

TAXONOMY, EVOLUTION, AND FUNCTIONAL MORPHOLOGY OF SOUTHERN AUSTRALIAN TERTIARY HEMIASTERID ECHINOIDS

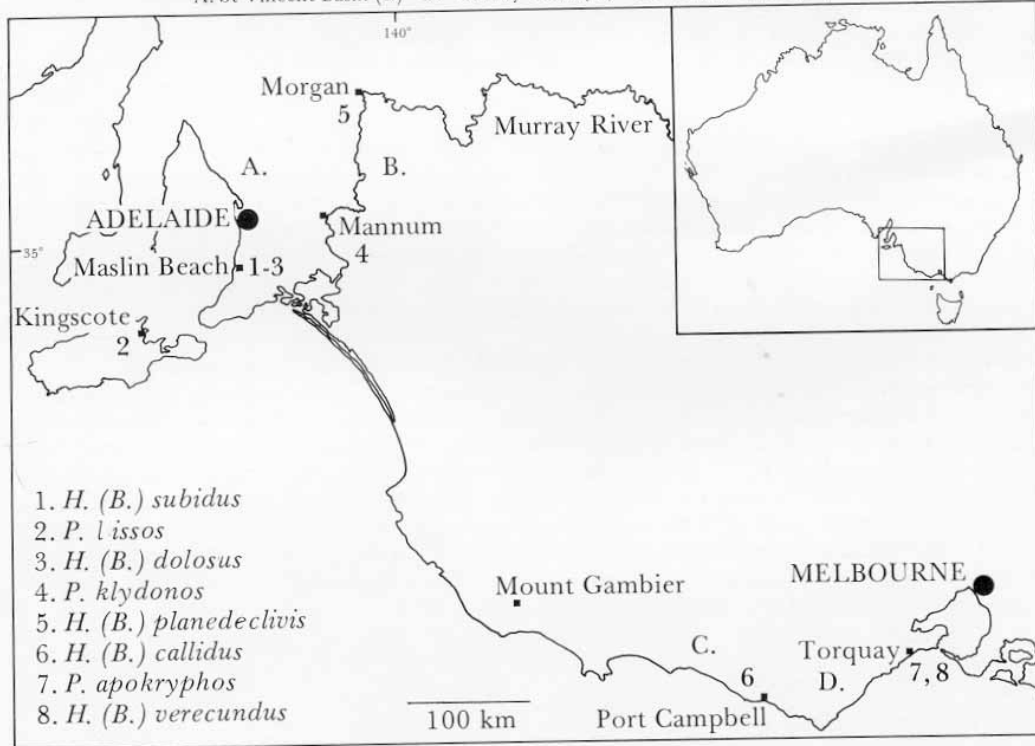
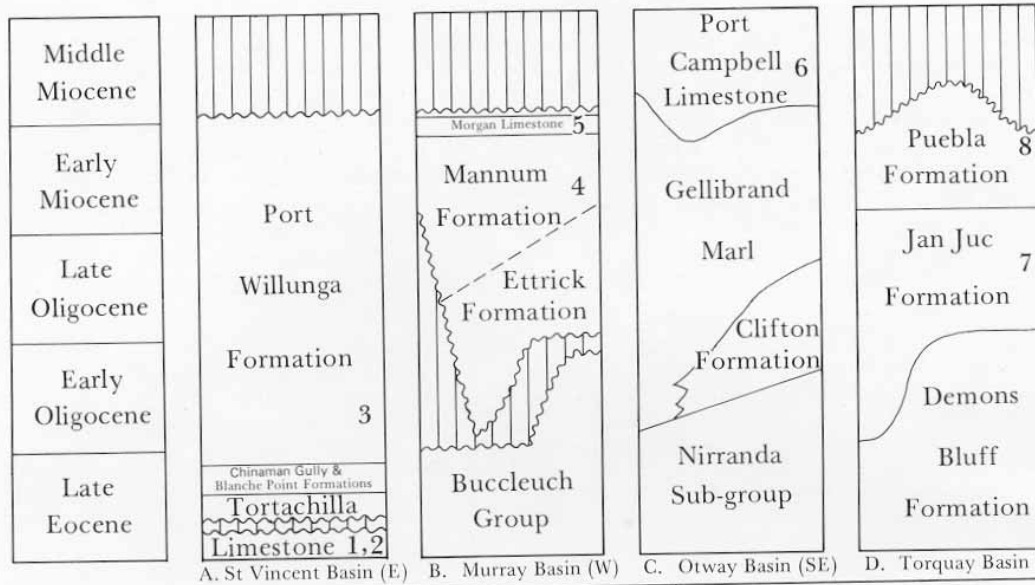
by KENNETH J. MCNAMARA

ABSTRACT. Eight species of hemiasterid echinoids, assigned to the genera *Hemiaster* (*Bolbaster*) and *Psephoaster* gen. nov., are described from Late Eocene to Middle Miocene strata of southern Australia. Seven of the species are new: the Late Eocene *H. (B.) subidus*, the Early Oligocene *H. (B.) dolosus*, the Early Miocene *H. (B.) verecundus*, the Middle Miocene *H. (B.) callidus*, the Late Eocene *P. lissos*, the Late Oligocene *P. apokryphos* and the Early Miocene *P. klydonos*. A neotype is selected for *H. (B.) planedeclevis* Gregory, 1890. The five species of *H. (Bolbaster)* are considered to have formed a single evolutionary lineage, as are the three species of *Psephoaster*. Directional trends in many morphological features in these two lineages are interpreted as reflecting both paedomorphosis and peramorphosis. The sediments in which the echinoids lived became progressively finer-grained from the Eocene to the Miocene and the morphological changes in the two lineages are considered to reflect adaptations by descendant morphotypes to the occupation of finer-grained sediments. Many of the morphological changes are common to both lineages. Species of *Psephoaster* are considered to have been shallow burrowers, while species of *H. (Bolbaster)* are interpreted as having burrowed more deeply in the sediment.

HEMIASTERID echinoids form a relatively minor part of an otherwise rich spatangoid echinoid fauna which occurs in parts of the Tertiary sedimentary sequence of southern Australia. The only hemiasterid species to have been described previously from these rocks is *Hemiaster planedeclevis* Gregory, 1890, from the Early/Middle Miocene Morgan Limestone exposed in the banks of the Murray River in South Australia. Since Gregory's description there has been a tendency to call any specimen of *Hemiaster* found in Australian Tertiary deposits *H. planedeclevis*, specimens attributable to *Hemiaster* having subsequently been found in Late Eocene to Early/Middle Miocene strata (Tate 1891; Clark 1946).

Extensive collecting in recent years, by R. and F. Foster, of Tertiary sequences in the St Vincent and Murray Basins, South Australia, and in the Torquay and parts of the Otway Basins, Victoria, has yielded a number of forms superficially resembling *H. planedeclevis*. These specimens have come from the Late Eocene Tortachilla Limestone and Early Oligocene Port Willunga Formation, in coastal cliff sections in the St Vincent Basin, south of Adelaide, South Australia; from coastal cliff sections in the Late Oligocene Jan Juc Formation and Early Miocene Puebla Formation in the Torquay Basin, south-west of Melbourne, Victoria; from the Early Miocene Mannum Formation and the Early/Middle Miocene Morgan Limestone in cliffs exposed by the Murray River in the Murray Basin, South Australia; and from a coastal section exposing the Middle Miocene Port Campbell Limestone, in the south-eastern Otway Basin, Victoria (text-fig. 1). Specimens collected from these units are described below and assigned to eight species, seven of which are new. Five of the eight species are placed in *Hemiaster*, all being members of the subgenus *Bolbaster*. The other three species are considered to belong in a separate, previously unrecognized genus, *Psephoaster* gen. nov.

The five species of *H. (Bolbaster)* and the three species of *Psephoaster* are considered to form two evolutionary lineages. Most of the diagnostic morphological features which separate members of the lineages show temporal, directional, morphological transformations. These morphological changes are examined and compared with the ontogenetic development of species of *Hemiaster* in



TEXT-FIG. 1. Simplified stratigraphy of Tertiary strata of the eastern St Vincent Basin, western Murray Basin, south-eastern Otway Basin, and the Torquay Basin in southern Australia (after Abele *et al.* 1976 and Lindsay 1985) and locality map showing distribution of hemiasterid species.

order to assess the importance of heterochrony in the evolution of the two lineages. The functional significance of these morphological changes is assessed, particularly in relation to the character of the sediment in which the echinoids are preserved. It is considered that the specimens are autochthonous, the frequent presence of fine spines still adhering to some tests indicating that the specimens both lived and died within the sediment. Discussion of the relationship between morphology and enclosing sediment is therefore considered to be valid.

The relationship of morphology to sediment type has been assessed for a number of spatangoid groups in recent times (McNamara 1982a, 1985; McNamara and Philip 1980, 1984; Smith 1980b, 1984). The present study of evolutionary trends and their functional significance in two closely related spatangoid genera provides further evidence to support the view that morphological evolution in many spatangoids was strongly affected by the character of the sediment in which the echinoid lived and upon which it fed.

Materials and Methods. The collections upon which this study is based are housed in the Museum of Victoria, Melbourne (NMV), the South Australian Museum, Adelaide (SAM), the Western Australian Museum, Perth (WAM), and the private collection of E. and F. Holmes. Measurements were made to an accuracy of 0.1 mm with a vernier calliper or an ocular graticule fitted to a Wild binocular microscope. A number of parameters are expressed as percentages of maximum test length (% TL).

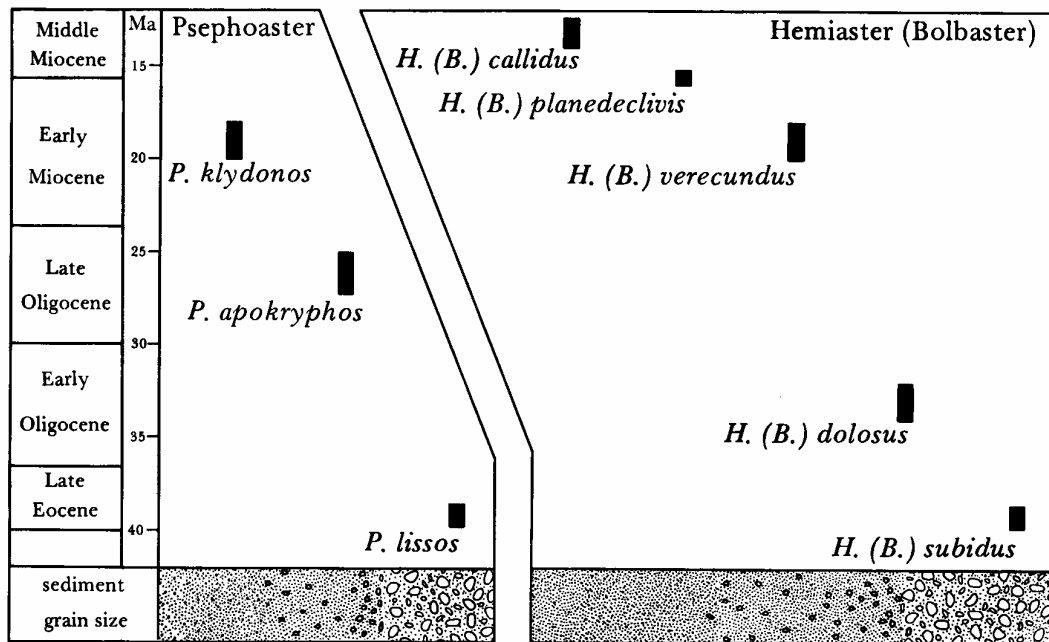
EVOLUTIONARY TRENDS AND THEIR FUNCTIONAL SIGNIFICANCE IN *HEMIASTER (BOLBASTER)* AND *PSEPHOASTER*

Morphological evolution of H. (Bolbaster)

Five species of *H. (Bolbaster)* occur in Eocene to Miocene strata in southern Australia. The oldest is the Late Eocene (Aldingan) *H. (B.) subidus* sp. nov., which is succeeded by the Early Oligocene (Willungan) *H. (B.) dolosus* sp. nov., the Early Miocene (Longfordian) *H. (B.) verecundus* sp. nov., the late Early/early Middle Miocene (Batesfordian/Balcombian) *H. (B.) planedeclevis* Gregory, and finally the late Middle Miocene *H. (B.) callidus* sp. nov. (text-fig. 2). It is considered that these five species form part of a single evolutionary lineage. They occur in relatively close geographical proximity to one another. The two earliest species occur in the Tortachilla Limestone and Port Willunga Formation, respectively, in the cliffs south of Adelaide. *H. (B.) verecundus* occurs 650 km to the south-east in the Puebla Formation on the southern Victoria coast, *H. (B.) callidus* 200 km to the west in the Port Campbell Limestone, and *H. (B.) planedeclevis* 500 km north-west in the Morgan Limestone, which outcrops in the Murray River Cliffs. The wide ranges of some modern Australian taxa, such as more than 4,000 km for both *Breynia desorii* (McNamara 1982a) and *Protenaster australis* (McNamara 1985), argue, in addition to the morphological criteria discussed below, for the five species of *H. (Bolbaster)* all forming part of a single evolutionary lineage.

Some ten morphological characters of the test undergo directional morphological change along the *H. (Bolbaster)* lineage over a period of twenty-eight million years from the Late Eocene to Middle Miocene. The characters which show these directional morphological transformations are: test height, width, and profile; length and depth of petals; length and depth of ambulacrum III, and extent of tuberculation; shape and disposition of the pore pairs in the petals; position of the apical system; thickness of the peripetalous fasciole; shape of the aboral interambulacra; density of ambital and aboral tuberculation; and form of the plastronal plating.

Test shape. During the course of the evolution of the *H. (Bolbaster)* lineage in southern Australia the test shape underwent a marked change, from ovoid in the earlier species, to near circular in outline in the later species (text-fig. 3b). In the Late Eocene *H. (B.) subidus* the width of the test is 90–96 % TL. The test widened in the three succeeding species (93–98 % TL in *H. (B.) dolosus*, 97 % TL in *H. (B.) verecundus* and 91–101 % TL in *H. (B.) planedeclevis*, apart from one specimen which is 88 % TL). In the youngest species, the Middle Miocene *H. (B.) callidus*, the width is even greater at 97–103 % TL.



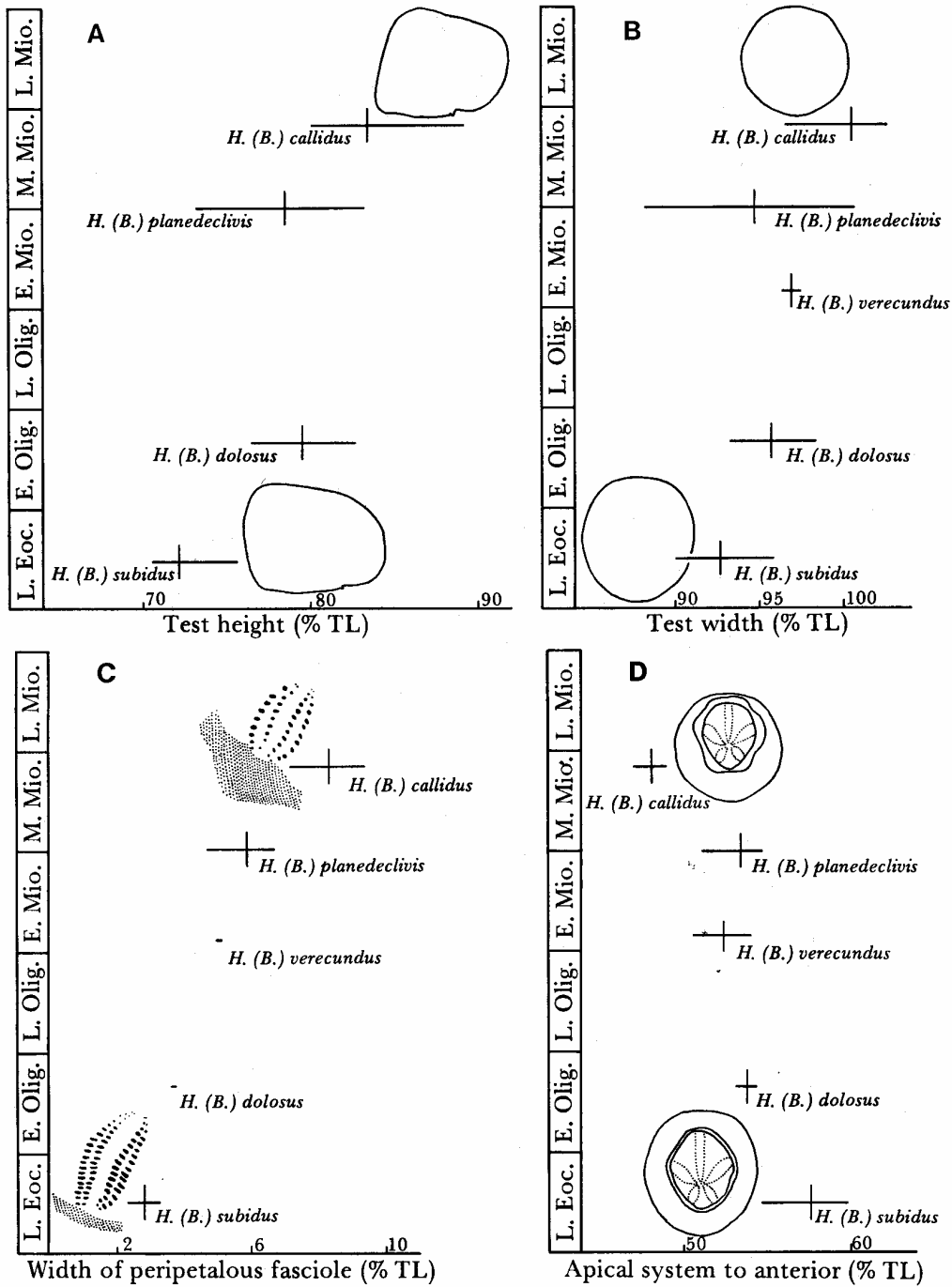
TEXT-FIG. 2. Stratigraphic and sedimentological distribution of species of *Hemiaster (Bolbaster)* and *Psephoaster* in the Tertiary of southern Australia.

Concomitant with this increase in test width there was an increase in test height and a change in the profile of the posterior surface of the test (text-figs. 3A, 8). In the Late Eocene *H. (B.) subidus* the posterior surface of the test is inclined such that interambulacrum 5 aborally overhangs the posterior of the plastron. With the evolution of the lineage the posterior face changed its orientation to become vertical in *H. (B.) dolosus* and *H. (B.) verecundus*, then slightly inclined forward in *H. (B.) planedecclivis*, and strongly inclined forward in the youngest species, *H. (B.) callidus*, such that both the periproct and posterior of the plastron are visible from above.

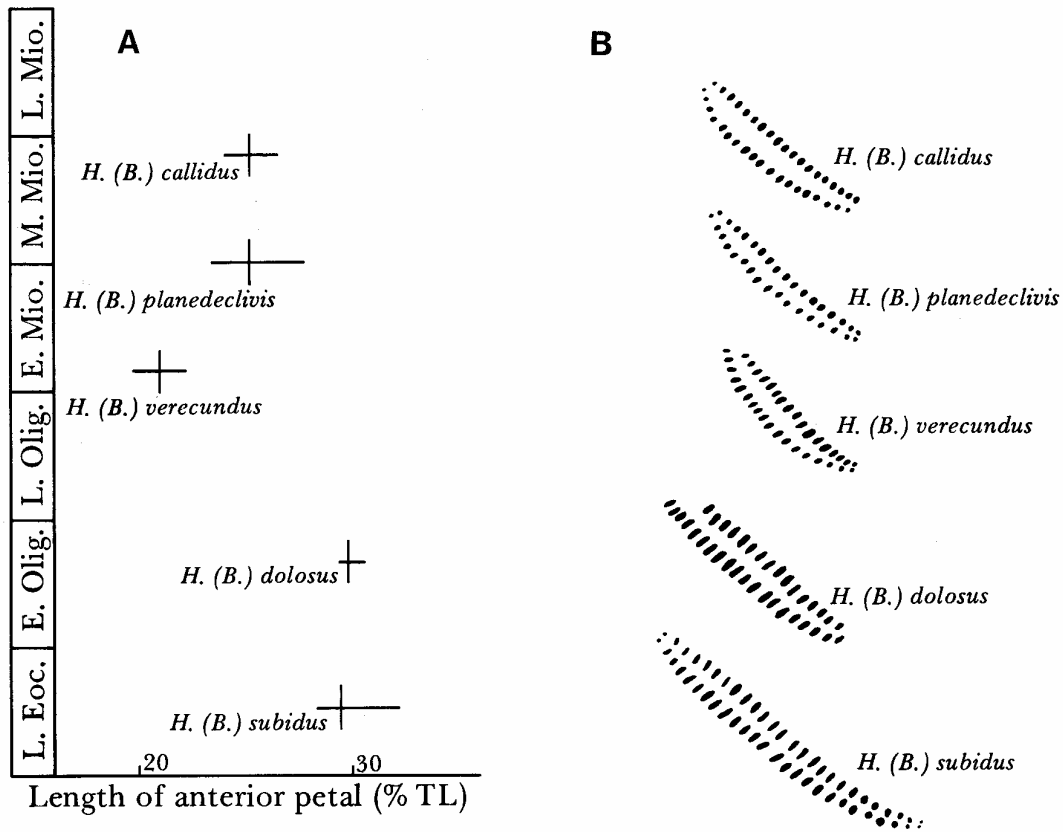
The general result of the increase in test width and height along the lineage was for the test to become more spherical in shape; the increase in relative test height occurred both by a foreshortening of the test and by increased swelling of interambulacrum 5.

Petals and ambulacrum III. These structures underwent a number of morphological changes, principally involving: progressive deepening; modest relative shortening of the anterior petals; change in the structure of the pore pairs in the petals, from each pore being elongate and proximal to the other pore of the pair in the early species, to nearly circular and widely separated in the later species; and decrease in primary tuberculation in the interporiferous zone.

In the two oldest species, the Late Eocene *H. (B.) subidus* and the Early Oligocene *H. (B.) dolosus*, the anterior petals are 28–32% TL and 29–30% TL in length, respectively. The Early Miocene *H. (B.) verecundus* is characterized by its particularly short anterior petals, 20–22% TL in length. The two youngest species, *H. (B.) planedecclivis* and *H. (B.) callidus*, have slightly longer petals, but shorter than those of the two oldest species, being 24–28% TL and 25–26% TL in length, respectively (text-fig. 4A). This reduction in petal length corresponds to a reduction in the number of pore pairs. For instance, the anterior petals of the oldest species, *H. (B.) subidus*, have eighteen to twenty-seven pore pairs, whilst the youngest species, *H. (B.) planedecclivis* and *H. (B.) callidus*, have thirteen to



TEXT-FIG. 3. Ranges (horizontal lines) and means (vertical lines), for species of *Hemiaster* (*Bolbaster*) in the Tertiary of southern Australia of test height, test width, width of peripetalous fasciole, and distance between apical system and anterior ambitus; all expressed as percentages of test length.



TEXT-FIG. 4. Ranges (horizontal lines) and means (vertical lines), for species of *Hemiaster (Bolbaster)* in the Tertiary of southern Australia, of the length of the anterior petals, expressed as percentages of test length (left); and illustrations of the posterior row of pore pairs of anterior petals of the five species of *H. (Bolbaster)*, illustrating the progressive temporal reduction in size of the pores and their increasing separation (right).

twenty-one and sixteen to twenty, respectively (text-fig. 4B). Similarly, the posterior petals show a reduction, with thirteen to nineteen pore pairs in *H. (B.) subidus*, eight to fourteen in *H. (B.) planedecclivis*, and eleven or twelve in *H. (B.) callidus*.

As the anterior petals became shorter, from the Late Eocene to the Middle Miocene, so both they and the posterior petals also became progressively deeper. A similar deepening also occurred in ambulacrum III. Furthermore, as the petals and ambulacrum III deepened, so the aboral interambulacra became increasingly swollen. This effectively increased the depth of the petals and ambulacrum III even further. Consequently, the smooth aboral surface of the early species of *H. (Bolbaster)* progressively changed through the Tertiary to give way to a coarsely corrugated surface in the youngest species, *H. (B.) callidus* (Pl. 47, fig. 4).

Along with these changes in petal topography, the shape and disposition of the pore pairs in the petals underwent a unidirectional morphological change. The pairs within each pore pair in the Late Eocene *H. (B.) subidus* are elongate and situated close together, the distance between the pores in each pair being less than the length of the pore (text-fig. 4B). In the descendant Early Oligocene *H. (B.) dolosus* the pores are still as elongate, but are set a little further apart within each pair. The

pores became less elongate in the Early Miocene *H. (B.) verecundus* and set even wider apart, the distance between the pores in each pair being greater than the length of the pore. In the Early/Middle Miocene *H. (B.) planedecclivis* the pores became almost circular and separated by a distance greater than their diameter. The final species in the lineage, the Middle Miocene *H. (B.) callidus*, also possesses nearly circular pore pairs, but they are more widely separated than those of its ancestor, *H. (B.) planedecclivis*, being separated by a distance up to twice the diameter of the pores.

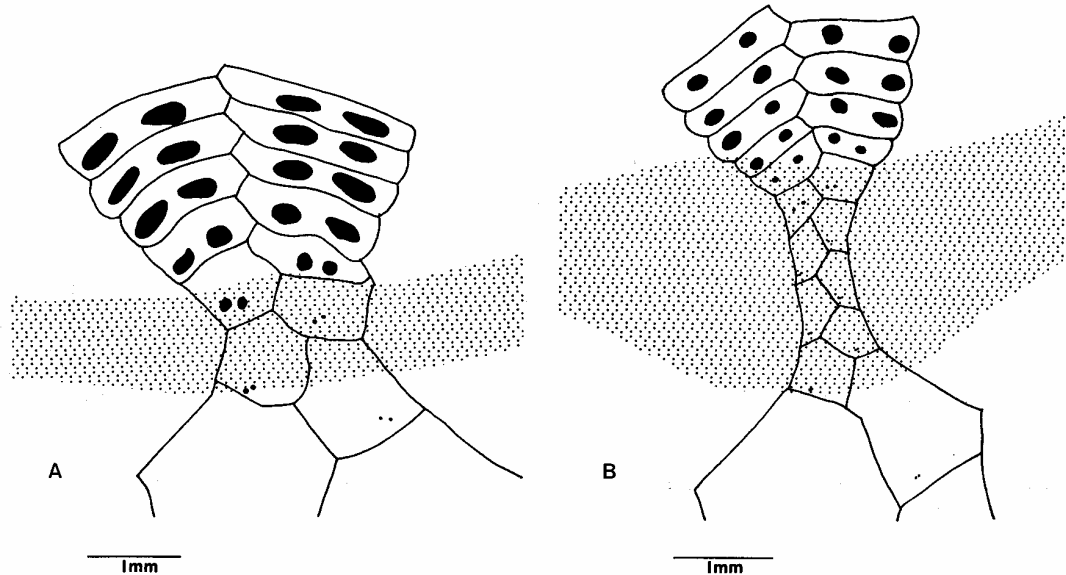
Although the pores within each pair became progressively more widely separated, the interporiferous zone between the anterior and posterior rows of pore pairs in each petal did not become narrower. Instead, the petals became slightly wider to accommodate the expansion. The widening rows were also accommodated by the increase in depth of the petals. However, although the interporiferous zone did not change in width as the lineage evolved, it underwent a change in character. In early species, such as *H. (B.) subidus* and *H. (B.) dolosus*, the interporiferous zone is covered by a mixture of primary and miliary tubercles (Pl. 44, fig. 4). As the lineage evolved, so the density of primary tuberculation decreased, with the result that the youngest species, *H. (B.) callidus*, possesses only miliary tubercles. The same degree of reduction in primary tubercles is also evident in ambulacrum III. *H. (B.) subidus* possesses a maximum of seventeen tubercles in ambulacrum III; *H. (B.) dolosus* has up to nine; *H. (B.) verecundus* five; *H. (B.) planedecclivis* six; *H. (B.) callidus* generally none, though rarely one or two. Tubercles were preferentially lost from the adapical part of the ambulacrum. Thus, in *H. (B.) subidus* primary tubercles are spread over the entire length of ambulacrum III, but are confined to the adambital half in *H. (B.) dolosus* and the adambital third in *H. (B.) verecundus* and *H. (B.) planedecclivis*. Where primary tubercles do occur in *H. (B.) callidus*, they are found close to the peripetalous fasciole.

Apical system. A consequence of the foreshortening of the test and the inclination of the posterior surface of the test was a relative anterior movement of the apical system. It is posterior of centre in the oldest species, *H. (B.) subidus* and *H. (B.) dolosus*, almost central in *H. (B.) verecundus* and *H. (B.) planedecclivis*, and slightly anterior of centre in *H. (B.) callidus* (text-fig. 3D). With the anterior migration of the apical system through the lineage, a change in the orientation of the anterior petals might be expected; but this was not the case. There was, however, a change in the outline of the peripetalous fasciole, from oval in the earlier species, with the long axis sagittal, to nearly circular in *H. (B.) callidus*. Ambulacrum III also shortened as the apical system migrated anteriorly, from 45% TL in the Late Eocene *H. (B.) subidus* to 40% TL in the Middle Miocene *H. (B.) callidus*.

Peripetalous fasciole. One of the more dramatic morphological changes along the lineage was the increase in width of the peripetalous fasciole (text-fig. 3C). This increase in width was not over the entire fasciole, but was confined to the plate margins. In the earliest species, the Late Eocene *H. (B.) subidus*, the fasciole is narrow (2.4–3.3% TL) and of nearly even width throughout its course (Pl. 48, fig. 8). Where it crosses the ambulacra it covers no more than two plates in each column (text-fig. 5A). As the species evolved along the lineage, so the fasciole progressively widened from 3.8% TL in the Early Oligocene *H. (B.) dolosus*, to 5.7% TL in *H. (B.) verecundus*, 5–7% TL in *H. (B.) planedecclivis*, and 7.3–9.5% TL in *H. (B.) callidus*. In the later species the fasciole broadened at all plate boundaries; at the centre of each ambulacral plate the fasciole is a little broader than in *H. (B.) subidus*. Whereas the fasciole covers only two plates in each ambulacral column in *H. (B.) subidus*, it covers five or six plates in each column in the youngest species, *H. (B.) callidus* (text-fig. 5B). The reduction in petal length and pore pair number in the petals along the lineage, and the increase in the number of small, fasciole-bearing ambulacral plates, implies that the fasciole increased in width at the expense of the pore pairs in the petals. In *H. (B.) callidus* the fasciole covers almost the entire lateral margin of the interambulacral plates (Pl. 48, fig. 7), whereas in *H. (B.) subidus* it covers only one-sixth of the lateral plate margin.

Aboral tuberculation. In the Late Eocene *H. (B.) subidus* the aboral and ambital tuberculation consists of relatively widely spaced primary tubercles set in a matrix of miliary tubercles (Pl. 48, fig. 8). As the lineage evolved, so the proportion of primary to miliary tubercles increased to such

an extent that in the Middle Miocene *H. (B.) callidus* the miliary tubercles are almost absent, the primary tubercles being densely concentrated (Pl. 48, fig. 7). The primary tubercle concentration (measured on the aboral surface between the peripetalous fasciole and the ambitus) increases from 3.2 mm^{-2} in the oldest species, *H. (B.) subidus*, to 7.8 mm^{-2} in the youngest species, *H. (B.) callidus* (text-fig. 9A).



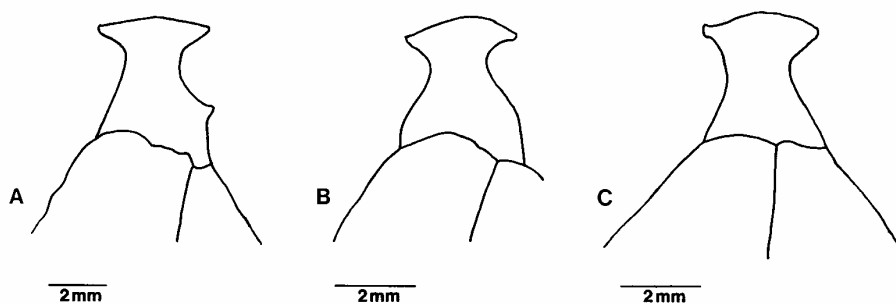
TEXT-FIG. 5. Camera lucida drawings of the distal portion of the posterior ambulacrum and the peripetalous fasciole (dotted). A, *H. (Bolbaster) subidus* sp. nov., SAM P26554, holotype. B, *H. (B.) callidus* sp. nov., NMV P100503, holotype, illustrating its wider peripetalous-fasciole, covering a greater number of ambulacral plates than in *H. (B.) subidus*.

Adoral surface. This underwent less morphological evolution than the aboral surface in the *H. (Bolbaster)* lineage. Changes were confined to the peristome and the plastron. The peristome became positioned further from the anterior ambitus in later species. The peristomial margin became increasingly raised and notched as the lineage evolved. The labrum also elongated and came to project more strongly anteriorly in later species. Furthermore, the adoral interambulacra surrounding the peristome became a little more swollen.

The only other morphological changes on the adoral surface of the test involved the two plastronal plates, interambulacra 5a and 5b. In *H. (B.) subidus* the plates are markedly asymmetric, being in a primitive amphisternous condition. In the youngest species, *H. (B.) callidus*, the plates are almost symmetrical (text-fig. 6).

Morphological evolution of Psephoaster

Three species of *Psephoaster* are known from Eocene to Miocene strata of southern Australia. The oldest species is the Late Eocene (Aldingan) *P. lissos* sp. nov., which is succeeded by the Late Oligocene (Janjukian) *P. apokryphos* sp. nov. and the Early Miocene (Longfordian) *P. klydonos* sp. nov. (text-fig. 2). These species probably form part of a single evolutionary lineage. Like the *H.*

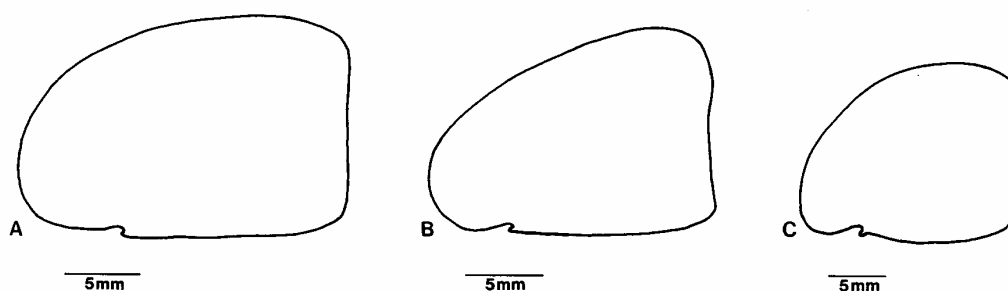


TEXT-FIG. 6. Camera lucida drawings of the labrum and anterior plastron. A, *Hemiaster (Bolbaster) subidus* sp. nov., SAM P26554, holotype. B, *H. (B.) planedecivis* Gregory 1890, NMV P78460. C, *H. (B.) callidus* sp. nov., NMV P100503, holotype. They illustrate the adaxial temporal migration of the interambulacrum 5 suture.

(*Bolbaster*) lineage, the species in this lineage occur over a geographical range of some 650 km, well within the extent of range of many modern spatangoid species.

Seven morphological characters of the test undergo directional morphological change along the *Psephoaster* lineage over a period of twenty million years from the Late Eocene to Early Miocene. Directional morphological transformations occur in the test height and profile, width and depth of the petals, position of the apical system, shape of the aboral interambulacra, size and position of the pore pairs in the petals, width of the peripetalous fasciole, and density of ambital tuberculation. Apart from the change in pore pair shape, all other changes parallel those which occur in the *H. (Bolbaster)* lineage.

Test shape. As the *Psephoaster* lineage evolved, so the test became relatively shorter and higher. This occurred by a preferential increase in height of the posterior of the test in interambulacrum 5 (text-fig. 7). The height of the test relative to the length of the test increased from 66% in the Late Eocene *P. lissos*, to 67–71% in the Late Oligocene *P. apokryphos*, and 79–87% (apart from one specimen at 72%) in the Early Miocene *P. klydonos*. A concomitant change was the development of a prominent rostrum in interambulacrum 5, both adorally and aborally. With this increase in test height, the aboral surface, particularly in the central part of the test, became more steeply inclined. The increase in height also resulted in the anterior movement of the apical system, from being 55% TL from the anterior ambitus in *P. lissos*, to 49% TL in *P. apokryphos*, and 44–49% in *P. klydonos*.



TEXT-FIG. 7. Camera lucida drawings of the lateral profiles of the three species of *Psephoaster*. A, *P. lissos* sp. nov., SAM P26560, holotype. B, *P. apokryphos* sp. nov., NMV P100506, holotype. C, *P. klydonos* sp. nov., SAM P24631, holotype. They illustrate the temporal relative increase in test height.

Petals. The petals of the Late Eocene *P. lissos* are relatively narrow (3% TL), very shallow, and bear very small, widely spaced, circular pore pairs. As the lineage evolved, so the petals widened (4–5% TL in the Late Oligocene *P. apokryphos*, 5–6% in the Early Miocene *P. klydonos*), became a little deeper, and the pore pairs enlarged, the two rows of pore pairs in each petal becoming situated closer together (text-fig. 13). The depth of the petals was effectively further increased by the development of gently swollen adapical interambulacra in *P. klydonos*, in a similar manner to those of *H. (Bolbaster) callidus*.

Peripetalous fasciole. The *Psephoaster* lineage parallels the *H. (Bolbaster)* lineage in its development of an increasingly broader peripetalous fasciole in younger species. In the Late Eocene *P. lissos* the fasciole is very thin (1.5% TL), thread-like, and of even width throughout (Pl. 47, fig. 3). The fasciole is almost twice as wide in the Late Oligocene *P. apokryphos*, reaching a maximum width of 2.5% TL where it crosses the ambulacra. It is slightly narrower across the interambulacra. This variation in fasciole width is accentuated in the Early Miocene *P. klydonos* (Pl. 48, fig. 1), which reaches up to 6% TL in width where it crosses the ambulacra and the interradial suture (text-fig. 13). Here it is about three times wider than where it crosses the middle of the interambulacral plates.

Tuberculation. Aboral and ambital primary tuberculation increased in density from the Late Eocene *P. lissos*, with a density of 3 mm⁻², through the Late Oligocene *P. apokryphos* with 5 mm⁻², to the Early Miocene *P. klydonos* with 7.5 mm⁻² (text-fig. 9b). As the primary tuberculation increased in density, so the intervening miliary tubercles decreased in density. The rate of change in density of primary tuberculation in *Psephoaster*, from 3 mm⁻² in the Late Eocene to 7.5 mm⁻² in the Early Miocene, was a little greater than the increase in *H. (Bolbaster)*, which over the same period increased from 3.2 to 4.8 mm⁻². However, by the end of the Middle Miocene the tuberculation density in *H. (Bolbaster)* reached a similar concentration to that of *Psephoaster*, being 7–8 mm⁻² in *H. (B.) callidus*.

Role of heterochrony in the evolution of the H. (Bolbaster) and Psephoaster lineages.

Nearly all of the morphological changes which occurred along the *H. (Bolbaster)* and *Psephoaster* lineages may be interpreted as being products of variation in the rate of ontogenetic development of various structures (heterochrony). Certain morphological features are considered to have undergone an increased rate of development (acceleration), resulting in peramorphosis (*sensu* Alberch *et al.* 1979; McNamara 1986), while others experienced a decreased rate of development (neoteny), resulting in paedomorphosis.

A number of examples of heterochrony in echinoid evolution have recently been documented. McNamara and Philip (1980) and McNamara (1982a) interpreted many of the morphological changes which occurred with the evolution of *S. (Schizaster)* from *S. (Paraster)* in the Australian Tertiary as having been produced by the action of both acceleration and hypermorphosis (extension of ontogenetic allometries) resulting in peramorphosis. Conversely, the living species of *Breynia* are thought to have evolved by paedomorphosis (McNamara 1982b). The changes in test architecture in Australian Tertiary species of *Pericosmus* are considered to have occurred by hypermorphosis, resulting in peramorphosis (McNamara and Philip 1984). Similarly, changes in the form of phylloidal plates in the Australian spatangoid *Protenaster* have been interpreted (McNamara 1985) as a product of acceleration, resulting in peramorphosis. Hypermorphosis has been invoked by Smith and Paul (1985) for the evolution of *Discoidea favrina* (Desor) from *D. subucula* (Leske) in the Cenomanian of Devon. In all of these examples the morphological evolution within each lineage is either paedomorphosis or peramorphosis. The species in each lineage lie along discontinuous morphological gradients, termed (McNamara 1982a) either paedomorphoclines (as in *Breynia*) or peramorphoclines (as in *Schizaster*, *Pericosmus*, and *Protenaster*).

Recently, McKinney (1984) has demonstrated that some structures in an *Oligopygus* lineage are paedomorphic, while others are peramorphic in the same species. A similar situation occurs in species in the *H. (Bolbaster)* and *Psephoaster* lineages where some of the morphological characters

of descendant species may be interpreted as paedomorphic, whilst others may be peramorphic. As McKinney (1984, p. 415) noted, such dissociated heterochronic events have been documented in a number of living organisms. Any particular developmental pattern for any structure may be disrupted to varying degrees, potentially producing an almost endless variety of descendant heterochronic morphotypes. The selection pressures which act on these descendant morphotypes in *H. (Bolbaster)* and *Psephoaster* are discussed below.

In order to assess which particular structures in the species of *H. (Bolbaster)* and *Psephoaster* are paedomorphic and which are peramorphic, it is necessary to be able to document the species' ontogeny. The only described ontogenies of species of *Hemiaster* are those of the living *H. expergitus* Lovén, 1874 (Mortensen 1907) and the Paleocene *H. (Leymeriaster) targari* McNamara and Philip, 1987. These two species both follow similar ontogenetic pathways. Comparison of adult morphologies of the five species of *H. (Bolbaster)* and the three species of *Psephoaster* with the ontogeny of *H. (L.) targari* allows heterochronic patterns to be assessed.

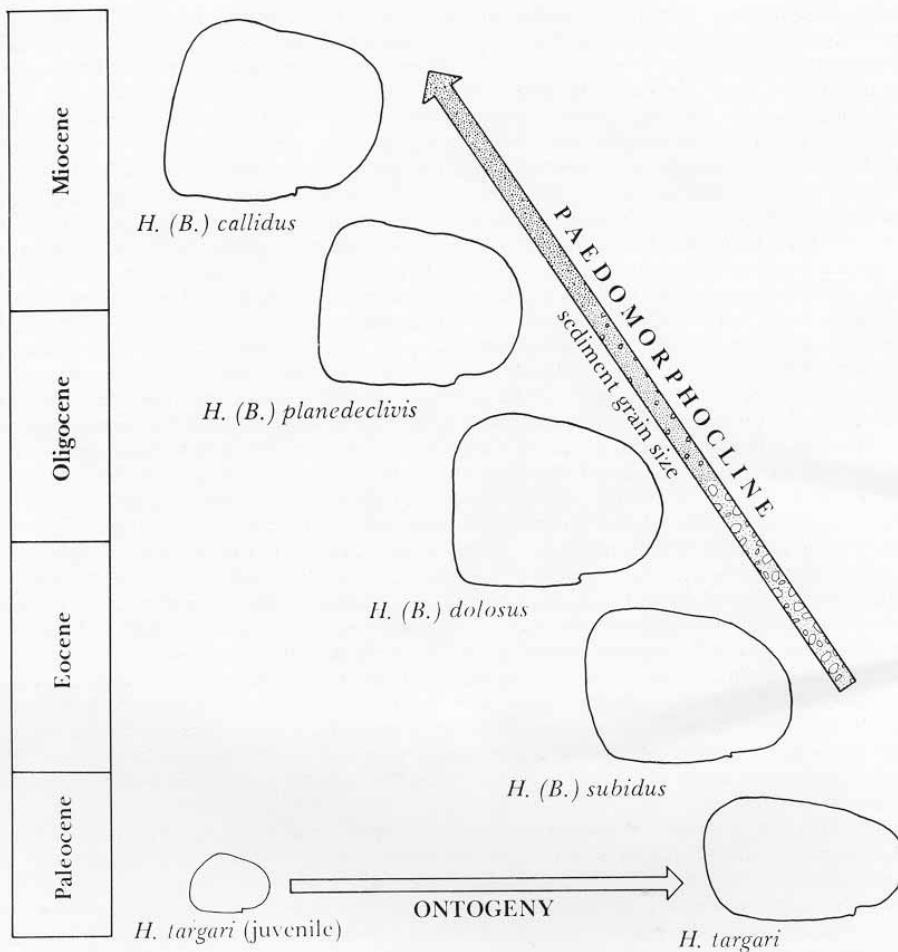
During the ontogeny of *H. (L.) targari* the test lengthened, narrowed, became less inflated, and the posterior face changed from being anteriorly inclined to near vertical; the petals lengthened and deepened, and the pore pairs changed from being circular to elongate; ambulacrum III also deepened and a weak anterior notch developed; the apical system underwent a relative posterior migration, moving from anterior of centre to posterior of centre; the density of the tuberculation increased; on the adoral surface the interambulacra became relatively less inflated close to the peristome; the peristome itself migrated anteriorly and the labrum developed an anterior lip; and the plastron, which was very convex in juveniles, became flatter during ontogeny (McNamara and Philip 1987).

Of the morphological trends which have been documented in the *H. (Bolbaster)* lineage, ten follow the opposite trend to the ontogenetic development, with the result that later species became increasingly juvenile in appearance in these particular characters. This increasing degree of paedomorphosis resulted in the establishment of paedomorphoclines for many of the structural changes. Paedomorphoclines can be observed in the change in test outline, from oval to circular; the relative increase in test height (text-fig. 8); the increasing inclination of the posterior surface of the test; the shortening of the petals and ambulacrum III, and reduction in number of pore pairs in the petals; the development of rounded pores from elongate pores in the petals; the reduction in primary tuberculation in the petals; the reduction in primary tuberculation in the petals and ambulacrum III; the relative anterior movement of the apical system; the broadening of the peripetalous fasciole; the posterior migration of the peristome; and the swelling of the interambulacra close to the peristome. Three evolutionary changes in the *Psephoaster* lineage which also occur in the *H. (Bolbaster)* lineage, namely increase in test height, anterior displacement of the apical system, and broadening of the fasciole, are also interpreted as being paedomorphic changes.

With structures such as the width of the peripetalous fasciole, in which the ancestral morphotypes underwent negative allometry during growth, the degree of negative allometry decreased along the lineage and approached isometry. Conversely, the petals grew with positive allometry, but the paedomorphocline developed because the degree of positive allometry was reduced along the lineage such that it approached closer to isometry. Reducing either positive or negative allometries closer to isometry results in paedomorphosis. Increasing positive or negative allometries away from isometry results in peramorphosis. Three structures form peramorphoclines in both the *H. (Bolbaster)* and *Psephoaster* lineages: the deepening petals, the swelling of the interambulacra adapically, and the increase in aboral primary tuberculation. Furthermore, the broadening petals and increase in pore pair size are peramorphic features in *Psephoaster*.

Psephoaster itself may be interpreted as a paedomorphic hemiasterid. Juvenile hemiasterid characters which it possesses as an adult include: the petals, which are shallow to flush with the test surface; the very small, simple pore pairs in the petals; and the lack of a sunken ambulacrum III, which also has very small pore pairs.

This obvious structural plasticity in the two lineages is comparable with that observed in other spatangoid and holasteroid lineages (McNamara and Philip 1980, 1984; McNamara 1982*a, b*, 1985; Gale and Smith 1982; Smith 1984). Such plasticity has been interpreted (McNamara *in press*) as



TEXT-FIG. 8. Camera lucida drawings of the lateral profiles of four of the Australian Tertiary species of *Hemaster (Bolbaster)* and the juvenile and adult profiles of an Australian Paleocene species of *Hemaster*. They illustrate the pedomorphic change in lateral test profile from the Paleocene to Middle Miocene and its relationship to the reduction in sediment grain size.

being caused by 'plate translocation'. This involves the dissociation of growth allometries of each coronal plate and the capacity of plates to resorb stereom, as well as grow, at their margins at different rates, thereby providing a great range of morphotypes available for selection and subsequent genetic stabilization.

Functional significance of the morphological evolution of the H. (Bolbaster) and Psephoaster lineages. Spatangoid echinoids are a highly successful group of echinoderms which are adapted to living on and within a wide range of sediment types. Not only have some evolved a number of morphological

structures which allow them to live buried in coarse to fine-grained sediments, but they are also adapted to feeding directly from the sediment. Consequently, any unidirectional morphological trends occurred in response to selection for test morphologies which are better adapted either to inhabiting, or feeding from, a different sediment grain size.

A number of spatangoid evolutionary lineages have been described. The morphological evolution in all these examples was directed toward the occupation of finer-grained sediments. Thus, morphological changes along the *S. (Paraster)*-*S. (Schizaster)* lineage have been interpreted (McNamara and Philip 1980) as adaptations to burrowing in progressively finer-grained sediment along a peramorphocline. The morphological changes involved: swelling of interambulacrum V aborally; a posterior migration of the apical system; decreased petal depth; increased depth of ambulacrum III and increase in the number of pore pairs; slightly anterior migration of the peristome; and increased development of an anterior rim on the labrum. These changes are thought to have allowed descendant species of *S. (Schizaster)* to occupy finer-grained sediments than their ancestors. This necessitated the development of structures which were adapted to optimum utilization of the water for respiration, such water being restricted to flowing down the funnel connected to the surface by the funnel-building tube feet of ambulacra III. Earlier species of the *S. (Paraster)* morphotype inhabited coarser-grained sediments which allowed water to bathe the entire test surface. The more impervious nature of finer-grained sediments resulted in only those morphotypes with the ability to construct mucus-lined funnels being able to inhabit such sediments.

Smith (1984) recently re-interpreted the evolution of the Cretaceous spatangoid *Micraster* in a similar light. Nichols (1959*a, b*) had previously interpreted the morphological changes in *Micraster* as adaptations to burrowing deeper in the sediment. However, Smith noted that changes such as increased test height, posterior movement of the apical system, development of a keel in interambulacrum 5, broadening of the test, deepening and increasingly tuberculate ambulacrum III, anterior movement of the peristome, labrum enlargement, and increase in petal length (many of which occur in the *Schizaster* and, as discussed below, in the *H. (Bolbaster)* and *Psephoaster* lineages) are all adaptations by descendant morphotypes to inhabiting finer-grained sediments. Similar morphological changes in the evolution of species of *Pericosmus* from the Australian Tertiary (McNamara and Philip 1984) are also considered to be adaptations to inhabiting finer-grained sediments. Changes in the structure of the phyllodal plates in *Protenaster* are similarly interpreted (McNamara 1985) but, in this case, the adaptation was concerned largely with the organism's ability to feed from a finer-grained sediment.

Many of the evolutionary trends which occurred in the *H. (Bolbaster)* and *Psephoaster* lineages are the same as those in the *Schizaster*, *Micraster*, and *Pericosmus* lineages, and for the same reason—the occupation by descendant morphotypes of progressively finer-grained sediments. In *H. (Bolbaster)* these adaptations included: broadening of the test, increase in test height, and development of a keel in interambulacrum III (all of which improved water flow over the test); elongation of the labrum; and reduction in primary tuberculation in the petals and ambulacrum III (allowing an increase in miliary currents and so improving ciliary current flow). Water flow over the test was likewise improved in descendant species of *Psephoaster* by the increase in test height, development of a keel in interambulacrum 5, deepening of the petals, and swelling of the aboral interambulacra adapically.

Smith and Paul (1985) recently demonstrated how the ecophenotypic increase in test height in a lineage of *Discoides subucula* corresponds to a decrease in sediment grain size. They interpreted the higher test shape, resulting in the attainment of a more conical profile, as an adaptation for assisting in preventing finer-grained sediment from falling through the shield of fine spines. *Discoides*, being a holoctypoid, lacked mucus-producing fascioles. The increase in test height in spatangoids is more likely to have helped water flow over the test and on to the respiratory tube feet-bearing petals at a faster rate.

Analysis of the calcarenites which the five Australian Tertiary species of *H. (Bolbaster)* inhabited reveals a progressive decrease in sediment grain size (text-fig. 9A), 98 % of sediment grains ranging in diameter from 0.5–2.0 mm (1 % up to 6 mm) in the Late Eocene, to 0.05–0.2 mm (up to 0.5 mm)

in the Middle Miocene. The Eocene and Oligocene sediments are predominantly coarse-grained bryozoal calcarenites. The finer-grained calcarenites of the Miocene deposits are composed largely of foraminifers, with a minor component of fragments of echinoid tests and spines, and of molluscan shells.

In studies of the relationship between grain size and permeability of both artificial (Fraser 1935; Beard and Weyl 1973) and natural (Pryor 1973) sediments, it was shown that with decreasing grain size there is a corresponding decrease in permeability. Although these authors also showed that porosity may sometimes increase with decreasing grain size, other factors, such as sphericity and angularity of the grains, play an important role in affecting sediment permeability. Sphericity of grains is much lower in the Eocene and Oligocene sediments, which are dominated by fragments of stick bryozoans. Fraser (1935) showed how permeability of sediments increases as particles depart in shape from a perfect sphere. Permeability is higher because such irregular-shaped grains act as bridges between other grains, resulting in looser packing of the sediment. Von Engelhardt and Pitter (1951) demonstrated that looser packing results in higher sediment permeability.

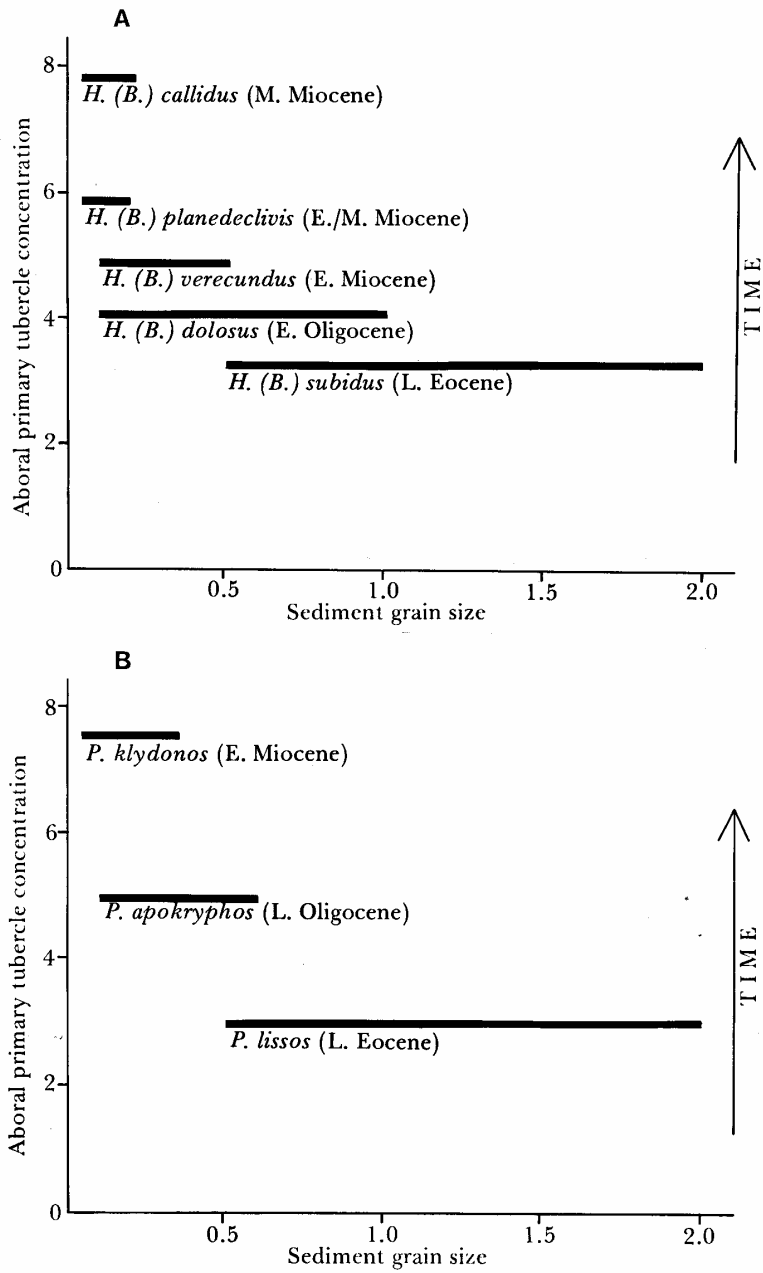
The overall decrease in grain size from the Late Eocene to Middle Miocene of sediments inhabited by species of *H. (Bolbaster)*, combined with an increase in grain sphericity, is likely to have had a greater impact on reducing overall sediment permeability than the small increase in sorting which accompanied the decrease in grain size. Consequently, only descendant morphotypes with morphological adaptations suitable for inhabiting sediments of lower permeability were selected. In the case of the *H. (Bolbaster)* lineage, the combination of paedomorphic and peramorphic features which evolved were the most successful adaptations.

A parallel situation occurred in the *Psephoaster* lineage (text-fig. 9B), the sediment grains ranging in diameter from 0.5–2.0 mm in the Late Eocene Tortachilla Limestone to 0.1–0.6 mm in the Late Oligocene Jan Juc Formation and to 0.1–0.33 mm in the Early Miocene Mannum Formation; the sediments inhabited by the three species therefore diminished in grain size and increased in sphericity.

In addition to the morphological trends common to *H. (Bolbaster)*, *Psephoaster*, *Schizaster*, *Micraster*, and *Pericosmus*, some have only been recognized in the *H. (Bolbaster)* and *Psephoaster* lineages. Three significant trends which provide strong evidence for the morphological changes reflecting adaptations to inhabiting finer-grained sediments are those involving the increase in peripetalous fasciole width, change in tubercle density, and change in size and shape of the pore pairs in the petals. All three character changes occur in both of these hemiasterid lineages.

It is likely that the reduction in density of aboral miliary tubercles, at the expense of the primary tubercles, and the increase in width of the peripetalous fasciole are closely related. The increase in fasciole width occurred by an increase in the density of tiny miliary tubercles which bear clavules. As Chesher (1963, p. 560) noted for the spatangoid *Moiria*, the clavules have a division of labour, some parts producing mucus, others generating water currents from cilia arranged along the clavule shaft. Increase in the density of mucus and current producing clavules will have benefited an echinoid inhabiting fine-grained sediments. Smith (1984) observed a similar change in the distribution of miliary tubercles on some later species of *Micraster* which inhabited finer-grained sediments than their ancestors. Early species possess no aboral fasciole, only a dense array of miliary tubercles. In some later species a peripetalous fasciole began to develop at the expense of the aboral miliaries. Although Smith (1980b) questioned how fasciole arrangement could be used to infer preferred substrata in fossil echinoids, the positive relationship between increasing peripetalous fasciole width and decreasing sediment grain size in *H. (Bolbaster)* and *Psephoaster* indicates that fasciole width may prove to be of some general significance in assessing substratum preference in spatangoids. The reduction in the number of primary tubercles in the interporiferous zones of the petals and ambulacrum III in later species of *H. (Bolbaster)*, at the expense of miliary tubercles, also suggests a further increase in current-generating spines to improve water flow over the respiratory tube feet.

The relationship between the concentration of aboral primary tubercles and decreasing sediment grain size has been examined by Smith (1980b); in spatangoids, he noted how the tubercle concentration increased as the sediment grain size decreased. Both *H. (Bolbaster)* and *Psephoaster* follow



TEXT-FIG. 9. Relationship of aboral primary tubercle concentration to sediment grain size. A, in five species of *Hemiaster (Bolbaster)*. B, in three species of *Psephaster*.

this relationship (text-fig. 9). The increase in tubercle concentration is particularly evident between the peripetalous fasciole and the ambitus, reflecting an increase in aboral spine concentration. Aboral spines are used by burrowing spatangoids to transport sand over the aboral surface of the test (Smith 1980*b*). An increase in concentration of aboral spines is a natural corollary of inhabiting a finer grained sediment, as a denser concentration is necessary to effectively transport smaller sediment grains. A similar relationship of high aboral spine density with fine-grained sediments has been observed in archiaciid cassiduloids by Smith and Zaghbib-Turki (1985).

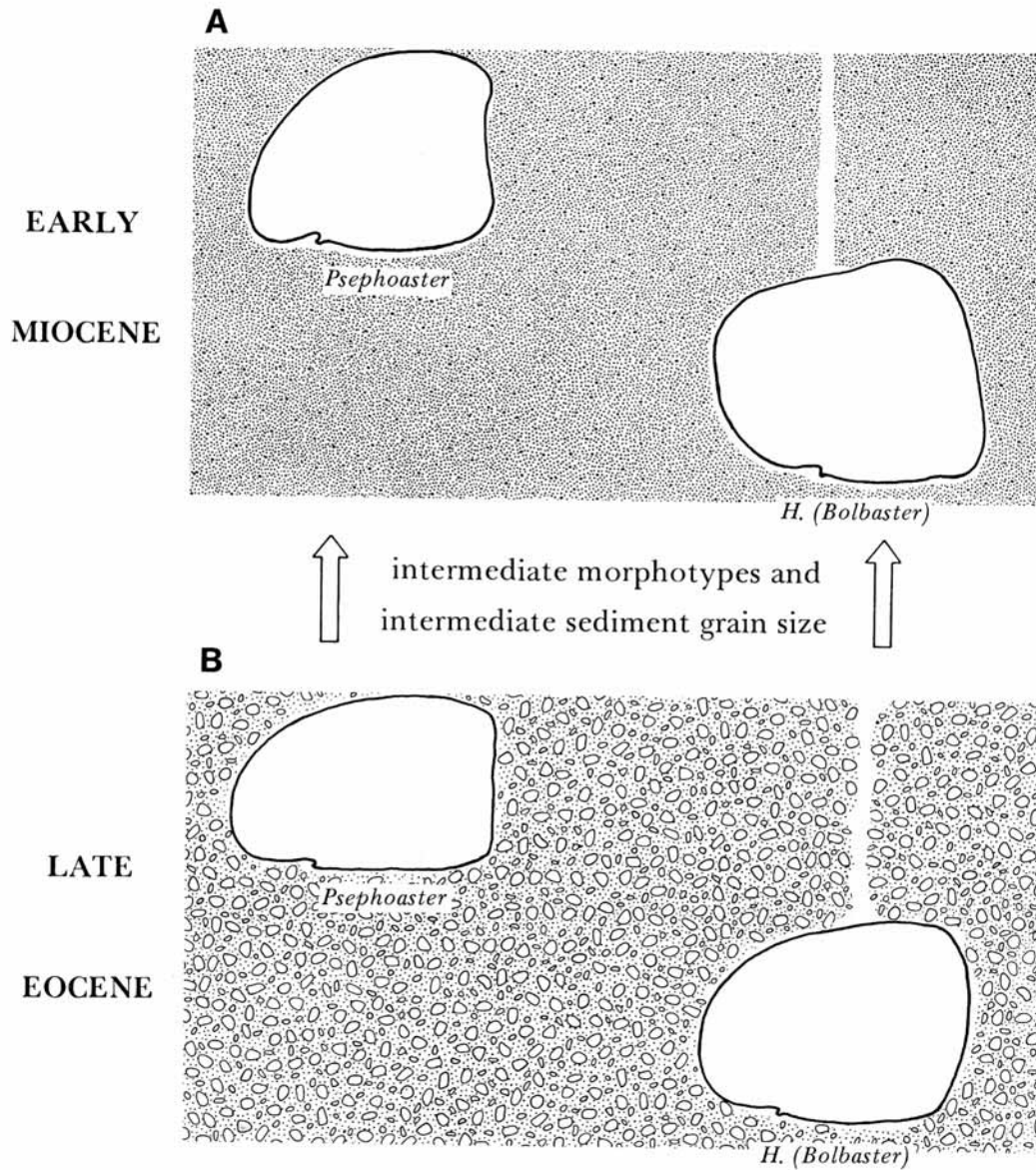
In the petals of *H. (Bolbaster)*, the paedomorphic evolution of widely spaced round pores from closely spaced elongate pores is yet another morphological feature which may be interpreted as an adaptation to inhabiting finer-grained sediments. Smith (1980*a*) noted how pores which are widely separated have a more efficient gas exchange system in the tube feet than those which are closely spaced. The wider spacing reflects the presence of a larger ampulla with many septa. It may be argued that the increased spacing of the pores along the *H. (Bolbaster)* lineage reflects the possession of more efficient respiratory tube feet in those species which inhabited finer-grained sediments. In *Psephoaster*, improvements in the respiratory capabilities of the aboral ambulacral tube feet occurred by an increase in size, thus allowing a greater degree of oxygen absorption.

The morphological adaptations in all eight species of the *H. (Bolbaster)* and the *Psephoaster* lineages indicate that they lived buried in the sediment. However, there is no direct evidence to indicate to what depth they burrowed. The co-existence of these two, probably closely related, hemiasterid genera suggests that niche partitioning between them may have occurred by differences in depth of burial within the sediment. Although five living species of *Hemiaster* are known (Mortensen 1950), including some such as *H. expergitus* which are morphologically very similar to some species within the *H. (Bolbaster)* lineage, little of their ecology was known until recently, beyond the fact that they generally occupy fine-grained sediments in relatively deep water (140–3,000 m).

Smith (1980*a*, p. 53) recognized the presence of funnel-building tube feet in *H. expergitus*. These are poorly specialized tube feet bearing a broad, circular disc, with scalloped margins, supported by a rosette of ten or eleven rods. Each tube foot is associated with a partitioned isopore. The presence of funnel-building tube feet in ambulacrum III, combined with the possession of a peripetalous fasciole, suggest that *H. expergitus* burrowed to some depth within the sediment. This prediction has recently been confirmed by Gage *et al.* (1985) who reported the recovery of a specimen of *H. expergitus* from a box core sample in which it was lying in its burrow 12 cm from the sediment surface. A long, slightly oblique funnel linked it to a shallow depression and opening in the sediment. The specimen was found in a soft, fine-grained sediment. Gage *et al.* (1985) suggested that the wide peripetalous fasciole of *H. expergitus* was capable of generating a strong current within its burrow.

The principal difference between *Hemiaster* and *Psephoaster* lies in the character of aboral ambulacrum III, which provides the possible key to the niche partitioning of the *H. (Bolbaster)* and *Psephoaster* lineages. *H. (Bolbaster)*, like all other members of the genus, possesses a sunken ambulacrum III aborally. Within this depressed ambulacrum the pore pairs occur as isopores which are divided by a prominent interporal partition and are very similar in morphology to the equivalent structure in *H. expergitus*. This, combined with the presence of a peripetalous fasciole which is very broad in later species, and other morphological adaptations consistent with optimizing water current flow over the test in a relatively fine-grained sediment, points to *H. (Bolbaster)* having burrowed quite deeply in the sediment (text-fig. 10), perhaps in the region of 10–12 cm below the sediment/water interface, similar to *H. expergitus*.

Psephoaster, on the contrary, has neither a sunken aboral ambulacrum III nor isopores with a swollen interporal partition. The pore pairs in ambulacrum III are extremely small and widely spaced, with an interporal partition flush with the surface of the test; they were probably sensory, not mucus-generating. The presence of a peripetalous fasciole which is relatively narrower in species of *Psephoaster* than in co-existent species of *H. (Bolbaster)*, and the probable absence of funnel-building tube feet, suggests that species of *Psephoaster* were shallow burrowers, perhaps burrowing only to sufficient depth to cover the aboral surface of the test (text-fig. 10).



TEXT-FIG. 10. Suggested niche partitioning. A, Early Miocene species inhabiting fine-grained sediment. B, Late Eocene species of *Psephoaster* (shallow burrower) and *Hemiaster (Bolbaster)* (deeper burrower) inhabiting coarse-grained sediment.

PALAEONTOLOGY, VOLUME 30
SYSTEMATIC PALAEONTOLOGY

Order SPATANGOIDA Claus, 1876
Family HEMIASTERIDAE Clark, 1917
Genus HEMIASTER Agassiz in Agassiz and Desor, 1847

Type species. Spatangus bufo Brongniart, 1822, p. 84.

Discussion. Lambert and Thiéry (1924) subdivided *Hemiaster* (s.l.) into seven sections: *Hemiaster* (s.s.), *Leymeriaster*, *Mecaster*, *Gregoryaster*, *Integraster*, *Bolbaster*, and *Holanthus*. Lambert (1931) later abandoned *Integraster*, regarding it as being synonymous with *Hemiaster* (s.s.), but introduced another, *Catoproctus*. Fischer (1966) regarded the sections as subgenera, but relegated *Catoproctus* to the class of 'doubtful nominal genera'. The many described species of *Hemiaster* and their wide range of morphologies makes the use of the seven subgenera reasonably effective. The only problems arise in the assignment of some species to particular subgenera, on account of the artificial nature of the generic subdivision. The Australian Tertiary species of *Hemiaster* (s.l.) described herein are assigned to *Bolbaster*.

Subgenus BOLBASTER Pomel, 1869

Type species. Spatangus prunella Lamarck, 1816, p. 33.

Emended diagnosis. Test spherical to subspherical, with anterior notch very faint or absent.

Discussion. The type species of *Bolbaster*, *H. (B.) prunella* from the Maastrichtian of Maastricht, southern Netherlands, was described by Lamarck in 1816, but figured earlier in his *Tableau encyclopédique et méthodique des trois règnes de la nature* (Lamarck 1798, pl. 158, figs. 3 and 4). It was later figured by d'Orbigny (1856, pl. 881, figs. 2-4); d'Orbigny's specimen (see Mortensen 1950, fig. 280) has a faint anterior notch, this feature being used as the principal diagnostic character of the subgenus, along with its subspherical form (Lambert and Thiéry 1924, p. 505; Mortensen 1950, p. 384; Fischer 1966, pp. U558-559). However, Lamarck's (1798, pl. 158, figs. 3 and 4) illustrations, and specimens of *H. (B.) prunella* which I have examined (collected by Dr J. Geys from the Maastricht Chalk at Limburg, Belgium), have no anterior notch present at all; these specimens are about one-third of the size of d'Orbigny's specimen. As shown below, in species of *Hemiaster* (s.l.) the anterior notch develops and deepens during ontogeny; thus its absence in juveniles and small adults of *H. (B.) prunella*, but presence in larger adults are both diagnostic characters of the subgenus. Mesozoic species of *Hemiaster* (s.l.) tend to be characterized by the presence of a relatively deep anterior notch which is likely to have begun development at an early stage of ontogeny. The delay in onset of development of the anterior notch in some Late Cretaceous and Tertiary species of *Hemiaster* (s.l.) (post-displacement of Alberch *et al.* 1979; see also McNamara 1986) has resulted in this character being paedomorphic in *H. (Bolbaster)*.

The five species of *Hemiaster* (s.l.) described below likewise do not possess an anterior notch and have a subspherical shape similar to the type species; they are therefore considered to belong in the subgenus *Bolbaster*. The few species of *Bolbaster* which have previously been described (see Lambert and Thiéry 1924, p. 505) range from the Maastrichtian to the Paleocene. Inclusion of the five Eocene to Miocene Australian species within *Bolbaster* therefore greatly extends the range of the subgenus.

Furthermore, it is considered that some of the living species referred to *Hemiaster* (s.s.), namely *H. expergitus* Lovén, 1874 and *H. gibbosus* Agassiz, 1879, which lack an anterior notch and are very similar in overall morphology to the Australian Tertiary species, also belong in *Bolbaster*.

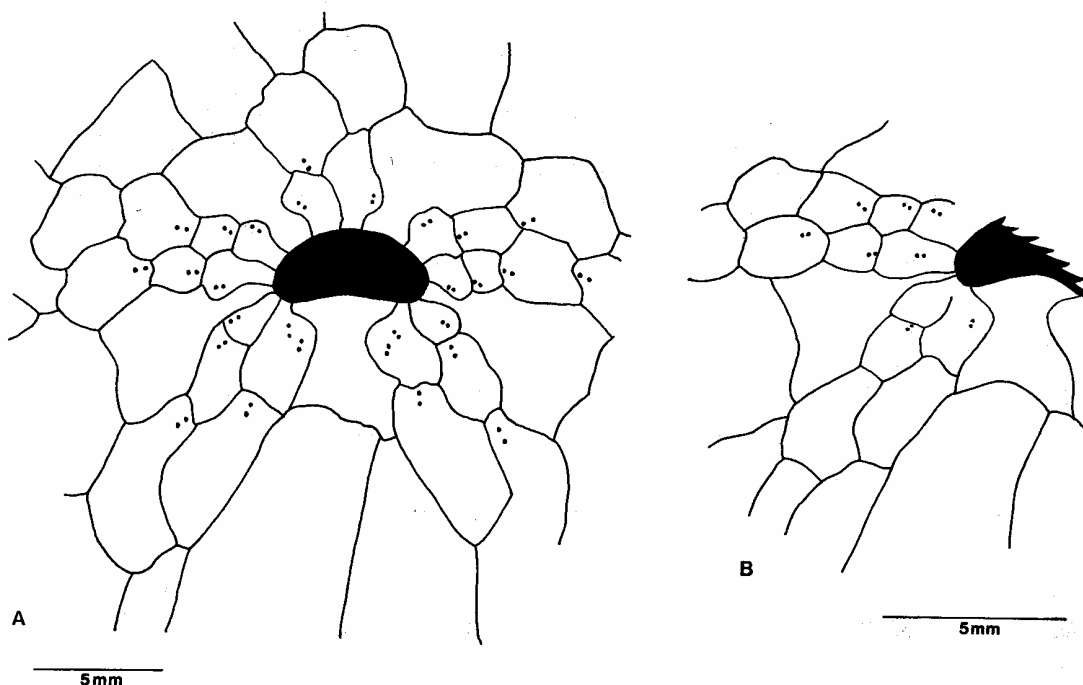
Hemiaster (Bolbaster) subidus sp. nov.

Plate 44; Plate 48, fig. 8; text-figs. 3, 4, 5A, 6A, 8, 10, 11A, 12A

Diagnosis. Test ovoid; apical system well posterior of centre; petals and ambulacrum III very shallow; pores narrow, elongate, and closely positioned within each row; peripetalous fasciole

narrow, 2-3 % TL in width. Labrum barely projected anteriorly; plastron relatively long. Posterior surface of test vertical.

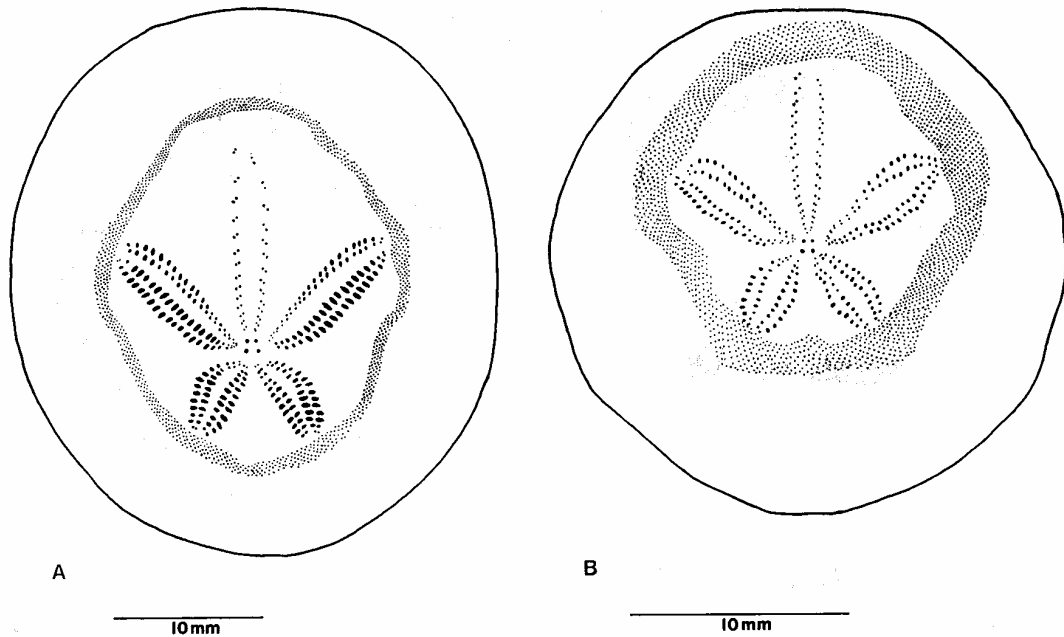
Material. Holotype SAM P26554 and paratypes SAM P26555, P26556 and NMV P20484, P53211, from Late Eocene (Aldingan) Tortachilla Limestone, Maslin Beach-Port Willunga district, south of Adelaide, South Australia.



TEXT-FIG. 11. Camera lucida drawings of adoral plating. A, *Hemiaster (Bolbaster) subidus* sp. nov., SAM P26554, holotype. B, *H. (B.) planedeclevis* Gregory, 1890, NMV P78460.

Description. Test reaching maximum known length of 38 mm; ovoid, maximum width anterior of centre; width 90-96 % TL; highest posterior of apical system close to posterior ambitus; height 71-75 % TL; posterior face vertical (text-fig. 8); aboral surface gently declined anteriorly. Interambulacra weakly raised adapically. Apical system slightly sunken and set 55-60 % TL from anterior ambitus. Ambital tubercle density 3.2 mm^{-2} . Ambulacrum III weakly depressed; parallel sided, width 6-7 % TL; bears up to eighteen isopores, pores within each pair being aligned at about 45° and being separated by a prominent interporal partition. Petals very shallow. Anterior pair diverge at $c. 105^\circ$; steadily increase in width distally to be 9 % TL wide; slightly flexed distally; length of each petal 28-32 % TL; bear up to twenty-seven pore pairs in each row, fewer in smaller specimens; pores slit-like (Pl. 44, fig. 4), pairs not conjugate; distance between pores in each row less than length of pore (text-fig. 4); pores in anterior row slightly smaller than those in posterior row adapically. Posterior petals also up to 9 % TL in width; diverge at $c. 80^\circ$; length 15-17 % TL; bear up to nineteen pore pairs, fewer in smaller specimens. Peripetalous fasciole not indented between petals; relatively narrow (Pl. 48, fig. 8), 2-3 % TL; shows little appreciable widening opposite tips of petals (text-fig. 5A).

Adoral surface gently convex. Peristome semicircular, entirely bordered by slightly raised rim; width 15-16 % TL; moderately sunken; posterior situated 28-29 % TL from anterior. Labrum long; posteriorly it narrows slightly before flaring toward plastron; relatively long, 12 % TL. Phyllode with seven isopores in ambulacra II and IV, four in ambulacrum III, and five in ambulacra I and V; pores separated by prominent interporal partition. Plastron relatively long, 46 % TL; width 33-36 % TL. Periproct oval, small, slightly sunken; length 10 % TL.



TEXT-FIG. 12. Camera lucida drawings of aboral surfaces. A, *Hemiaster (Bolbaster) subidus* sp. nov., SAM P26555, paratype. B, *H. (B.) callidus* sp. nov., NMV P100503, holotype.

Discussion. *H. (Bolbaster) subidus* is the oldest of the five known species of this subgenus. It is a rare component of the rich Late Eocene Tortachilla Limestone fauna of South Australia. Comparison with other species of *H. (Bolbaster)* is made under those species. *H. (B.) subidus* can be distinguished from the type species, *H. (B.) prunella*, on the basis of its more posterior apical system, relatively shorter petals, narrower test, and larger peristome. *H. (B.) subidus* is similar to *H. integer* Lambert (1933, pl. 3, figs. 5 and 6) from the early Turonian of D'Antantilokey, Madagascar, but can be distinguished by its narrower ambulacrum III, more posterior apical system, and more evenly sloping aboral surface. *H. integer* is herein considered to belong in *Bolbaster*. *H. (B.) subidus* also compares with *H. madagascariensis* Cottreau from the Late Maastrichtian of Madagascar (Besairie 1930, pl. 26, fig. 12), but can be distinguished by its more posterior apical system and longer, broader petals. *H. madagascariensis* also belongs in *Bolbaster*.

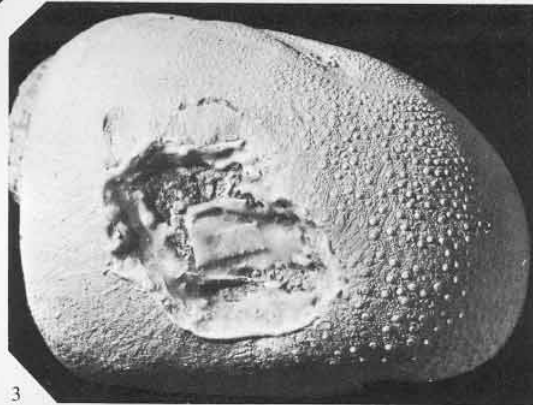
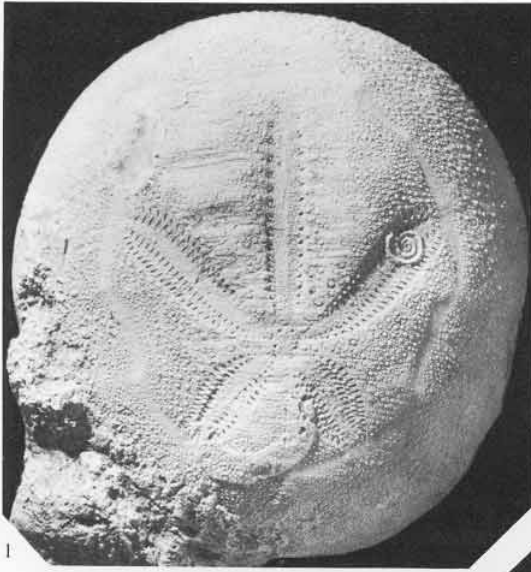
Hemiaster (Bolbaster) dolosus sp. nov.

Plate 45, figs. 1-3, 6; text-figs. 4 and 8

Diagnosis. Species of *Bolbaster* with nearly vertical posterior surface; nearly circular outline; moderately impressed, distally flared anterior petals; relatively deeply impressed, broad ambulacrum III; and short plastron.

EXPLANATION OF PLATE 44

Figs. 1-5. *Hemiaster (Bolbaster) subidus* sp. nov. 1-3, SAM P26554, holotype. 4 and 5, SAM P26555, paratype; both from Late Eocene (Aldingan) Tortachilla Limestone, Maslin Beach-Port Willunga district, south of Adelaide, South Australia. All $\times 2$ except fig. 1 ($\times 2.1$) and fig. 4 ($\times 5$).



McNAMARA, *Hemiaster (Bolbaster)*

Material. Holotype NMV P53172, from the Early Oligocene (Willungan) Ruwarung Member of the Port Willunga Formation, Maslin's Beach, Aldinga, South Australia. Paratypes SAM P26557-26559 and WAM 86.1206-1209 from the Port Willunga Formation in the sea cliffs at Seaford, South Australia. J. Murray Lindsay (South Australian Department of Mines and Energy) has sampled Foraminifera from the section and reports that it is Early Oligocene (planktic foraminiferal zones P19/20) in age. One further specimen, SAM P22111 from the Gambier Limestone, Mt Gambier, South Australia, is probably also a member of this species.

Description. Test circular, reaching maximum known test length of 37 mm; maximum width at mid-test length, being 93-98 % TL; highest mid-way between apical system and posterior ambitus; height 77-83 % TL; posterior surface very slightly inclined; aboral surface moderately declined anteriorly. Interambulacra 2 and 3 moderately raised adapically; other interambulacra only weakly raised adapically. Apical system slightly sunken, set 53-54 % TL from anterior ambitus. Ambulacrum III relatively strongly impressed, particularly adapically; with slight adambital taper; width 7-8 % TL; bears up to seventeen isopores in each row; pores elongate and within each pair separated by a distance equal to length of pore. Petals moderately impressed. Anterior pair diverge at *c.* 115°; increase in width distally to be more than 10 % wide; length of each petal 29-30 % TL, bearing up to twenty-four pore pairs in each row. Posterior petals slightly narrower than anterior pair; diverge at *c.* 70°; length 13-18 % TL; bear up to fourteen pore pairs. Peripetalous fasciole follows similar path to that in *H. (B.) subidus*; width 4 % TL, widening slightly opposite tips of petals.

Adoral surface moderately convex. Peristome semicircular, bordered by entire, raised rim; width 17 % TL; slightly sunken; posterior situated 35 % TL from anterior. Labrum long; constricts to half width at about mid-length, then widens slightly toward plastron. Phyllode with eight isopores in ambulacra I and IV, four in ambulacrum III, and six in ambulacra I and V. Plastron relatively short, 43 % TL; width 36 % TL. Periproct subcircular, small, situated high on posterior face; barely sunken; maximum diameter 9 % TL.

Discussion. *H. (Bolbaster) dolosus* occurs in the lower part of the Port Willunga Formation, the base of which occurs 33 m above the top of the Late Eocene Tortachilla Limestone, within which *H. (B.) subidus* occurs. *H. (B.) dolosus* can be distinguished from the older species by its more circular test, which is relatively higher and has a slightly more anteriorly inclined posterior face (text-fig. 8). It is further distinguished by its deeper ambulacrum III and deeper petals, straighter anterior petals, less divergent posterior petals, possession of keeled anterior interambulacra adapically, slightly wider peripetalous fasciole, more posteriorly positioned peristome, less constricted labrum, and more swollen plastron.

H. (B.) dolosus can be distinguished from the similar *H. (B.) integer* from the early Turonian of Madagascar (Lambert 1933) by its more posteriorly situated apical system, more evenly declined aboral surface, and more swollen plastron. *H. (B.) dolosus* differs from *H. (B.) madagascariensis* from the Late Maastrichtian of Madagascar (Besairie 1930) in its longer, more distally flared petals and wider ambulacrum III. In its circular test, *H. (B.) dolosus* compares with *H. (B.) prunella* Lamarck, 1816, from the Maastrichtian at Maastricht, but is distinguished by the complete absence of a frontal notch in large adult specimens, its broader petals, less divergent posterior petals, and possession of a peristome further from the anterior ambitus.

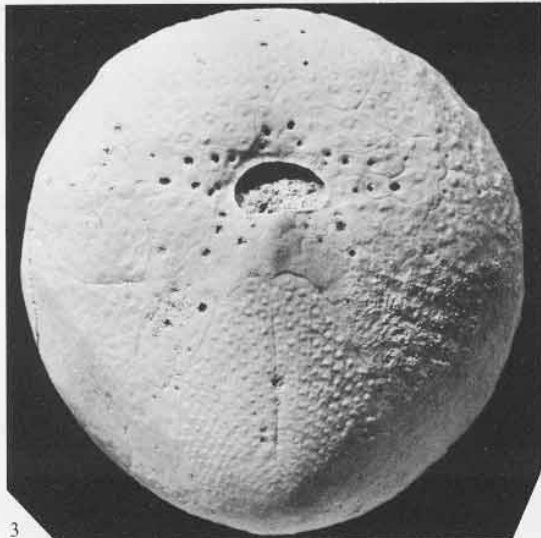
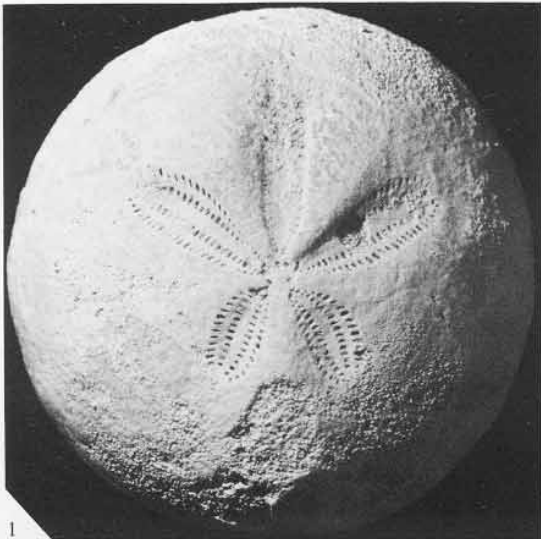
Hemiaster (Bolbaster) verecundus sp. nov.

Plate 45, figs. 4 and 5; Plate 46, figs. 1 and 2; text-figs. 4 and 8

Diagnosis. Species of *H. (Bolbaster)* with short, broad petals; anterior pair diverge at 100°; pores in

EXPLANATION OF PLATE 45

Figs. 1-3, 6. *Hemiaster (Bolbaster) dolosus* sp. nov. 1, 3, 6, NMV P53172, holotype, from the Early Oligocene (Willungan) Ruwarung Member of the Port Willunga Formation, Maslin Beach, Aldinga, South Australia. 2, SAM P26557, paratype, from same horizon as holotype, in the sea cliffs at Seaford, South Australia. Figs. 4 and 5. *H. (B.) verecundus* sp. nov. 4, NMV P18578, holotype; 5, NMV P78458, paratype; both from the Early Miocene (Longfordian) Puebla Formation, Fisherman's Steps, Torquay, Victoria. All × 2.



McNAMARA, *Hemiaster (Bolbaster)*

petals slightly elongate; short poriferous ambulacrum III; and nearly centrally positioned apical system.

Material. Holotype NMV P18578, from the Early Miocene (Longfordian) Puebla Formation, Fisherman's Steps, Torquay, Victoria. Paratypes NMV P18761, 20145, and 78458, from essentially the same locality and horizon as the holotype.

Description. Test subcircular, reaching a maximum known test length of 30 mm; maximum width near mid-test length, 97% TL; apex mid-way between apical system and posterior ambitus; posterior face almost vertical; aboral surface evenly and gently declined anteriorly. Apical system slightly sunken, set 51–54% TL from anterior ambitus. Poriferous zone of ambulacrum III relatively short, 30–31% TL; width 5% TL; moderately incised, bearing up to fourteen isopores; interporal region swollen. Petals short; anterior pair 20–22% TL; relatively broad, 11% TL; bearing up to seventeen pore pairs in each row; diverge at *c.* 100°; pores slightly elongate; within each pair, pores separated from one another by a distance slightly greater than length of pore; pores not conjugate. Posterior petals short, 13–14% TL, bearing up to ten pore pairs in each row; diverge at *c.* 70°. Peripetalous fasciole not indented between petals; 5.5% TL in width; narrows slightly between petals.

Adoral surface poorly known. Moderately convex. Plastron short and wide. Labrum projects quite strongly across peristome; bordered by raised rim; posteriorly labrum widens steadily toward plastron. Nature of phyllode unknown.

Discussion. *H. (Bolbaster) verecundus* compares with the Early Oligocene *H. (B.) dolosus* in its nearly circular test outline, almost vertical posterior surface of the test, and relatively broad petals. However, it can be distinguished by its much shorter petals, shorter poriferous zone of ambulacrum III aborally, slightly more centrally placed apical system, marginally deeper petals, wider peripetalous fasciole, and more widely separated, less elongate pores in each row of pore pairs in the petals.

H. (B.) verecundus is easily distinguished from the Late Eocene *H. (B.) subidus* by its wider, shorter, deeper petals, more centrally placed apical system, less elongate test, wider peripetalous fasciole, more widely spaced and less elongate pores in each pore pair in the petals, and deeper, shorter poriferous tract of ambulacrum III aborally.

The Paleocene species *H. (B.) hawkinsi* Lambert, 1933, from Madagascar, is similar to *H. (B.) verecundus*, but differs in its longer petals and poriferous tract of ambulacrum III. *H. (B.) prunella* is also similar to *H. (B.) verecundus*, but the Australian species has less divergent, shorter, and wider petals, as well as lacking the anterior notch in large adults.

Hemiaster (Bolbaster) planedecivis Gregory, 1890

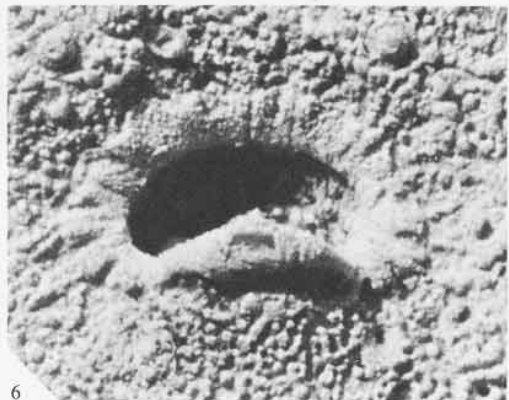
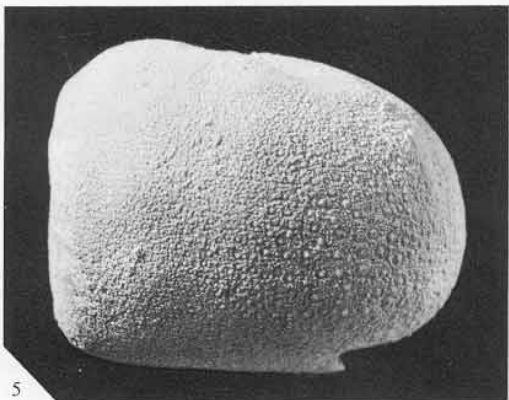
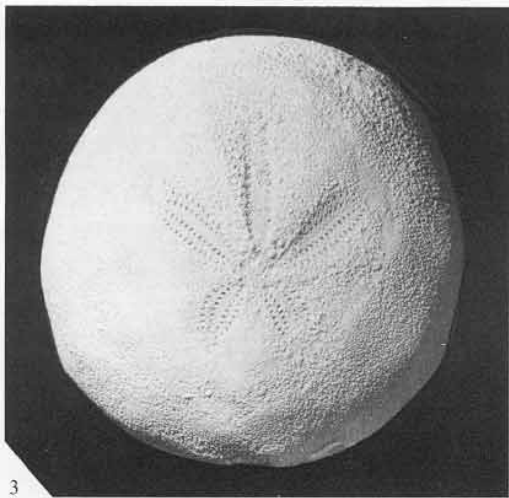
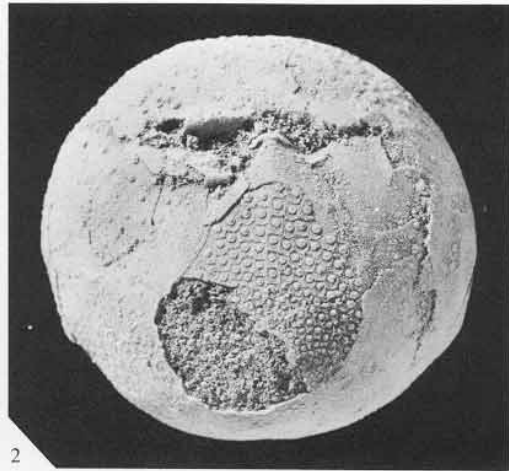
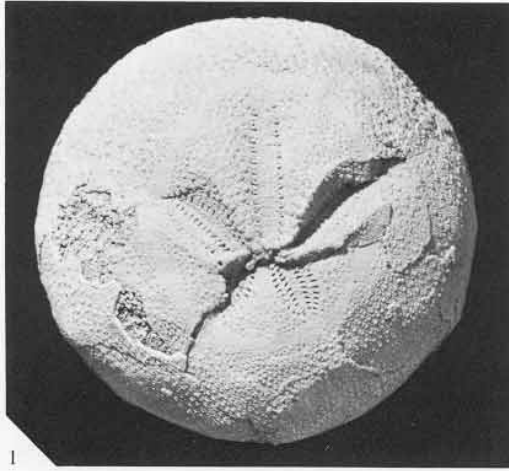
Plate 46, figs. 3–6; Plate 47, figs. 1 and 2; text-figs. 4, 6B, 8, 11B

- 1890 *Hemiaster planedecivis* Gregory, pp. 488–489, pl. 14, figs. 6 and 7.
 1891 *Hemiaster planedecivis* Gregory; Tate, p. 277.
 1892 *Hemiaster planedecivis* Gregory; Bittner, pp. 366–367, pl. 2, fig. 4.
 1914 *Hemiaster planedecivis* Gregory; Chapman, p. 147, fig. 81A.
 1924 *Hemiaster (Integraster) planedecivis* Gregory; Lambert and Thiéry, p. 504.
 1946 *Hemiaster planedecivis* [sic] Gregory; H. L. Clark, p. 364.

Diagnosis. Posterior surface of test slightly inclined anteriorly. Petals moderately impressed, bearing nearly circular pores; ambulacrum III narrow. Labrum projects quite strongly forward. Peristomial margin with strongly indented raised rim.

EXPLANATION OF PLATE 46

- Figs. 1 and 2. *Hemiaster (Bolbaster) verecundus* sp. nov., NMV P18761, paratype, from the Early Miocene (Longfordian) Puebla Formation, Fisherman's Steps, Torquay, Victoria, × 2.
 Figs. 3–6. *H. (B.) planedecivis* Gregory, 1890. 3–5, NMV P78461, neotype, from the late Early to early Middle Miocene (Batesfordian/Balcombian) Morgan Limestone, Morgan, South Australia, × 2. 6, NMV P18016, from the same horizon and locality as the neotype, showing detail of the peristome, × 10.



McNAMARA, *Hemiaster* (*Bolbaster*)

Material. Gregory's (1890) type specimen, said to be from Morgan, South Australia, was lodged in the Ipswich Museum. However, it can not now be located. In order to provide taxonomic stability, a neotype NMV P78461 (Pl. 46, figs. 3-5), from the late Early to early Middle Miocene (Batesfordian/Balcombian) Morgan Limestone at Morgan, South Australia, is chosen. This species is relatively common in the fine-grained calcarenites of the Morgan Limestone in the region of Morgan on the Murray River, South Australia. NMV P18016 is from the same horizon and locality as the neotype. Six specimens (SAM P22111) are also known from the upper siliceous horizon in the Gambier Limestone, Mt Schank, South Australia, preserved as flint moulds.

Description. Test reaching a maximum length of 31 mm; ovoid to circular, maximum width slightly posterior of centre, 88-100% TL; highest mid-way between apical system and posterior surface, forming a keel; height 74-84% TL; posterior face inclined forward at *c.* 10° to the vertical. Interambulacra 2 and 3 moderately raised adapically. Interambulacra 1 and 4 slightly swollen in region of peripetalous fasciole. Apical system slightly sunken, set 51-55% TL from anterior. Ambulacrum III moderately depressed; width 5-7% TL; bearing up to twenty-one isopores. Petals moderately impressed. Anterior pair diverge at *c.* 115°; of even width for much of that length; slightly flexed distally; length of each petal 24-28% TL; bearing up to twenty-one sub-circular pore pairs in each row; pores within each pair separated by a distance greater than width of pores; pores in anterior row very much smaller than those in posterior row. Posterior petal slightly curved; diverge at *c.* 70°; length 12-16% TL; bearing up to fourteen pore pairs in each row, fewer in smaller specimens. Peripetalous fasciole variable in width, being broadest at distal extremities of petals in middle of interambulacra, in other words widest at suture lines between columns of plates; maximum width 5-7% TL.

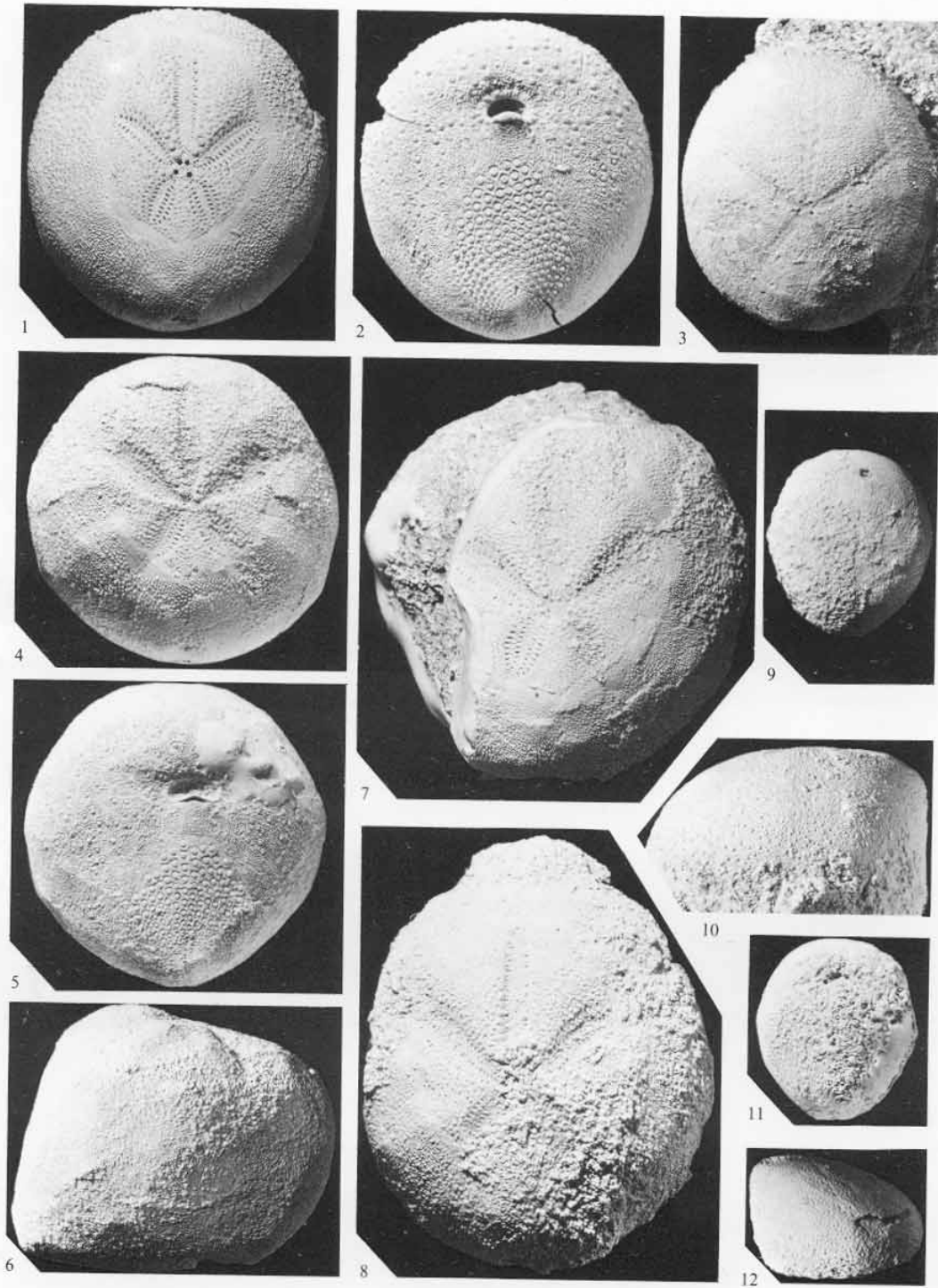
Adoral surface moderately convex. Peristome (Pl. 46, fig. 6) lunate; entirely bounded by raised rim which is often strongly indented; indentations consist of a narrow slit, corresponding to an intercolumnal suture line, and a deeper, broader pit situated equidistantly between sutures. Labrum projects anteriorly to variable degree and also ventrally; posteriorly constricted at one-third labral length from anterior, flaring toward plastron. Phyllode with eight isopores in ambulacra II and IV, five in ambulacrum III, and six in ambulacra I and V. Second plate of interambulacrum 1b not generally bisecting first plate of interambulacrum 1 and second plate of 1a; however in one specimen (NMV P78460) plate translocation has occurred resulting in bisection of these plates (text-fig. 11b). Plastron nearly flat; length 43-51% TL; width 34-38% TL. Periproct small, circular; diameter 8-11% TL; not sunken.

Discussion. *H. (Bolbaster) planedecivis* is most easily distinguished from all other species of *H. (Bolbaster)* by the strongly indented nature of its peristomial margin. This is a most unusual feature and is only found elsewhere, less well developed, in *H. (B.) callidus*. The notches in the margin probably reflect attachment sites for the peristomial plates. Normally, in spatangoids, these have only a membranous attachment. It seems that *H. (B.) planedecivis* and, to a lesser degree, *H. (B.) callidus* developed a notched peristomial margin, into which the distal margin of the peristomial plates could fit. This would necessitate the presence of an enlarged process on the marginal peristomial plates. Such a notched peristomial margin seems to be unique in spatangoids.

H. (B.) planedecivis can further be distinguished from the older species *H. (B.) subidus*, *H. (B.) dolosus*, and *H. (B.) verecundus* by its more anteriorly situated apical system, deeper petals, more

EXPLANATION OF PLATE 47

- Figs. 1 and 2. *Hemiaster (Bolbaster) planedecivis* Gregory, 1890, NMV P18016, from the late Early to early Middle Miocene (Batesfordian/Balcombian) Morgan Limestone, Morgan, South Australia.
- Figs. 3 and 10. *Psephoaster lissos* sp. nov., SAM P26560, holotype, from the Late Eocene (Aldingan) Kingscote Limestone, Kingscote, Kangaroo Island, South Australia.
- Figs. 4-8. *H. (B.) callidus* sp. nov. 4-6, NMV P100503, holotype, from the late Middle Miocene (Bairnsdalian) Port Campbell Limestone, near the mouth of the Sherbrooke River, near Port Campbell, Victoria. 7, NMV P100504, paratype, from same horizon and locality as holotype. 8, NMV P100505, paratype, from same horizon and locality as holotype.
- Figs. 9, 11, 12. *P. apokryphos* sp. nov., NMV P100507, paratype, from the Late Oligocene (Janjukian) Jan Juc Formation between Bird Rock and Fisherman's Steps, Torquay, Victoria.
- All × 2.



McNAMARA, *Hemiaster* (*Bolbaster*), *Psephoaster*

circular pores in the petals, more anteriorly inclined posterior surface of the test, broader peripetalous fasciole, and more strongly projecting labrum. Furthermore, it has longer petals than *H. (B.) verecundus*, a narrower ambulacrum III and more anteriorly positioned peristome than *H. (B.) dolosus*, and much denser ambital tuberculation than *H. (B.) subidus*.

Of all the Australian species of *H. (Bolbaster)*, *H. (B.) planedeclevis* is the most similar to *H. integer* from the early Turonian of Madagascar (Lambert 1933). The Australian species can be distinguished by its narrower ambulacrum III and slightly shorter petals. *H. (B.) planedeclevis* can be distinguished from *H. (B.) prunella* by its shorter, less divergent posterior petals, more posterior peristome, and more swollen aboral interambulacrum 5. *H. (B.) planedeclevis* is also quite similar to *H. (B.) madagascariensis* (Besairie 1930), but has a more circular test outline and broader anterior petals.

Hemiaster (Bolbaster) callidus sp. nov.

Plate 47, figs. 4–8; Plate 48, fig. 7; text-figs. 3, 4, 5B, 6C, 8, 10, 12B

Diagnosis. Test broad, with strongly anteriorly inclined posterior surface and swollen aboral interambulacra. Apical system central or slightly anterior of centre. Petals depressed. Peripetalous fasciole very broad.

Material. Holotype NMV P100503 and paratypes NMV P100504, 100505, 100508, from the late Middle Miocene (Bairnsdalian) Port Campbell Limestone near the mouth of the Sherbrooke River, near Port Campbell, Victoria. Paratype NMV P100509 from the same horizon, 22 m above sea level, Amphitheatre, east of Port Campbell, Victoria.

Description. Test reaching maximum test length of 35 mm; subcircular, often wider than long, width 97–103 % TL; highest point at prominent keel in interambulacrum 5; height 81–89 % TL; posterior face inclined anteriorly at about 15° to the vertical. Interambulacra all strongly raised aborally, reaching their apex close to course of peripetalous fasciole; intercolumnal sutures run in depression. Ambital tubercle density 7.8 mm⁻². Ambulacrum III depressed; narrow, width 6–7 % TL; maximum number of pore pairs unknown; floor covered by dense concentration of fine tubercles. Petals deep. Anterior pair diverge at 115°; steadily increase in width distally; length of each petal 24–26 % TL; bearing up to twenty pore pairs in each row; pores almost circular and, within each row, widely separated, interporal distance being about twice diameter of pores. Posterior petals diverge at c. 80°; length 14–15 % TL; bearing up to twelve pore pairs in each row. Peripetalous fasciole (Pl. 48, fig. 7) very broad at intercolumnal sutures, particularly at distal extremities of petals (text-fig. 5), ranging from 7 to 10 % TL in width. Ambital spines 2–3 mm long, with flattened distal tips. Subanal spines 5 mm long, with broad, spatulate tips.

Adoral surface moderately convex. Peristome slightly sunken; with raised rim, weakly notched, marginal rim width 14–17 % TL; situated 31–40 % TL from anterior ambitus. Labrum anteriorly acuminate; narrows slightly posteriorly, then flares broadly to plastron. Plastron gently convex; relatively broad, length 39–46 % TL, width 37–42 % TL. Periproct small, circular, with diameter 9–10 % TL; not sunken.

Discussion. *H. (Bolbaster) callidus* can be distinguished from the other species in this subgenus by its high, wide test with anteriorly inclined posterior surface, swollen aboral interambulacra, very broad peripetalous fasciole, deeper petals, more widely separated pores within each petaliferous row, and more anteriorly positioned apical system. In having relatively short petals, it resembles the Early Miocene (Longfordian) *H. (B.) verecundus*. It can be distinguished, however, by its deeper petals and deeper ambulacrum III, more anteriorly positioned apical system, and swollen aboral interambulacra.

The anteriorly projecting labrum of *H. (B.) callidus* resembles that of *H. (B.) planedeclevis*, but the more posteriorly situated peristome of *H. (B.) callidus* distinguishes the two species. In this respect *H. (B.) callidus* resembles the Early Oligocene *H. (B.) dolosus*. However, the nature of the aboral surface is sufficient to distinguish the two taxa. The near spherical test of *H. (B.) callidus* resembles that of *H. (B.) prunella*. The two species can be distinguished by the relatively shorter, deeper petals of *H. (B.) callidus*, its deeper ambulacrum III, more swollen adapical interambulacra, and less swollen, non-tuberculate labrum.

Of all the Australian Tertiary species of *H. (Bolbaster)*, *H. (B.) callidus* most closely resembles the living Indo-West Pacific species *H. (B.) gibbosus* (Agassiz 1879, pl. 20, figs. 5-16) and the Atlantic species *H. (B.) expergitus* (Mortensen 1907, pl. 2, figs. 1, 4, 18, 20). *H. (B.) callidus* can be distinguished from these species by its more central apical system, broader petals, and narrower peristome.

Genus PSEPHOASTER gen. nov.

Type species. Psephoaster klydonos sp. nov.

Diagnosis. Test subspherical without anterior notch. Ambulacrum III not sunken at all aborally, with much reduced pore pairs. Petals narrow, flush with test surface or slightly depressed; pores circular, pairs not conjugate. Apical system ethmophract with four genital pores.

Discussion. *Psephoaster* can be distinguished from *Hemiaster* (*s.l.*) by the absence of a sunken ambulacrum III and anterior notch, and by the single, parallel sided petals which are flush with the test, or almost so. The only other hemiasterid with such simple aboral ambulacra is the Late Cretaceous *Vomeraster* (see Mortensen 1950, p. 407). However, *Psephoaster* can be distinguished by its more truncate posterior margin, shallower, more parallel-sided petals, and lack of intersutural depressions (a distinctive character of *Vomeraster*).

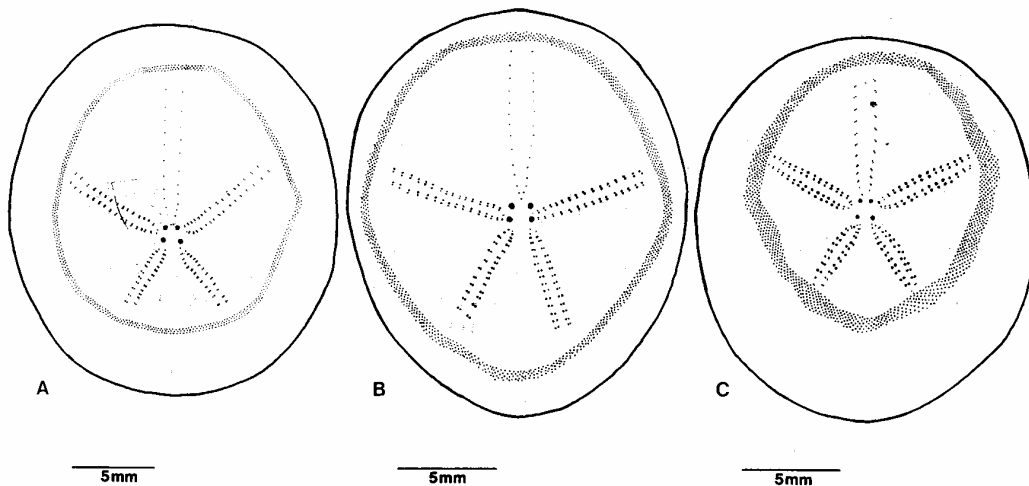
Psephoaster lissos sp. nov.

Plate 47, figs. 3 and 10; text-figs 7A, 10, 13A

Diagnosis. Species of *Psephoaster* with relatively low test; apical system set well posterior of centre; very narrow, slightly sunken petals with extremely small pore pairs.

Material. Holotype SAM P26560, from the Late Eocene (Aldingan) Kingscote Limestone, Kingscote, Kangaroo Island, South Australia. Paratype SAM P26561, from the Late Eocene (Aldingan) Tortachilla Limestone, Maslin Beach, south of Adelaide, South Australia.

Description. Test reaching maximum known length of 24 mm; ovoid, maximum width central; width 84-90% TL; highest point midway between apical system and posterior; height 66% TL; posterior face inclined slightly



TEXT-FIG. 13. Camera lucida drawings of aboral surfaces. A, *Psephoaster lissos* sp. nov., SAM P26560, holotype. B, *P. apokryphos* sp. nov., NMV P100506, holotype. C, *P. klydonos* sp. nov., SAM P24631, holotype.

anteriorly; aboral surface gently inclined anteriorly in posterior half progressively steepening anteriorly. Apical system slightly sunken and set 55 % TL from anterior ambitus. Ambital tubercle density 3 mm⁻². Ambulacrum III flush with test surface; narrow, width 5 % TL; bears about twelve minute pore pairs, pores within each pair being aligned almost exsagittally. Petals slightly depressed, very narrow, 2.3 % TL. Anterior pair diverge at about 120°; straight, parallel-sided; length 35 % TL; bearing up to twenty minute pore pairs, the distal four or five of which are extremely reduced in size; pores circular, pairs not conjugate; rows separated by a distance equal to about three times pore pair widths. Posterior petals diverge at about 75°; length 24 % TL; bearing up to fourteen pore pairs, similar in size to those of anterior pair, and similarly degenerating distally before reaching peripetalous fasciole. Peripetalous fasciole not indented between petals; narrow, 1.5 % TL.

Adoral surface poorly known. Peristome situated 23 % TL from anterior ambitus. Plastron strongly convex, transversely. Periproct nearly circular, 14 % TL in diameter; situated high on posterior surface. This surface slightly depressed below periproct.

Discussion. Of the two known specimens of *P. lissos* only one, the holotype, has its aboral and posterior surfaces preserved, while the paratype is largely covered by growths of bryozoans. However, sufficient details are preserved to indicate their conspecificity and close morphological similarity. *P. lissos* occurs in the Late Eocene Kingscote and Tortachilla Limestones with the other hemiasterid, *H. (B.) subidus*. *P. lissos* can be distinguished by its finer aboral tuberculation, narrower and longer petals which are hardly depressed, and much smaller pore pairs.

Psephoaster apokryphos sp. nov.

Plate 47, figs. 9, 11, 12; Plate 48, figs. 4-6; text-figs. 7B and 13B

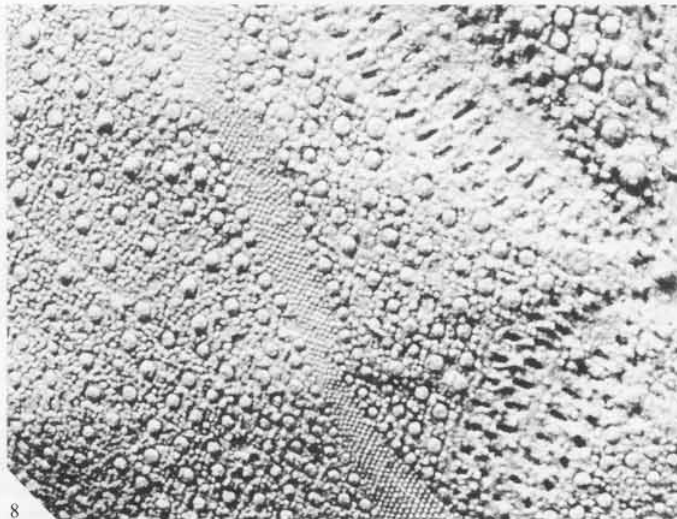
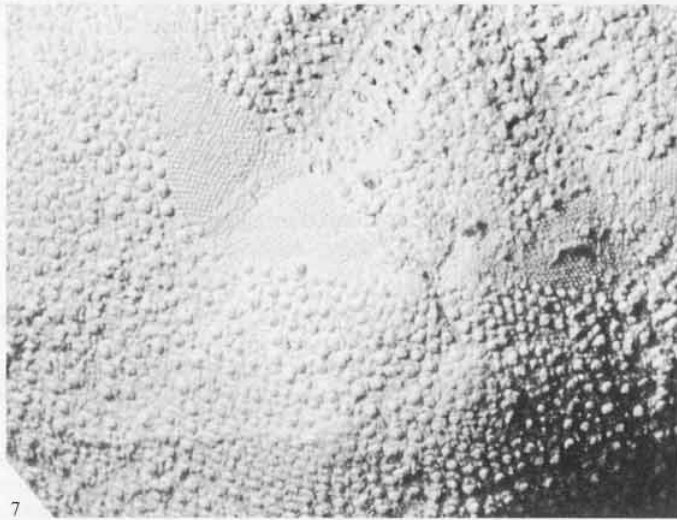
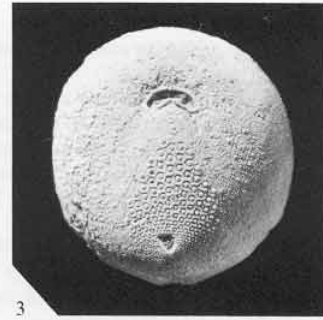
Diagnosis. Species of *Psephoaster* with a test which has a strongly inclined, though flat, aboral surface; petals and ambulacrum III not sunken; relatively long posterior petals; central apical system; narrow plastron; prominent subanal rostrum.

Material. Holotype NMV P100506 and paratype NMV P100507 from the Late Oligocene (Janjukian) Jan Juc Formation between Bird Rock and Fisherman's Steps, Torquay, Victoria.

Description. Test reaching maximum known length of 20 mm; ovoid, maximum width slightly anterior of centre, 83-87 % TL; highest point close to posterior ambitus in interambulacrum 4; height 67-71 % TL; posterior face slightly overhung by aboral interambulacrum 5; aboral surface steeply inclined, but nearly flat, until it plunges vertically to anterior ambitus. Apical system central at 49 % TL; not sunken. Ambital tubercle density 5 mm⁻². Ambulacrum III flush with surface of test, with indeterminate number of minute pore pairs. Petals not depressed and poorly defined, aboral tuberculation on ambulacra of the same size and density as on interambulacra. Anterior pair diverge at c. 110°; straight, parallel-sided, and relatively long; bearing up to sixteen small single pore pairs which fail to reach peripetalous fasciole. Pairs separated by a distance equal to one and a half to two times width of pore pairs. Posterior petals diverge at about 65°; length 28 % TL;

EXPLANATION OF PLATE 48

- Figs. 1-3. *Psephoaster klydonos* sp. nov. 1, SAM P24631, holotype, from the Early Miocene (Longfordian) Mannum Formation, Murray River, South Australia, × 2. 2, WAM 86.296, paratype, from same horizon and locality as holotype, × 2. 3, SAM P22017, paratype, from the same horizon as the holotype at Punyelroo, South Australia, × 2.
- Figs. 4-6, *P. apokryphos* sp. nov., NMV P100506, holotype, from the Late Oligocene (Janjukian) Jan Juc Formation between Bird Rock and Fisherman's Steps, Torquay, Victoria, × 2.
- Fig. 7. *Hemiaster (Bolbaster) callidus* sp. nov., NMV P100503, holotype, from the late Middle Miocene (Bairnsdalian) Port Campbell Limestone, near the mouth of the Sherbrooke River, near Port Campbell, Victoria, showing detail of dense aboral tuberculation and broad peripetalous fasciole, × 8.
- Fig. 8. *H. (B.) subidus* sp. nov., SAM P26555, paratype, from Late Eocene (Aldingan) Tortachilla Limestone, Maslin Beach-Port Willunga district, south of Adelaide, South Australia, showing detail of sparse aboral tuberculation and narrow peripetalous fasciole, × 8.



McNAMARA, *Psephoaster*, *Hemiaster* (*Bolbaster*)

bearing up to twelve small pore pairs in each row. Peripetalous fasciole narrow, 2.5 % TL; situated quite close to ambitus.

Adoral surface strongly convex transversely, with prominent subanal rostrum. Peristome small, width 16–17 % TL, situated 22–23 % TL from anterior ambitus; slightly sunken. Labrum slightly projecting anteriorly; long, parallel-sided. Nature of phyllode not known. Plastron narrow, width 43 % TL. Posterior face of test depressed below periproct, depressed area narrowing adorally. Periproct situated high on posterior face, slightly wider than long, 10–12 % TL.

Discussion. The Late Oligocene *P. apokryphos* can be distinguished from the Late Eocene *P. lissos* by its flatter and more steeply inclined aboral surface, narrower test, less conspicuous petals with slightly larger pore pairs, more central apical system, longer posterior petals, wider peripetalous fasciole, and small periproct.

In the same cliff section near Torquay, Victoria, the hemiasterid *H. (B.) verecundus* occurs in the Early Miocene Puebla Formation, which conformably overlies the Jan Juc Formation. *P. apokryphos* differs in its narrower test and inconspicuous, though longer, petals and ambulacrum III.

Psephoaster klydonos sp. nov.

Plate 48, figs. 1–3; text-figs. 7c, 10, 13c

Diagnosis. Species of *Psephoaster* with high test, slightly inflated interambulacra adapically; slightly sunken, relatively broad petals; apical system anterior of centre; relatively broad peripetalous fasciole and short posterior petals.

Material. Holotype SAM P24631 and paratypes SAM P565, P8933, and WAM 86.296, from the Early Miocene (Longfordian) Mannum Formation, Murray River, South Australia. Paratypes SAM P22017 from the same horizon at Punyelroo, South Australia and NMV P13167 from the same horizon near Morgan, South Australia. Other material: three specimens from the Mannum Formation north of Younghusband, and from Mannum, South Australia, in the private collection of E. and F. Holmes.

Description. Test reaching a maximum known length of 23 mm; ovoid, maximum width central; width 85–96 % TL; highest point midway between apical system and posterior; height 79–87 % TL (although holotype is only 72 % TL); posterior face vertical and slightly overhung by keel in interambulacrum 5; aboral surface steeply inclined. Apical system slightly sunken and set 44–49 % TL from anterior ambitus. Ambital tubercle density 7.5 mm⁻². Ambulacrum III flush with test surface; narrow, width 4–5 % TL; bears up to eleven very small pore pairs, pores within each pair being aligned 30° to exsagittal line. Petals slightly depressed, narrow, 5 % TL. Anterior pair diverge at c. 120°; straight parallel-sided, open distally; length 31–38 % TL, bearing up to nineteen small pore pairs; pores circular, not conjugate; rows separated by a distance equal to width of pore pairs. Posterior petals diverge at about 75°; length 17–19 % TL; bearing up to thirteen pore pairs, similar in size to those of anterior pair. Peripetalous fasciole relatively broad; wider at coronal sutures than in centre of plates, reaching up to nearly 6 % TL in width.

Adoral surface moderately arched transversely. Peristome situated 24–29 % TL from anterior ambitus; lunate, width 15–20 % TL; slightly sunken; has raised marginal rim. Phyllode with isopores, pores being separated by prominent interporal partition; nine in ambulacra II and IV, seven in ambulacra I and V, and five in ambulacrum III. Labrum moderately constricted, expanding posteriorly to plastron; projects strongly anteriorly, more than halfway across peristome; marginal rim well developed. Plastron length 39–47 % TL, width 34–36 % TL. Periproct small, 11 % TL in diameter; subanal area between periproct and projecting subanal rostrum slightly depressed.

Discussion. *P. klydonos* differs from the Late Eocene *P. lissos* in its higher test, more anteriorly eccentric apical system, broader petals, larger and more closely spaced pore pairs, more densely tuberculate ambitus, broader peripetalous fasciole, and relatively smaller periproct. *P. klydonos* differs from the Late Oligocene *P. apokryphos* in its higher test with more pronounced keel in interambulacrum 5, more sunken and shorter petals, longer pore pairs, slightly more eccentric apical system, broader fasciole, wider plastron, less strongly developed subanal rostrum, and more prominent labrum.

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