A new genus of brissid echinoid from the Miocene of Australia

K. J. McNAMARA* & C. AH YEE†

* Department of Palaeontology, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia
†20 Bayley Street, Hamilton, Victoria 3300, Australia

(Received 9 September 1987; revised version received 20 September 1988; accepted 22 September 1988)

Abstract – The brissid echinoid *Amoraster* (gen. nov.) is described from Miocene strata in southern Australia on the basis of two species: *Amoraster paucituberculata* sp. nov., which ranges from the Batesfordian (latest Early Miocene) Bochara Limestone to the Bairnsdaled–Mitchellian (Middle–Late Miocene) Port Campbell Limestone in Victoria; and *Amoraster tuberculata* sp. nov. from the Longfordian (Early Miocene) Mannum Formation in South Australia. Morphological changes which occurred with the evolution of *A. paucituberculata* from *A. tuberculata* are interpreted as being adaptations to the occupation of a finer grained sediment by the descendant species.

1. Introduction

It is now more than 120 years since the first brissid echinoid species was described from the Tertiary deposits of southern Australia (Tenison Woods, 1867). Since that time 16 further species, placed in eight genera, have been described (Kruse & Philip, 1985; McNamara, Philip & Kruse, 1986). Brissid echinoids form the major part of the rich Australian Tertiary spatangoid fauna, comprising 44% of genera and 38% of species.

It is therefore a little surprising that our collecting in recent years has yielded a further two undescribed brissid species which cannot be accommodated within any known living or fossil echinoid genus. Even more surprising, perhaps, is that one of the species should have been collected from the cliffs of the Murray River near Mannum in South Australia, one of the most well-known fossil collecting sites in Australia. Furthermore, this undescribed genus is particularly large, being exceeded in size amongst Australian Tertiary echinoids only by *Victoriaster* (one of the largest echinoids ever to have lived) and some of the larger species of *Pericosmus* (McNamara & Philip, 1984).

The aim of this paper, therefore, is to describe the new species and the new genus into which they are placed. In addition, the morphological evolution which occurred between the two species is analysed and the functional significance of these changes is assessed.

Measurements on the specimens were made with a vernier calliper to an accuracy of 0.1 mm. A number of parameters are expressed as percentages of maximum test length (%TL). The labrum index is a measure of maximum length/maximum anterior width. Specimens are housed in the collections of the Western Australian Museum (WAM).

One new term, *bifastigate*, is introduced. This refers to the presence of two raised points on the plastronal keel.

2. Stratigraphy

The earliest occurrence of the new genus is in the Mannum Formation which is Longfordian (Early Miocene) in age (Lindsay, 1985). This is a sequence of yellow, bioclastic calcarenites which transgresses onto bedrock on the western margin of the Murray Basin in South Australia. The Mannum Formation is exposed as cliff sections about 15 m thick on the banks of the Murray River in the Mannum region (Fig. 1). In total the formation is about 45 m thick. It is a very fossilsiferous unit, being dominated by echinoids, principally *Loenia forbesi* (Tenison Woods), *Eupatagus murrayensis* (Laube) and *E. wrighti* (Laube).

A single specimen of the new genus is known from the Batesfordian (latest Early Miocene) Bochara Limestone in the Otway Basin at Muddy Creek, Victoria. This is a porous, yellow-brown bedded bryozoa carbonite, attaining a maximum thickness of 23 m (Spencer-Jones, 1971). The Bochara Limestone is considered to have been deposited in a relatively shallow, high-energy environment (Abele et al. 1976) and is likely to represent a marginal equivalent of the Port Campbell Limestone.

The new genus has also been collected from the Port Campbell Limestone at Portland, Victoria (Fig. 1). Here the unit is a relatively fine-grained foraminiferal calcarenite, thought to have accumulated offshore in deeper water than the Bochara Limestone (Abele et al. 1976). The Port Campbell Limestone is a thick unit, in excess of 150 m (Baker, 1950). In the Port Campbell Embayment it is Bairnsdaled (Middle Miocene) in age (Ludbrook, 1973), although the upper part of the formation at Portland may be a little
younger, representing the upper part of foraminiferal zone N16 and the basal part of zone 17 (Singleton, McDougall & Mallett, 1976). This would place it in the Late Miocene Mitchellian stage.

3. Systematic descriptions

Order SPATANGOIDA Claus, 1876
Family BRISSIDAE Gray, 1855
Genus Amoraster nov.

Diagnosis. Test inflated; apex coincident with, or anterior of, apical system; primary tuberculation absent or weakly developed and confined to the posterior plate series in each of the paired interambulacra; petals sunken and poriferous zones deeply incised; pore pairs in petals deeply conjugate; ambulacrum III sunken adapically; labrum short, wider than long; periproct wider than long; and plastronal keel bifastigate.

Derivation of name. From the Greek 'amora', a cake, alluding to the shape of the test; and 'aster', a star.

Type species. Amoraster paucituberculata sp. nov.

Age and distribution. From the Early to Late Miocene (Longfordian to Mitchellian) of the Murray and Otway Basins in southern Australia.

Remarks. While a number of brissid genera may share the same morphological character, each can be distinguished from all others by its unique combination of characters. Thus although Amoraster cannot be distinguished from other brissids on the basis of any one major characteristic feature, a unique combination of morphological features which characterizes the two species placed in Amoraster militate against their emplacement within any known genus. Although it might be argued that the superficial similarity which the species bear to species of Eupatagus indicates that they could be included within that genus, such a course of action would mean a wholesale extension of the generic concept of Eupatagus. Moreover, it would result in many other currently established brissid genera being synonymized into Eupatagus. All this would achieve is a false picture of the true extent of brissid generic diversity during Tertiary time.

A further argument for the establishment of a new genus is the fact that two species have been recognized as forming part of a single lineage, evolving in parallel with a plexus of Eupatagus species (Kruse & Philip, 1985). These Oligocene to Miocene southern Australian species cover almost the entire spectrum of morphotypes currently regarded as belonging within Eupatagus. Thus, they are most appropriate for comparing with the two species described herein and for highlighting the fact that these two species lie well outside of the range of the generic concept of Eupatagus.

Amoraster differs in many important respects from Eupatagus (Table 1). Whereas primary tubercles in Eupatagus are always present within the aboral area bounded by the peripetalous fasciole, in Amoraster they may be absent, or if present they are confined to the posterior series of plates in the paired interambulacra, that is, plates 1a, 2a, 3b and 4b. Amoraster can further be distinguished from Eupatagus by the shape of the test. In Eupatagus the apex of the test is posterior of the apical system, whereas in Amoraster it is either coincident with, or anterior to it. Amoraster further differs from Eupatagus in having sunken petals, slightly indented peripetalous fasciole, shorter labrum (Table 1), and a periproct which is transversely oval, rather than dorso-ventrally elongate (see Fig. 5). The plastron shows an important difference in that the posterior keel is bifastigate.
New Miocene echinoid genus

Table 1. Distinguishing morphological features of *Amoraster* and the four genera with which it is most similar

<table>
<thead>
<tr>
<th>Features</th>
<th>Amoraster</th>
<th>Eupatagus&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Granobrissoides&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Gillechimus&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Lajanaster&lt;sup&gt;3&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test height</td>
<td>High arched</td>
<td>Low arched</td>
<td>Low arched</td>
<td>Low arched</td>
<td>Low arched</td>
</tr>
<tr>
<td>Oral surface</td>
<td>Sunken to peristome</td>
<td>Flat</td>
<td>Slightly sunken to peristome</td>
<td>Flat</td>
<td>Flat</td>
</tr>
<tr>
<td>Paired amb.</td>
<td>Closed &amp; sunken</td>
<td>Closed &amp; not sunken</td>
<td>Open &amp; sl. sunken</td>
<td>Closed &amp; sl. sunken</td>
<td>Closed &amp; sl. sunken</td>
</tr>
<tr>
<td>Pore zones</td>
<td>Deeply incised</td>
<td>Weakly incised</td>
<td>Weakly incised</td>
<td>Not incised</td>
<td>Weakly incised</td>
</tr>
<tr>
<td>Frontal amb.</td>
<td>Sunked adapically</td>
<td>Not sunken</td>
<td>Not sunken</td>
<td>Sunken</td>
<td>Sunken adapically</td>
</tr>
<tr>
<td>Peripetalous fasciole</td>
<td>Slightly indented between petals</td>
<td>Not indented between petals</td>
<td>Not indented between petals</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>Labrum</td>
<td>Short-index 0.75–0.9</td>
<td>Long-index 1.5–3</td>
<td>Short-index 1</td>
<td>Long-index 2–2.5</td>
<td>Unknown</td>
</tr>
<tr>
<td>Plastron</td>
<td>Bifastigate keel and not parallel-sided</td>
<td>Keel and not parallel-sided</td>
<td>Keel and parallel-sided</td>
<td>Very narrow</td>
<td>&quot;Circular&quot;</td>
</tr>
<tr>
<td>Periproct</td>
<td>Wider than long</td>
<td>Longer than wide</td>
<td>Longer than wide</td>
<td>Longer than wide</td>
<td>&quot;Circular&quot;</td>
</tr>
<tr>
<td>Primary tubercles</td>
<td>Absent, or, if present, restricted to 1a, 2a, 3b, 4b</td>
<td>Present in 1a/b, 2a/b, 3a/b, 4a/b</td>
<td>Absent</td>
<td>Present in 1a, 2a, 3b, 4b</td>
<td>Present in 1a, 2a, 3b, 4b</td>
</tr>
</tbody>
</table>

<sup>1</sup> Data from Mortensen (1951) and Kruse & Philip (1985).
<sup>2</sup> Data from McNamara, Philip & Kruse (1986).
<sup>3</sup> Data from Kier (1984).

Another endemic Australian brissid with which *Amoraster* shows some similarities is *Granobrissoides*. This Late Oligocene genus has a similar petal configuration to *Amoraster* and also lacks primary tubercles (McNamara, Philip & Kruse, 1986). *Amoraster* can be distinguished, however, by its much larger size, anterior apex, more parallel-sided, sunken petals, wider periproct and broader, bifastigate plastron, which unlike *Granobrissoides* is not parallel-sided.

The only other Australian Tertiary brissid echinoid to have primary tubercles confined to the posterior plate series in paired aboral interambulacra is *Gillechimus*. *Amoraster* differs, however, in having closed petals with deeply incised pore zones, shorter labrum (Table 1), bifastigate keel and wider periproct.

Of brissid genera which do not occur in Australia, *Amoraster* most closely resembles the Miocene Cuban genus *Lajanaster* (Kier, 1984). Both have lanceolate petals, no anterior notch, and few primary tubercles confined to the posterior interambulacral plates series. However, *Amoraster* can be distinguished by its more tumid test; more deeply conjugate pore pairs; more flexuous anterior petals, which are equal to, or longer than the posterior; the more anteriorly prominent labrum and much broader plastron (Table 1).

Derivation of name. Alluding to the paucity of primary tubercles.

Type material. Holotype WAM 87.303, from the Middle–Late Miocene (Bairnsdalian–Mitchellian) Port Campbell Limestone, Portland, Victoria. Paratypes WAM 85.1271, 85.522, 87.523 from the Port Campbell Limestone in coastal cliffs, 3.5 m above ground level below the lighthouse, Portland, Victoria; WAM 85.1356 from same locality and formation as 85.1271, but from a higher level, at the top of the cliff immediately below the lighthouse, possibly Mitchellian (Late Miocene) in age; WAM 87.304, from the same locality and horizon as the holotype; WAM 86.293, from the latest Early Miocene (Balcombian) Bochra Limestone, Muddy Creek, 400 m downstream from wooden bridge near old Yulecart bore.

Description. Test large, reaching a maximum known length of 117 mm; slightly narrower than long, maximum width posterior of centre, 97% TL; apex high, 68% TL, confluent with or anterior of apical system; anterior surface of test strongly declined, posterior surface moderately steeply declined (Fig. 4d). No anterior notch present. Apical system anterior of centre, 35% TL from anterior ambitus; ethmolytic, with four genital pores, madreporite extending posteriorly by more than half length of apical system (Figs. 3a, 4e). Ambulacrum III flush with test surface adambitally, but adapically is slightly depressed; bears an unknown number of minute isopores. Petals slightly depressed; slightly flexed distally, with deeply conjugate pore pairs and swollen interporiferal zone (Fig. 2a), which is half as wide again as the pore pairs; up to 24 large pore pairs in each row, and about eight very small pairs adapically. Anterior pair longer than posterior, being 36–38% TL, compared with 28–30% TL; 9% TL wide; diverge at 135°; distally open.

*Amoraster paucituberculata* sp. nov.

Figures 2–4

Diagnosis. Test tumid and strongly vaulted; primary tubercles absent or very rare; petals slightly sunken, anterior longer than posterior; interporiferous zones swollen; periproct moderately sunken; and labrum strongly anteriorly elongate.
Figure 2. *Amoraster paucituberculata* sp. nov. Holotype, WAM 87.303 from the Middle–Late Miocene (Bairnsdalian–Mitchellian) Port Campbell Limestone, Portland, Victoria; (a) aboral view, (b) adoral view. Both × 1.

Posterior petals diverge at 55°; 7% TL wide; distally closed. Peripetalous fascicle slightly re-entrant between petals, particularly between anterior pair and ambulacrum III. Posterior half of each posterior series of paired interambulacral plates inclined along margins of petals. Rarely these areas bear one or two tubercles per plate (Fig. 2a). Margins of interambulacra 2b and 3a adjacent to ambulacrum III
New Miocene echinoid genus

181

Figure 3. Plating drawings of Amoraster paucituberculata; (a) apical system (WAM 86.293), (b) adoral surface (WAM 87.522).

may bear irregular scatterings of tubercles slightly larger than general covering of secondary tubercles.

Adoral surface gently convex. Peristome slightly sunken; anterior margin located 26–28 % TL from anterior ambitus; relatively small, width 13–16 % TL. Labrum projects almost halfway across peristome in large specimens, but less so in small ones (Figs. 2b, 3b); posteriorly narrows abruptly, then broadens before constricting to half this width where it abuts the plastron. Phyllode with 12 unipores in ambulacra II and IV, eight in III and five in I and V. Plastron small, width 25 % TL; with weakly bifastigate keel (Fig. 4b). Subanal fasciole broad, elliptical, width 36 % TL, enclosing five pore pairs in both ambulacra I and V (Fig. 4c). Periproct slightly sunken; wider than long (Figs. 4c, 5).

Remarks. With the size of specimens ranging only between 66 and 117 mm, there is little opportunity to assess the extent of ontogenetic variation in the species. However, even over this size range there is a small degree of apparent morphological change. In the smallest known specimens the petals appear slightly more sunken than in larger individuals. This, in part, is a function of the interporiferous zones being more swollen in the larger specimens. The proportions of large to small pore pairs in the petals increases during growth of the test, while the petal length also increases slightly. Adorally, the labrum projects a little further across the peristome in larger individuals (Figs. 2b, 4b).

Amoraster paucituberculata is a relatively long-ranging species, ranging from latest Early Miocene through to Late Miocene time. The oldest specimen of A. paucituberculata shows minor differences from the younger specimens. There is no trace whatsoever of primary tubercles in the older form and the interporiferous zone in the petals is a little less swollen. In all other respects the two forms are identical. A. paucituberculata is coeval with the superficially similar E. rotundus Duncan in the Bochara Limestone, but can readily be distinguished by its anteriorly vaulted test; much weaker primary tuberculation; more sunken and flexed petals; broader subanal fasciole; more anteriorly projecting labrum; and laterally elongate periproct.

Amoraster paucituberculata is a relatively long-ranging species, ranging from latest Early Miocene through to Late Miocene time. The oldest specimen of A. paucituberculata shows minor differences from the younger specimens. There is no trace whatsoever of primary tubercles in the older form and the interporiferous zone in the petals is a little less swollen. In all other respects the two forms are identical. A. paucituberculata is coeval with the superficially similar E. rotundus Duncan in the Bochara Limestone, but can readily be distinguished by its anteriorly vaulted test; much weaker primary tuberculation; more sunken and flexed petals; broader subanal fasciole; more anteriorly projecting labrum; and laterally elongate periproct.

Amoraster tuberculata sp. nov.

Figure 6

Diagnosis. Primary tubercles present in posterior plate series of paired interambulacra; petals of similar length; peristome slightly sunken; labrum only slightly anteriorly projecting; plastron with prominent bifastigate keel; periproct not sunken.

Derivation of name. Alluding to the presence of primary tubercles.

Type material. Holotype WAM 87.116, from the Early Miocene (Longfordian) Mannum Formation, cliffs on Ponde Road, on east side of the Murray River, 2.5 km from the Mannum Ferry, South Australia. Paratypes WAM 86.322 b, d–g from same horizon and locality as holotype.

Description. Test reaching a maximum known length of 84 mm; slightly narrower than long, maximum width at about mid-test length, 93–100 % TL; maximum height 54 % TL; apex anterior of apical system (Fig. 6b); anterior surface steeply declined, posterior of apical system gently declined; posteriorly truncate. No anterior notch present. Apical system anterior of
Figure 4. *Amoraster paucituberculata* sp. nov.; aboral (a), adoral (b), posterior (c) and lateral (d) views of paratype WAM 87.304 from the Middle–Late Miocene (Bairnsdalian–Mitchellian) Port Campbell Limestone, Portland, Victoria; (e) aboral view of WAM 86.293 from the Early Miocene (Batesfordian) Bochara Limestone, Muddy Creek, Victoria. All × 1.
centre, 33% TL from anterior ambitus. Ambulacrum III flush with test adambitally, but slightly depressed adapically, bearing about 15 unipores. Anterior petals slightly depressed and slightly flexed; 35% TL long; bearing about 22 large, deeply conjugate pore pairs and about 6-8 pore pairs adapically; anteriorly divergent at 150°; interporiferous zone slightly swollen. Posterior petals almost as long as anterior pair (Fig. 6a) being 33% TL long; posteriorly divergent at 40°; bearing a similar number of pore pairs as anterior pair. Peripetalous fasciole follows same course as that in the type species. Bevelled posterior plate series in the paired interambulacra bear a scattering of relatively small primary tubercles (Fig. 6a). In interambulacra 2a and 3b there are up to about 10 in each; in 1a and 4b there are about 25. These tend to be arranged in regular rows running parallel to the long axes of the coronal plates.

Adoral surface flat apart from presence of prominent bifastigate keel in anterior peristome (Fig. 6c). Peristome barely sunken; anterior margin located 28% TL from anterior ambitus; relatively small, width 15% TL. Labrum projects only slightly across peristome; posteriorly narrows abruptly to two-thirds anterior width, then progressively undergoes a slight narrowing posteriorly. Phylloide with eight unipores in ambulacra II and IV; six in III and five in I and V. Plastron relatively small, maximum width 30% TL. Subanal fasciole broad, elliptical, width 36% TL; enclosing five pore pairs in both ambulacra I and V (Fig. 6d). Periproct not sunken; wider than long (Fig. 5).

Remarks. Amoraster tuberculata can be distinguished from its presumed descendant A. paucituberculata by:

- its lower test; its petals of more equal length, the anterior pair of which are more divergent, the posterior less divergent; the more tuberculate interambulacral areas between the apical system and peripetalous fasciole; the flatter adoral surface; less anteriorly projecting labrum; more prominent plastronal keel; and periproct which is not sunken.
- Like the Balcombian form of A. paucituberculata, A. tuberculata occurs with the long-ranging Eupatagus rotundus. While both species possess aboral primary tubercles, they are smaller, more densely concentrated and are restricted to the posterior plate series of the paired interambulacra in A. tuberculata. This species can further be distinguished from E. rotundus by the more anteriorly situated apex of the test; the more deeply conjugate pore pairs in the petals which are sunken; its shorter, wider peristome; shorter labrum, bifastigate plastronal keel; wider subanal fasciole; and transverse periproct.

4. Functional significance of the morphological evolution of Amoraster

The origins of Amoraster lie, most probably, with Eupatagus. Like the endemic Granobrissoides, which also evolved from Eupatagus, but in Late Oligocene time (McNamara, Philip & Kruse, 1986), the Miocene Amoraster shows a reduction in aboral tuberculation, as one of its diagnostic characters. Even within Eupatagus itself, some species, such as E. collabus Kruse & Philip 1985, show this trend. However, it should be noted that even in such species of Eupatagus impoverished in primary tubercles, tuberculation still occurs in eight interambulacral columns, whereas in Amoraster it is restricted to four.

A number of Caenozoic brissids and loveniids possess large primary aboral tubercles, supporting prominent spines (see McNamara, 1982, fig. 10E). Their role was almost certainly one of defence. This has been demonstrated in Miocene species of Lovenia from southern Australia (McNamara, in prep.), where gastropod predation occurred on all parts of the test, except in the tuberculated areas and in the region immediately posterior which would have been covered by the dense array of posteriorly directed spines. The reduction and eventual loss of primary tubercles and spines in Amoraster and Granobrissoides may be related to the occupation of deeper burrows in the sediment in a zone of reduced predation pressure. Living, spinose species, such as Lovenia elongata (Gray), are known to be shallow burrowers and use their spines in a defensive role (Ferber & Lawrence, 1976). Deeply burrowing spatangoids, however, such as Brissopsis, Sehizaster and Moira, do not possess large, primary tubercles and spines.

The morphological evolution of A. paucituberculata shows some parallels with the evolutionary changes seen in a number of other
Figure 6. *Amoraster tuberculata* sp. nov.; (a) aboral, (b) lateral, (c) adoral, (d) posterior views of holotype, WAM 87.116, from the Early Miocene (Longfordian) Mannum Formation, Mannum, South Australia. All × 1.

echinoid lineages. The most noticeable change is the increase in height in the anterior region of the test, resulting in an increase in declination of the posterior aboral surface of the test. A similar increase in test height has been documented within a number of other echinoid lineages, where it has been correlated with a decrease in grain size of the enclosing sediment. Examples include species of *Discoides* from the Early Cenomanian strata of southern England (Smith & Paul, 1985), and the southern Australian Tertiary spatangoids *Pericosmus* (McNamara & Philip, 1984) and *Hemiaster* (McNamara, 1987). Similarly, species
New Miocene echinoid genus

of arachiacid cassiduloids which have prominently swollen apical parts of the test, also in an anterior position, have been regarded as having inhabited relatively muddy sediments (Smith & Zaghbibi-Turki, 1985).

The similar increase in anterior test height in Amoraster can, to some degree, also be correlated with a decrease in sediment grain size. A. tuberculata is preserved in calcarenites which range in size from 0.1 to 0.4 mm in diameter, whereas A. paucituberculata occurs in more well-sorted sediments, 0.1 to 0.2 mm in diameter, in the Port Campbell Limestone. This unit is considered to have been deposited in relatively deep water (Bock & Glenie, 1965). The coarse-grained calcarenites of the Mannum Formation represent sedimentation in a very shallow water environment. However, the evolution of A. paucituberculata from A. tuberculata is not simply a case of adaptation by the descendant species to inhabiting a finer-grained sediment. The earliest known specimen of A. paucituberculata, which lacks primary tubercles entirely, occurs in coarse-grained bryozoal calcarenites of the Bochara Limestone. It is tempting to speculate that this earliest form of A. paucituberculata, in lacking tubercles, and thus defensive spines, was adapted initially to burrowing deeper in coarse-grained sediments than its ancestor, A. tuberculata. But A. paucituberculata, by also having evolved a higher test, longer labrum, deeper petals and more sunken poriferous zones in the petals, was also suitably preadapted to occupying the finer-grained, deeper-water sediments of the Port Campbell Limestone.

The increase in petal depth which occurs in the A. tuberculata–paucituberculata lineage parallels the situation seen in the Schizaster lineage (McNamara & Philip, 1980) and the Pericosmus lineage (McNamara & Philip, 1984). Development of more sunken petals is thought to optimize water flow over the respiratory tube feet in finer-grained sediments. Amoraster further refined this adaptation by a swelling of the inter-poriferous zone, thus setting each row of respiratory tube feet in a deeper channel. Two other morphological changes in Amoraster have also been documented in the Schizaster and Pericosmus lineages. These are the evolution of a more sunken peristome and anterior elongation of the labrum. McNamara & Philip (1980) considered that these changes were also adaptations to the habitation of an environment where the flow of water around the echinoid test was limited to an entrance above the apical system. Ingestion of food, particularly if the source of the food was from the sediment surface, was improved by the elongation of the labrum. The absence of pore pairs in ambulacrum III, characteristic of species which possess funnel-building tube feet, suggests that Amoraster did not burrow very deeply into the sediment. However, as noted above, the reduction in tubercle number between A. tuberculata and A. paucituberculata may, perhaps, be interpreted as an adaptation to slightly deeper burrowing in the sediment by the descendant species.

Most interspecific morphological changes in echinoids occur by heterochrony (McNamara, 1988). Amoraster was no exception. Although little is known about the ontogenetic changes in the genus, the greater degree of anterior elongation of the labrum in A. paucituberculata during growth, compared with that attained by the ancestral A. tuberculata, indicates an acceleration in labral growth resulting in the evolution of a peramorphic trait. The reduction in primary aboral tubercle number, on the other hand, is a paedomorphic feature. Such dissociated heterochrony, with some traits being peramorphic, others paedomorphic, was probably the rule rather than the exception in echinoid evolution (McNamara, 1988) and likely to have been a major factor in the high degree of speciation in spatangoid echinoids during Tertiary time.

Acknowledgements. We should like to thank Frank Holmes for the donation of a specimen and Kris Brimmel for the photography.

References


Ludbrook, N. H. 1973. Distribution and stratigraphic utility of Cenozoic molluscan faunas in southern Australia. Science Reports of the Tohoku University,
New Miocene echinoid genus

Sendai, Japan, Second series (Geology), Special Volume, No. 6 (Hatai Memorial Volume), 241–61.


McNamara, K. J. (in prep.). The role of gastropod predation in directing speciation in spatangoid echinoids.


