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The spatangoid echinoid *Schizaster (Schizaster) compactus* (Koehler, 1914) in Western Australia

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Abstract – The spatangoid echinoid *Schizaster (Schizaster) compactus* (Koehler, 1914) is recorded from Australian waters for the first time. A sample consisting of a juvenile and adults collected from off the Dampier Archipelago, Western Australia is shown to undergo significant ontogenetic variation in a number of parameters, notably number of pore pairs in all aboral ambulacra; relative size and shape of the peristome and periproct; relative width of ambulacrum III aborally; and relative length of the posterior petals. A number of morphological characters also show appreciable intraspecific variation, in particular the number of gonopores; position of the peristome; the width of the plastron; test width; and position of the apical system. An understanding of the degree of phenotypic variation in this species aids in the delimitation of species of *Schizaster* and in the characterisation of the taxa *Schizaster* and *Paraster*.

INTRODUCTION

On July 27, 1982 a number of large steel pipes destined for the North-West Shelf Gas Project was inadvertently sunk in about 45 m of water north of Dampier, Western Australia at 20°19'33.1"S, 116°33'22.11"E. Nearly 10 months later, on May 18, 1983, the pipes were recovered. They were found to be packed with soft, foraminiferal-rich silt, within which were living five species of spatangoids. In addition to 33 complete and broken specimens of a species of *Schizaster*, single specimens of *Moira lethe* Mortensen, 1930; *Metalia sternalis* (Lamarck, 1816); and *Lovenia elongata* (Gray, 1845) were found in the silt, along with three specimens of an undescribed species of *Metalia*.

The species of *Schizaster* (Figure 1) is identical to a single specimen described by McNamara and Philip (1980a) from Rosemary Island in the Dampier Archipelago, and referred by them to *Schizaster (Schizaster) lacunosus* (Linnaeus, 1758). Examination of the larger population has revealed the species to be conspecific with a form described by Koehler (1914) from the Bay of Bengal and called by him *Paraster compactus*. However, in one character the Western Australian form differs from the features described by Koehler, and that is in the number of gonopores. Koehler's description was based on only two specimens. This difference is not considered to be of sufficient importance to warrant placing the Australian form in a separate species, as other species of *Schizaster* have been shown to possess variable numbers of gonopores (McNamara and Philip 1980a).

In addition to describing this species from the eastern side of the Indian Ocean for the first time, the aim of this paper is to demonstrate not only the variability in the number of gonopores within a single, presumably genetically homogeneous, population. This feature has been used as a generic or subgeneric character within schizasterids. In this paper characters other than gonopore number are used to differentiate the three subgenera of *Schizaster* (*Schizaster*, *Paraster* and *Ova*) and revised diagnoses of these subgenera given. This paper also aims to illustrate the extent of morphological variation present in other characters throughout ontogeny. Phenotypic variation encompasses not simply the morphological differences between adults within a population, but also differences that occur through the ontogenetic development. After all, the adult phenotype is a product of the morphological variation that the individual undergoes throughout its ontogeny.

It is particularly important to determine the degree of morphological variation present within species of *Schizaster* in order to delineate fossil taxa effectively. In the past many species have been described, particularly last century, on the basis of few specimens (Koehler's *Paraster compactus* being a case in point). Consequently, Lambert and Thiéry (1925) and Kier and Lawson (1978) recorded that up until 1970, 275 species of *Schizaster* and *Paraster* had been described. Categorising the degree of intraspecific morphological variation within this northwestern Australian species of *Schizaster* will therefore provide a useful tool to further studies aimed at clarifying the number of species of *Schizaster*.

The other aspect of this study is to document the ontogenetic development of the species, as both juvenile and adult specimens are present within the population that was collected. McNamara and Philip (1980a) documented a number of ontogenetic changes in another Australian species, *Schizaster (Ova) myorensis*. Defining the characters that undergo morphological change during ontogeny in the northwestern Australian species of *Schizaster* will assist in determining the universality of ontogenetic change in suites of characters within the genus *Schizaster* and so aid the elucidation of the phylogenetic history of the genus.

MATERIALS AND METHODS

Measurements were carried out on 26 specimens. These are registered in the collections of the Western Australian Museum under the numbers 132–93 to 135–93. Measurements were made using electronic callipers to an accuracy of 0.1 mm. Measurements were made of test length; maximum test width; maximum test height; centre of apical system to anterior ambitus; width of aboral ambulacrum III; length and width of anterior petals; length and width of posterior petals; width and length of peristome; width and length of periproct; length from anterior of peristome to anterior ambitus; maximum width of plastron. Furthermore, counts were made of the number of gonopores and number of pore pairs in ambulacra I, II and III aborally. For the purposes of ascertaining the number of gonopores present in the species 27 specimens were studied.

SYSTEMATIC PALAEONTOLOGY

Order Spatangoida Claus, 1876

Family Schizasteridae Lambert, 1905

Genus *Schizaster* L. Agassiz, 1836

Type species

Schizaster studeri L. Agassiz 1836, by subsequent designation of the Thirteenth International Congress of Zoology in Paris; opinion 209, 1954.

Subgenus *Schizaster* L. Agassiz, 1836

Emended diagnosis

Moderate to deeply incised ambulacrum III aborally, in which pore pairs are numerous (more than 15 in each row), occur in regular, single series and are aligned transversely, or only slightly obliquely.

Remarks

In his description of the fossil spatangoid echinoids of Cuba, Kier (1984) addressed the question of the validity of the taxon *Paraster*. Traditionally, *Schizaster* and *Paraster* had been distinguished on the basis of the number of genital pores, *Paraster* having four, *Schizaster* having two (Mortensen 1951). The two taxa had either been regarded as being of separate generic status (Mortensen 1951; Chesher 1966, 1972; Kier 1975) or only subgeneric status (Kier 1957; Henderson 1975) on the basis of this character.

With the discovery that within a single population of *Schizaster (Ova) myorensis* the number of genital pores may vary between two, three and four (McNamara and Philip 1980b), other criteria were employed to distinguish *Paraster* from *Schizaster*. McNamara and Philip (1980a,b) regarded the two as subgenera and characterised *Paraster* as having a more shallow ambulacrum III than *Schizaster*, with fewer, oblique pore pairs; a more circular test; more central apical system; and straighter, more divergent anterior petals. They noted, however, that the two subgenera lie at either end of a morphological continuum, and that some species are therefore likely to be transitional between the two subgenera.

In their analysis of the evolution of the Australian species of *Schizaster* (s.l.) in the Tertiary, McNamara and Philip (1980b) noted that those species with the *Paraster* morphology were restricted to coarser sediments than those species with the *Schizaster* (s.s) morphology. They suggested that this indicated evolution of the finer-grained sediment dwelling *Schizaster* (s.s.) morphotype from the coarser-grained sediment inhabiting *Paraster* morphotype. A similar evolutionary trend has been observed in the genus in the Pyrennees (J. Villatte, pers. comm.). Although both the Australian living and fossil species of *Schizaster* (s.l.) can be accommodated comfortably within the two subgenera *Schizaster* and *Paraster* on the basis of characters suggested by McNamara and Philip (1980a,b), Kier (1984) was unable to separate all of the 16 Cuban species of *Schizaster* (s.l.) into the subgenera *Schizaster* and *Paraster*.

However, it may be possible to subdivide *Schizaster* (s.l.) on the basis of the nature of ambulacrum III aborally, principally using a combination of the depth of ambulacrum III and the number and orientation of pore pairs. In those species with very shallow ambulacrum III, the number of pore pairs is much fewer than in those species with a deeper, broader ambulacrum III. Furthermore, the pore pairs are much more obliquely aligned, with the inner pore of each pair set much farther forward than the corresponding outer pore, such as in the sand-inhabiting *Paraster*

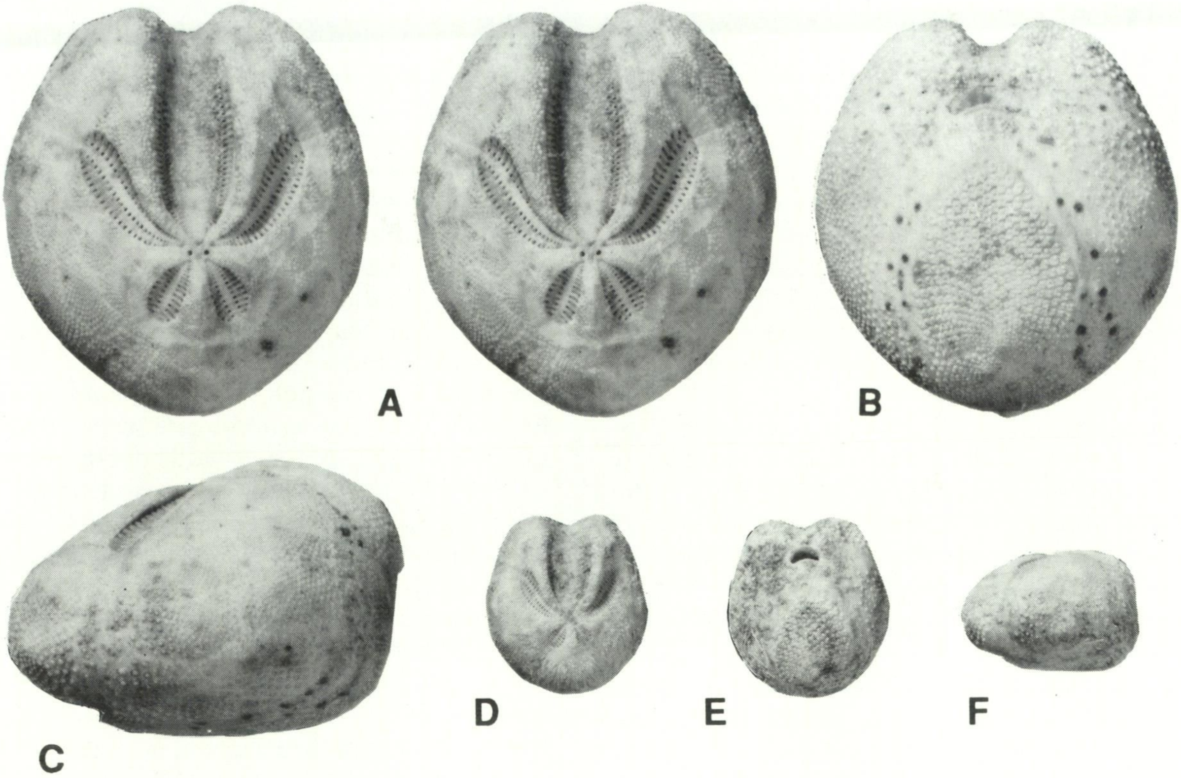

Figure 1 *Schizaster (Schizaster) compactus* (Koehler, 1914) from the Dampier Archipelago, Western Australia. WAM 133–93: A, aboral surface, stereo pair; B, adoral surface; C, lateral view. WAM 132–93, juvenile: D, aboral surface; E, adoral surface; F, lateral view. All x2.

floridiensis Kier and Grant 1965 (see also Chesher 1966). In *Schizaster* (s.s.) ambulacrum III is deeper, the pore pairs are more numerous (although in single rows) and aligned transversely, or nearly so (e.g., Mortensen 1951, p.301, figure 140; McNamara and Philip 1980a, figure 4D). Species with this morphology are known to be able to burrow in mud. Thus of the Cuban species of *Schizaster* recognised by Kier (1984), *S. camagueyensis, S. cubitabellae, S. fernandezi* and *S. subcylindricus* can all be assigned to the subgenus *Paraster*, as all have a shallow ambulacrum III with a relatively small number (less than 15) of obliquely aligned pore pairs, whereas *S. bathypetalus, S. delgadoi, S. egozcuei, S. gerthi, S. llagunoi, S. munozi, S. nuevitasensis, S. formelli, S. rojasi, S. sanctamariae* and *S. santanae*, with their greater number of transversely orientated pore pairs, can be accommodated within the subgenus *Schizaster*. It is worth noting that one of the principle characteristics of the type species of *Paraster, P. gibberulus*, is its possession of very obliquely arranged pore pairs in ambulacrum III aborally (Mortensen 1951, p.220, figure 104b), while in *S. studeri*, the type species of *Schizaster*, the pore pairs are closely spaced, transverse and numerous (Mortensen 1951, p.297, figure 136) .

Species of *Schizaster* in which the pore pairs are so crowded in ambulacrum III that they effectively form multiple rows (see McNamara and Philip 1980a, figure 5C), are classified as a third subgenus, *S. (Ova)*, as typified by forms such as *S. (Ova) myorensis* McNamara and Philip 1980a. Consequently a morphocline of increasing concentration of pore pairs in ambulacrum III aborally exists from *S. (Paraster)*, through *S. (Schizaster)* to *S. (Ova)* (Figure 2).

Schizaster (Schizaster) compactus (Koehler, 1914)
Figure 1

Paraster compactus Koehler, 1914: 180; Mortensen 1951: 221–223, plate 24, figures 3–8, plate 52, figures 1,3; Ghiold 1989: 117, 140.

Schizaster (Schizaster) lacunosus (Linnaeus): (pars) McNamara and Philip 1980a: 129–131, figure 1.

Schizaster (Schizaster) compactus (Koehler): McNamara and Kendrick 1994: 46.

Material Examined

Australia: Western Australia: WAM 1488–75, dredged from a depth of 4–5 m outside Norbill Bay, Rosemary Island, Dampier Archipelago; WAM 132–93 to 135–93, 33 complete and broken specimens from a depth of 45 m north of Dampier, at 20°19'33.1"S, 116°33'22.11"E.

Description

Test tumid (Figure 1A,C), reaching up to 33.5 mm TL; anterior notch moderately developed (Figure 1A,B); highest posteriorly in interambulacrum 5, just posterior of apical system, forming a prominent keel (Figure 1C); height 63–72%TL (mean 67.5;SD=2.6; n=23); wider than long, ranging between 87–97%TL (mean 91.7; SD=4.6; n=26). Position of apical system variable; posteriorly eccentric, 56–65%TL (mean 60.0; SD=2.4; n=25) from anterior ambitus; ethmolytic, with two to four genital pores (Figure 3) (see below).

Ambulacrum III relatively broad (Figure 4A), 18–25%TL (mean 20.8; SD=1.7; n=25); moderately deeply incised (Figure 1A), shallowing slightly near ambitus; bears up to 38 pore pairs; smallest with 18 (Figure 5C); within a pair each pore separated by raised interporal partition; pores almost transversely aligned in a pair, although becoming slightly oblique abapically. Anterior petals moderately deep; broad, width 9–13%TL (mean 11.1; SD=0.87; n=26); diverge anteriorly at about 80° (Figure 1); slightly flexed distally; relatively long, 33–42%TL (mean 36.3; SD=2.0; n=26); bear up to 31 pore pairs (Figure 5B); pores within each pair widely spaced, elongate, not conjugate. Posterior petals slightly shallower and much shorter than anterior pair (Figure 1A), length 12–21%TL (mean 17.5; SD=1.8; n=25); width 8–10%TL (mean 8.7; SD=0.67; n=25); bear up to 20 pore pairs in each row (Figure 5A). Peripetalous fasciole very broad (Figure 1A) and moderately indented between anterior and posterior petals. Lateroanal fasciole very thin.

Peristome lunate (Figure 1B), width 14–20%TL (mean 17.4; SD=1.6; n=24); slightly sunken; situated 16–24%TL (mean 19.0; SD=2.1; n=24) from anterior ambitus. Labrum narrow and long; anteriorly acuminate medially and projecting antero-ventrally (see McNamara and Philip 1980a, Figure 1D). Phyllode with unipores: 10 in ambulacra II and IV; 5 in ambulacrum III; 6 in ambualcra I and V. Periporal area slightly swollen around abambital unipores, but flat around adambital unipores. Plastron slightly convex; width 38–46%TL (mean 41.9; SD=2.1; n=23). Periproct ovate; length (Figure 6D) 13–21%TL (mean 16.3; SD=1.6; n=26); width (Figure 6C) 11–15%TL (mean 11.4; SD=0.92; n=26).

Ontogenetic Variation

The 26 specimens of *Schizaster compactus* range in test length from 12.1 mm to 33.5 mm (Figure 7). Mean length is 24.8 mm (SD=4.6). The smallest specimen has unopened gonopores and therefore can be considered to be a juvenile. Gonopores open between 12 mm and 17.7 mm, the next largest specimen being 17.7 mm in test length, having fully opened gonopores.

Of the characters measured on the aboral surface of the test, significant ontogenetic changes occur in the width of ambulacrum III, the length of the

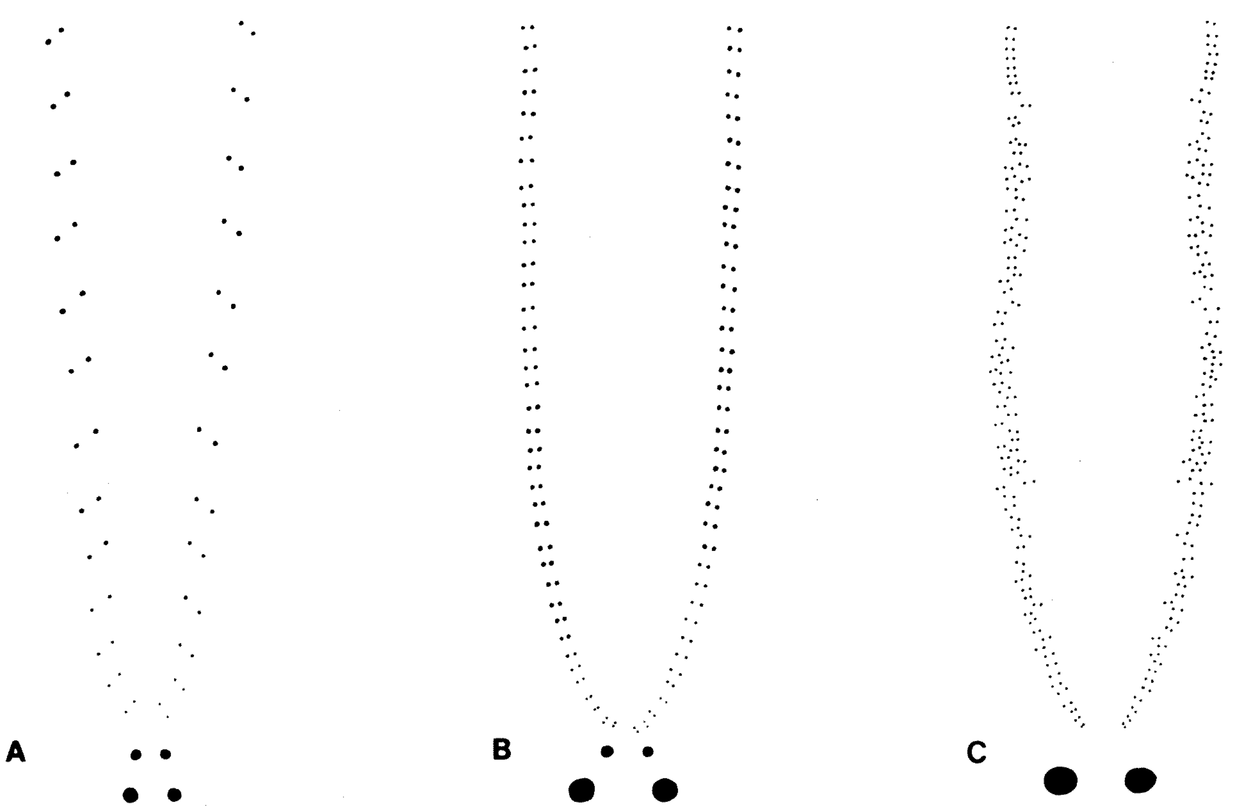

Figure 2 Arrangement of pore pairs in ambulacrum III aborally in the three subgenera of *Schizaster*: A, *S. (Paraster)*; B, *S. (Schizaster)*; C, *S. (Ova)*.

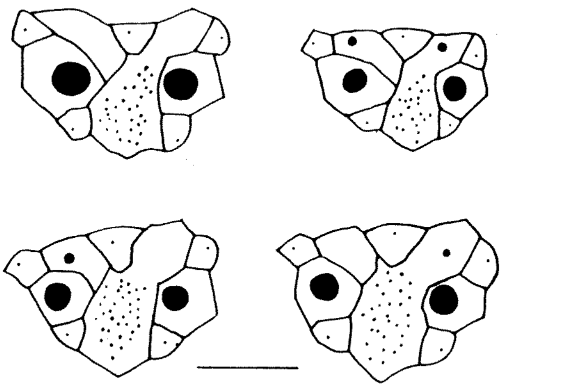

Figure 3 Variation in gonopore number in four adult specimens of *Schizaster (Schizaster) compactus* showing individuals with either two, three of four gonopores. In those specimens with three gonopores, the anterior gonopore may be either gonopore 2 or 3. Bar represents 1 mm.

posterior petals and the number of pore pairs in the ambulacra. As the test increases in size ambulacrum III becomes relatively narrower (Figure 4A), the width being 24.8%TL in the smallest specimen, decreasing to 18–19%TL in the largest specimens. A similar relative decrease in the width of ambulacrum III adorally was recorded in *Schizaster (Ova) myorensis* by McNamara and Philip (1980a, figure 6D). Ambulacrum III also shows a progressive increase in number of pore pairs throughout ontogeny, from 18 in each row in the smallest specimen to a maximum of 38 in the largest specimens (Figure 5C). However, this is not achieved by a lengthening of ambulacrum III and a posterior migration of the apical system, which is the situation in *Schizaster (Ova) myorensis*, rather the rate of pore pair production within the ambulacrum would have been greater during ontogeny.

Of the other ambulacral characters, the only other to show significant shape changes are the posterior petals, which show a slight relative increase in length (from about 14%TL to almost 20%TL) (Figure 4B). This length increase coincides with the increase in number of pore pairs from eight to an average of 17 in the largest specimens (Figure 5A). The anterior petals similarly show an increase in the number of pore pairs in each row, from 17 to 30 (Figure 5B). This persistent production of pore pairs throughout ontogeny also occurs in *S. (Ova) myorensis* (McNamara and Philip 1980a). Although there is a slight increase in length of the anterior petals during ontogeny, it is highly variable (see below). There appears to be no correlation between those individuals with longer anterior petals and a greater number of pore pairs. This implies that the pore pairs are relatively more closely packed in larger individuals. Petal width, position of the apical system, and test height and length all show little or no ontogenetic variation. This is in contrast to the situation in *S. (Ova) myorensis*, in which the test shape changes markedly during growth, becoming both relatively flatter and narrower (McNamara and Philip 1980a), and the apical system migrates posteriorly.

Mortensen (1951, p.222) observed that the three specimens of *S. (Schizaster) compactus* at his disposal, which were twice the size of Koehler's specimens, showed a more prominent development of the keel in interambulacrum 5 aborally. The Western Australian material similarly shows the adult specimens to have a more pronounced keel than the small juvenile (Figures 1C,F).

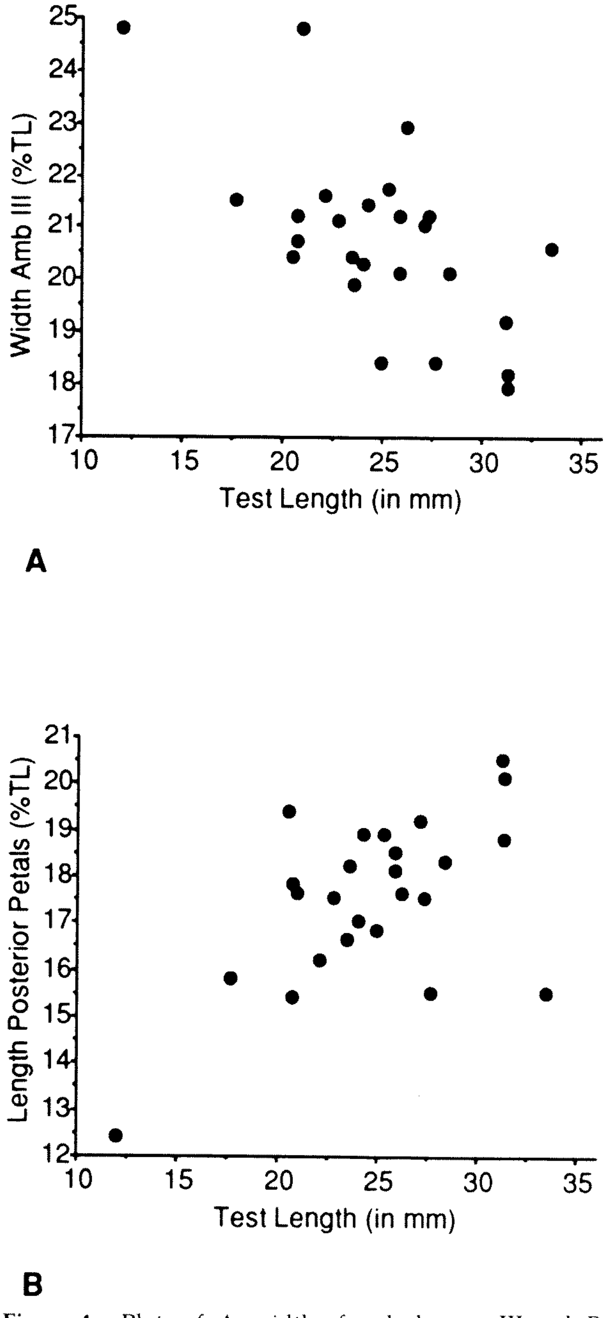

Figure 4 Plots of, A, width of ambulacrum III and, B, length of posterior petals, expressed as percentages of test length against test length for *Schizaster (Schizaster) compactus*.

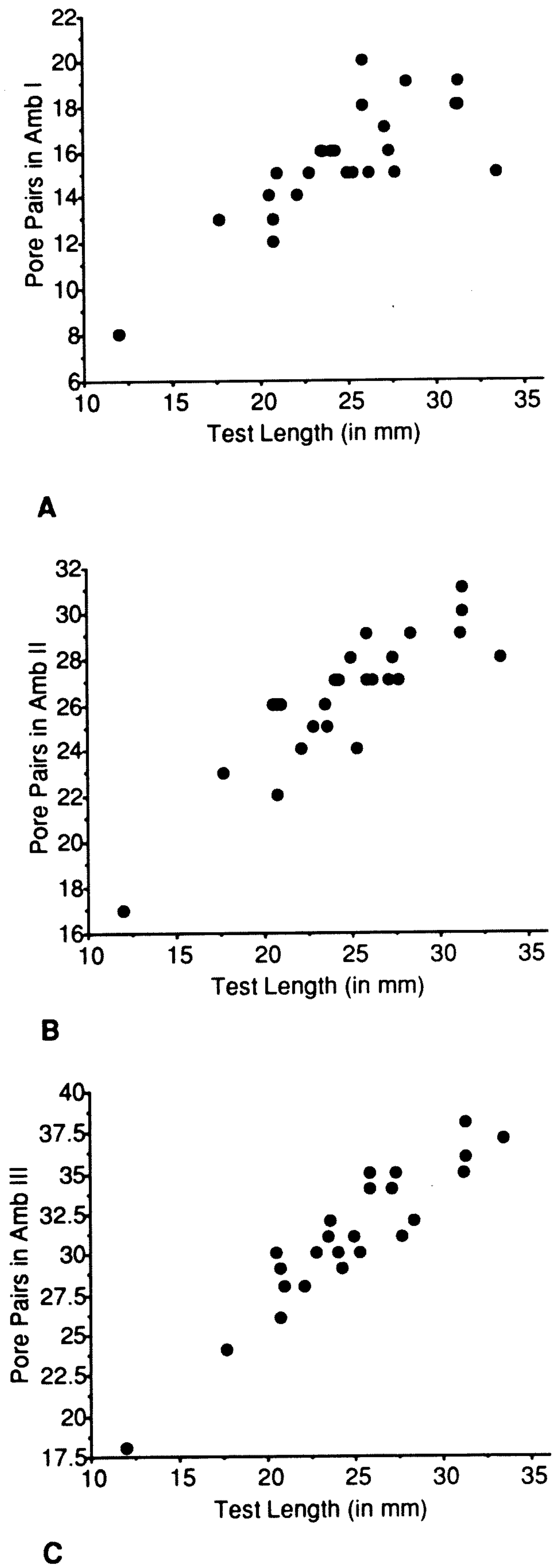

Figure 5 Plots of pore pairs in, A, ambulacrum I, B, ambulacrum II and, C, ambulacrum III aborally against test length for *Schizaster (Schizaster) compactus*.

On the adoral surface significant ontogenetic changes occur to the relative size and shape of the peristome and the periproct (Figure 6). The peristome becomes relatively smaller with growth, decreasing in width, from 20%TL to 16%TL (Figure 6A). Likewise, the peristome length (Figure 6B) decreases from 9%TL to a little over 4%TL. This relatively greater reduction in length, compared with width, arises, in part, from a relative increase in anterior growth of the labrum, which projects more across the peristome in larger specimens than in smaller ones (Figure 1). Unlike *S. (Ova) myorensis*, where the peristome becomes positioned relatively closer to the anterior ambitus through ontogeny, the peristome position in *S. (Schizaster) compactus* is highly variable (see below) and shows no such anterior trend. However, like *S. (Schizaster) compactus*, the peristome in *S. (Ova) myorensis* also becomes relatively smaller during ontogeny (McNamara and Philip 1980a).

The periproct likewise becomes relatively smaller during ontogeny. It is particularly wide in the juvenile specimen, being almost 15%TL, reducing during adult ontogeny from 12.5%TL to about 11%TL (Figure 6C). The slightly greater degree of reduction in relative length (Figure 6D), from 19%TL to 15%TL, compared with relative width, is reflected in a change in periproct shape, from subcircular to distinctly elongate. *S. (Ova) myorensis* similarly shows a decrease in periproct size during ontogeny. Other characters to undergo ontogenetic change are the anterior notch, which becomes relatively deeper and narrower (Figure 1), and the periplastronal area which becomes relatively narrower (Figure 1).

Intraspecific variation

The most notably variable character in *S. (Schizaster) compactus* is the number of gonopores, which vary between two and four (Figure 3). Of the 27 specimens used in this study that had fully opened gonopores, 8 had two, 4 had three, and 15 had four. Thus, while Koehler (1914) defined the species, in part, on its possession of four gonopores, the examination of a larger population size than the two specimens Koehler used in his description, shows that only 55.6% of specimens had, in fact, four gonopores. A further 29.6% had three and 14.8% two (Figure 8). It would be interesting if sufficient numbers of specimens from the type locality in the Bay of Bengal ever became available, to see if similar variation exists in topotype material. The relative percentages of specimens with two, three and four gonopores show quite a close correspondence with the situation in *S. (Ova) myorensis* (Figure 8), where 14.3% had two gonopores, 11.5% had three and 74.2% four.

There is no correlation between number of

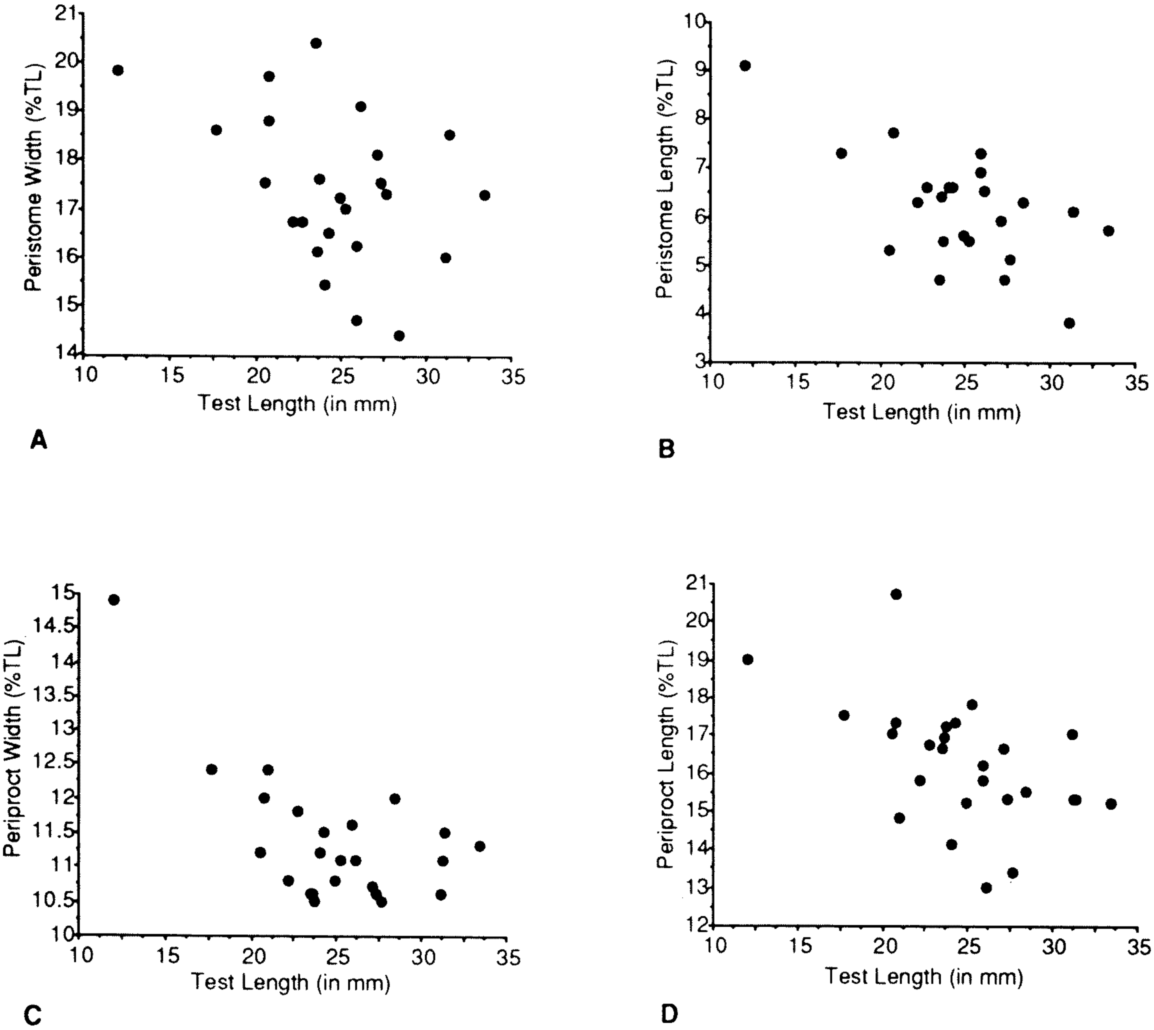

Figure 6 Plots of, A, peristome width, B, peristome length, C, periproct width and, D, periproct length, expressed as percentages of test length against test length for *Schizaster (Schizaster) compactus*.

gonopores and test size, the same proportion of large and small specimens having only two genital pores as have four gonopores. Of those that have three gonopores, the odd anterior pore may be either on the right side or the left side (that is, either gonopore 2 or 3). The anterior pair of pore pairs are consistently smaller than the posterior pair (Figure 6), a feature of the species noted by Mortensen (1951). They may be as large as about one third the diameter of the posterior gonopores, or as little as one tenth. The posterior pair open before the anterior pair and expand in area at a greater rate. The onset of opening of the anterior pair would seem to vary between individuals.

From a phylogenetic viewpoint these variations to the timing of opening of the anterior gonopores can be considered in a heterochronic context. The plesiomorphic condition within schizasterids is the possession of four open gonopores. In those individuals that produce only three, the delayed opening of the fourth gonopore occurs by postdisplacement, that is a delay in the time of opening of the gonopore (on the assumption that test size is providing a reasonably valid metric for time). In those individuals that produce only two gonopores, there is also postdisplacement of the other gonopore. The three states therefore lie along a paedomorphocline (*sensu* McNamara 1982, 1990)

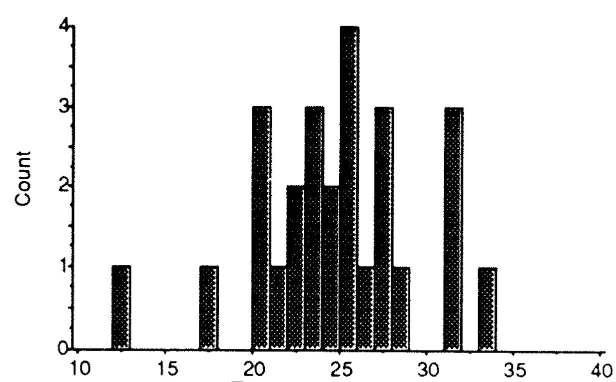

Figure 7 Histogram showing number of specimens in each 1 mm size class in the northwestern Australian population of *Schizaster (Schizaster) compactus*.

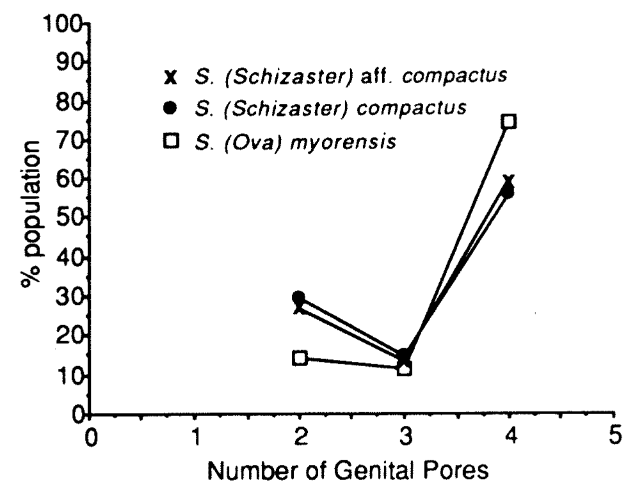

Figure 8 Similarity in percentage variation in gonopore number in the living species *Schizaster (Schizaster) compactus* and *Schizaster (Ova) myorensis* (data from McNamara and Philip 1980a), and the fossil species *Schizaster (Schizaster)* aff. *compactus* from the Middle Miocene Trealla Limestone, Gnargoo Range, Western Australia.

of four, three and two gonopores. This developmental flexibility in *S. (Schizaster) compactus* highlights the impracticality of using gonopore number as a generic or subgeneric diagnostic character. It may, however, serve as a useful character for the delineation of species, as the very flexible nature of the gonopore production may in itself be a species character.

The shape of the test shows a high degree of intraspecific variability. At mean test length, the test can vary in height between 64 and 72%TL (n=22). Similarly, the test width varies between 88 and 97%TL (n=24). *S. (Ova) myorensis* shows similar degrees of intraspecific variation in mature specimens (McNamara and Philip 1980a, figure 6A,B), but the ontogenetic variation that it displays does not occur in *S. (Schizaster) compactus.* On the aboral surface of the test the only character to show appreciable intraspecific variation is the position of the apical system. Specimens of mean test size show a variation in the distance of the apical system from the anterior ambitus of between 56 and 64%TL.

On the adoral surface the position of the peristome in relation to the anterior ambitus is highly variable, varying in mean specimens between 17 and 24%TL from the anterior ambitus. The maximum width of the plastron also shows a degree of variability, varying between 38 and 46%TL.

CONCLUSIONS

The ontogenetic development of *Schizaster (Schizaster) compactus* shows some similarities and some dissimilarities to the ontogeny of *Schizaster (Ova) myorensis*. Both species share a narrowing of ambulacrum III adorally, an increase in number of pore pairs in the aboral petals and ambulacrum III, and relative decrease in size of the peristome and periproct. Other changes seen in *S. (Ova) myorensis*, but not observed in *S. (Schizaster) compactus*, are changes in shape of the test, the posterior migration of the apical system and increase in petal sinuosity. The greater extent of morphological development during ontogeny in *S. (Ova) myorensis* occurs because, compared with *S. (Schizaster) compactus*, it is a more peramorphic species, lying further along the peramorphocline between the *"Paraster"* morphotype and *"Schizaster"* morphotype (McNamara and Philip 1980b). The morphological changes that are common in the ontogenies of the species reflect changes during growth associated with feeding (peristome and periproct size), funnel construction (ambulacrum III size and pore pair number) and respiration (pore pair number in the petals).

The presence of variable pore pairs numbers in these two Australian species suggests the possibility that if large populations of other species of *Schizaster* from other regions are examined, the same effect will be seen. It is unlikely to be a purely Australian phenomenon. Neither is it likely to be a feature restricted to extant species. Indeed, an examination of fourteen specimens of an undescribed species of *Schizaster* from the Middle Miocene Trealla Limestone of the Gnargoo Range in the Carnarvon Basin, Western Australia, referred to as *S. (Schizaster)* aff. *compactus* by McNamara and Kendrick (1994), shows a similar variation of individuals with either two, three or four genital pores. Moreover, there is a startlingly similar ratio between the two species, with the Miocene species having 28.6% of specimens with two gonopores (compared with 29.6% in *S. compactus*), 14.3% with three (compared with 14.6%) and 57.1% with four (compared with 55.6%).

It has been demonstrated elsewhere (McNamara 1988, 1989, 1990) how important heterochrony has been to the evolution of spatangoid echinoids, and to *Schizaster* in particular (McNamara and Philip 1980b). Heterochrony has been shown to be more important as an evolutionary mechanism in those species that show both high degrees of ontogenetic and adult morphological variation. Many characters in *S. (Schizaster) compactus* fulfil these two criteria. If, as seems likely from other studies of phenotypic variation in species of *Schizaster* (McNamara and Philip 1980a), suites of characters covary, then perturbations to the characters that undergo morphological change during ontogeny are likely to have been an important factor in the evolution of the large number of species of *Schizaster* during the Tertiary.

The characterisation of species of *Schizaster*, and of echinoid species in general, needs to take into account both ontogenetic and general adult variation. The ontogenetic variation arises either from differentiation of novel features during growth (such as pore pairs or tubercles) or from growth of particular structures, such as coronal plates (McNamara 1988). Allometric growth of particular plates, either positive or negative, characterise species, but small variations to the allometries are the factors that produce adult phenotypic variation. The degree of variation itself can be a feature that characterises a species. High degrees of variation certainly make it harder to characterise species, but it is vital that both ontogenetic and adult phenotypic variation be taken into account when characterising species, either living or fossil.

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