Rec. West. Aust. Mus. 1982, 10 (2): 167-197

Taxonomy and Evolution of Living Species of *Breynia* (Echinoidea: Spatangoida) from Australia

K.J. McNamara*

Abstract

Three living species of *Breynia* are described: *B. australasiae* (Leach, 1815) from eastern Australia; *B. desorii* Gray, 1851 from western and northern Australia; and *B. neanika* sp. nov. which is described on the basis of specimens from north-eastern Australia and from the Arafura Sea. Speciation is shown to relate to variation in rates of morphological development, *B. desorii* undergoing most morphological change during its ontogeny, *B. neanika* the least. The post-larval ontogeny of *Breynia* is described in detail for the first time. A revised key for the living species of *Breynia* is presented.

Introduction

The spatangoid echinoid *Breynia,* although being one of the commonest of the larger heart urchins around the coast of Australia, has been little studied. Indeed, surprisingly few detailed taxonomic studies have been carried out on any of the living irregular echinoids of Australia apart from recent papers by McNamara and Philip (1980) and McNamara (1982*a*). These authors established that in living Australian schizasterid echinoids it is important to examine large collections as there is often a high degree of intraspecific variation. This is the case with eastern and Western Australian forms of *Breynia* in which a certain amount of confusion over the taxonomic status has occurred during the last hundred years.

Gray (1851, 1855) originally distinguished the Western Australian *B. desorii,* from the eastern species, *B. australasiae* (Leach, 1815). However, many later workers (Agassiz 1872-74; Studer 1880; H.L. Clark 1914, 1917, 1925, 1938, 1946; Alexander 1914; Mortensen 1918) synonymized *B. desorii* with *B. australasiae* without having examined adequate material. Some workers (Mortensen 1951; James 1966; A.M. Clark and Rowe 1971) have considered *B. desorii* to be specifically distinct from *B. australasiae,* although for different reasons.

The aim of this paper is to describe the western form of *Breynia* in detail, on the basis of a large collection from Norbill Bay, Rosemary Island, Western Australia, in order to re-evaluate its taxonomic status. The range of variation between

---

* Department of Palaeontology, Western Australian Museum, Francis Street, Perth, Western Australia 6000.

adults, both within and between populations, and the ontogeny of *Breynia* are described, and the relationship between ontogeny and phylogeny within the genus is assessed. Furthermore, examination of the eastern Australian form, largely on the basis of material from Lord Howe Island, and a collection recently made from the Arafura Sea by the CSIRO vessel *Soela,* reveals the presence of two species, both distinct from the western species; one of these is described as new.

Specimens used in this study are housed in the Western Australian Museum (WAM), Australian Museum (AM), Queensland Museum (QM) and British Museum (Natural History) (BM). In species descriptions 'percentage of test length' is abbreviated to % TL. All measurements made are self-evident, except for width of internal fasciole; this is measured across the apical system.

Key to Living Species of *Breynia*

1	Test with flattened aboral surface; short petals	2
	Test with vaulted aboral surface; long petals	3
2	Internal fasciole narrow; periproct oval	*B. neanika*
	Internal fasciole narrow; periproct circular	*B. vredenburgi*
3	Many primary tubercles	4
	Few primary tubercles	*B. australasiae*
4	Internal fasciole long; plastron long	*B. desorii*
	Internal fasciole short; plastron short	*B. elegans*

Systematics

Order Spatangoida Claus, 1876
Family Loveniidae Lambert, 1905
Genus *Breynia* Desor, 1847

Type Species

Spatangus australasiae Leach, 1815: 68.

Breynia australasiae (Leach, 1815)

Figures 1, 2

Spatangus australasiae Leach, 1815: 68, Pl. 82.

Breynia australasiae – Mortensen 1951: 132-139, Pl. 10, figs 1-5, Pl. 12, figs 8, 9, 11, 13, Pl. 14, figs 3-5, Pl. 49, figs 1-5, 20, 25-30, 32; with full synonymy.

Breynia desorii Gray, 1851; – Mortensen 1951, Pl. 12, fig. 7, Pl. 14, figs 6, 7.

Diagnosis (emended herein)

Aborally test bears up to 15 primary spines and tubercles in each of the anterior interambulacra, 2 and 3, and up to 25 in 1 and 4. Peripetalous fasciole only close to ambitus anteriorly; broad and relatively short internal fasciole. Peristome broad and sunken; periproct large. Generally between 5 and 6 subanal pore pairs.

Remarks

This species has been described by a number of authors (see Mortensen [1951] for detailed synonymy) and in detail by Mortensen (1951). Further general description would be superfluous. However, a number of further observations can be made, amplifying, in particular, characters hitherto not considered to be of great taxonomic significance, but in this study shown to be important in characterizing the species.

Compared with other species of *Breynia* the peristome is wide (Figure 5) occupying up to 16% TL. In large adults the labrum may project slightly anteriorly giving a slight lunate shape to the peristome, in contrast to the semicircular shape in juveniles and young adults. Mortensen (1951) characterized *B. australasiae* as having a labrum which reaches only to the second ambulacral plate, although rarely just approaching the third. Examination of almost 100 specimens has revealed that the labrum reaches the second ambulacral plate in only 40% of the specimens; in the remaining 60% it reaches the third.

The periproct is large for the genus, its long axis reaching almost 15% TL. It is enclosed by plates 4-8 of interambulacrum 5. Although Mortensen (1951) observed no more than 6 pore pairs either side of the mid-line within the subanal fasciole, specimens are known which have 7; others have as few as 4. Generally there are 5 or 6.

The internal fasciole is relatively broad (Figures 1, 7) occupying generally 20-24% TL, but up to almost 30% in some large individuals. It is relatively short (Figure 6), between 36 and 44% TL. As a result of the peripetalous fasciole being set well in from the ambitus anterolaterally, the width across the anterior petals is only about 56-60% TL (Figure 9). The smaller interambulacral area within the peripetalous fasciole results in fewer primary tubercles than in species in which the peripetalous fasciole approaches closer to the ambitus (Figure 7). In anterior interambulacra 2 and 3 there are no more than 15 primary tubercles, while in the lateral interambulacra 1 and 4 there are up to 25. Rate of production of primary tubercles through ontogeny is slow compared with *B. desorii* (Figure 8).

Examination of an ontogenetic suite shows similar morphological development to *B. desorii* (described below), although rate of development is reduced. The significance of this is discussed below in the section dealing with the phylogenetic relationships between the Australian species. Opening of genital pores is thought to correspond to onset of maturity. This generally occurs between test lengths of 38 and 44 mm.

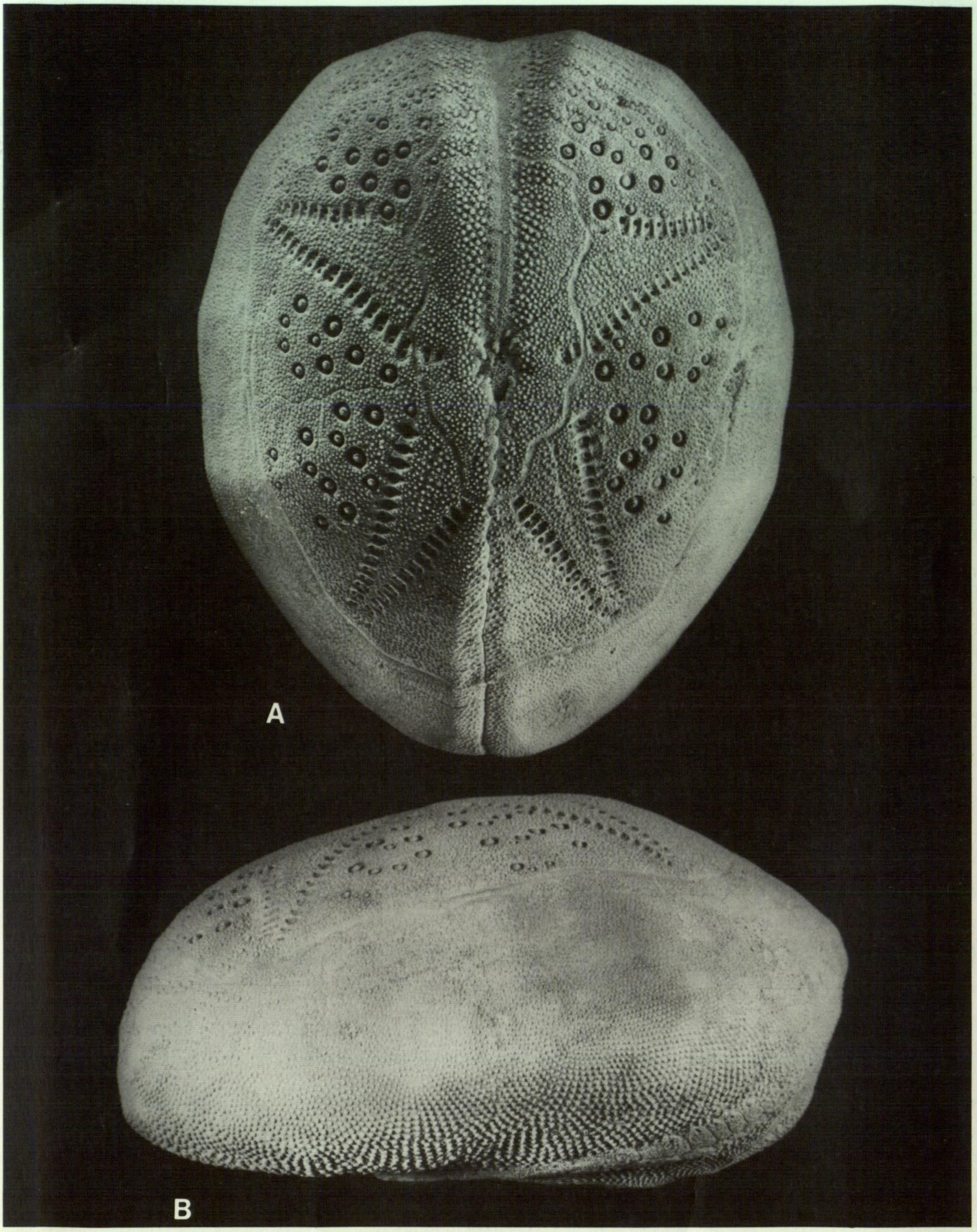

Figure 1 *Breynia australsasiae* (Leach, 1815); AM G12604, from Lord Howe Island; (A) aboral view; (B) lateral view; both x 1.

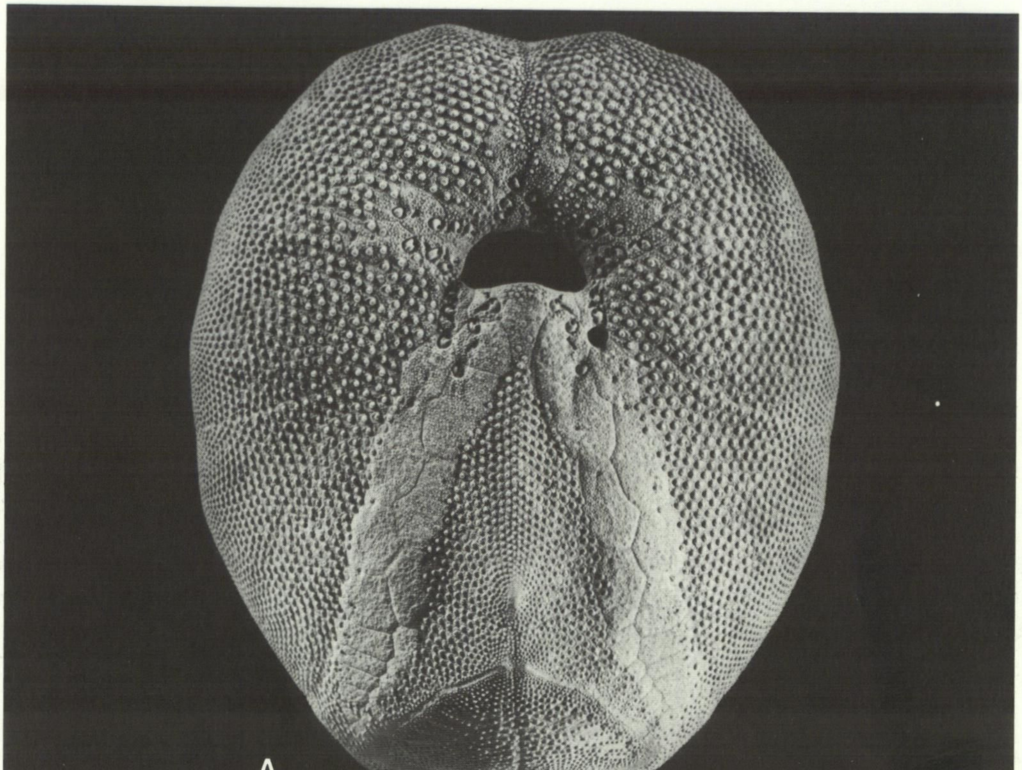

Figure 2 *Breynia australasiae* (Leach, 1815); AM G12604, from Lord Howe Island; (A) adoral view; (B) posterior view; both x 1.

Distribution

H.L. Clark (1946) and Mortensen (1951), following Tenison Woods (1878), recorded *B. australasiae* along the entire Queensland coast from 'Cape York to Port Jackson'. It does not appear, however, to be common from the Queensland coast on the basis of material held in Museum collections. Single specimens are known from East Tongue Reef, north of Cairns; Lindeman Island; Swain Reef and Turtle Head Island, Cape York (all Australian Museum specimens); north Wistari Reef; Bowen; Yepoon (all Queensland Museum specimens); and Hervey Bay (Endean 1961). Four specimens from Torres Strait are in the British Museum (Natural History) collection.

B. australasiae is particularly common around Lord Howe Island in the Tasman Sea, where it burrows in sand in shallow water depths. Although Tenison Woods (1878) recorded the species from Port Jackson there are no specimens from N.S.W. in the collections of the Australian Museum or any other collections examined. There is no record of *B. australasiae* from either the Victorian or South Australian coasts (Figure 14).

Although Mortensen (1951: 137) considered *B. australasiae* to be restricted to the eastern coast of Australia and *B. desorii* to the west, three of the specimens he figured from eastern Australia, one from Bowen (Mortensen 1951, Pl. 12, fig. 7) and two from 'Queensland' (Mortensen 1951, Pl. 14, figs 6, 7) he called *B. desorii,* contrary to his opinion on their distribution expressed in the text. These specimens appear to be *B. australasiae.*

Breynia desorii **Gray, 1851**

Figures 3, 4, 10

Breynia desorii Gray, 1851: 131; – Gray 1855: 46; – Mortensen 1951: 129-131, 139-141, Pl. 11, figs 3-5, Pl. 12, figs 1, 12, *non* 7, Pl. 14, figs 1, 2, *non* 6, 7; – James 1966: 79; – A.M. Clark and Rowe 1971: 146-149, 165, fig. 81b.

Breynia australasiae – Agassiz 1872-74: 578 (pars.); – Studer 1880: 881; – Alexander 1914: 112; – H.L. Clark 1914: 169; – H.L. Clark 1917: 250 (pars.); – Mortensen 1918: 20, Pl. 5, figs 2, 18, 19, 22; – H.L. Clark 1925: 228; – H.L. Clark 1938: 438-439; – H.L. Clark 1946: 381.

?*Breynia australasiae* var. *aroensis* Currie, 1924: 63-66, Pl. 4.

Holotype

British Museum (Natural History) specimen 39.6.10.36, a dry test lacking spines; probably female. Purchased from a Mr Turner prior to 1839 when it was registered. Miss A.M. Clark of the British Museum informs me (litt. comm. 21.10.80) that the specimen is the only one in the collections registered as coming from 'Swan River, Western Australia', the type locality, even though Gray (1851: 131) recorded several specimens being in existence at the time of his description of the species. It must therefore be regarded as the holotype as it is the sole remaining specimen from the type series. It had earlier been considered by A.M. Clark and Rowe (1971) that all of Gray's original series was lost.

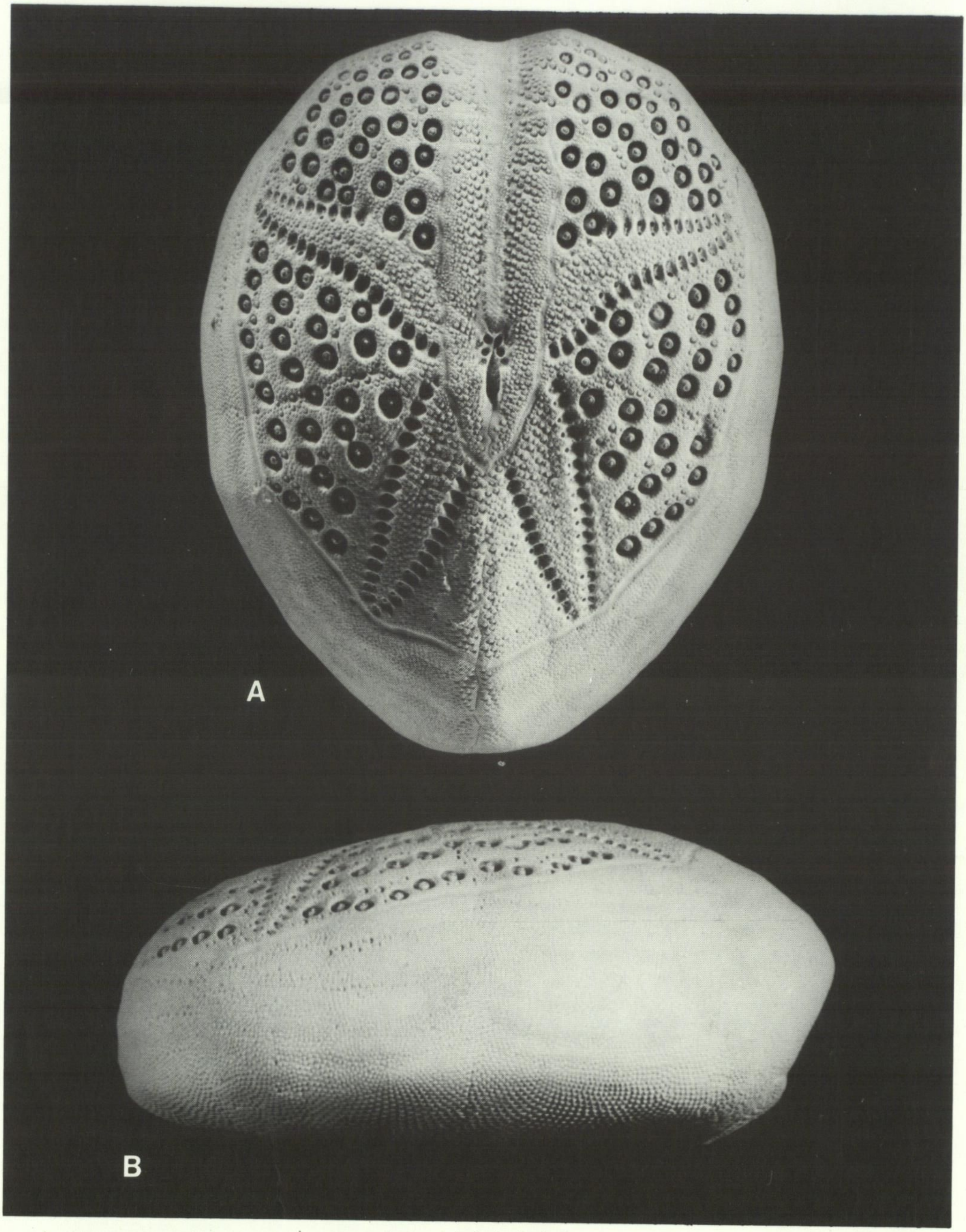

Figure 3 *Breynia desorii* Gray, 1851; BM 39.6.10.36, holotype, from 'Swan River, Western Australia'; (A) aboral view; (B) lateral view; both x 1.

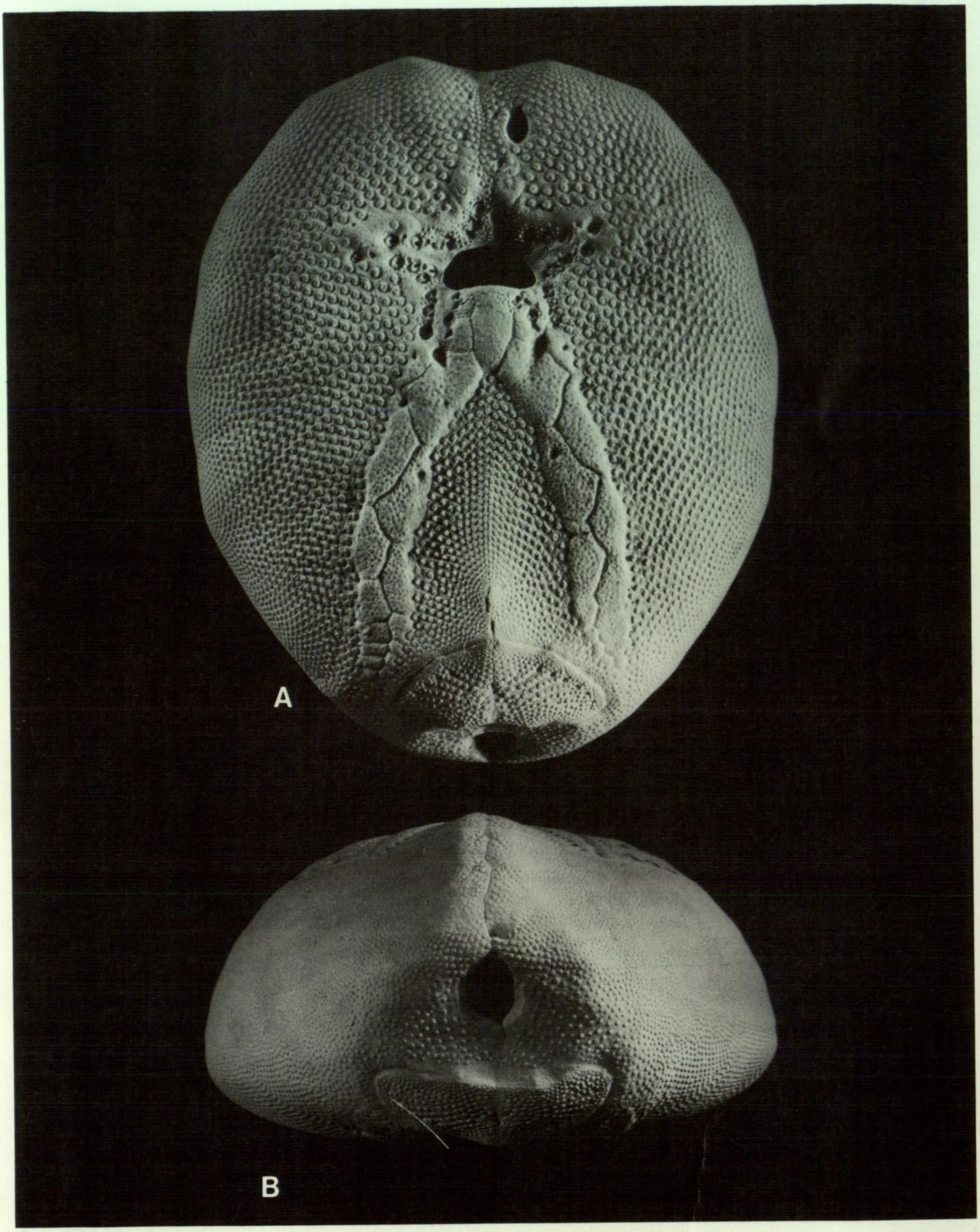

Figure 4 *Breynia desorii* Gray, 1851; BM 39.6.10.36, holotype, from 'Swan River, Western Australia'; (A) adoral view; (B) posterior view; both x 1.

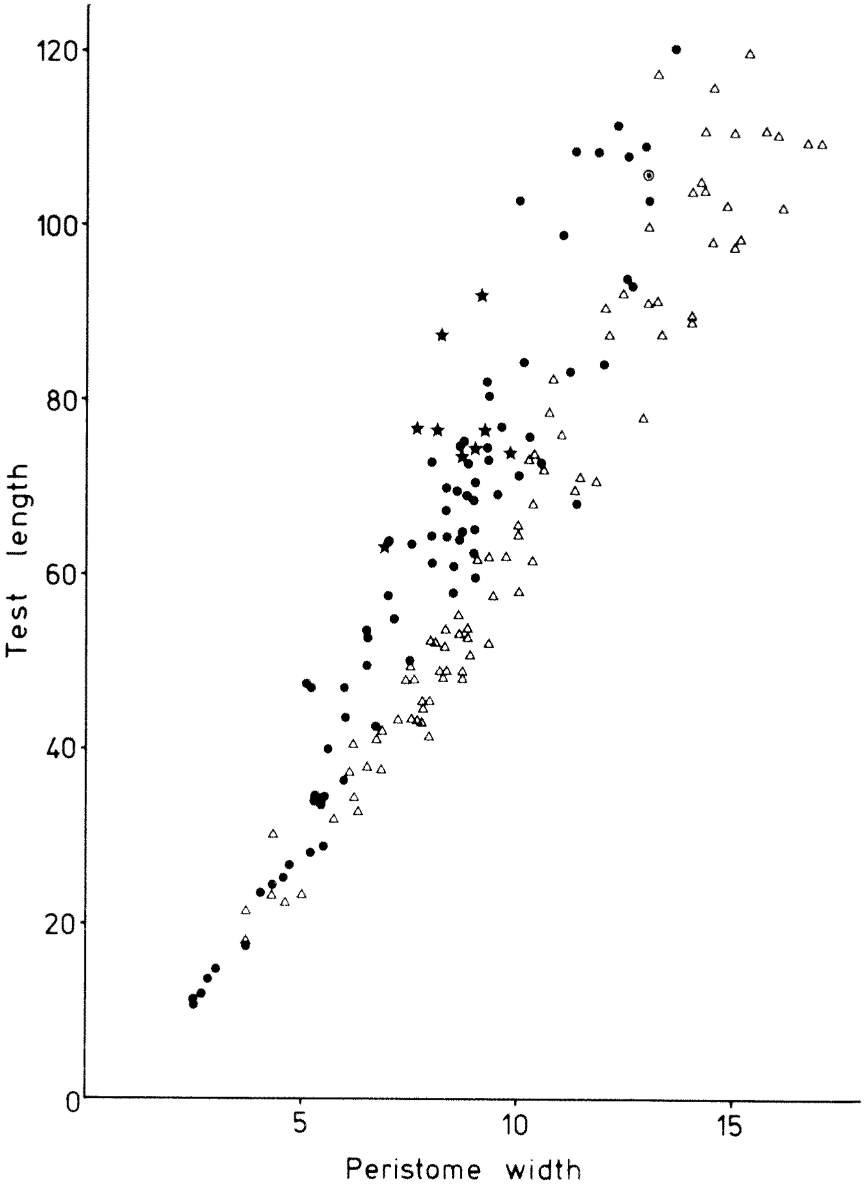

Figure 5 Plot of test length against peristome width for *B. australasiae* (triangles), *B. desorii* (circles) and *B. neanika* (stars).

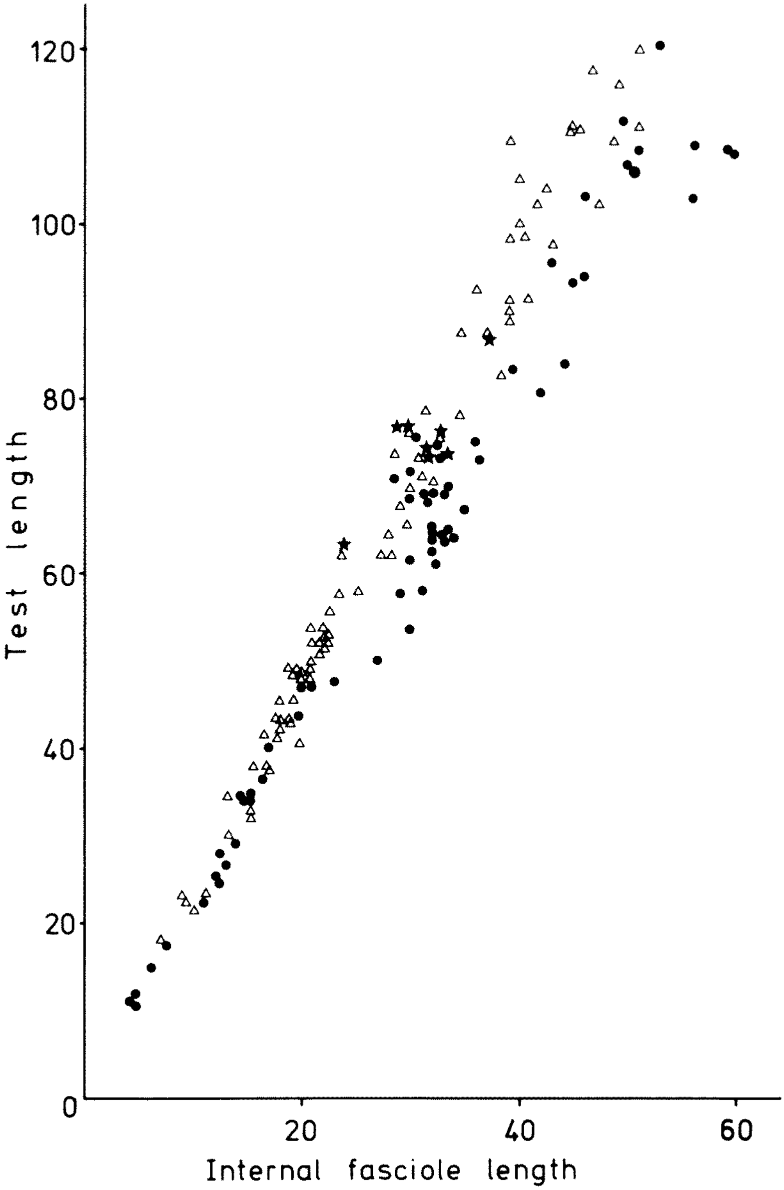

Figure 6 Plot of test length against internal fasciole length for *B. australasiae* (triangles), *B. desorii* (circles) and *B. neanika* (stars).

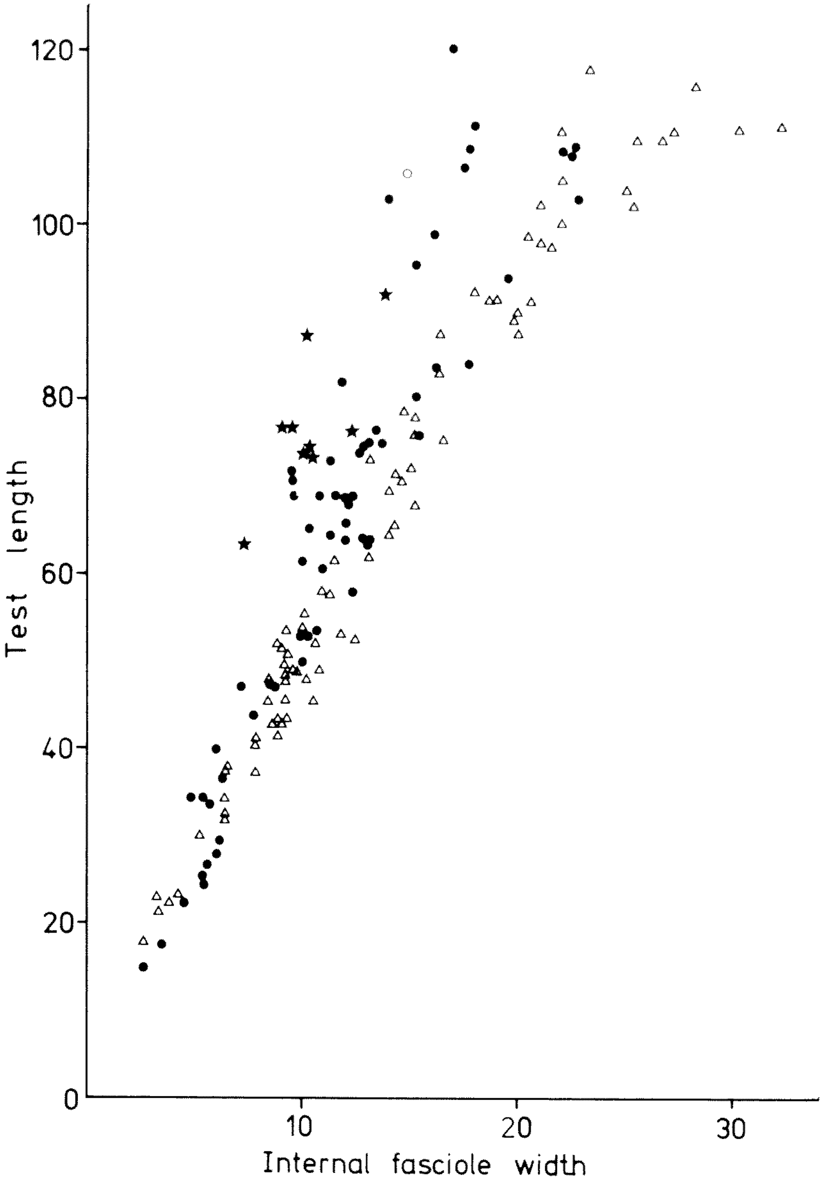

Figure 7 Plot of test length against internal fasciole width for *B. australasiae* (triangles), *B. desorii* (circles) and *B. neanika* (stars).

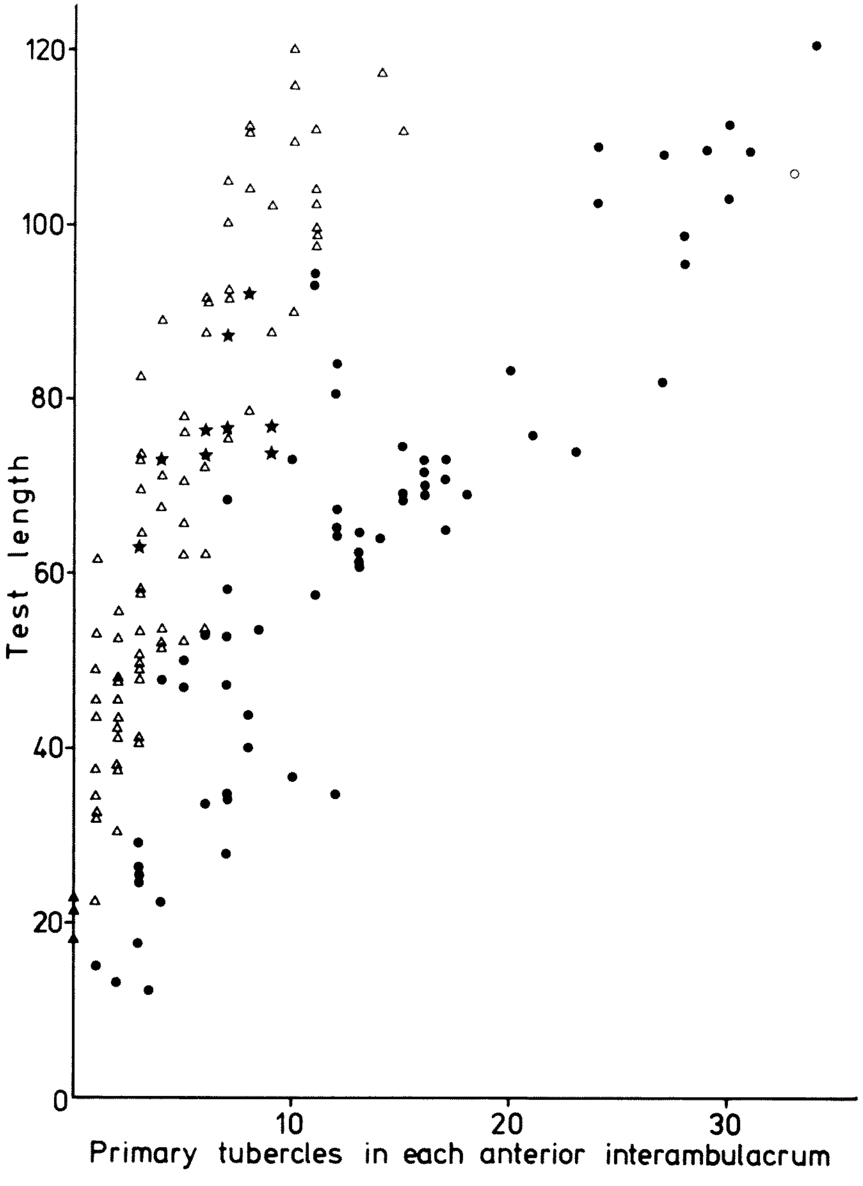

Figure 8 Plot of test length against number of primary tubercles in anterior interambulacra for *B. australasiae* (triangles), *B. desorii* (circles) and *B. neanika* (stars).

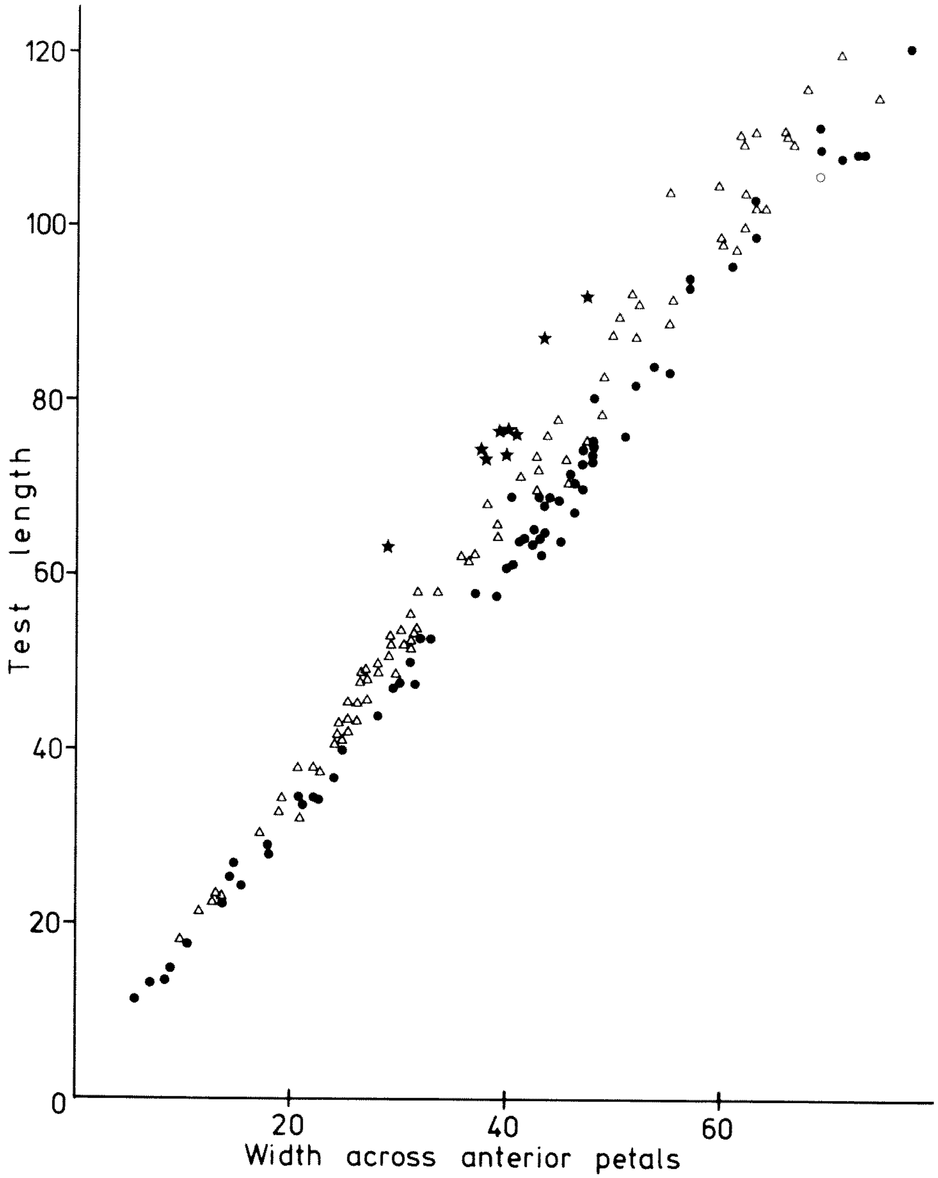

Figure 9 Plot of test length against width across anterior petals for *B. australasiae* (triangles), *B. desorii* (circles) and *B. neanika* (stars).

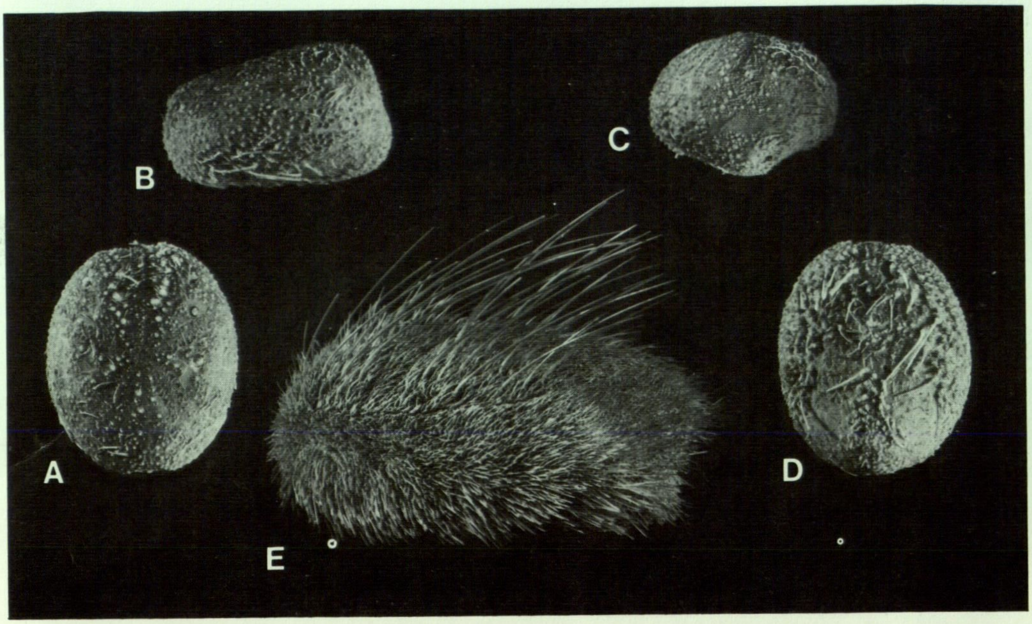

Figure 10 *Breynia desorii* Gray, 1851; WAM 50-82, juvenile (A) aboral view; (B) lateral view; (C) posterior view; (D) adoral view; all x 3; (E) WAM 51-82, lateral view of specimen with spines, x 1. Both specimens from Norbill Bay, Rosemary Island, Western Australia.

Diagnosis (emended herein)

Aborally test bears up to 42 primary spines and tubercles in each of the anterior interambulacra, 2 and 3, and up to 45 in lateral interambulacra 1 and 4. Peripetalous fasciole close to ambitus anteriorly and laterally; long and generally narrow internal fasciole. Peristome narrow and sunken. Generally between 6 and 7 subanal pore pairs.

Description

Test reaches a maximum known length of 120 mm; widest slightly anterior to mid-test length, width varying between 73 and 85% TL (holotype 82% TL). Test generally highest at two-thirds test length in keel formed by swelling of interambulacrum 5; often, however, test swollen apically; height varies between 44 and 55% TL (holotype 46% TL). Test has broad, shallow anterior notch and tapers gently posteriorly. Posterior keel overhangs periproct. Apical system tetrabasal; depressed and set anterior of centre, about 40% TL from anterior; ethmolytic with four genital pores; a bimodal size distribution of pore size probably reflects sexual dimorphism; posterior pair more widely spaced than anterior pair, which are almost in contact; occasionally some specimens possess only 3 pores due to failure of one to open at onset of maturity. Madreporite very long, up to 6% TL. Ocular plates very small.

Aborally ambulacrum III shallow, deepening slightly abapically; bears very small pore pairs which decrease in size and become more widely spaced abapically; pores within each pair aligned abaxially; ambulacral plates bear many, relatively large, secondary tubercles abaxially, largest being close to pore pairs; adaxially covered by dense accumulation of very small, granular tubercles.

Anterior petals broad adapically, narrowing abapically to terminate close to ambitus; anterior rows of pore pairs run almost transversely; posterior rows diverge anteriorly at about 115°; pore pairs large in ambulacra between the peripetalous and internal fascioles; width across anterior petals 64% TL (Figure 9); anterior row of large pore pairs relatively short, extending for only two-thirds distance between peripetalous and internal fascioles; large pore pairs replaced by very small pore pairs which extend directly to apical system, the two rows of small pore pairs in ambulacra II and IV diverging at about 90°. Posterior row straight to gently sinuous, almost twice as long as anterior row and reaching much closer to apical system, terminating in transverse line with it at internal fasciole; very small pore pairs extend inside internal fasciole transversely to apical system; rarely one or two of the pore pairs within the internal fasciole may be large. Large pore pairs in petals deeply sunken and conjugate, outer pore of each pore pair slightly larger than inner; abapically pores diminish in size slightly close to ambitus; 10-13 pore pairs in anterior rows of petals; 16-20 in posterior rows; frequently 11 in anterior, 17 in posterior (as in holotype). Plates 13 or 14 of the anterior ambulacra have first petaloid pore pairs. Ambulacra between pore pairs covered by numerous small, granular tubercles.

Posterior petals with outer poriferous rows being much longer than inner (16-20 pore pairs, compared with 13-16); rows straight, widely spaced anteriorly, converging posteriorly at peripetalous fasciole. Within internal fasciole inner row continues its course as very small pore pairs; very small pore pairs in outer row run transversely within internal fasciole. Plates 21 of each of the posterior ambulacra have first petaloid pore pairs. This plate is occluded by plates 20 and 22, and so fails to touch the interambulacra.

Within peripetalous fasciole, interambulacra 1 to 4 bear large, sunken, primary tubercles; larger adapically, diminish in size toward peripetalous fasciole. Number of tubercles is quite variable (Figure 8), a test 109 mm in length having only 24 in interambulacrum 2, but one 106 mm in length having 42. Tests 100 to 120 mm test length generally have 28-33 in the anterior interambulacra 2 and 3. There are generally a few more tubercles in posterolateral interambulacra than in anterolateral interambulacra. Tubercles bear large spines which may reach up to half test length (Figure 10E). One aberrant specimen (WAM 631-71), which has the highest known number of tubercles in interambulacra 1 to 4, has, contrary to generic diagnosis, six tubercles in interambulacrum 5.

Peripetalous fasciole may extend to ambitus anteriorly and close to ambitus laterally; posteriorly it reaches to within almost 90% TL of posterior; frequently branched anteriorly, branches running parallel to main fasciole, but often discontinuous; indeed it is unusual for fasciole not to have many branches anteriorly. Laterally it passes across plate 6 of interambulacra 1 and 4. Internal fasciole long and generally narrow (Figures 3, 6, 7); parallel-sided throughout most of its length; length 45-55% TL; width 14-20% TL (though higher in a Shark Bay population – see below); also often branched anteriorly; extends a long distance, up to 20% TL behind apical system.

Peristome lunate, sunken and narrow (Figures 4, 5), width being only 9-13% TL. Oral unipores, with tube feet being terminated by a disc which bears many fine papillae, arranged in phyllode around peristome: 9 or 10 in ambulacra II and IV; 6 in ambulacrum III; 7 or 8 in ambulacra I and V. Although pores are generally unipores, occasionally anisopores are present. Labrum very long, up to 15% TL; broad anteriorly, constricting at one-quarter length, then approximately parallel-sided until tapers posteriorly almost to point; reaches plastron except in eight specimens: two (WAM 1788-74, 192-78) from Wallabi Island, Abrolhos; three from the southern end of Eighty Mile Beach; and three from Louisa Bay, Dirk Hartog Island. In these specimens third plates of ambulacra I and V are in contact, thus labrum and plastron are separated (Figure 11C). In about 80% of specimens labrum extends posteriorly to be in line with third ambulacral plate; in remainder extends only to second plate (Figure 11A). This is not a function only of varying length of labrum, but is largely a consequence of great variability in size of second ambulacral plate. Generally it is only about one-quarter the size of third ambulacral plate, but in some individuals it is at least half the size and extends posteriorly. Anteriorly labrum is transverse to anteriorly projecting, particularly in large adults.

Plastron triangular and widest posteriorly; width half to one-third length; posteriorly forms a slightly raised keel; plastron covered by tubercles which increase in size abaxially; areole around tubercles extends postero-adaxially. Ambulacra I and V smooth, swollen; width 8-11% TL. Periproct longitudinally oval; longer axis 10-12% TL. Subanal fasciole large; triangular to sub-oval; width up to 35% TL. Generally 6-7 pore pairs within each ambulacra within fasciole, though range is from 3-8; associated tube feet with disc-like termination bearing numerous fine papillae. Test between periproct and subanal fasciole sunken. Large adoral anterior and lateral interambulacral surfaces covered by large, closely spaced tubercles; areoles directed posterolaterally in lateral interambulacra, but anterolaterally in anterior interambulacra.

Pedicellariae very numerous; small ophicephalous, which are particularly common on adoral ambulacra I and V; large, 1.5 mm long, and small rostrate; 1 mm long tridentate; small triphyllous. There is no apparent difference in form of these pedicellariae from those of *B. australasiae*, but, as Mortensen (1951) observed, small globiferous pedicellariae infrequently occur in *B. desorii*.

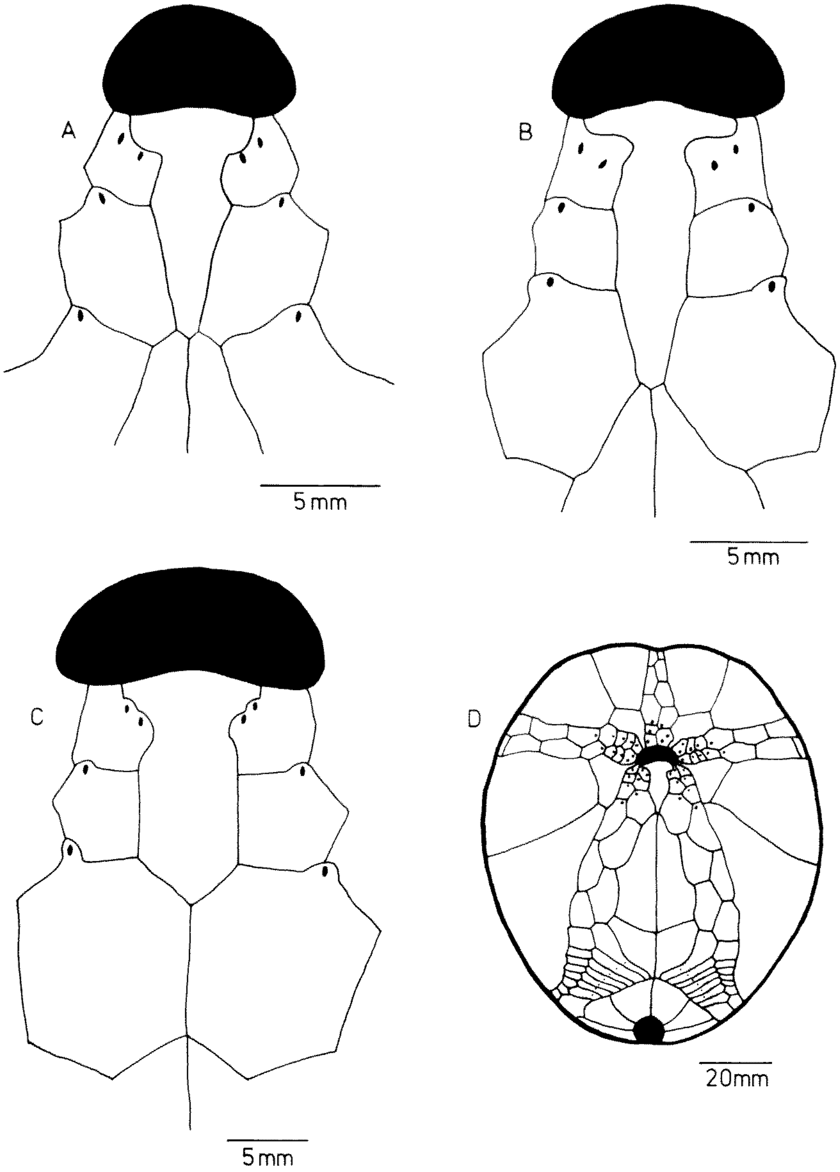

Figure 11 (A-C) Variation in plating around the labrum in *B. desorii:* (A) WAM 49-82, from Laura Bay, Dirk Hartog Island, labrum extends posteriorly to second ambulacral plates; (B) WAM 6-65, from Shark Bay, labrum extends to third ambulacral plates; (C) WAM 192-78 from East Wallabi Island, Abrolhos, labrum separated from plastron by enlarged third ambulacral plates; (D) adoral plating of holotype of *B. desorii*, BM 39.6.10.36.

Ontogeny

Smallest known specimen (Figure 10A-D) has a test length of 10.8 mm. Other specimens of test length 11.0 and 11.8 mm are known. In these small juveniles test is nearly as wide as long, being 85-90% TL. During growth test length progressively increases to adult proportions, i.e. width to as low as 73% TL. Pore pairs open when test length between 32 and 38 mm; this is thought to correspond with onset of sexual maturity. Apical system becomes relatively more anteriorly positioned with growth, from about 50% TL in smallest juveniles to about 40% TL from anterior in adults.

Smallest juveniles have short petals. In anterior pair there are 5 pore pairs in anterior row and 11 in posterior row. In posterior pair there are 8 in inner row and 9 in outer. Petals lengthen through ontogeny initially by increase in number of pore pairs until full adult complement is reached, then by a relative increase in size and spacing of the pore pairs. Pore pairs are neither conjugate nor sunken in juveniles; deepening occurs with growth. The two rows of pore pairs in each petal are sub-parallel in small juveniles and interporiferous zones are a little narrower than width of pore pairs. During growth interporiferous zones of anterior petals increase greatly in width adapically, resulting in anterior rows running almost transversely in adults, and not divergent at about 120° as in juveniles. Petals lengthen such that anterior pair come to lie with distal extremities close to ambitus, width across anterior petals increasing from 50% TL in small juveniles to 66% in adults (Figure 9). Posterior pair lengthen from 25% TL to 40% TL for a ten-fold increase in test length from 10.8 mm. Lengthening of posterior petals occurs at a relatively greater rate than anterior on account of the anterior movement of the apical system; thus posterior petals lengthen both adapically and abapically, whereas anterior petals increase in length only abapically. Anterior and posterior petals of a similar length relatively through adult growth.

Internal fasciole relatively very wide anteriorly in small juveniles, occupying 32-38% TL, whereas in adults it is only half this proportion (Figure 7). With growth, inverted triangular shape of fasciole changes to parallel-sided as most lateral growth occurs posteriorly. Fasciole increases in length from as little as 32% TL to 45-55% TL in adults (Figure 6). In small juveniles fasciole close to apical system posteriorly. Moves posteriorly away from apical system during growth. In small juveniles large area of outer ambulacral plates within internal fasciole carries most prominent tubercles and longest spines. In individuals of test length of 14 mm, spines up to 7 mm long. One to two primary tubercles are present in each interambulacrum between internal and peripetalous fascioles, but spines carried are shorter than those on plates of ambulacrum III. With growth interambulacral spines lengthen relative to ambulacral spines, such that at test length of 20 mm they are of similar length. At maturity (32-38 mm) interambulacral spines are longer and continue to increase relatively during adult growth. Production of primary tubercles and spines increases throughout adult growth.

Adorally, second plate in posterior row of interambulacrum 1 has junction with third plate meeting tenth ambulacral plate in juvenile 8 mmTL. At 34 mm TL it meets twelfth plate, whilst in adults 100 mm TL it meets the sixteenth plate.

Peristome relatively large in juveniles, length equalling nearly one-quarter test length. There is a relative size decrease during growth such that in adults peristome length half relative juvenile length; a similar relative reduction occurs in peristome width (Figure 5). Furthermore, during growth peristome becomes more sunken and in large adults labrum, which is transverse anteriorly in juveniles, may project forward. Ambulacra I and V are relatively very broad in small juveniles, width being up to 25% TL, decreasing to 8-11% TL in adults. Plastron elongates anteriorly during growth. Subanal area moves forward during growth; in juveniles it is orientated vertically at posterior of test; it moves anteriorly to lie adorally in adults, as does periproct which, in juveniles, is visible from above. Periproct large in small juveniles: long axis 25% TL in 12 mm long juvenile, decreasing to 17% TL at onset of maturity, thence to 10-12% TL in adults. Number of subanal pore pairs increases steadily from 2 at test length of 12.5 mm to full adult complement of 6-7 at onset of sexual maturity, i.e. test length between 32 and 38 mm.

Morphological Variation

The extent of phenotypic variation in *B. desorii* is best exemplified by a population collected from Laura Bay on the eastern side of Dirk Hartog Island in Shark Bay (WAM 1066.81, 1062. 81). Unlike *B. desorii* populations from Eighty Mile Beach and Rosemary Island to the north, and from the coast near Fremantle to the south, the majority of the Shark Bay specimens are characterized by possession of a narrower test, fewer primary tubercles and broader internal fasciole. In the last two characters they resemble *B. australasiae.* Of 33 specimens measured, the mean internal fasciole width (% TL) is 22.03, which is outside the range for other populations of *B. desorii* (14-20% TL). The range of the Shark Bay populations is 16.8 to 26.7% TL. In *B. australasiae* the range is 20-24% TL.

The internal fasciole length of the Shark Bay specimens is, however, characteristic of *B. desorii,* ranging from 41-58% TL (compared with 45-55% TL in other populations of *B. desorii* and 36-44% TL in *B. australasiae*).

The peripetalous fasciole is not positioned quite as close to the ambitus in the Shark Bay material. This, combined with the broader internal fasciole, restricts the production of primary tubercles. Although generally possessing fewer tubercles than specimens in other populations of *B. desorii,* the Shark Bay specimens have more tubercles than specimens of *B. australasiae* of comparable size.

The reasons for interspecific morphological differences in *Breynia* are discussed below. It may be noted here, however, that this morphological variation reflects paedomorphosis, that is retention of characters into moderate to large-sized adults which occur in juveniles and small adults of other populations of *B. desorii.* The rate of morphological change is lower in the Shark Bay material. The population is therefore a neotenic population.

It should be stressed that although the majority of specimens in the Shark Bay population have a relatively longer test than in other populations, and also have fewer primary tubercles, and a broader internal fasciole, some Shark Bay individuals are indistinguishable from individuals from other populations. Furthermore, all the Shark Bay specimens have the characteristic adoral features of *B. desorii.* Morphological variation in other populations affects similar structures to those in the Shark Bay population, but the range of variation is very much less.

Another interesting feature of morphological variation in *B. desorii* is the shape and disposition of the plates in ambulacrum I and V adorally. Variation in size of the second ambulacral plates, as already discussed, results in the labrum reaching posteriorly either to the second or third plates. In addition, a small number of specimens possess third ambulacral plates which are in contact with each other, consequently separating the labrum from the peristome. This feature has not previously been described in living species of *Breynia,* but all described fossil species invariably have the labrum separated from the plastron by greatly enlarged third ambulacral plates. This feature has been noted by Gerth (1922) in the Miocene *B. multituberculata* and by Mortensen (1951) in *B. paucituberculata* (Gerth, 1922). It also occurs in the Miocene *B. carinata* d'Archiac and Haime, 1853 and in an undescribed species from the Middle Miocene Trealla Limestone on Barrow Island and in the Gnargoo Range. It is interesting to note that in juveniles of this undescribed species the labrum and plastron are not separated, suggesting that the lack of separation of these plates in living species is a paedomorphic feature. Separation of the labrum from the plastron also occurs in the brissid *Spatangomorpha,* which occurs in Miocene-Pliocene rocks of the Indo-West Pacific region, and in the loveniid *Verbeekia* from the Eocene of Borneo.

Distribution

Although Mortensen (1951) recorded *B. desorii* from only between Swan River and Dampier, specimens in the Western Australian Museum have been collected from the entire length of the western coast of Australia (Figure 14), being particularly common between Dampier and Broome on the north-west coast. On the southern coast it has been collected from as far east as Lucky Bay (122°15'E). On the northern coast it has been collected from as far east as Darwin (131°E). One fossil specimen of *B. desorii* is known: WAM 60.17, from River Cave, Lake Arramel; this is the Pleistocene Tamala Limestone. The specimens from the Aru Islands, Papua New Guinea described by Currie (1924) as *B. australasiae aroensis* appear to be indistinguishable from *B. desorii.* They are said to be Pliocene in age (Currie 1924: 66).

Information with specimens in the Western Australian Museum collection records *B. desorii* as having been collected only from a sandy substrate. One specimen is recorded as having been found buried in sand 8 cm below the sediment/water interface. The species has been collected from water depths as great as 140 m and in intermediate depths to intertidal sandflats.

Remarks

Gray (1851, 1855) distinguished *B. desorii* from *B. australasiae* principally on the basis of the greater number of primary tubercles; he also noted the elongate, narrow nature of the internal fasciole. Following Agassiz (1872), H.L. Clark (1914, 1917, 1938, 1946), amongst others, placed *B. desorii* in synonymy with *B. australasiae* as he considered the greater number of primary tubercles to be insufficient basis on which to distinguish the western form as a separate species. The nature of the internal fasciole was not considered. Mortensen (1951) was the first worker to reinstate *B. desorii* on the basis of a number of characters. He believed that an important distinguishing character, noted also by James (1966), was the length of the labrum. He believed it extended posteriorly to the third adjoining ambulacral plate in *B. desorii,* but only to the second in *B. australasiae.* A.M. Clark and Rowe (1971) noted a marked variation in this character between species. Rather than the labrum reaching either the second or third ambulacral plate, depending on the species, it is more appropriate to note that, on the basis of examination of large samples, the labrum reaches the third ambulacral plate in *B. desorii* in about 80% of specimens and the second in 20%, whereas in *B. australasiae* the third plate is reached in about 60% of specimens and the second 40%.

Mortensen (1951) further distinguished *B. desorii* from *B. australasiae* on the basis of *B. desorii* possessing 8 pore pairs in each of the ambulacra within the subanal fasciole, whereas *B. australasiae* was said to have only 6. A.M. Clark and Rowe (1971) noted no more than 7 in the largest of the eleven Western Australian specimens of *B. desorii* which they studied; one had as few as 4. Examination of a large sample of adult specimens of *B. desorii* showed a range from 3 to 8, but generally there were 6 or 7. Frequently there will be more pore pairs in one ambulacrum than the other. In *B. australasiae* the number of pore pairs varies between 3 and 7, though generally there are 5 or 6.

The principal character noted by Gray, the greater number of primary tubercles in *B. desorii,* is particularly noticeable in large adults. Even small juveniles of *B. desorii* possess more primary tubercles than equivalent sized specimens of *B. australasiae* (Figure 8); rate of production of tubercles is greater in *B. desorii* than in *B. australasiae.*

B. desorii can further be distinguished from *B. australasiae* on its possession of longer petals, both anterior and posterior (Figures 1, 3), though there is little difference in number of pore pairs; a tendency for a slightly deeper anterior peripetalous fasciole extending closer to the ambitus laterally and posteriorly; longer and generally narrower internal fasciole (Figures 6, 7); narrower peristome (Figure 5); and smaller periproct.

Breynia neanika sp. nov.

Figures 12, 13

Holotype

AM J14324; adult ?female; dry test with some spines preserved; collected from the Arafura Sea on the CSIRO *Soela* Cruise on 14.11.80 at Station S07/80/35 (10°29'S, 132°01'E) at a depth of 80-82 m by J. Paxton.

Paratypes

AM J14325, from the Arafura Sea; collected on the CSIRO *Soela* Cruise at Station S07/80/43 (10°13'S, 133°58'E) at a depth of 72 m; AM J14326a-d, from the Arafura Sea; collected on the CSIRO *Soela* Cruise at Station S07/80/34 (10°27'S, 132°01'E).

Other Material

AM J5295, J5296 from Albany Passage, Torres Strait (10°44-47'S, 142°36-39'E), 'from 9-12 fathoms on gravelly bank'; AM J9993, from 14°24'S, 144°48'E (about 18 km ESE of Barrow Point, Queensland) at a depth of '10 m from mud with *Halimeda* and *Gracilaria*'; AM G7448, from Bowen, Queensland; BM 1881.11.23.29 from Torres Strait, collected on the *Challenger* expedition.

Diagnosis

Test flattened aborally; bears few primary tubercles, no more than 9 tubercles in interambulacra 2 and 3, and 16 in interambulacra 1 and 4. Apical system almost central. Peripetalous fasciole set far from ambitus laterally and posteriorly; internal fasciole short and narrow. Posterior petals short, same length as short anterior petals. Peristome narrow and only slightly sunken; plastron and subanal fasciole narrow; ambulacra I and V broad adorally. No more than 5 subanal pore pairs.

Description

Test reaches a maximum known length of 92 mm; widest at, or slightly posterior, to mid-test length, width generally varying between 80 and 85% TL; 91% in one specimen. Aborally surface of test flattened, but inclined gently anteriorly; highest posterior of apical system; height 44-58% TL. Test has broad, shallow anterior notch; posterior of test almost vertical. Apical system almost flush with surface of test and situated slightly anterior of mid-test length; in form like that of *B. australasiae* and *B. desorii.*

Ambulacrum III aborally very shallow, deepening slightly anteriorly; about 20 widely spaced, very small pore pairs aligned exsagittally; abaxially ambulacral plates bear few larger tubercles. Anterior petals with rows widely spaced adapically, converging abapically; anterior rows not transverse, but anteriorly divergent at 150-160°; posterior rows diverge at 90° initially, then half petal length at 110-120°; width across petals short (Figure 9), 46-54% TL; 9-12 pore pairs in anterior row, 14-16 in posterior row; pore pairs conjugate and deeply sunken. Posterior petals short, same length as anterior petals; converge anteriorly at about 50°; 15-16 pore pairs in outer row, 13-15 in inner row.

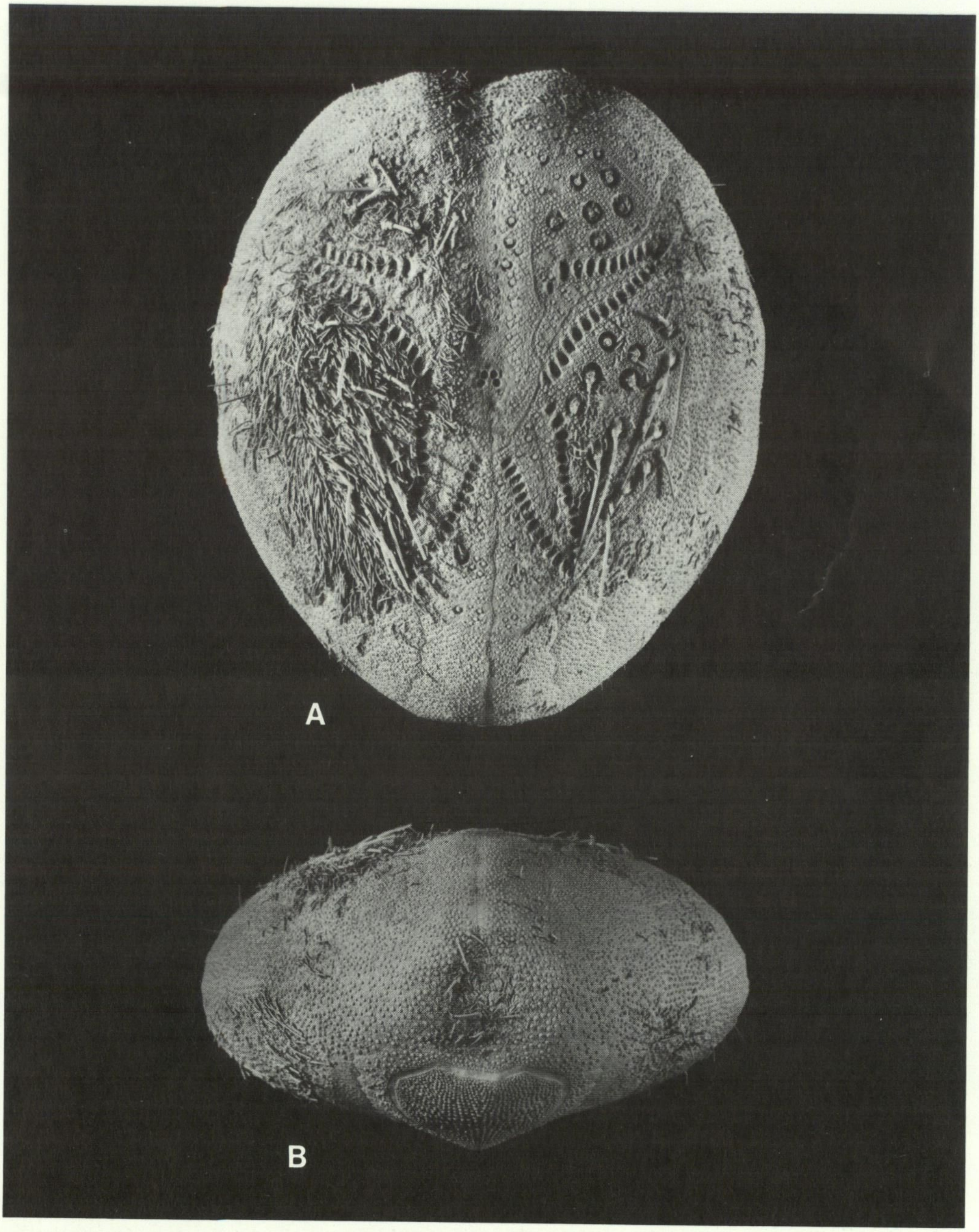

Figure 12 *Breynia neanika* sp. nov.; AM J14324, holotype from the Arafura Sea at 10°29′S, 132°01′E. (A) aboral view; (B) posterior view; both x 1.

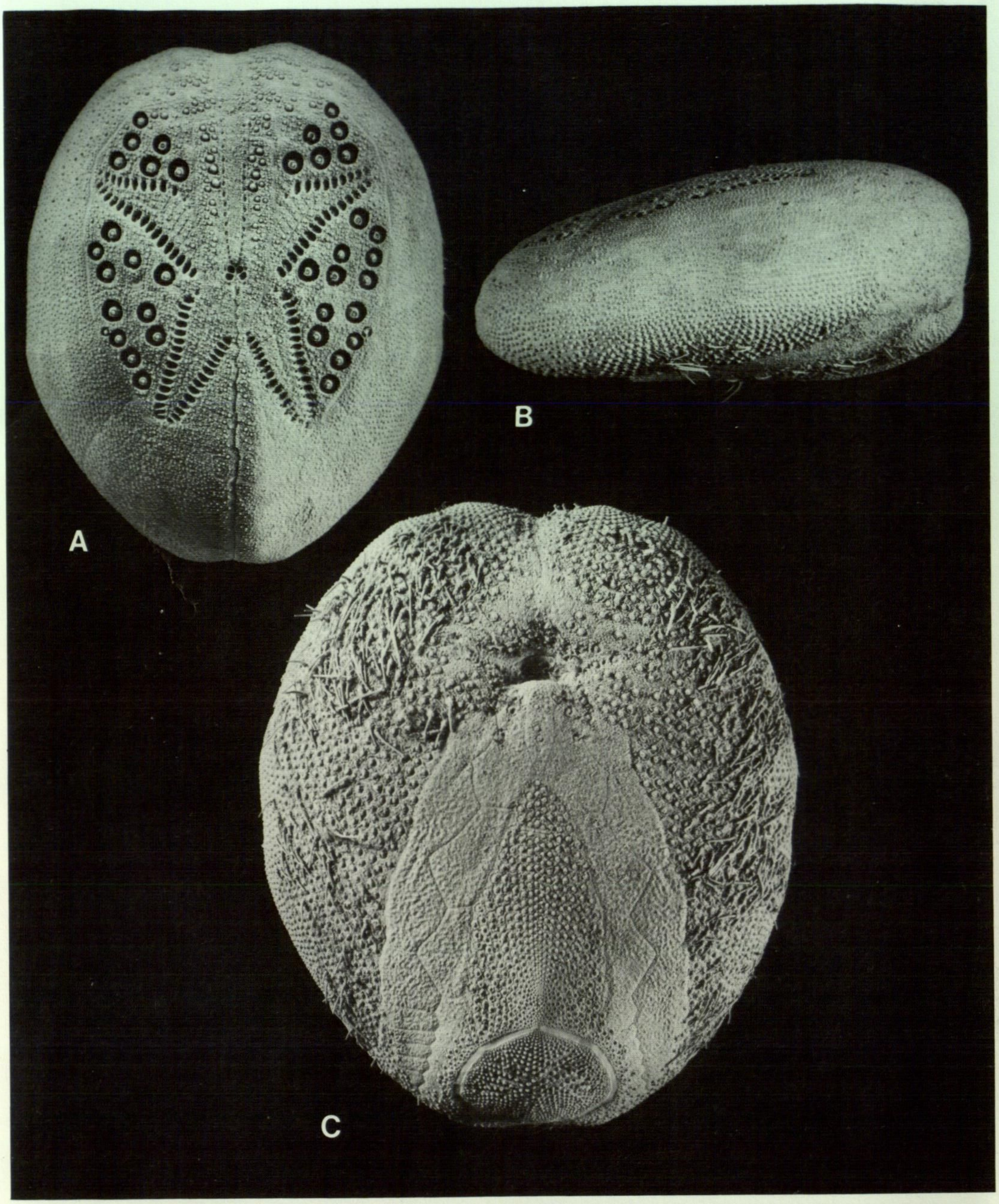

Figure 13 *Breynia neanika* sp. nov.; (A, B) AM J5295, from Albany Passage, Queensland; (A) aboral view; (B) lateral view. (C) AM J14324, holotype, from the Arafura Sea at 10°29′S, 132°01′E, adoral view; both specimens x 1.

Within peripetalous fasciole interambulacra 1 and 4 bear 9-16 primary tubercles; interambulacra 2 and 3 bear 3-9. In holotype and one other specimen (AM J5296) there is one primary tubercle in interambulacrum 5. Peripetalous fasciole is 20% TL from ambitus posteriorly; does not extend to ambitus laterally, passing across plate 7 of interambulacra 1 and 4; anteriorly in interambulacra 2 and 3 fasciole turns through almost a right angle and runs adambitally for a short distance before turning adaxially to run close to ambitus across anterior of test. In many specimens a branch of fasciole extends line of lateral course of fasciole to run across ambulacrum III 15% TL posterior of anterior ambitus. Internal fasciole short (Figure 6) occupying 37-44% TL, and narrow (Figure 7), width being 12-15% TL across apical system; gradually broadens anteriorly.

Peristome semicircular and only slightly sunken; narrow (Figure 5), 9-13% TL. Eight unipores in phyllode in ambulacra II and IV; 6-7 in ambulacra I and V and 5 in ambulacrum III. Labrum long, 14% TL; does not project anteriorly; posteriorly extends to third ambulacral plate; tapers posteriorly. Plastron narrow, posteriorly being 35% TL; subanal fasciole also narrow, 28-30% TL; triangular to suboval; encloses up to 5 pore pairs in each ambulacrum. Ambulacra I and V flat and broad, width 16-17% TL. Periproct longitudinally oval, 12-15% TL. Test between periproct and subanal fasciole almost flat. Adoral interambulacral tuberculation relatively sparsely distributed.

Remarks

B. neanika differs from *B. australasiae* and *B. desorii* in the possession of a flatter test, the posterior of which is more vertically orientated; shorter petals, which are of equal length; anterior row of anterior petals being less transversely directed; more centrally situated apical system; peripetalous fasciole not as distally positioned laterally and posteriorly; less sunken peristome; broader ambulacra I and V adorally; narrower, more oval subanal fasciole; sparser adoral tuberculation; and fewer phyllode unipores. It can further be distinguished from *B. australasiae* by its narrower internal fasciole and narrower peristome; and from *B. desorii* by the possession of fewer primary tubercles, shorter internal fasciole, absence of anteriorly projecting labrum, and less sunken area between the periproct and subanal fasciole.

It can be distinguished from *B. elegans* Mortensen, 1948, by its possession of a less tapering test; fewer primary tubercles; broader and shorter petals; more centrally situated apical system; longer internal fasciole; and longer plastron. *B. neanika* has more primary tubercles than *B. vredenburgi* Anderson, 1907, which also has a flattened aboral test surface. On the basis of data provided by James (1966), *B. neanika* would also appear to differ from *B. vredenburgi* in its possession of more poriferous petals; more oval periproct and narrower internal fasciole.

James' (1966) key for the separation of species of *Breynia* was based solely on the relationship between the position of the posterior of the labrum with respect to the adjoining ambulacral plate. It has been shown (above) that, contrary to the opinion of Mortensen (1951), there is little difference between *B. australasiae*, *B. desorii* and *B. neanika* in this highly variable character. The revised key, presented above, is based on a combination of other characters.

Etymology

Neanikos (Gr.): youthful, alluding to the possession of adult characters which occur in the juveniles of other Australian species of *Breynia.*

Phylogenetic Relationships

Many of the morphological characters which vary within populations, and which differentiate the three living Australian species of *Breynia,* are characters which undergo appreciable change during the ontogeny of the species, as their growth is allometric. The principal ontogenetic changes observed in both *B. desorii* and *B. australasiae* can be summarized as: a narrowing of the test; a relative anterior movement of the apical system; an increase in petal length and resultant abapical shift of the peripetalous fasciole toward the ambitus; an increasingly transverse orientation of the anterior row of the anterior petals; a narrowing and lengthening of the internal fasciole; an increase in the number of primary tubercles; a relative decrease in size of the peristome and periproct; development of a more deeply sunken peristome; a decrease in width of adoral ambulacrum I and V; and an increase in the number of subanal pore pairs.

B. desorii undergoes greater morphological changes in the majority of these characters during ontogeny than the other Australian species. *B. australasiae* undergoes less morphological change than *B. desorii* during ontogeny but more than *B. neanika,* which thus retains in its late adult form characters which occur only in juveniles and small adults of the other two species (paedomorphosis).

The rate of anterior movement of the apical system is similar in both *B. desorii* and *B. australasiae,* but in *B. neanika* it shows less anterior movement and remains in a more central position, like juveniles of the other two species. Both anterior and posterior petals lengthen more through ontogeny in *B. desorii* than in *B. australasiae,* which in turn has petals which lengthen more than those of *B. neanika.* Like juvenile *B. desorii* the petals of adult *B. neanika* are of similar length; the posterior becomes longer in adults of the other two species. As a consequence the peripetalous fasciole migrates out toward the ambitus most in *B. desorii* and least in *B. neanika.* This results in adults of *B. desorii* possessing larger interambulacral areas between the internal and peripetalous fascioles, so enabling a greater number of primary tubercles to be generated in *B. desorii* than in the other two species.

The anterior rows of the anterior petals change orientation during growth in *B. desorii,* from being anteriorly divergent at 120° in juveniles to almost transverse in adults. The change in orientation, which occurs as the petals lengthen, is least pronounced in *B. neanika,* the adults of which have anterior rows divergent at 150-160°.

The internal fasciole changes from being short and broad in juveniles of *B. desorii,* to long and generally narrow in the adult; in *B. australasiae* this fasciole remains broad and short, whilst in *B. neanika* it remains relatively short, but does become narrower. The peristome, which relatively decreases in size during ontogeny in proportion to the whole test, decreases at a less pronounced rate in *B. australasiae* than in *B. desorii.* Consequently adults of *B. australasiae* have a relatively larger peristome. Whereas *B. neanika* generally retains the most juvenile characters, it has a relatively small peristome, like *B. desorii.* This illustrates the potential for development of large numbers of morphotypes from a *B. desorii*-type ancestor, as decreased rates of morphological development may operate on different combinations of characters. Adults of *B. neanika* do, however, like the juvenile *B. desorii,* retain only a slightly sunken peristome in the adult. As with the peristome, the periproct also undergoes an appreciable decrease in relative size through ontogeny in *B. desorii.* This change is less pronounced in *B. australasiae,* which consequently possesses a larger adult periproct. *B. neanika* also has a relatively larger periproct than adult *B. desorii.* The adoral ambulacra I and V are very wide in juvenile *B. desorii.* They decrease in relative width through growth in *B. desorii* and *B. australasiae*; the ambulacral plates also become tumid with growth. *B. neanika* retains the juvenile flat, relatively broad ambulacral plates into the adult. Another juvenile character retained by *B. neanika* is the possession of sparsely distributed adoral tubercles.

The number of subanal pore pairs in each ambulacrum progressively increases during juvenile growth in *B. desorii* to the adult complement of 6-7. *B. australasiae* generates only 5-6, whilst *B. neanika* has no more than 5.

Consequently, speciation in *Breynia* may be considered to have occurred by selection of paedomorphic forms. *B. australasiae* evolved by selection of an extreme paedomorph of *B. desorii* which possessed a morphology which was sufficiently different from the ancestral *B. desorii* morphology to allow ecological and, subsequently, genetic isolation.

It is clear that the adaptive threshold which must be crossed in order for speciation to occur has not been reached by the Shark Bay population of *B. desorii.* Like *B. australasiae* there has been a reduced rate of morphological development of some characters, compared with the more normal populations of *B. desorii.* Fewer characters have changed in the Shark Bay population than in *B. australasiae,* however, and they are insufficient to allow ecological separation of this morphotype from the ancestral *B. desorii* morphotype.

B. neanika is neotenic with respect to *B. australasiae,* from which it is considered to have evolved by the same process as *B. australasiae* evolved from *B. desorii.* By showing increasing degrees of paedomorphosis, from the apaedomorph, *B. desorii,* though *B. australasiae,* to the most paedomorphic, *B. neanika,* the three species form a paedomorphocline (McNamara 1982*b*) (Figure 15).

Fossil species of *Breynia* have never been found in the Miocene deposits of southern Australia (principally the Murray River in South Australia and the Nullarbor in Western Australia). Neither, it would seem, was it present in south-west Australia during the Pliocene as no specimens have ever been recorded from the richly fossiliferous Roe Calcarenite, despite intensive collecting in recent years. The presence of *B. desorii* along the western part of the south coast at the present day suggests it is a relatively recent immigrant.

In addition to the occurrence of Miocene and Pliocene species of *Breynia* in the western Sind and Kachh regions of Pakistan, in Taiwan, Japan and Java, it also occurs in the Middle Miocene of north-west Australia (McNamara in prep.). Modern distribution suggests a migration from this general Indo-West Pacific region eastwards to encompass western, northern and eastern Australian coasts.

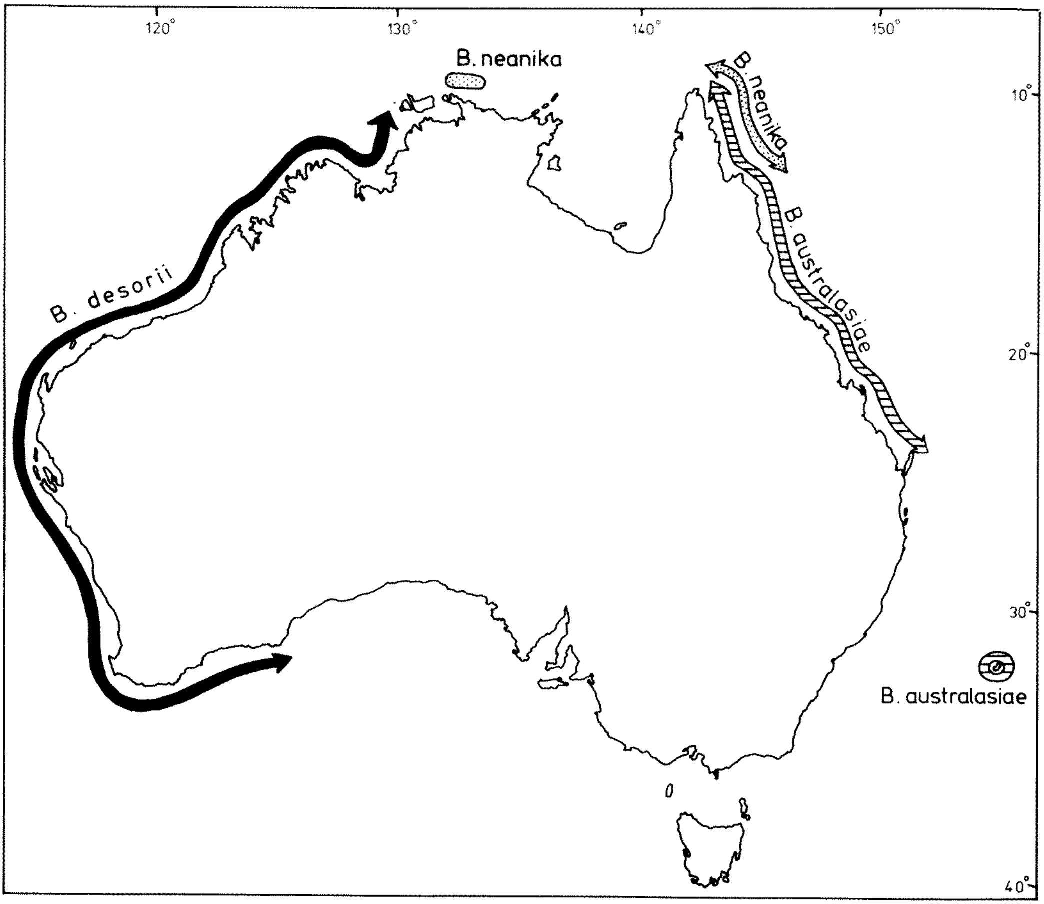

Figure 14 Map showing known distribution of species of *Breynia* around Australia.

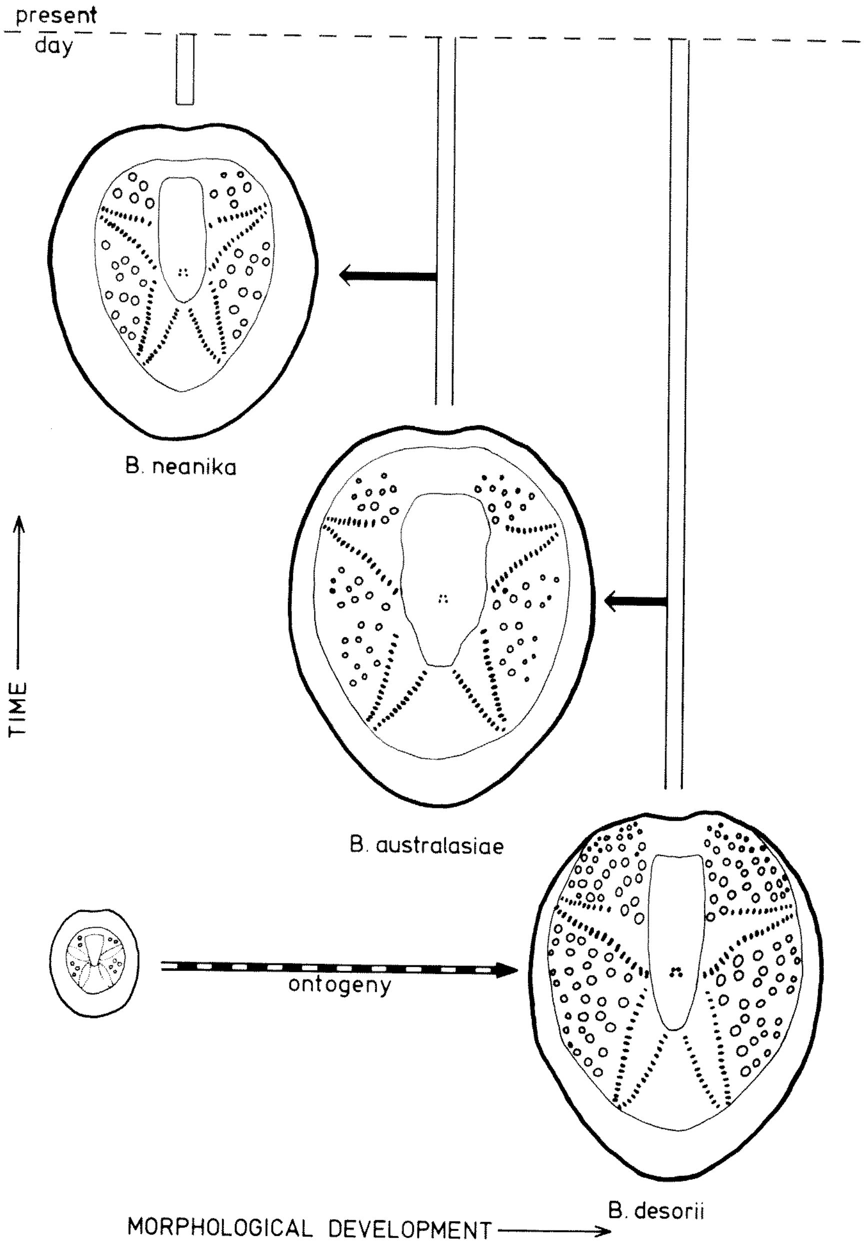

Figure 15 Suggested phylogeny of Australian species of *Breynia*. The three species form a paedomorphocline. *B. australasiae* is thought to have evolved pre-Late Pleistocene, and *B. neanika* post-Late Pleistocene. Reconstructions are x ½, except for juvenile *B. desorii* which is x 1½.

Outside of the Australian region the genus is now rare, being known only from the Kei Islands (*B. elegans*) and Andaman Island (3 specimens of *B. vredenburgi*).

The absence of *Breynia* from both the fossil and living records from much of southern Australia, suggests derivation of the eastern Australian species, *B. australasiae* and *B. neanika,* along the northern coast from species to the west. This is in keeping with the suggested paedomorphic derivation of these species from the western Australian *B. desorii.* The localized, uncommon occurrence of the paedomorphic *B. neanika* in north-east Australia (where it occurs with *B. australasiae*) and in the Arafura Sea, is consistent with a suggested development by paedomorphosis from the morphologically closest species, *B. australasiae,* perhaps in relatively recent times. The geographic spread of *B. neanika* east and west of Torres Strait, which was emergent between 80 000 and 8 000 years ago (Jennings 1972; Chappell 1976), suggests evolution of the species may have occurred after that time. Genetic isolation of *B. australasiae* in the east (it is not known west of Torres Strait) from *B. desorii* in the west, may have been facilitated by the long periods of emergence of Torres Strait during periods of Pleistocene glaciation.

Acknowledgements

I would like to thank G.M. Philip for making specimens freely available to me and for reading the manuscript; F.W.E. Rowe (Australian Museum), L. Marsh (Western Australian Museum, and A. Clark (British Museum, Natural History) for loan of specimens; L. Cannon (Queensland Museum) for supplying photographs of specimens; V.A. Ryland for photography and E. Ioannidis for typing the manuscript.

References

Agassiz, A. (1872-1874). Revision of the Echini. *Mem. Mus. comp. Zool. Harv.* 3: 383-762.

Alexander, W.B. (1914). Western Australian echinoderms. *Rec. West. Aust. Mus.* 1 (3): 105-112.

Chappell, J.M.A. (1976). Aspects of late Quaternary palaeogeography of the Australian-East Indonesian region. In: *The Origins of the Australians* (Ed. R.L. Kirk and A.G. Thorne): 11-22. (Humanities Press: New Jersey).

Clark, A.M. and Rowe, F.W.E. (1971). *Monograph of shallow water Indo-West Pacific echinoderms.* (British Museum [Nat. Hist.] : London).

Clark, H.L. (1914). The echinoderms of the Western Australian Museum. *Rec. West. Aust. Mus.* 1 (3): 132-173.

Clark, H.L. (1917). Hawaiian and other Pacific Echini. Spatangina. *Mem. Mus. comp. Zool. Harv.* 46 (2): 81-283.

Clark, H.L. (1925). *A catalogue of the recent sea urchins (Echinoidea) in the collection of the British Museum (Natural History).* (British Museum [Nat. Hist.] : London).

Clark, H.L. (1938). Echinoderms from Australia. *Mem. Mus. comp. Zool. Harv.* 55: 1-597.

Clark, H.L. (1946). The echinoderm fauna of Australia. Its composition and its origin. *Publ Carneg. Inst.* 566: 1-567.

Currie, E.D. (1924). On fossil Echinoidea from the Aru Islands. *Geol. Mag.* 61: 63-72.

Endean, R. (1961). Queensland faunistic records. Part VII. Additional records of Echinodermata (excluding Crinoidea). *Pap. Dep. Zool. Univ. Qld* 1 (13): 289-298.

Gerth, H. (1922). Echinoidea. *In:* Die fossilien von Java, K. Martin. *Samml. geol. Reichsmus. Leiden* 2 (4): 497-520.

Gray, J.E. (1851). Description of some new genera and species of Spatangidae in the British Museum. *Ann. Mag. nat. Hist. ser. 2,* 7: 130-134.

Gray, J.E. (1855). *Catalogue of the Recent Echinida, or sea eggs, in the collection of the British Museum.* Part 1 – *Echinida Irregularia.* (British Museum [Nat. Hist.] : London).

James, D.B. (1966). Studies on Indian echinoderms – 1. Rediscovery of the echinoid, *Breynia vredenburgi* Anderson from Andaman Sea, with an emended description. *J. Mar. biol. Ass. India* 8: 76-81.

Jennings, J.N. (1972). Some attributes of Torres Strait. In: *Bridge and barrier: the natural and cultural history of Torres Strait* (Ed. D. Walker): 29-38. (ANU Press: Canberra).

Leach, W.E. (1815). *The zoological miscellany; being descriptions of new, or interesting animals.* Vol. II. (Nodder: London).

McNamara, K.J. (1982*a*). A new species of the echinoid *Rhynobrissus* (Spatangoida: Brissidae) from north-west Australia. *Rec. West. Aust. Mus.* 9 (4): 349-360.

McNamara, K.J. (1982*b*). Heterochrony and phylogenetic trends. *Paleobiology* 8: 130-142.

McNamara, K.J. and Philip, G.M. (1980). Living Australian schizasterid echinoids. *Proc. Linn. Soc. N.S.W.* 104: 127-146.

Mortensen, T. (1918). Echinoidea of Dr Mjöberg's expedition to Australia. *K. svenska Vetensk. – Akad. Handl. Stockholm* 58 (9): 1-22.

Mortensen, T. (1951). *A monograph of the Echinoidea* 5 (2), *Spatangoidea* II. (Reitzel: Copenhagen).

Studer, T. (1881). Übersicht uber die wahrend der Reise SMS 'Gazelle' um die Erde. *Mber, K. preuss. Akad. Wiss.* 1880: 861-885.

Tenison Woods, J.E. (1878). The echini of Australia. *Proc. Linn. Soc. N.S.W.* 2: 145-176.

Received 29 January 1982 Accepted 15 June 1982 Published 13 December 1982