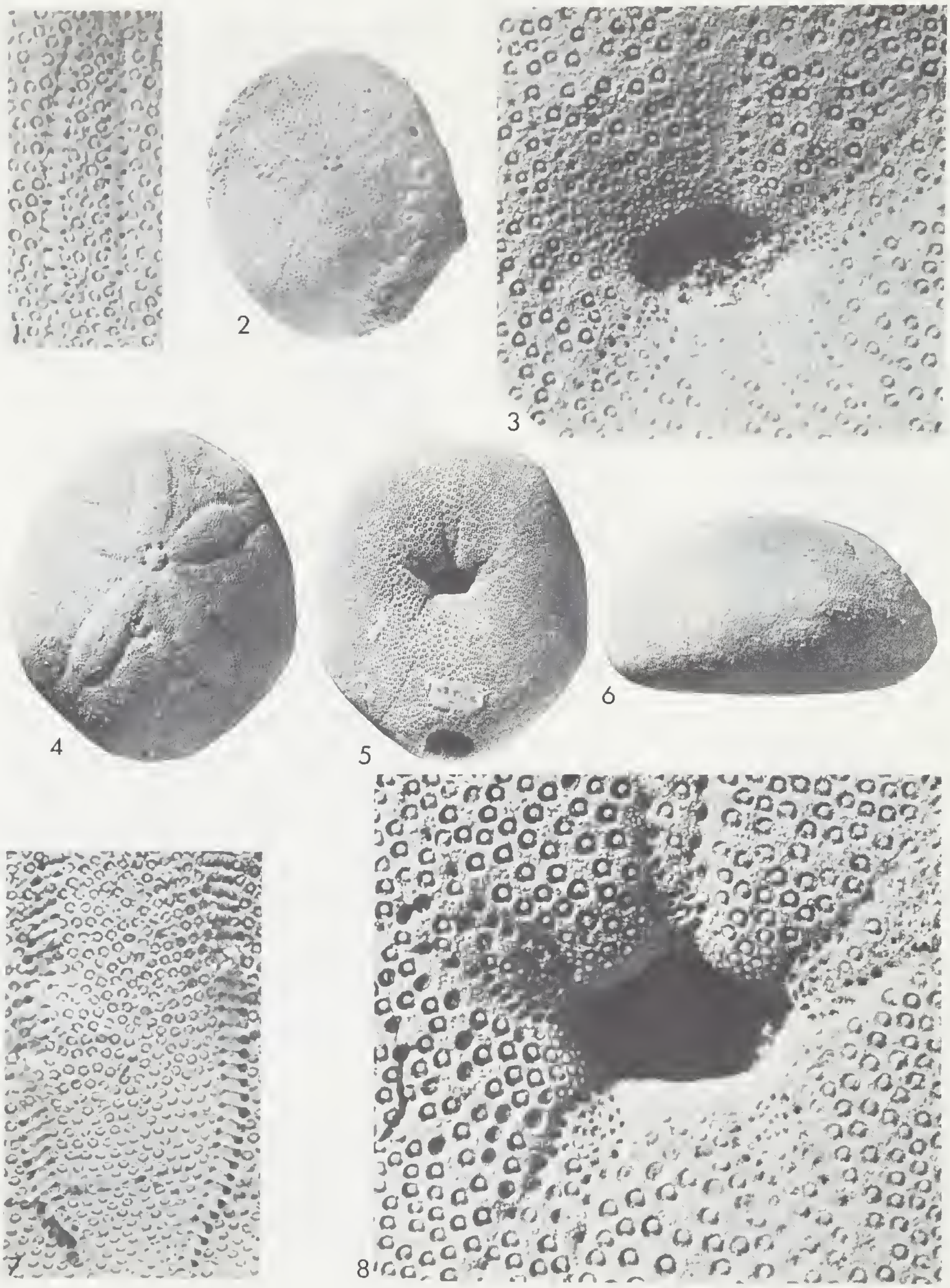
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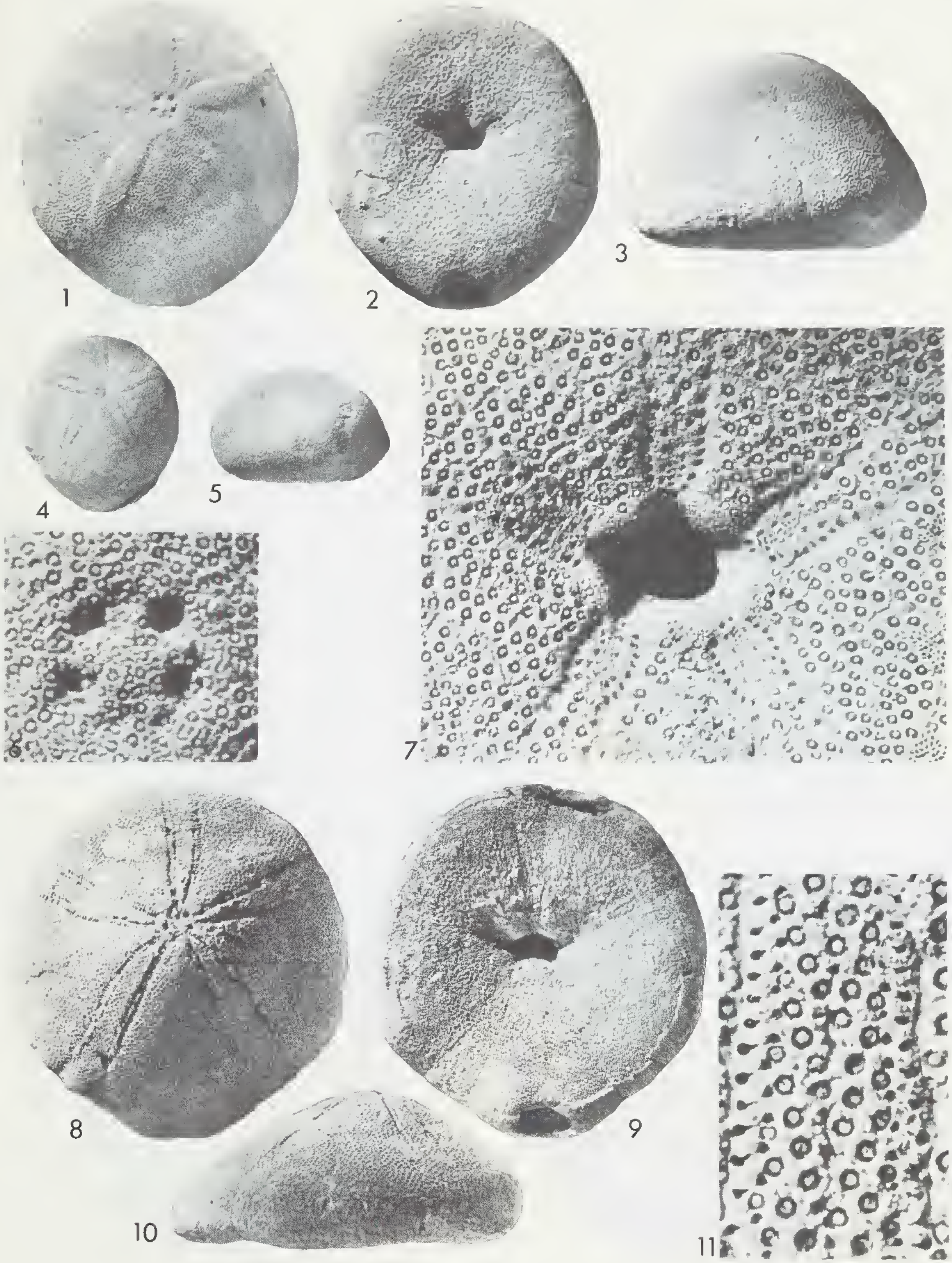
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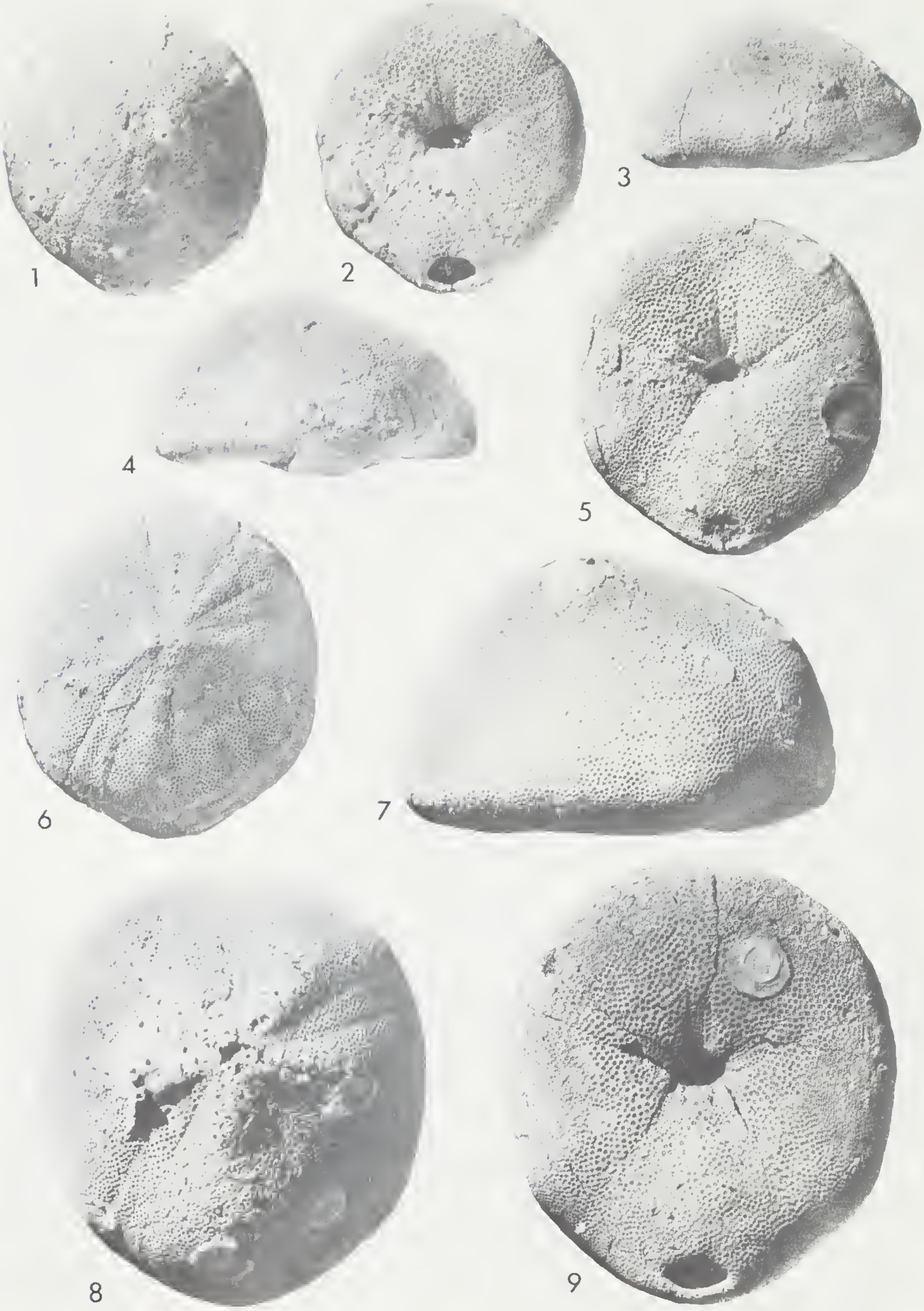
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