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Fasciole pathways in spatangoid echinoids: a new source of phylogenetically informative characters

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Fascioles are important early-forming structures that play a key role in allowing irregular echinoids to burrow. They have traditionally been grouped into a small number of types according to their general position on the test, but this masks some significant differences that exist. The precise course that fasciole bands follow over the test plating has been mapped in detail for 89 species of spatangoid echinoids, representing the great majority of fasciole-bearing genera both living and fossil. Within each fasciole type, discrete and conserved patterns can be distinguished, differing both in which plates they are initiated on, and on whether they cross plate growth centres or are late-stage bands positioned towards the edge of the plate. Fasciole position is most highly conserved in the anterior and lateral interambulacral plates and on the earliest forming bands. The existence of different subanal fasciole patterns in the Micrasteridae and Brissidae suggests that these may have evolved independently. Schizasterid and hemiasterine spatangoids can each be subdivided into two major clades, and brissid spatangoids into three clades based on detailed patterns of their fascioles. Plotting fasciole pathways over test architecture provides a rich new source of phylogenetically informative characters.

ADDITIONAL KEYWORDS: echinoderms – functional morphology – spines – taxonomy.

INTRODUCTION

Spatangoids are an immediately recognizable group of largely heart-shaped echinoids. They first evolved in the early Cretaceous (Valanginian, *c*. 135 Mya), underwent a major diversification in the Tertiary, and today constitute the largest and most successful of all irregular echinoid groups. Although there are over 220 named genera (Smith, 2004), the higher classification of this large group has traditionally relied on just two features: apical disc structure and the presence and placement of fascioles, which are bands of tiny specialized spines that form linear features running around the test (Fig. 1). These fascioles are named by reference to their general position; for example, a marginal fasciole runs around the test ambitus, a peripetalous fasciole bounds the ends of the petals, and a subanal fasciole forms a closed loop beneath the anal opening.

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However, this simple classification ignores important information about how fascioles develop. Mortensen (1910: 78, 1951: 207) and more recently Markov & Kushlina (1990) and Markov (1994), for example, have pointed out that the fascioles named ‘peripetalous’ in schizasterids and hemiasterid spatangoids form in very different ways. Furthermore, there are differences in the detailed form they take. Neraudeau, David & Madon (1998) undertook a broad survey of fascioles, concentrating on their detailed structure. Based upon the sharpness of their edges, tuberculation density and continuity, and the presence or absence of intercalated primary tubercles, they recognized three types of fasciole: protofascioles (weakly aligned and discontinuous bands of miliaries), parafascioles (dense bands of miliaries which include primary tubercles and have diffuse boundaries) and orthofascioles (sharply defined and densely packed bands of miliaries free of primary tubercles). This highlighted important differences between the micrasterid and toxasterid fascioles on the one hand, and those of more derived spatangoids.

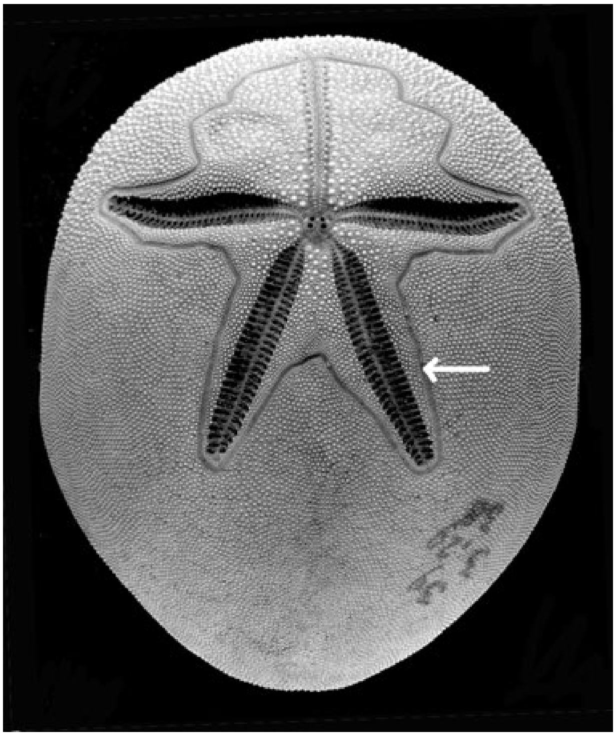

Figure 1. Aboral surface of the test of *Brissus unicolor* (Leske, 1778) (NHM 39.3.29.38). The peripetalous fasciole shows up clearly as a narrow dark band (arrowed). Length of test 50 mm.

However, with the notable exceptions of Chesher (1968) and Mooi & David (1996), the detailed pathway followed by the fascioles over the echinoid test has generally been ignored. This is surprising because fascioles start to form at an extremely early stage of development, shortly after the plates have been initiated (Mortensen, 1907; Gordon, 1929; Kier, 1975; Markov & Kushlina, 1990). Fascioles therefore generally radiate outwards from the growth centre of individual plates and remain fixed in position through ontogeny (David & Laurin, 1991), despite marked changes in test architecture. Furthermore, within species of the same genus the path followed by individual fascioles is relatively conservative (Chesher, 1968). The one complicating factor is that fascioles can be secondarily lost during growth in some taxa (e.g. Chesher, 1970).

Since fascioles become established at a very early stage of development, it is possible that mapping the precise course they take may help refine concepts of homology and provide phylogenetic markers for the higher-level relationships of the group. Here we document the path followed by fascioles for 89 spatangoid echinoids both Recent and fossil using a reference system based on plate architecture.

FASCIOLE STRUCTURE AND FUNCTION

Fascioles are bands of small and densely packed spines, termed clavulae, which are unique to atelostomate echinoids (i.e. members of the orders Spatangoida and Holasteroida). Clavulae are slender cylindrical calcite rods with a rounded to slightly oval cross-section, little more than 50 μm in diameter, and covered by epithelium. The histology of clavulae was first described in detail by Nichols (1959a) and their structure and function detailed in Nichols (1959b) and Chesher (1968). A single clavula has two bands of cilia that run the length of the shaft, placed on diametrically opposite sides parallel to the line of the fasciole. Distally, each clavula ends in an enlarged fleshy bulb containing numerous mucous glands. Each clavula is attached at its base by a ring of connective tissue and articulates onto a minute tubercle, usually around 100–150 μm in diameter. The clavulae and their tubercles generally take up a hexagonal close-packed arrangement, creating organized lines of tubercles that run oblique to the length of the fasciole. Individual fasciole bands range in breadth from no more than two or three tubercles to as much as 15–20 tubercles. In most spatangoids, fascioles are constrained to pass through the growth centre (point of initiation) of the plates they cross, a clear indication that they must form very early in plate development. The thickness of the fasciole in some taxa varies across a plate, narrowest at the growth centre and expanding towards the plate margins (Fig. 2). This demonstrates that although the width of fascioles on individual plates expands peripherally as the plate grows, the earlier formed parts of the fasciole remain at their original width.

Fascioles serve two purposes (Nichols, 1959a; Chesher, 1968; Lawrence, 1987), both related to the adoption of an infaunal mode of life. The ciliated clavulae are responsible for generating a current of water through the burrow. The alignment of ciliary bands parallel to the length of the fasciole ensures that the cilia work in tandem to draw water currents at right angles across the fasciole. These currents irrigate the burrow, drawing fresh oxygenated water past the respiratory tube feet and helping to remove waste products to the rear. The mucous glands at the clavula tips generate a cohesive mucous sheath that is carried conveyor-belt-like over the spine canopy and is compacted into the overlying sediment. This mucous sheath functions to seal the walls of the burrow thereby preventing fine particles from falling through the spine canopy and clogging the water-filled space between the spine tips and the surface of the test. Fascioles are best developed in taxa living in relatively fine and impermeable sediments and are absent or poorly developed in epibenthic taxa or those

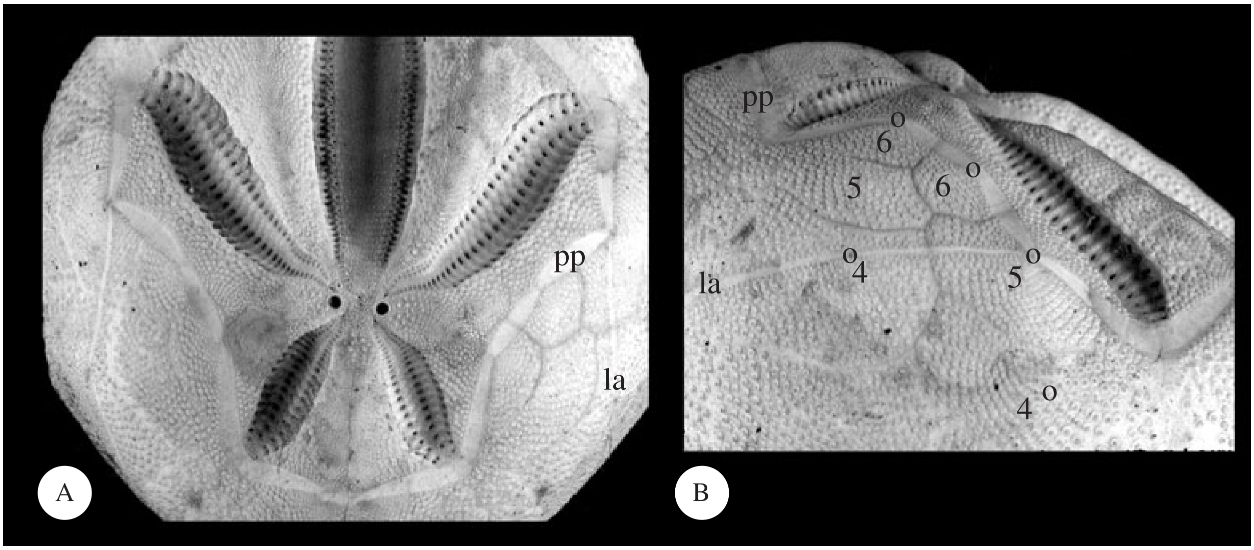

Figure 2. Test of *Ova lacunosus* (L., 1758) (NHM 81.11.22.39) in A, apical, and B, lateral views. The peripetalous (pp) and lateroanal (la) fascioles stand out as paler bands of fine tuberculation. Note the highly angular pathway and variable thickness of the fascioles, with angles coincident with the growth centres (o) of individual plates. Plates labelled according to Loven's system (see text for details).

inhabiting coarse, permeable sediments. A small number of taxa completely lack fascioles as adults. In some cases it is clear that fascioles have been secondarily lost since they are present in juveniles (e.g. Mortensen, 1951; Chesher, 1970). In other cases there is no evidence that fascioles were ever developed during ontogeny.

In fossils, the track of individual fascioles can usually be readily identified because the close-packed granules that supported the clavulae are much finer and denser than the surrounding tubercles, and stand out even to the naked eye.

Fascioles have been named according to their position on the adult test. There are six patterns commonly referred to in the literature, not all of which are mutually exclusive:

1. *Peripetalous:* an aboral band that passes around the distal ends of the petals and between the periproct and apical disc in interambulacrum 5 (Figs 1, 3, 4).
2. *Marginal:* a fasciole that runs around close to the ambitus of the test, usually at some distance from the distal ends of the petals, and which passes beneath the periproct.
3. *Subanal:* a fasciole forming a closed loop, either oval, lozenge-shaped or kidney-shaped in outline, beneath the periproct (Figs 3, 6).
4. *Anal:* a band that runs up the posterior interambulacrum on either side of the periproctal opening. The two bands may unite beneath the periproct forming a U-shaped fasciole.
5. *Latero-anal:* a band that branches from the peripetalous fasciole usually immediately behind the anterior paired petals, and which runs posteriorly, passing underneath the periproct (Figs 4, 5).
6. *Inner:* a band that crosses the lateral and posterior paired ambulacra adapical to the distal ends of the petals, effectively cutting the petals into two parts, the inner part commonly without conjugate pore-pairs (Fig. 8). It encloses the aboral part of ambulacrum III.

MATERIAL AND METHODS

We examined fasciole patterns in 89 species of spatangoid drawn from a wide range of living and fossil genera, with representatives from all families (Appendix 1). The position of fascioles was documented by reference to the plates they crossed, and we noted whether they passed through the growth centre of these plates or simply impinged on a plate edge.

Plate nomenclature

The spatangoid test, as in all post-Palaeozoic sea urchins, is composed of 20 columns of plates that run from the mouth to the apical disc. These columns are arranged in pairs, alternately of ambulacral and interambulacral plates. The ambulacral series form in association with the five radial water vessels and each plate is pierced by a pore or pore-pair that marks the position of a tube-foot. The interambulacral series are imperforate. Plates are added at the apical disc during the early stages of growth and continue to enlarge by peripheral accretion throughout life. Consequently the first formed plates are those closest to the peristome.

The standard nomenclature for test plating (Loven, 1874) is used here, in which the five ambulacral zones are numbered with Roman numerals I–V and the interambulacral series with Arabic numerals 1–5 (Fig. 3). The anterior ambulacrum in the bilaterally symmetrical spatangoids is ambulacrum III, and the interambulacrum to the posterior that houses the anal opening is interambulacrum 5. In oral view, the ambu-

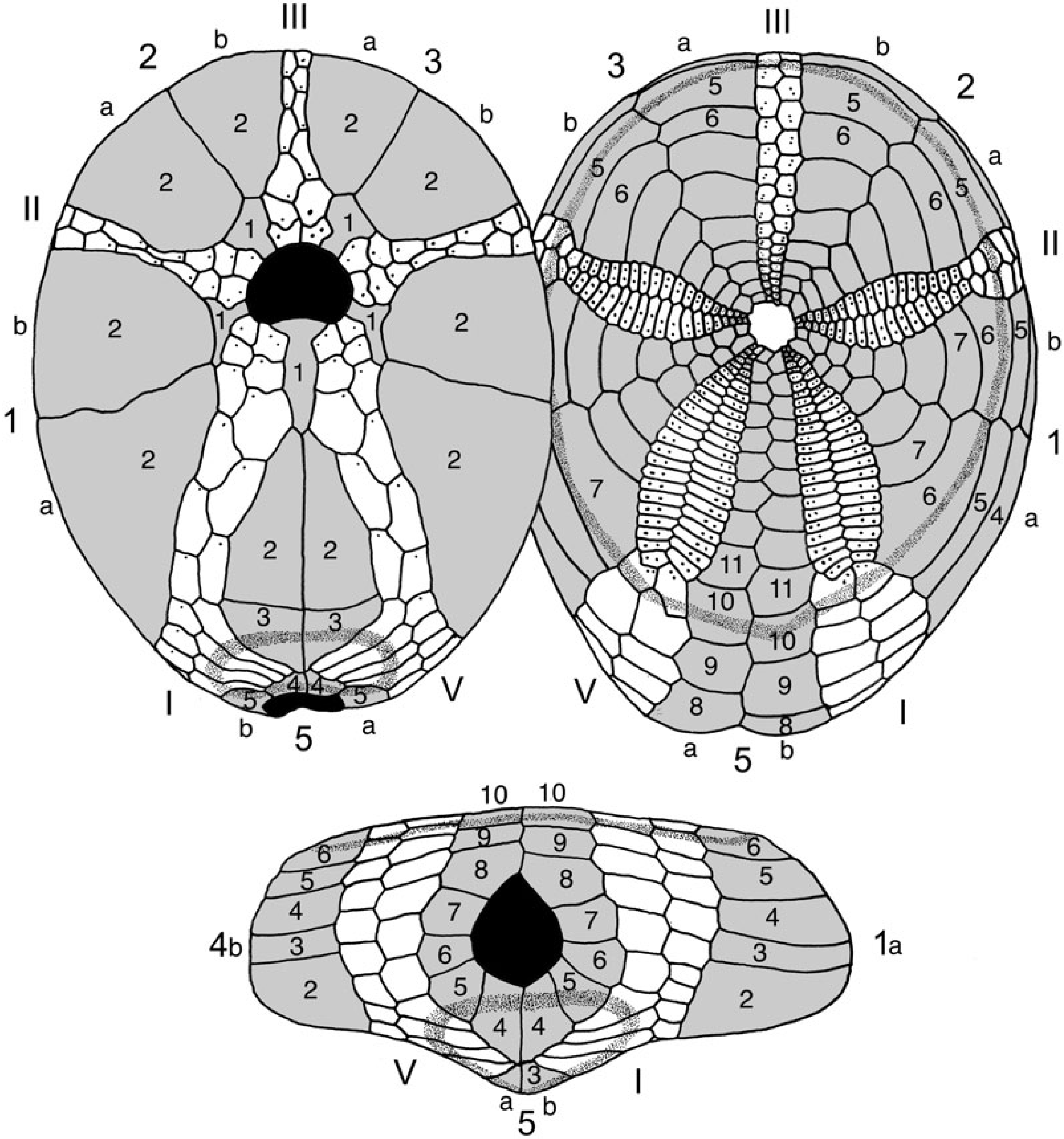

Figure 3. Fasciole pathways in *Eupatagus valenciennesi* (Agassiz & Desor, 1847). Camera lucida plating diagrams of oral, apical and posterior surfaces. Fascioles are shown as densely stippled bands. Interambulacral plates are numbered according to Loven's system and shaded grey. Ambulacral zones are unshaded.

lacral and interambulacral zones are numbered clockwise. Each interambulacral zone starts with a single plate, the basicoronal plate, adjacent to the mouth opening. This is plate 1. Subsequent plating is biserial and the two series of plates in each zone are labelled a and b as indicated in Figure 3. Facing the peristome, the column on the right-hand side is designated 'a'. Individual plates can then be specified by stating the zone, column and plate number, e.g. 5.b.2 indicates the second plate in the left-hand column (in oral view) of interambulacrum 5.

In interambulacrum 5 the oral plates are differentiated to form the plastron, specialized to carry the powerful spines used in pushing the animal forward through the sediment. The basicoronal plate in interambulacrum 5 is termed the labral plate, 5.a.2 and 5.b.2 are termed the sternal plates and 5.a.3 and 5.b.3 the episternal plates.

The periproct, or anal opening, forms at metamorphosis and is initially apical in position. However, as development proceeds the periproct becomes associated with specific plates in interambulacrum 5 (usually plates 5–9) and starts to shift in position adorally as new interambulacral plates are added at the apex.

Fasciole pathway reference system

It is useful to be able to describe the path followed by fascioles around the test in notational form. Since the position of fascioles is more conserved across genera on interambulacral than on ambulacral plates, only the former need be considered. Starting from the anterior ambulacrum (III) and in apical view working clockwise to the posterior, the fasciole crosses interambulacral columns 2.b, 2.a, ambulacrum II, interambulacral columns 1.b, 1.a, ambulacrum I and interambulacral column 5.b. The fasciole path can then be annotated to the number of the plate in each interambulacral column. In this way a fasciole that crosses columns 2.b and 2.a on plate 5, 1.b and 1.a on plate 6, and 5.b on plate 10 (Fig. 3) has the formula [5, 5 :: 6, 6 :: 10]. The symbol :: indicates an ambulacral zone.

Several factors can complicate the formula. First, the fasciole path commonly differs slightly on left and right sides of the test. Invariably the path is identical in the two anterior interambulacra 2 and 3, and in columns 1.b and 4.a. However, in columns 1.a, 4.b and 5.a, 5.b the fasciole is commonly one plate different. Variation between left and right columns can be easily indicated by listing the fasciole position in column 1.a first and that in 4.b in parentheses immediately afterwards. Thus if the fasciole crosses plate 6 in column 1.a and plate 7 in column 4.b (Fig. 3) the formula becomes [5, 5 :: 6, 6(7) :: 10]. The same approach can be used to indicate variation in columns 5.a and 5.b.

Another complicating factor is that fascioles can run vertically across two or more plates in a single interambulacral column. Where this occurs, plates that are crossed within a single column are linked by arrows and listed in clockwise order. In *Protenaster* (Fig. 4) for example, the fasciole crosses columns 2.a and 2.b on plate 4, then rises and runs to the growth centre of plate 5 in columns 1.b and 4.a, where it divides. The peripetalous band then rises through the plate growth centres of plates 6 and 7 in columns 1.b and 4.a before crossing to plate 7 in columns 1.a and 4.b. The formula for this peripetalous fasciole is thus [4, 4 :: 5→7, 6(7) :: 9].

Finally, fascioles can split and merge in schizasterids and palaeopneustids. This usually occurs in columns 1.b and 4.a, where a single anterior fasciole splits into two posterior bands, one passing beneath the periproct, the other above. For example, in *Agassizia* (Fig. 5) a single fasciole crosses columns 2.a and 2.b on plate 3, and runs to the growth centre of plate 4 in column 4.a. From there, one band rises from plate 4 to plate 7, passing through plate growth centres before crossing into column 4.b on plate 8 and continuing posteriorly above the periproct, crossing column 5.a on plate 9. The lower band continues on plate 4.a, crossing to plate 4 in column 1.a and plate 5 in column 4.b, before passing beneath the periproct running from plate 5 to 4 in column 5.a. The fasciole formula can then be shown as:

Peripetalous [3, 3 :: 4→7, 7(8) :: 9]

Lateroanal [–, – :: 4, 4(5) :: 5→4].

Although fasciole positions are generally conserved across individuals of the same species, a small amount of variation can be encountered (see Appendix). Where the position is variable the range of possible plates is indicated by separated slashes. For example, [9/10/11] indicates that the fasciole may cross plate 9 or 10 or 11 in different individuals.

Classification

For ease of reference, the classification of spatangoids in the following discussion follows Mortensen (1951). Subsequently we make recommendations as to how this classification can be modified in the light of our findings.

RESULTS

Subanal fasciole

The subanal fasciole forms a closed loop beneath the periproct and can be ovate, lozenge-shaped or kidney-shaped. Despite this variability, the precise course followed by this fasciole is highly conserved and only two discrete pathways are found.

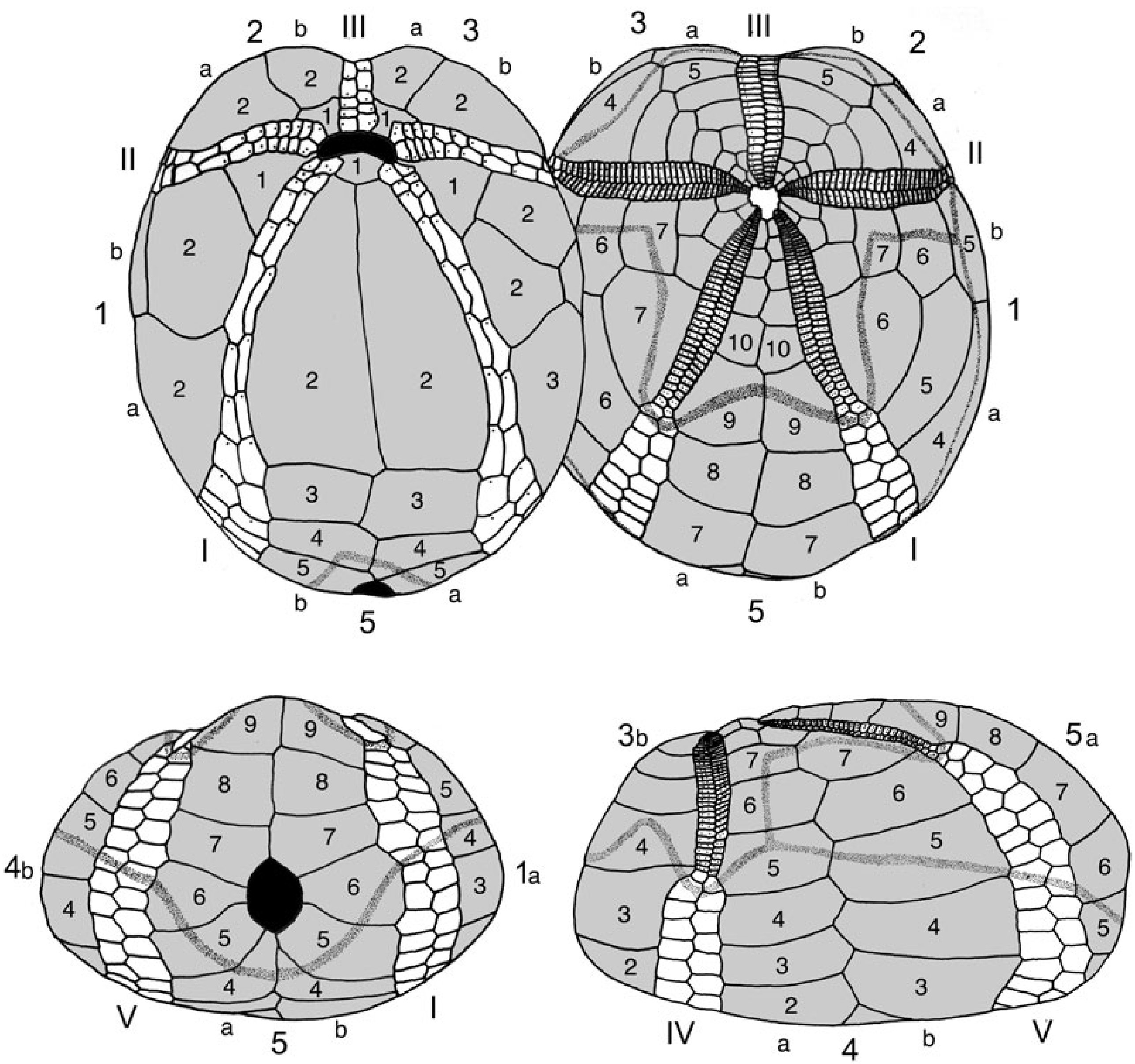

Figure 4. *Protenaster australis* (Gray, 1851). Camera lucida plating diagrams of oral, apical and posterior surfaces. Fascioles are shown as densely stippled bands. Length of test 63 mm.

Micrasterid pattern (Fig. 6)
The fasciole crosses the posterior interambulacrum running along the boundary between plates 5.b.2 and 5.b.3 and along the posterior of 5.a.2 on its oral side, and usually across 5.a.5 and 5.b.5 (the latter on its adapical side), though extending onto the upper margins of 5.a.4 in a few taxa. The fasciole is not constrained to run through the growth centres of these plates. It extends on either side over the inner series of plates in ambulacra I and V, these plates never being laterally elongated. The first ambulacral plates that bear the fasciole are I.a.5 and V.b.5.

This pattern is found in all Micrasteridae examined that develop a subanal fasciole: *Micraster, Gibbaster, Pseudomicraster, Cyclaster* (including *Brissopneustes*) and *Isopneustes*.

Brissid pattern (Figs 3, 7)
The fasciole crosses the posterior interambulacrum passing through the growth centres of plates 5.a.3 and 5.b.3 on its adoral side and the growth centres of 5.a.4, 5.b.4, and usually also 5.a.5 and 5.b.5, on its adapical side. This pattern holds true irrespective of whether

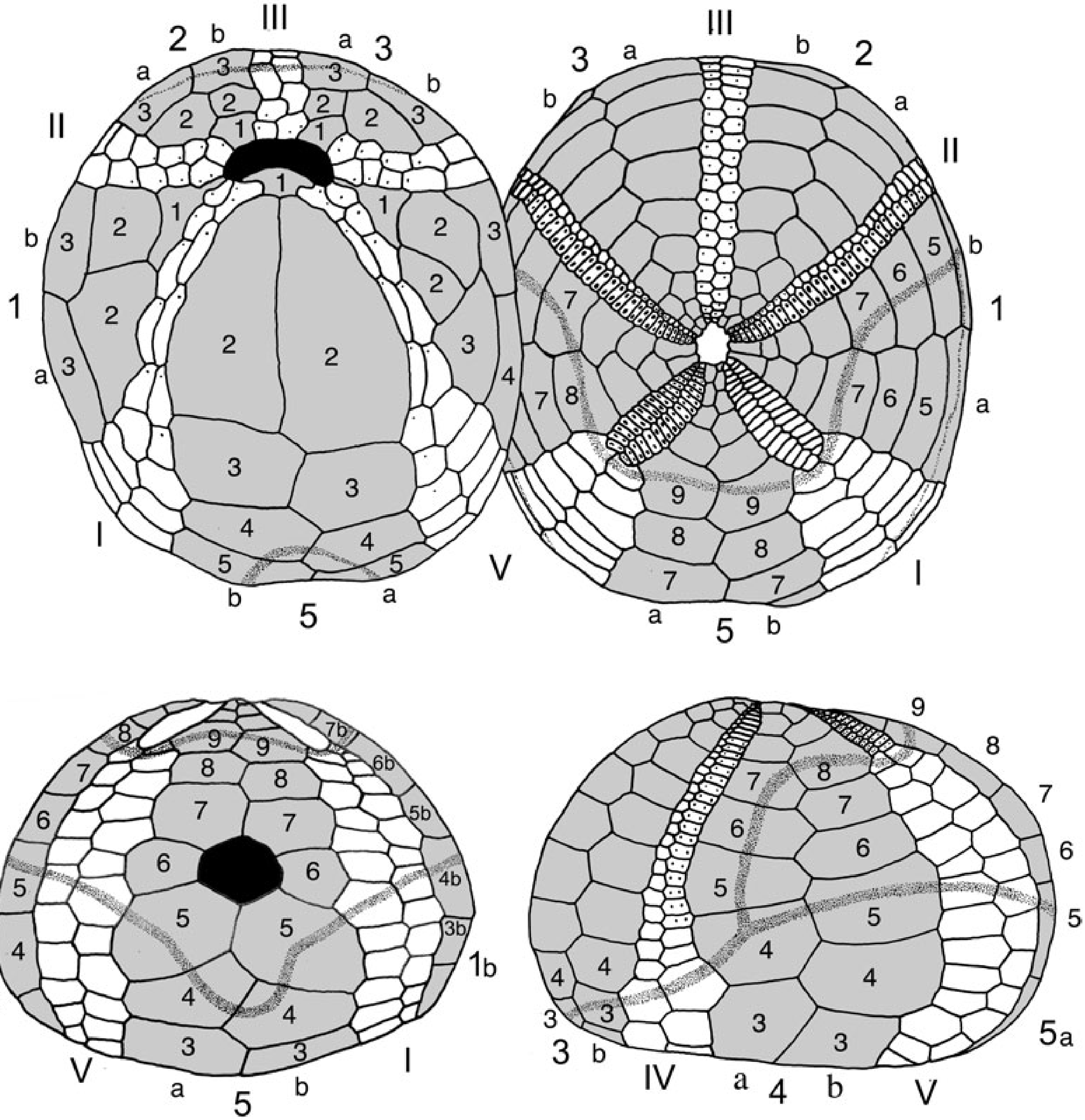

Figure 5. *Agassizia scrobiculata* (Valenciennes, 1846). Camera lucida plating diagrams of oral, apical, lateral and posterior surfaces. Fascioles are shown as densely stippled bands. Length of test 35 mm.

the fasciole is bilobed or lozenge-shaped, although in the latter the incursion across plate 5 is generally rather minor while in the former it may extend up to the growth centre of plate 6. This pattern is true of all Brissidae (e.g. *Brissus, Eupatagus*, *Maretia*, *Metalia, Meoma, Brissopsis*), Loveniidae (*Lovenia, Hemimaretia, Echinocardium, Breynia*) (Appendix). In a very few species (e.g. *Spatangobrissus, Rhinobrissus*) the fasciole does not extend onto plate 5 in interambulacrum 5 but is restricted to 5.a.4 and 5.b.4 only, while in *Plagiobrissus* it may even extend to 5.a.6 and 5.b.6.

The fasciole extends onto the ambulacra on either side, running across the inner series of plates I.a and V.b only. The number of ambulacral plates incorporated varies from taxon to taxon but is never less than three and usually is four or five. The first ambulacral plates to be crossed on the oral side are, with rare exceptions, I.a.6 and V.b.6.

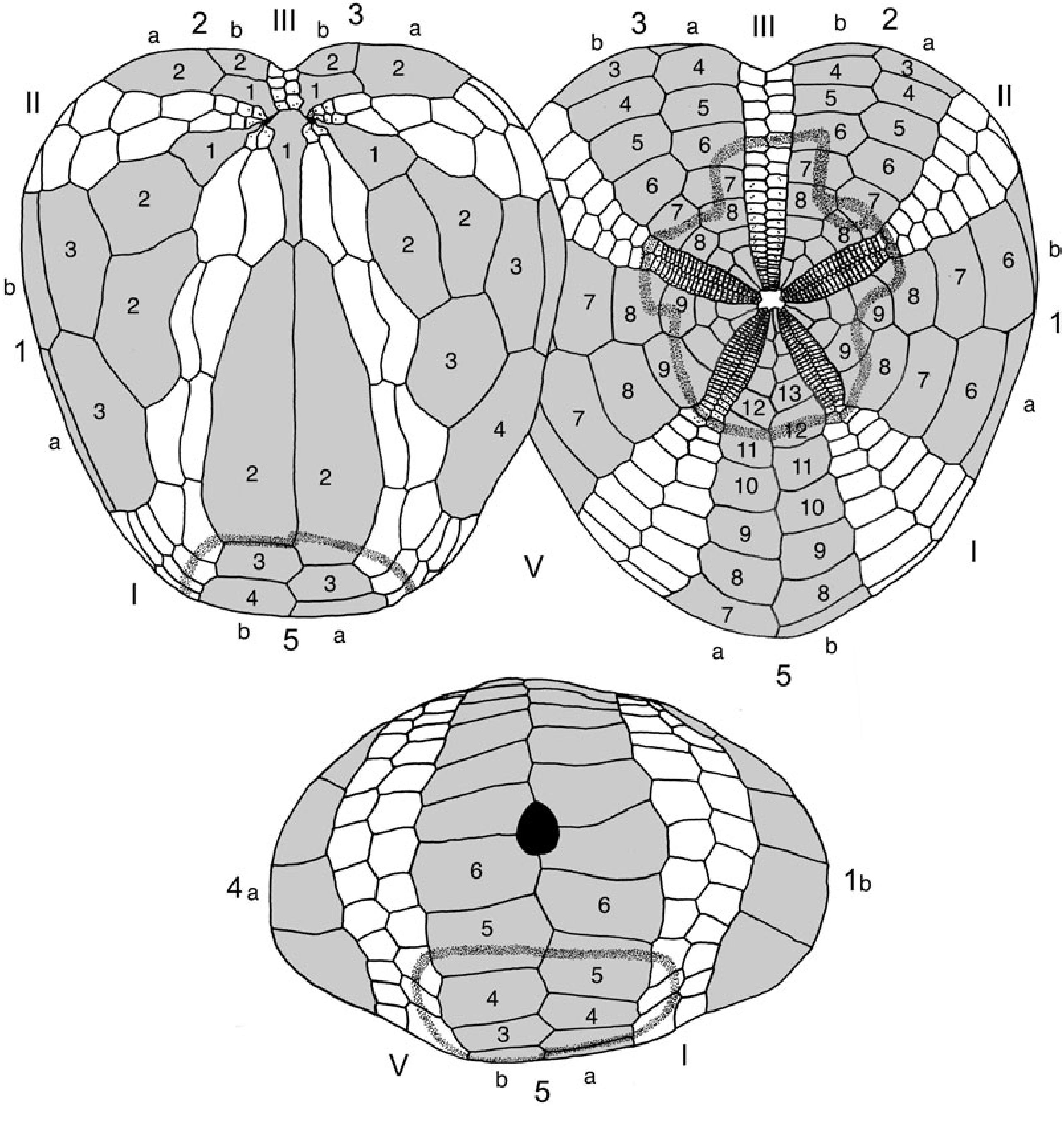

Figure 6. *Cyclaster regalis* Baker, 1969. Camera lucida plating diagrams of oral, apical and posterior surfaces. Fascioles are shown as densely stippled bands. Length of test 65 mm.

Anal fascioles

Only a few taxa within the Brissidae and Loveniidae develop an anal fasciole. This band runs up either side of the periproct and invariably passes through the growth centres of plates 5–8 or higher in interambulacrum 5. There are two patterns; either the two lateral bands merge with the subanal fasciole so that a single combined band crosses plates 5.a.4 and 5.b.4, or the anal fasciole is a separate U-shaped structure that remains discrete from the subanal fasciole and crosses below the periproct on plates 5.a.5 and 5.b.5.

Rhinobrissus and *Echinocardium* have discrete anal and subanal bands, whereas the two are coalesced in *Brissopsis, Metalia*, *Plagiobrissus* and *Rhabdobrissus*.

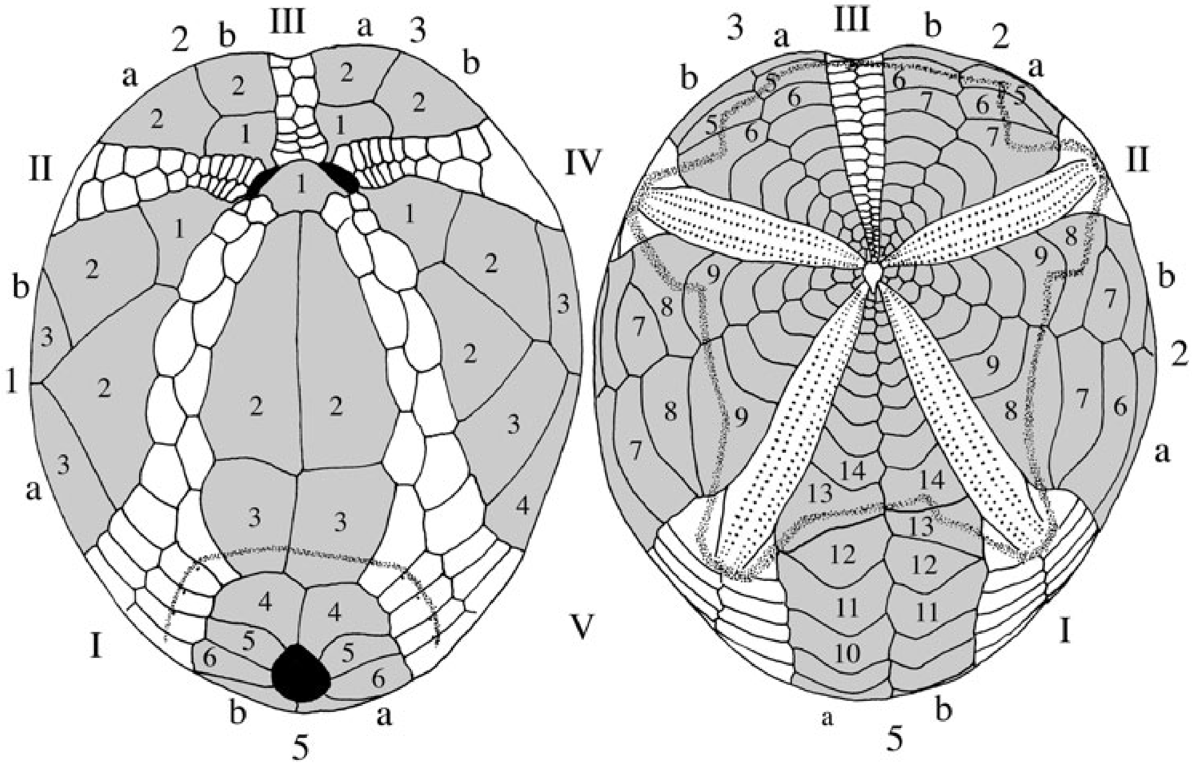

Figure 7. *Meoma ventricosa* (Lamarck, 1816). Camera lucida plating diagrams of oral and apical surfaces. Fascioles are shown as densely stippled bands. Length of test 119 mm.

MARGINAL FASCIOLE

A discrete marginal fasciole forming a ring that passes beneath the periproct is developed only in Palaeopneustidae (*Palaeopneustes* and *Plesiozonus*) and Pericosmidae (*Pericosmus*). In all three cases the marginal fasciole crosses plates 2.b.3 and 2.a.3, sometimes rising to 2.a.4, passes laterally over 1.a.4 and then 1.b.4 or 1.b.5, and then dips below the periproct crossing 5.a.5 and 5.a.4. The fasciole in interambulacrum 1 runs across plate 4 in both columns whereas in interambulacrum 4 it crosses from 4.a.4 to 4.b.5. *Faorina* also possesses a marginal fasciole, although only the subanal portion is retained in adults and we have not studied juveniles where the complete fasciole pathway can be traced. In all taxa studied the notation for the marginal fasciole is: [3 (3→4), 3 :: 4, 4(5) :: 5→4].

PERIPETALOUS FASCIOLES

Peripetalous fascioles are widely developed amongst spatangoids. They are present as the sole fasciole in hemiasterids, aeropsids, corasterids and palaeostomatids, and occur in association with a subanal fasciole in brissids, and occasional loveniids and micrasterids. Peripetalous bands are also present in pericosmids, palaeopneustids and schizasterids, associated with a marginal or lateroanal fasciole. In detail, however, the peripetalous fasciole follows different pathways in many of these groups and within species is more highly conserved in position around the anterior of the test than around the posterior. The following arrangements can be distinguished.

Micrasteridae, Pericosmidae and Palaeopneustidae

Cyclaster is the only micrasterid to develop a reasonably distinct peripetalous band, although this is a diffuse parafasciole that is commonly lost around the anterior (Fig. 6). It is always developed on relatively late-forming plates, never passing below plate 6 in interambulacra 2 and 3 or plate 7 in interambulacra 1 and 4. It has the formula [6→8, 7/8 :: 9→10, 9→8(9) :: 13].

The peripetalous fasciole in Pericosmidae is also confined to relatively late forming plates but the precise pathway taken is variable even within the same genus: *Pericosmus latus* [6→7, 7 :: 7/8→9, 9→8 :: 11/12→12/13], *P. macronesius* [?, 7 :: 8→9, 9→8 :: 11(12)] and *Faorina* [5, 5 :: 7, 7 :: 10]. Likewise, in *Palaeopneustes* [7→8, 8→7 :: 9→10, 10(11→10) :: 11→12(12)] and *Plesiozonus* [8→9, 9 :: 8→10, 9(10→9) :: 10→11] the peripetalous fasciole is similarly confined to relatively late-forming plates.

Brissidae and Loveniidae
Three different fasciole pathways can be distinguished amongst brissids:

1. In *Plagiobrissus, Metalia, Linopneustes*, *Eupatagus, Granobrissoides, Brissus, Brissopsis* and *Cionobrissus*, the fasciole crosses interambulacra 2 and 3 on plates 2.b.4, 3.a.4 passing onto 2.a.4, 3.b.4 before rising to 2.a.5, 3.b.5 (Fig. 3). An alternative seen in some species of *Brissopsis* is for the fasciole to run vertically from plate 4 to 5 in interambulacral columns 2b and 3a. The fasciole then crosses into columns 1b and 4a on plate 6. In *Plagiobrissus, Linopneustes*, *Granobrissoides* and *Cionobrissus* the fasciole continues directly from anterior to posterior column in interambulacra 1 and 4 without indentation, and then crosses interambulacrum 5 somewhere between plates 10 and 13 (the precise path is rather variable). A typical formula (*Metalia*) is [4, 4→5 :: 6→7, 6(7) :: 12/13]. A similar pattern is also seen in *Breynia,* the one loveniid to develop a peripetalous fasciole. In *Brissus, Brissopsis and Metalia* the fasciole is indented in columns 1.b and 4.a and runs vertically across two or three plates giving a formula of [4, 4→5 ::.6→7, 7→ 6(8→7) :: 10/11/12]
2. In a smaller number of brissids the peripetalous fasciole is positioned slightly higher on interambulacra 2 and 3, crossing plate 5 in both columns. This pattern is seen in *Anametalia, Eupatagus, Rhynobrissus, Gillechinus*, *Lissospatangus* and *Spatangobrissus.* In all these taxa the fasciole crosses interambulacra 1 and 4 on plates 6 and 7 without indentation. The formula is [5, 5 :: 6, 6(7) :: 10/11] or [5, 5 :: 7, 7(8) :: 11/12]
3. The highest pathway followed by the peripetalous fasciole is found in *Meoma* (Fig. 7), *Macropneustes* and *Plethotaenia*. In these taxa the fasciole crosses interambulacra 2 and 3 on plates 5 and 6 (indented in *Meoma* but unindented in the other two) and plate 8 or 9 in interambulacra 1 and 4.

Hemiasterina
Heterolampas, Bolbaster, *Psephoaster* and most species of *Hemiaster* and *Leymeriaster* all share a very similar fasciole pattern, namely [5, 5 :: 6→7, 6(7) :: 9/10]. *Hemiaster bufo,* the type species of *Hemiaster* and stratigraphically one of the earliest, has its fasciole slightly higher, crossing anteriorly on plates 2.a.6, 2.b.6 and 3.b.6, 3.a.6. The same is also true of *Leymeriaster leymerei*.

By contrast, in the hemiasterids *Proraster, Opissaster*, *Palaeostoma*, *Holanthus* and *Mecaster* species, the peripetalous fasciole develops on more adoral plates with a formula [4, 4 :: 5→6, 5(6) :: 9/10]. The same is true of all Somaliasteridae [4, 4 :: 5, 5(6) :: 8/9]) and most Aeropsidae (*Aceste* [4, 4→5 :: 4→5, 5(6) :: 8]; *Sphenaster* [4, 5 :: 5→6, 6(7) :: 10]; *Coraster* [4, 4 :: 5→6, 6(7) :: 9→10(9)]; *Homoeaster* [4, 4 :: 5, 5(6) :: 9(8)]). However, *Aeropsis* itself has a very different arrangement, much closer to the peripetalous fasciole of schizasterids.

Peripetalous/marginal fascioles

A combined peripetalous/marginal fasciole is developed in schizasterids and is very highly conservative in its path. *Schizocomus* is the only extant taxon in which the peripetalous and marginal fascioles coalesce in interambulacra 2 and 3. The peripetalous fasciole in *Schizocomus* [– (6), 4→6 (6) :: 6(6→7), 6(7) :: 9] basically runs parallel to the marginal fasciole only two plates higher (see de Ridder *et al*., 1992). The fossil *Lambertonia* has a more or less identical fasciole path.

In all other schizasterids the peripetalous and marginal fascioles coalesce in interambulacral columns 1b and 4a. There are three basic patterns.

Pattern 1
In *Prenaster*, *Agassizia* (Fig. 5) and *Saviniaster* the peripetalous fasciole passes inframarginally around the anterior on plates 2.a.3, 2.b.3, and also at some distance beyond the ends of the anterior petals. The fasciole branches on plates 1.b.4 and 4.a.4 give rise to a lateroanal band and a peripetalous band. The former continues on plates 1.a.4, 4.b.5 of the lateral interambulacra and crosses 5.a.5 and 5.a.4 beneath the periproct. The latter rises vertically for two or three plates in columns 1b and 4a before crossing 1a and 4b on plate 6 or 7. *Unifascia* has an identical peripetalous fasciole but lacks any trace of the lateroanal band, at least as adults. The formula for all of these is:

Peripetalous [3, 3 :: 4→7, 7(8) :: 9/11/12/13/14]
Lateroanal [–, – :: 4, 4(5) :: 5→4].

Pattern 2
In the great majority of schizasterids (*Schizaster, Protenaster* (Fig. 4), *Brisaster, Tripylaster, Paraster, Moira, Hypselaster, Diploporaster, Aguayoaster, Ova, Hypselaster, Pseudabatus, Linthia, Periaster*) the fasciole crosses anteriorly over plates 2.a.4 and 2.b.4, and passes immediately beneath the distal ends of the anterior petals onto 1.b.5 where the peripetalous and lateroanal bands split. A typical formula (from *Linthia*) is:

Peripetalous [4, 4 :: 5→6/7, 6(7) :: 10]
Lateroanal [–, – :: 5, 4(5) :: 5→4].

Pattern 3

In a smaller number of schizasterids (*Abatus, Parapneustes, Tripylus*) the peripetalous fascioles crosses anteriorly over plates 2.a.4 and 2.b.4, as in pattern 2, but then crosses onto 1.b.4 (and 4.a.4), where the lateroanal and peripetalous branches diverge. The formula is:

Peripetalous [4, 4 :: 4→5/6, 5(6) :: 8/9]

Lateroanal [–, – :: 4, 4(5) :: 5→4].

Inner fascioles

Only Loveniidae develop fascioles that enclose the frontal ambulacrum but not the petals aborally (Fig. 8A). The pathway followed by these fascioles is variable amongst species within the same genus. In *Echinocardium* it runs vertically up columns 2b and 3a starting from plate 5, 6 or 7 crossing to column 2a/3b at around plate 7 and continuing adapically for at least one further plate. The fasciole crosses interambulacra 1 and 4 on plate 10 and interambulacrum 5 on plate 14 or 15. *Lovenia subcarinata* has a rather similar pattern, with the fasciole running [4→6, 6→8 :: 10, 10 :: 16] but *L. elongata* and *Breynia* show a different pattern, with the inner fasciole starting on plate 8 and rising to plate 10 in interambulacra 2 and 3.

DISCUSSION

It should be clear from this review of fascioles and test architecture that there is important information to be gained from considering the precise pathway taken by fascioles. Taxa that traditionally have been grouped together because of their superficially similar fasciole patterns can often be subdivided on the basis of the actual plates crossed by that fasciole. Thus for example, there is a clear and consistent difference between the subanal fasciole of micrasterid and brissid spatangoids, and there are two distinct pathways for peripetalous fascioles amongst hemiasterine spatangoids. Depending upon which plates the combined peripetalous and marginal fasciole crosses in the anterior interambulacra, and on which plate they separate in interambulacral columns 1.b and 4.a, two major groups of schizasterid are distinguishable. These differences are consistent and clear-cut within species and genera and are likely to provide important phylogenetic markers.

Fascioles initiated on early forming plates are more consistent in their position than those that appear later in ontogeny. For example, fascioles on interambulacral plates 3 and 4 are much more invariant in position across taxa than the fasciole that crosses between the periproct and the apical disc and which cannot be initiated until eight or more plates have formed. This latter fasciole position is often variable even amongst individuals of the same species. We conclude that the later a fasciole forms in ontogeny the more variable is its pathway.

The earliest fascioles

Primitive spatangoids lack fascioles altogether, and the earliest fasciole-bearing taxa do not appear until the Albian (Neraudeau *et al*., 1998). At this time certain toxasterids start to display a diffuse band of small and semiorganized tubercles running around the base of their petals, forming a protofasciole (Neraudeau *et al*., 1998). The protofasciole in these early forms invariably forms a diffuse band on plates 6–8 in interambulacra 1, 2, 3 and 4 and plates 9–11 in interambulacrum 5. In *Hemiaster bufo*, the oldest hemiasterid examined with a true fasciole (orthofasciole), the band crosses plate 6 in ambulacra 2 and 3 and plate 6 or 7 in interambulacra 1 and 4. Since they are initiated on identical plates, it seems likely that the peripetalous fasciole of hemiasterids evolved by progressive specialization of the protofasciole band.

The first species with more complex fascioles appeared slightly later, in the Cenomanian. *Mundaster* has a peripetalous fasciole and an independent marginal fasciole (see Markov & Solovjev, 2001) and is the oldest known representative of the Pericosmidae. In *Mundaster* the marginal fasciole crosses plates 1.b.4 and 4.a.4. *Periaster,* which also comes from the Cenomanian, has the schizasterid fasciole pattern of a combined peripetalous and marginal band running around the anterior of the test over plates 2.a.4 and 3.b.4. This subsequently splits on plates 1.b.5 and 4.a.5 into a peripetalous band and a lateroanal band.

Slightly later, by the Turonian, the first taxon with a subanal fasciole appears, namely *Micraster*. However, all Upper Cretaceous forms follow the micrasterid subanal fasciole pattern and species showing the brissid pattern do not appear until much later, in the Eocene.

Homology of fascioles

Subanal fasciole

Although the micrasterid and brissid subanal fascioles develop in a similar position on the test, they consistently cross different plates. In brissids and their relatives the fasciole crosses interambulacral plates 5.a.3 and 5.b.3 orally and 5.a.4, 5.b.4 adapically, while ambulacral plate 6 is the first plate on the oral side that the fasciole crosses. By contrast, in micrasterids the fasciole runs close to the edge of interambulacral plates 5.a.2 and 5.b.2 adorally and 5.a.5, 5.b.5 adapically, while ambulacral plate 5 is the most adoral to be incorporated into the fasciole. A further difference is that the fasciole band is constrained to pass through

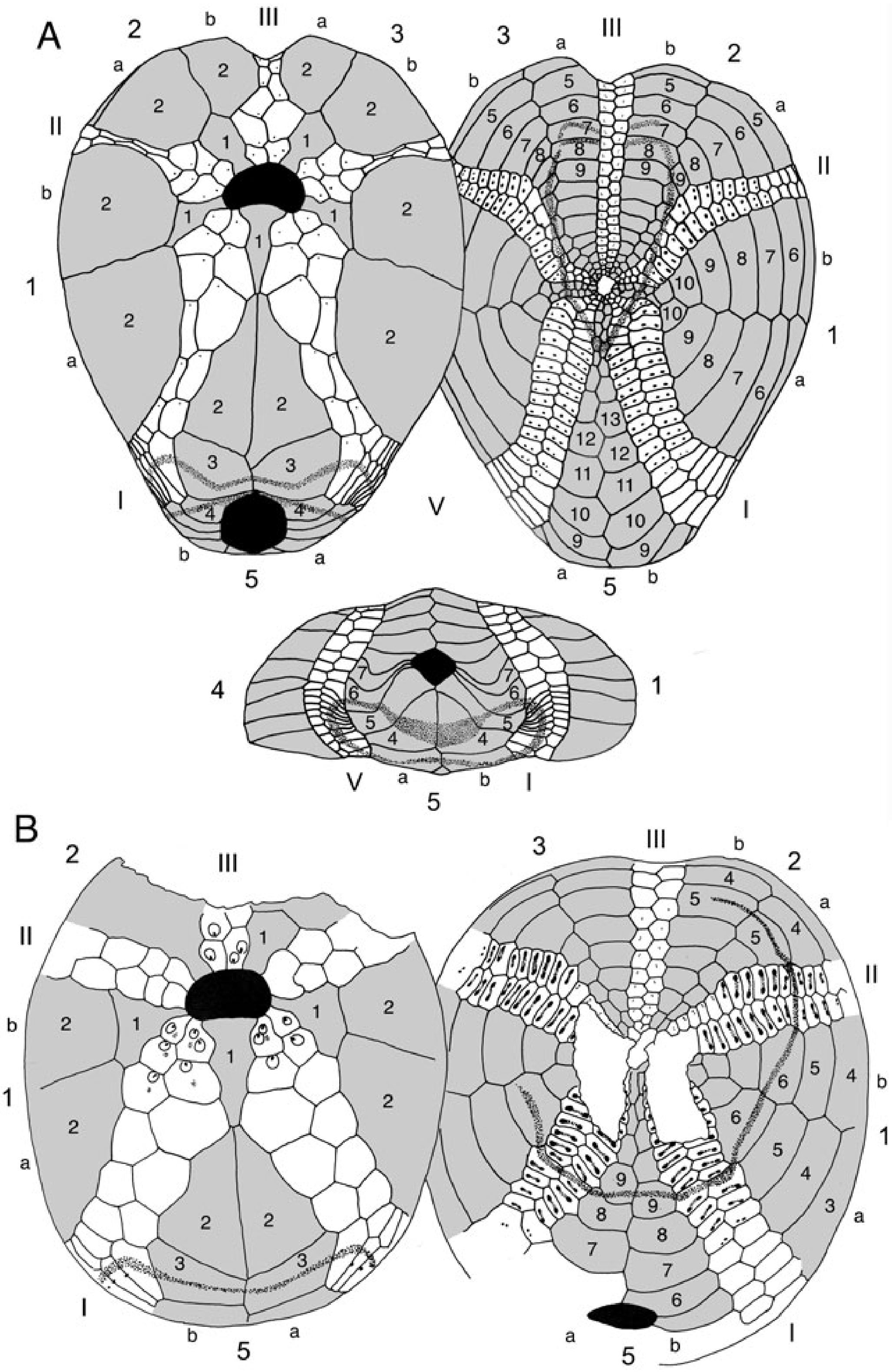

Figure 8. Camera lucida plating diagrams indicating fasciole pathways for: A, *Lovenia elongata* (Gray 1845), length of test 61 mm; B, *Gualtieria orbignyana* (Agassiz & Desor, 1847), length of test 39 mm.

growth centres of plates in the brissid pattern, but passes along plate margins in the micrasterid pattern. This indicates a difference in their time of formation, with the brissid pattern being established at a much earlier ontogenetic stage than the micrasterid pattern. These consistent differences strongly suggest that the fasciole is not homologous in the two groups.

Latero-anal and marginal fascioles

As first demonstrated by Mortensen for *Brisaster* and *Abatus*, the fasciole that forms initially in schizasterids is a marginal band that crosses the fourth or occasionally fifth plate in each interambulacral column. This therefore follows an identical pathway to the marginal fasciole of palaeopneustids, except anteriorly where it is one plate higher. This is very convincing evidence for them being homologous structures, as has been previously postulated (e.g. Mortensen, 1950; Markov & Kushlina, 1990).

Subanal and marginal fascioles

A fasciole band is initiated at the growth centres of plates 4 and 5 in both columns of interambulacrum 5 in many spatangoids. In one group this band goes on to form a closed subanal ring, while in another it forms part of a marginal or latero-anal fasciole. Because the subanal fasciole and the marginal fasciole both hold an identical and invariant position, it seems likely that the subanal fasciole of brissids and the marginal fasciole of schizasterids and palaeopneustids both developed from a homologous simple subanal fasciolar band. In holasteroids there is often only a partial marginal fasciole developed around the posterior of the test beneath the periproct (see Smith & Wright, 2003). It is envisaged that a similar partial band could have given rise to both subanal and marginal fascioles in spatangoids. By contrast, the peripetalous fasciole is clearly a separate independent innovation, since it is consistently initiated on much later forming plates.

Peripetalous fasciole

Since Mortensen (1910) observed that the peripetalous fasciole band formed secondarily in schizasterids, workers such as Markov & Kushlina (1990) and Neraudeau *et al*. (1998) have accepted that the peripetalous fascioles of schizasterids and brissids/hemiasterids are not homologous. However, the peripetalous fasciole is also a later forming structure. Kier (1975) showed it to be only a discontinuous single row of spines in a 5.8 mm long individual of the brissid *Meoma*. The band does not start to form until 10–11 interambulacral plates have been initiated in the posterior interambulacrum and the periproct has become separated from the apical disc. Thus in timing the appearance of the peripetalous fasciole of brissids and the semipetalous band of schizasterids is identical. Furthermore, the semipetalous fasciole merges into the marginal fasciole, to continue around the anterior on plate 3 or 4, which is also the path followed by the peripetalous fasciole of many hemiasterines and in the majority of brissids.

Consequently, rather than the peripetalous and semipetalous fascioles being independent derivatives, it seems more likely that they are homologous, and the anterior band in schizasterids represents a combined peripetalous and marginal fasciole.

Support for this view comes from taxa such as *Parapneustes, Hemigymnia, Schizocosmus* and *Eopericosmus,* where the semipetalous and marginal fascioles remain separate from the anterior interambulacra before eventually merging. Furthermore, in some specimens of *Periaster*, from the Cenomanian of Tunisia, independent peripetalous and marginal fascioles are present around the anterior and posterior of the test; these coalesce at the ends of the anterior paired petals.

The peripetalous fasciole was originally a rather late forming structure. In the more primitive hemiasterids (e.g. *Hemiaster*) the peripetalous fasciole is initiated on plate 6 or higher in the anterior interambulacra. However, in many other hemiasterine groups (*Mecaster*, Aeropsidae, Somaliasteridae) formation of fascioles appears to have been initiated earlier and the anterior part of the fasciole runs across plate 4. A similar trend towards earlier initiation of fasciole development around the anterior is also apparent in schizasterids and brissids. Amongst brissids the most primitive members are the macropneustids, and these have a fasciole position as in *Hemiaster*. In other brissids the fasciole crosses the anterior interambulacra one or two plates lower down.

Inner fasciole

This structure is restricted to the family Loveniidae and probably arose from delayed development of a peripetalous band. In *Echinocardium* and *Lovenia* there is an inner fasciole that encloses the anterior ambulacrum, cutting through the petals close to their apex. Mortensen (1951) suggested that this inner fasciole had nothing to do with peripetalous fascioles, because a third loveniid, *Breynia*, has both inner and peripetalous fascioles. Although this is true, in both *Echinocardium* and some species of *Lovenia* the anterior portion of the fasciole transverses the growth centres of plate 4 or 5 in interambulacra 2 and 3, as does the peripetalous fascioles of Brissidae.

However, instead of running laterally, the inner fasciole extends adapically to pass over very late-forming plates in interambulacra 1, 4 and 5. The transformation of peripetalous to inner fasciole thus simply requires delayed development. The fossil *Gaultieria* is often thought to show an intermediate stage, since its fasciole bisects the petals (Fig. 8B). However, its fasciole formula is [5, 5 :: 6, 6 :: 9] and, in interambulacra 2 and 3, the fasciole passes laterally without any vertical displacement. This is a more primitive arrangement than seen in any living Loveniidae and strongly points to its homology with peripetalous fascioles of brissids.

Functional implications

The change from a near horizontal periapical fasciole band to an oblique and anteriorly inclined peripetalous fasciole has occurred independently in all three major groups of spatangoid. This change in orientation presumably has a functional explanation related to the direction in which water is pumped through the burrow. In forms with a periapical fasciole, water is drawn vertically downwards, whereas in spatangoids with an oblique fasciole it is pumped downwards and to the rear, clearly an advantage for infaunal echinoids. Marginal fascioles create vertical flow across the test, which is a more appropriate strategy for epibenthic forms and is widely developed in holasteroids. In hemiasterids, where the adapical tube-feet of ambulacrum III construct and maintain an open passageway to the sediment–water interface, it is clearly advantageous to have a fasciole encircling the base of the opening that can act as a pump drawing water into the burrow. In taxa such as *Hemiaster* and *Brissopsis* the peripetalous fasciole is well placed to fulfil this role as it follows the edge of the frontal groove closely. The same is true of loveniids and many schizasterids such as *Moira* and *Schizaster,* where the fasciole has moved to encircle the frontal groove. This has been achieved through changes in plating architecture and not by a migration of the fasciole band onto more adapical plates, emphasizing how highly conserved fasciole pathways are in spatangoids. In forms that inhabit coarser, more permeable substrates and do not require a direct tunnel to the sediment-water interface, the fasciole does not have this close association with the adapical portion of the frontal ambulacrum.

Taxonomic conclusions

The utility of our more refined definitions of fascioles that are tied to specific plate homologies can only be tested by their incorporation into a more comprehensive cladistic analysis of all pertinent phylogenetic characters. This is currently being undertaken, but on fasciole evidence alone we recommend the following five taxonomic changes:

1. The grouping of Micrasteridae and Brissidae together on account of their shared subanal fasciole (e.g. Fischer, 1966) should be rejected as the fasciole follows a different pathway within each family and is likely to have evolved independently.
2. There are two major groups of hemiasterine taxa that differ in their peripetalous fasciole pattern: a primitive grade in which the fasciole is relatively late-forming and which passes across interambulacra 2 and 3 on plate 5 or above, and a clade in which it forms at an earlier stage and passes through the growth centre of plate 4 in interambulacra 2 and 3. These include *Mecaster*, the Aeropsidae and the Somailasteridae.
3. There are three groupings of Brissidae based on the course taken by the peripetalous fasciole around the anterior of the test. In the largest group it crosses interambulacra 2 and 3 on plate 4, while there is a small and apparently primitive group comprising *Meoma* and *Macropneuses*, that has a high, late-forming fasciole.
4. There are two major clades of schizasterids: in the first, the combined marginal-peripetalous fasciole passes over plate 3 in interambulacra 2 and 3 and branches on plate 4 in columns 1b and 4a; in the second, it passes over plate 4 in interambulacra 2 and 3 and branches on plate 5 in columns 1b and 4a. The first clade includes *Prenaster, Agassizia* and *Unifascia* and the second includes *Schizaster,* the type of the family Schizasteridae. *Prenaster*, *Agassizia* and *Unifascia* are separated as a distinct family for which the oldest available name is Unifasciidae Cooke, 1959.
5. The schizasterids + unifasciids share with palaeopneustids the presence of an early marginal fasciole crossing plate 3 in interambulacra 2 and 3 and plate 4 in interambulacra 1, 4 and 5, suggesting common ancestry. Markov & Solovjiev (2001: 80) named this clade the Palaeopneustoidea.

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APPENDIX

Fasciole pathways for 89 species of spatangoid mapped according to the plates they cross. Fasciole abbreviations: A, anal fasciole; IF, inner fasciole; M, marginal fasciole PP, peripetalous fasciole; SA, subanal fasciole; SP, semipetalous fasciole. Columns record plates that fasciole cross in ambulacrum III, interambulacrum 2b, 2a, ambulacrum II, interambulacrum 1b, 1a, ambulacrum I and interambulacrum 5b, 5a respectively. Plate numbering follows Loven (1874) (see text for details). Numbers in parentheses indicate less common conditions, or differences between left and right sides; numbers separated by a / indicate variability amongst individuals; → = fasciole crosses vertically over two or more plates in the same series: + = paths of two independent fasciole bands.

PERICOSMIDAE	IIIa,b	2a	2b	IIa,b	1a	1b	Ia,b	5a	5b
Faorina chinensis: M							8, 10	5→4	4→5
Faorina chinensis: PP	5,6 + 7,8	5,6	5	11,12	7	7	14–15	10	10
Lambertonia agassizia: M		3	4	7	4	4(5)	?	5→4	4→5
Lambertonia agassizia: PP		6→7	6	10,11	6→8	7(8)	?	9–10	10
Pericosmus blanquiszalensis: M	4,4	3 (3→4)	3	?	4	4(5)	?	5→4	4→5
Pericosmus blanquiszalensis: PP	6,7	6→7	7	?	7→9	9→8	?	12→13	13→12
Pericosmus crawfordi: M	?	3 (3→4)	3	?	4	4(5)	?	5→4	4→5
Pericosmus crawfordi: PP	?	6	6→9	?	7→9	9→8	?	12	12→11
Pericosmus latus: M	3,4	3 (3→4)	3	7,8	4	4(5)	?	5→4	4→5
Pericosmus latus: PP	6,7	6→7	7	12	7/8→9	9→8	?	12	11→12
Pericosmus macronesius: M	3,4	3 (3→4)	3	10	4	4(5)	9,10	5→4	4→5
Pericosmus macronesius: PP	–	–	7	16–17	8→9	9→8	18	12	11
Pericosmus melanostomus: M	–	3	3	6,7	4	4(5)	9,10	5→4	4→5
Pericosmus melanostomus: PP	5,6	6	6(5→6)	12	7	7(8)	?	11	10
PALEOPNEUSTIDAE	IIIa/b	2a	2b	Iia/b	1a	1b	Ia,b	5a	5b
Paleopneustes cristatus: M		3	3	10	4	4	12	5,4	4,5
Paleopneustes cristatus: PP	14	7,8	7,8	17,18	9,10	10	20,21	11,12	12
Paleopneustes tholoformis: M	6	3	3	10	4	5	12	5–4	4–5
Paleopneustes tholoformis: PP	14	7–8	8–7	19,20	9–10	10	22	11–12	12
FAMILY UNCERTAIN	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Schizocosmus abatoides: M	6,7	4	4	11	4	4	12,13	5→4	4→6
Schizocosmus abatoides: PP	10	(6)	6	13–14	6 (6→7)	6	16–17	9	9
BRISSIDAE	IIIa/b	2a	2b	IIa,b	1a/4b	1b	Ia,b	5a	5b
Anametalia sp.: PP	6,7	5	5	10,11	6	6(7)	16–17	11	11
Anametalia sp.: SA								3 + 5→4	3 + 4→5
Brissopsis atlantica: PP	6,7	4→5(6)	5	11	6→7	7→6(8→7)	19	11	11
Brissopsis atlantica: SA								3 + (6)5→4	3 + 4→5

Brissopsis capensis: PP	6,6	4→5	5	9,10	6→7	6(7)	14–15	10	10
Brissopsis capensis: SA								3 + 5→4	3 + 4→5
Brissopsis luzonica: PP	6,6	4→5	5	9,10	6→7	7→6(8→7)	17–18	11	11→10
Brissopsis luzonica: SA								3 + 5→4	3 + 4→5
Brissopsis lyrifera: PP	6	4	4→5	10	6→7	6(7)	14–16	10,11	10,11
Brissopsis lyrifera: SA								3 + 5→4	3 + 4→5
Brissopsis oldhami: PP	6,6	4→5	5	11	6→7	6(7)	15–16	10	10
Brissopsis oldhami: SA								3 + 5v4	3 + 4→5
Brissus latecarinatus: PP	9, 10	4	4→5	12,13	6→7	7→6(8→7)	18–19	11–12	12
Brissus latecarinatus: SA								3 + 6→4	3 + 4→6
Brissus scillae: PP	10,11	4	4→5	16	6→7	7→6(8→7)	21	11	11
Brissus scillae: SA									
Brissus unicolor: PP	11, 11	4	4→5	15–16	6→7	7→6(8→7)	21	11	11
Brissus unicolor: SA								3 + 6→4	3 + 4→6
Cionobrissus revinctus: PP	6,6	4	4→5	10, 11	6	6(7)	16–17	10	10
Cionobrissus revinctus: SA								3 + 4	3 + 4
Eupatagus rotundus: PP	9	6	6		6	6(7)		10,11	10
Eupatagus rotundus: PP									
Eupatagus valeniennsis: PP	9,10	5	5→6(5)	11,12	6	6(7)	15	10	10
Eupatagus valeniennsis: SA								3 + 5→4	3 + 4→5
Gillechinus cudmorei: PP	–	5	5	14–15	7	6(7)	20–21	11	12
Gillechinus cudmorei: SA								3 + 5→4	3 + 4→5
Linopneustes murrayi: PP	5,6	4→5	5	8,9	6	6(7)	13–14	10	9
Linopneustes murrayi: SA								3 + 5→4	3 + 4→5
Linopneustes spectabile: PP	6 + 8	3 + 5	3 + 5	9	6	6(7)	13–14	10	9
Maretia ovata: SA								3 + 5→4	3 + 4–5
Maretia planulata: SA								3 + 5→4	3 + 4→5
Maretia subcarinata: SA								3 + 6→4	3 + 4→6
Meoma ventricosa: PP	10,11,12	5→6(6)	5→6/7	14–16	8→9	8(9)	17–20	13→14	13
Meoma ventricosa: SA								3	3
Metalia dichrana: PP	5,6	4	4→5	10, 11	6→7	6(7)	18	12	12
Metalia dichrana: SA								3 + 5→4	3 + 4→5
Metalia nobilis: PP	8,8	4	4→5	12	6	6(7)	19–20	13	13
Metalia nobilis: SA								3 + 5→4	3 + 4→5
Metalia spatangus: PP	7, 8, 9	4	4→5(4→6)	13	6→7	6(7)	19	11, 12	12, 13
Metalia spatangus: SA								3 + 5→4	3 + 4→5
Metalia sternalis: PP	6, 6	4	4→5	10	6→7	6(7)	18	11	12
Metalia sternalis: SA								3 + 5→4	3 + 4→5
Metalia townsendi: PP	8, 8	4	4→5	12	6→7	6(7)	?	13	13
Metalia townsendi: SA								3 + 5→4	3 + 5→4

APPENDIX *Continued*

Palaeotrema loveni: SA								3 + 4	3 + 4
Plagiobrissus costae: PP	8,9	4	4→5	13,14	6	6(7)	21–22	13	13
Plagiobrissus costae: SA								3 + 5→4	3 + 4→5
Plagiobrissus grandis: A								8→4	4→8
Plagiobrissus grandis: PP	7,8	4	4→5	12	6	6 (7)	?	12	12,13
Plagiobrissus grandis: SA								3 + 5→4	3 + 4→5
Plethotaenia angularis: PP	(8–10)	6/7+8	6/7+8	15–17	8	8(9)	19–22	12,13	12,13
Plethotaenia angularis: SA								3 + 5→4	3 + 4→5
Plethotaenia spatangoides: PP	(7–10)	(5–8)	(5–8)	(9–17)	(6–9)	(6–9)	18–25	11	11,12
Plethotaenia spatangoides: SA							6–8	3 + 5→4	3 + 4→5
Rhynobrissus tumulus: A								9→5	5→9
Rhynobrissus tumulus: PP	7,6	5	5	10	7	7(8)	18	11	11
Rhynobrissus tumulus: SA								3 + 4	3 + 4
Spatangobrissus laubei: PP	7,8	5	5	10	6	6(7)	16–17	10	11
Spatangobrissus laubei: SA								3 + 4	3 + 4
SPATANGIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Spatangus purpureus: SA								3 + 5→4	3 + 4→5
LOVENIIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Breynia australis: IF	10,12,13,14	9	9→11	23–29	?10,11	?10,11	32–34	15	15
Breynia australis: PP	7,8	4	4→5	11,12	6	6(7)	18–19	9,10	10
Breynia australis: SA								3 + 5→4	3 + 4→5
Echinocardium cordatum: A								7→4	4–7
Echinocardium cordatum: IF	6,6	5→7	7	19–22	?10	?10	?	14	15
Echinocardium cordatum: SA								3 + 4	3 + 4
Echinocardium flavescens: A								7→4	4→7
Echinocardium flavescens: IF	10, 11	7	7→8	17–18	10,11	10,11	22–23	14	14
Echinocardium flavescens: SA								3 + 5→4	3 + 4→5
Echinocardium pennatifidum: IF	11, 11	6→8	7→8	20–22	10,11	10,11	?	14	15
Echinocardium pennatifidum: SA								3 + 5→4	3 + 4
Lovenia elongata: IF	10, 11, 12	8→9	10–11	21–25	12,13	12	35	16,17	17
Lovenia elongata: SA								3 + 6→4	3 + 4→6
Lovenia subcarinata: IF	6, 6	4→6	6→7,8		?10	?10		?15/16	?15/16
Lovenia subcarinata: SA								3 + 6→4	3 + 4→6
AEROPSIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Coraster villanovae: PP	4,5	4	4	8	5→6	6(7)	14–15	9	9,10
Homoeaster tunetanus: PP	4	4	4	7	5	5(6)	11,12	8	9

Homoeaster auberti: PP	4,5	5	5	9, 10	6→7	6(7)	17	11	11
Sphenaster larumbensis: PP	4	4,5	5		5	5(6)	?	10,11	10,11
Aceste bellidifera: PP	3,4	4	4→5	7	4→5	5(6)	11	8	8
Aeropsis rostrata: PP	3	3	3	7,	5	5(6)	12	9	8
SOMALIASTERIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Iraniaster morgani: PP	5	4	4	10	5	5(6)		8	8
Iraniaster affinimorgani: PP	4,5	4	4	11,12,13	5	5(6)	17–19	8,9,10	8,9,10
Iraniaster affinidouvillei: PP	5	4	4	11	5	5(6)	15	8,9	8,9
HEMIASTERIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Bolbaster prunella: PP	6,7	5	5	11–13	6→7	6(7)	17–18	9	9
Hemiaster subsimilis: PP	6,6	5	5	11–12	6→7	6(7)		9, 10	9, 10
Hemiaster ameliae: PP	6,6	4→5	5	11–12	6→7	6(7)		10	10
Hemiaster angustipneustes: PP	6,7	5	5	13	6→7	6(7)	20	10	10
Hemiaster bufo: PP	6,6	6	6	11–12	6→7	6(7)	18–20	10	10
Hemiaster calvini: PP	(6,7)	(6,7)	(6,7)	11–12	6→7	6(7)	(18–20)	(10)	(10)
Hemiaster desvauxi: PP	6,7	5	5	13–14	6→7	6(7)	22	9	10
Hemiaster (Holanthus) expurgitus: PP	7,8,9	4(5)	4/5(4)	13–14	5	5(6)	19–21	9	9
Hemiaster grossouverei: PP	6,6	5	5	13	6→7	6(7)		10	10
Hemiaster hypocastanum: PP	6,6	4	4	12–13	6→7	6(7)	22, 23	9	9
Hemiaster ligeriensis: PP	7,8	5	5	10–11	6	6(7)		9	9
Heterolampas maresi: PP		5	5	13	6: 6→7	6(7)	18	9	9
Holanthus hawkinsi: PP	?	5	5	6	6, 6→7	6(7)	17–19	10	11
Leymeriaster forbesi: PP	?	5	5	?	6→8	6(7)	16	10	10
Leymeriaster leymerei: PP	8	6	7		6→8	7(8)		?	?
Leymeriaster nuciformis: PP	8	5	5	13	6→7	7(8)	18–20	10	11
Leymeriaster regulusi: PP	8,	5	5	?	6	7(8)	19–20	10	10,11
Mecaster batnensis: PP	5,6	4	4	11,12	5→6	6(7)		9	10
Mecaster cubicus: PP	6,7	5	5	12,13	6→8(9)	(9→8) 8→7	19–21	9	9,10
Mecaster fourneli: PP	5	4	4	10,11	5→7	6(7)	19–20	9	9
Palaeostoma mirabile: PP	3,4	4	4 (3)	6	5→6	6(7)	12	9	9
Palaeostoma zitteli: PP	4,4	4	4	9, 10	5→6	6(7)	15–16	8	8
Proraster geayi: PP	4	4	4	?	5→6	6(7)	?	9	9
Psephoaster klydonos: PP	6,7	5(6)	5(6)	11,12	6	6(7)		9	10
MICRASTERIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Cyclaster recens: PP	9,9	6→8	8	16,16	8→9	9→8(9)	20–20	12	13
Cyclaster recens: SA								2 + 5	2/3 + 5
Plesiaster peini: PP	(6,7)	(5/6)	(5/6)	(11–13)	(6,7,8,9)	(7,8,9)	18–19	10,11	10,11
Plesiaster peini: SA								2 + 5→4	2/3 + 5

APPENDIX *Continued*

Cyclaster archeri: PP					9,10	9	21–22	12,13	13
Cyclaster archeri: SA								2 + 5→4	2/3 + 4
Cyclaster integer: PP					7,8	7,8		11	11
Cyclaster integer: SA								2 + 5	2/3 + 4→5
Cyclaster regalis: PP	9,10	6→8	8→7 (7)	15,16	9→10	9→8: (9)	19–20	12	13
Cyclaster regalis: SA								2 + 5	2/3 + 5
Micraster coranguinum: SA								2 + 5(4)	2/3 + 5→6
Gibaaster gibbus: SA								2 + 5	2/3 + 5
Diplodetus sp.: SA								2 + 5(4)	2/3 + 5
SCHIZASTERIDAE	IIIa/b	2a	2b	IIa/b	1a	1b	Ia,b	5a	5b
Abatus cavernosus: M/SP	6,7	4	4	40117	4→6	5(6)	17–19	9	9,10
Agassizia scrobiculata: M	3	3	3	6	4	4(5)	10,11	5→4	5→6
Agassizia scrobiculata: SP					4→7	7(8)	15	9	9
Agassizia excentrica: M	3	3	3	6	4	4(5)	10	5→4	5→4
Agassizia excentrica: SP					4→7	6(7)	15	9	9
Aguayoaster aguayoi: M	4	4	4	9,10	5	4(5)	13	5→4	4→5
Aguayoaster aguayoi: SP					5→7	6(7)	?	11	11
Aplospatangus eurynotus: M	4	4	4	8	5	4(5)	?	6→4	4→6
Aplospatangus eurynotus: SP					5→6	6	?	10	10
Arguayoaster shickleri: M	4	4	4	8,9	5	?	?	6→4	4→5
Arguayoaster shickleri: SP					5→6	6	?	11	11
Brisaster fragilis: M	4	4	4	11,12	5	4(5)	11,12	5→4	4→5
Brisaster fragilis: SP					5→7	6(7)	17–18	10	10
Caribbaster loveni: M	4	4	4	9,10	5	?	?	?	?
Caribbaster loveni: SP					5→6	?	?		10
Diploporaster savigni: M	4	4	4	10,11	5	4(5)	13–14	6→4	?
Diploporaster savigni: SP					5→6	6(7)	19–20	10	10
Hypselaster jukesii: M	4	4	4	10,11,12	5	–	10	5→4	4→5
Hypselaster jukesii: SP					5→6	6(7)	16–18	10,11	10,11
Hypselaster limicolus: M/SP	4	4	4	11,12	5→6	6(7)	18–19	10	10
Linthia oblonga: M	4,5	4(5)	4(5)	11,12	5	4(5)		5→4	5→6
Linthia oblonga: SP					5→6	6(7)		8	8,9
Linthia somaliensis: M	6	4	4	9,10	5	4(5)	10,11	5→4	4→5
Linthia somaliensis: SP					5→6	6(7)	15	8,9	9
Linthia sudanensis: M	4	4	4	8,9	5	4(5)	10–13	6,5,4	4,5
Linthia sudanensis: SP					5→7	6(7)	16–17	10	10
Linthia variabilis: M	4,5	4	4	9,10	5	4(5)	13,12	6–4	4–6

Linthia variabilis: SP					5→7	6(7)	18	10	10
Lutetiaster cavernosus: M	5,6	4	4	11	5	4(5)	12,13	6→4	4→5
Lutetiaster cavernosus: SP					5→7	6(7)	17–18	10	10
Moira atropos: M	4	4	4	11,12	5	4(5)	9,10	6→4	4→6
Moira atropos: SP					5→7	6(7)	14–15	11	11
Opissaster cotteaui: M/SP					5→ 7	6(7)	17–18	11	11
Opissaster farquharsoni: M					5			4	4
Opissaster farquharsoni: SP	4,5	4	4	11,11	5→6	6(7)	18–19	9	10
Ova canaliferus: M	4	4	4	10	5	4(5)	12,13	6→4	4→6
Ova canaliferus: SP					5,6	6(7)	18–19	10	10
Parapneustes cordatus: M/SP	6,7	4	4	10,11	4→5	5(6)	15–16	9	8,9
Paraster compactus: M	4	4	4	10,11,12	5	4(5)	14	6→4	4→6
Paraster compactus: SP					5→7	6(7)	19–21	11	11
Periaster sp.: M	6	4	4	?	5	4(5)		6→4	4→6
Periaster sp.: PP	7	5	5		5→7	7→6(6)		9	9
Periaster elatus: M	4, 5	5	5(6)	10–12	5	4(5)	13	5→4	4→5
Periaster elatus: PP					5→7	6(5)	18–19	8–9	10–8
Periaster sp. nov of Turki: M	5,6	5(4/5)	5	11,12	5	4(5)	12,13?	6→5	4→6
Periaster sp. nov of Turki: SP					5→6	6→5	17,18,19	9,10	9
Periaster undulatus: M	4	4(5)	5	9,10	5	4(5)	?	6→4	4→5
Periaster undulatus: SP					5→7	6(7)	?	10,11	10
Phrymnaster investigatoralis: M	4	4(5)	5	11	5	4(5)	10,11	5→4	4→5
Phrymnaster investigatoralis: SP					5→6	6(7)	15–16	10	10
Prenaster excentricus: M	4,4	3	3	7,8	4	4(5)		5→4	4→5
Prenaster excentricus: SP					4→8	7(8)		13/14	13/14
Protenaster australis: M	7,8	4 (4→5)	4	12,13	5	4(5)	13–14	6→4	4→6
Protenaster australis: SP					5→7	6(7)	22–23	10	10
Pseudabatus nimrodi	10	4	4	14,15	5→7	7	18–19	8,9	9
Saviniaster enodatus: M	3	3	3	7	4	4(5)	9,10	5→4	4→5
Saviniaster enodatus: SP					4→7	7(8)	20	11	11
Schizaster floridanus: M	4	4	4	11,12	5	4(5)	13–14	6→4	4→6
Schizaster floridanus: SP					5→7	6(7)	20–22	11	11
Schizaster lacunosus: M	4	4	4	10	5	4(5)	14–15	10	10
Schizaster lacunosus: SP					5→6	6(7)	18	6→4	4→6
Schizaster studeri: M	5	4(5)	4	?	5	4(5)	?	6→4	4→5
Schizaster studeri: SP					5→7	6(7)	?	11	11
Tripylaster philippii: M	5,6	4	4	12,13	5	4(5)	11	5→4	4→5
Tripylaster philippii: SP					5→7	6(7)	18	11	10
Tripylus excavatus: M	6,7	4	4	10,11	4	4(5)	13	5→4	4→5
Tripylus excavatus: SP					4→6	6(7)	18	9	8,9