A reassessment of the Lower Cambrian psammocoral *Spatangopsis costata*

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Abstract. The sand button of the psammocoral (vendobiont) *Spatangopsis costata* from the Early Cambrian Mickwitzia Sandstone of Sweden possessed radial rays on its uppermost surface that extended outward, in the living organism, farther than previously recognized. With intact rays, the button reached a diameter three or more times larger than its normally preserved central portion. The rays were likely housed in soft-tissue slots in close proximity to the external environment, and may have become directly exposed and easily broken off if the soft tissues contracted during storm-induced transportation, thus producing the normally observed short rays.

A large individual, exceptionally preserved in situ, shows the true length of rays, as well as a major portion of a circular, radially ribbed mechanical impression of a soft-tissue surface underneath the button. Back-filling of this impression suggests a slight, active upwards movement to counter sedimentation. Small individuals are more commonly preserved with complete rays.

A reconstruction of the *S. costata* organism as a solitary polyp appears unlikely, since the above evidence leaves insufficient space for an actinian-like gut above the sand button. More likely alternatives are a colonial organism in which a large, central polyp/zooid was specialized as a sand-weighted anchor and supported a number of smaller feeding individuals, or a solitary or colonial descendant of frond-bearing Ediacaran vendobionts that replaced the basal holdfast with a weighted anchor, as an evolutionary response to the Early Paleozoic decrease in biomats suitable for the disc type of attachment, and probably carried multiple fronds. Fragmentary impressions of suitable candidates for these fronds are preserved in the same sediments.

Key words: adaptation, Cambrian, Mickwitzia Sandstone, Psammocorallia, *Spatangopsis*, Vendobionta

Introduction

The Mickwitzia Sandstone in the areas of Lugnås and Kinnekulle (Early Cambrian, Vestrogothia, southern-central Sweden) contains a variety of ichnofossils, including *Bergaueria* (frequently interpreted as an actinian burrow; e.g. Seilacher, 2007), the arthropod-made *Cruziana* and *Rusophycus* (Rydell *et al.*, 2001; Seilacher, 2007, and references therein), abundant *Eophyton* toolmarks and a few types of peculiar body fossils, discussed below. Structures often interpreted as related to biomats ("elephant-skin" and other wrinkle structures, as well as *Kinneya*-type "peanut blisters"; see, e.g. Porada and Bouougri, 2007; Seilacher, 2007) are also relatively common. Accumulations of mat chip (or sand chip) structures, generally regarded as originating from microbial mats (Pflueger and Gresse, 1996; Gerdes,

2007; Mei *et al.*, 2007), also occur in these beds (e.g. Savazzi, 2007, figure 3a–b). Jensen (1997) reviewed the ichnofossils of these localities and summarized the relevant geological and paleontological literature.

The sediment is siliciclastic, coarsely bedded and with frequent ripple marks, indicative of relatively shallow water subjected to waves and currents (above references, especially Jensen, 1997). Storm activity is suggested by thick individual beds that grade from coarse granulometry at their bottom to fine at their top (above references).

Among the fossils of the above localities, *Spatangopsis costata* Torell, 1870 and *Protolyellia princeps* Torell, 1870 are relatively common. Both species are preserved as "buttons" of relatively coarse and well sorted sand particles. These sand buttons are granulometrically distinct from the surrounding sediment, which consists prevalently of finer particles (Seilacher, 1992;

Savazzi, 2007, and references therein). Both genera were interpreted as psammocorals by Seilacher (1992), *i.e.*, as organisms lacking a mineralized skeleton and gradually forming a permanent accumulation of cemented sediment particles within an internal body cavity (see also below).

P. princeps is circular in outline and generally lens-shaped (Seilacher, 1992; Seilacher and Goldring, 1996; Savazzi, 2007), while *S. costata* possesses an overall radiate symmetry, often superposed onto a roughly circular shape (Seilacher, 1992; Seilacher and Goldring, 1996, and below). The shapes and sizes of the sand buttons are quite variable among specimens of both genera. The geometry of individual specimens is often somewhat irregular, albeit their basic circular or radiate organization is always apparent.

The *P. princeps* button has a convex, smooth side displaying coarse sediment particles on its outer surface (and most of the button interior) and a usually flatter opposite side covered with an irregular network or "beehive" pattern in relief on a thin layer of fine-grained sediment particles (above references). *Spatangopsis* consists of a sand button with three to five (or occasionally more) radial ridges in relief on one face, originating from the center of this face. The opposite side of the button is convex and smooth, often with a central depression (Seilacher, 1992; Seilacher and Goldring, 1996).

Both genera are almost invariably preserved in a constant orientation, *i.e., Protolyellia* with its beehive pattern uppermost, and *Spatangopsis* with its rays uppermost. This orientation was interpreted by Seilacher (1992) as corresponding to the life orientation. He further argued that the placement of the heavy button lowermost within the soft parts facilitated a passive reorientation of the organism after transportation by water currents or waves. This interpretation has been supported by subsequent literature (see below).

Spatangopsis and *Protolyellia* were variously interpreted in the literature as sediment infillings of jellyfish internal cavities (e.g. Walcott, 1898; Nathorst, 1910), ichnofossils (Jensen, 1991) and Problematica (Campbell and Paul, 1983). Since Seilacher's (1992) interpretation of these genera as psammocorals, *Spatangopsis* and *Protolyellia* have largely been regarded as body fossils, although their affinities are still uncertain. Seilacher (1992) regarded both genera as representatives of the Vendozoa, originally established by him at the time not as a formal taxon, but rather as an informal group of organisms sharing partly similar body plans that differ from those of modern phyla. This group was formally renamed Kingdom Vendobionta (Seilacher in Seilacher and Goldring, 1996). Within the Vendozoa/Vendobionta, Seilacher (in Seilacher and Goldring, 1996) further characterized the Class Psammocorallia as a group of organ-isms possessing an internal sand skeleton, which often is the only preserved portion of the organism. In the present paper, the writer uses the psammocoral denomination as a morphologic grouping, without strict taxonomic implications.

The sand button of psammocorals consists of an aggregation of sediment particles, apparently collected by the organism from its immediate surroundings. Selective granulometric sorting with respect to surrounding sediment is evident. Sediment particles of the sand button also seem to be preferentially oriented with their longer axes parallel to the ventral button surface (see below). The sand skeleton appears to have been weakly cemented during the life of the organism, thus allowing its preservation if buried relatively quickly (Seilacher, 1992). Specimens are sometimes penetrated and partly reworked by infaunal burrowing organisms. This indicates that the button reverted to unconsolidated sediment in a relatively short time after the death of the organism.

Savazzi's (2007) interpretation of *P. princeps* differs from earlier studies (e.g. Seilacher, 1992; Seilacher and Goldring, 1996). He interpreted the wrinkled layer as part of a sand-covered external epithelium enclosing a column of soft tissues extending above the sand button, rather than as a part of the sand button *in vivo*. Fragments of this sand-covered epithelium, in various states of preservation, are frequent in sediments containing the *P. princeps* button, and laterally felled columns are occasionally preserved in direct proximity to the buttons (Savazzi, 2007). After the burial and death of the organism, sedimentary compaction and decay of the soft parts caused the lowermost portion of the column, and its wrinkled epithelium, to be pressed against the dorsal surface of the button. Thus, the placement of the dorsal wrinkled layer of *P. princeps* is a taphonomic artifact caused by the post-decay fusion of two structures originally not juxtaposed in the living organism.

The present paper reexamines *S. costata* in order to assess its anatomy, mode of life, and possible affinities with *Protolyellia* and other psammocorals.

Materials and methods

A few tens of specimens of *S. costata* from the Early Cambrian Mickwitzia Sandstone of localities of the Vestrogothia (Västergötaland in Swedish language) region of southern-central Sweden, stored in the collections of the Swedish Museum of Natural History, Stockholm, Sweden, were examined for this study. Inventory numbers, if available, are indicated in the figure captions.

Most of the larger specimens are isolated from the matrix, either by weathering or mechanical extraction by collectors. Several small specimens, and a large one, are
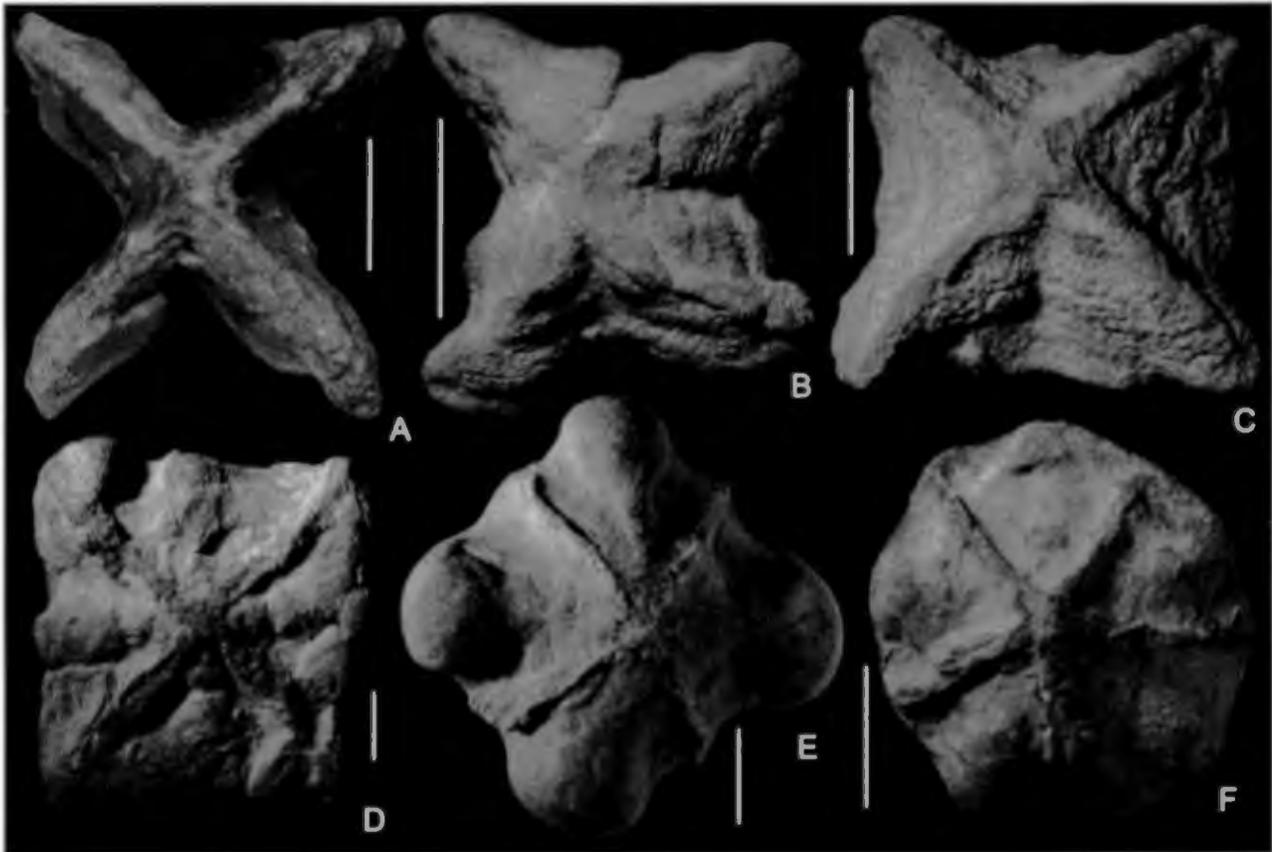
Figure 1. Dorsal surface of isolated *Spatangopsis costata*. Four-rayed (**A–E**) and five-rayed (**F**) specimens displaying a varying development of cheeks and a varying volume of the sand button. Lugnås (A–C, E–F) and Kinnekulle (D), Vestrogothia, Sweden. Scale bars represent 20 mm.

still partly embedded in the matrix.

Discussion

Terminology

In order to discuss the morphology and preservation of *S. costata*, it is necessary to define a few descriptive terms. Further morphologic terms referring to features of the *Spatangopsis* sand button are discussed in the introduction.

The side of the *Spatangopsis* sand button that carries a radially arranged relief is normally preserved uppermost, and is called *dorsal* in the following discussion (Figure 1). The opposite side is smoothly convex or flat, sometimes dimpled at its center (see below), and is called *ventral*. (Figure 2). This nomenclature carries no anatomical implications. The terms *dorsal view* and *ventral view* are used for illustrations that display the corresponding regions.

The *periphery* of the button is the curved surface that gradually joins the dorsal and ventral regions (Figure 3). The term *lateral view* is used for figures that illustrate this peripheral region from a direction perpendicular to the dorso-ventral axis.

The narrow, radial relief ridges displayed on the dorsal surface are hereby referred to as *rays* (see Figure 1A–F). The portion of sand button delimited by two adjacent rays is called a *sector*. In specimens in which sectors possess a central indentation (e.g. Figure 1A–C), it is convenient to use the term *arm* to indicate the radially protruding region located underneath each ray.

In some specimens, the sand button displays peripheral swellings in the middle of each sector (Figure 1D–F). These swellings are called *cheeks* (Seilacher and Goldring, 1996). Figure 1C displays moderately developed cheeks, while the specimen in Figure 1D is an extreme example of protruding cheeks.

In addition to a "fat" morphotype with protruding and well developed cheeks, a "skinny" morphotype is also common. It is characterized by deep indentations,
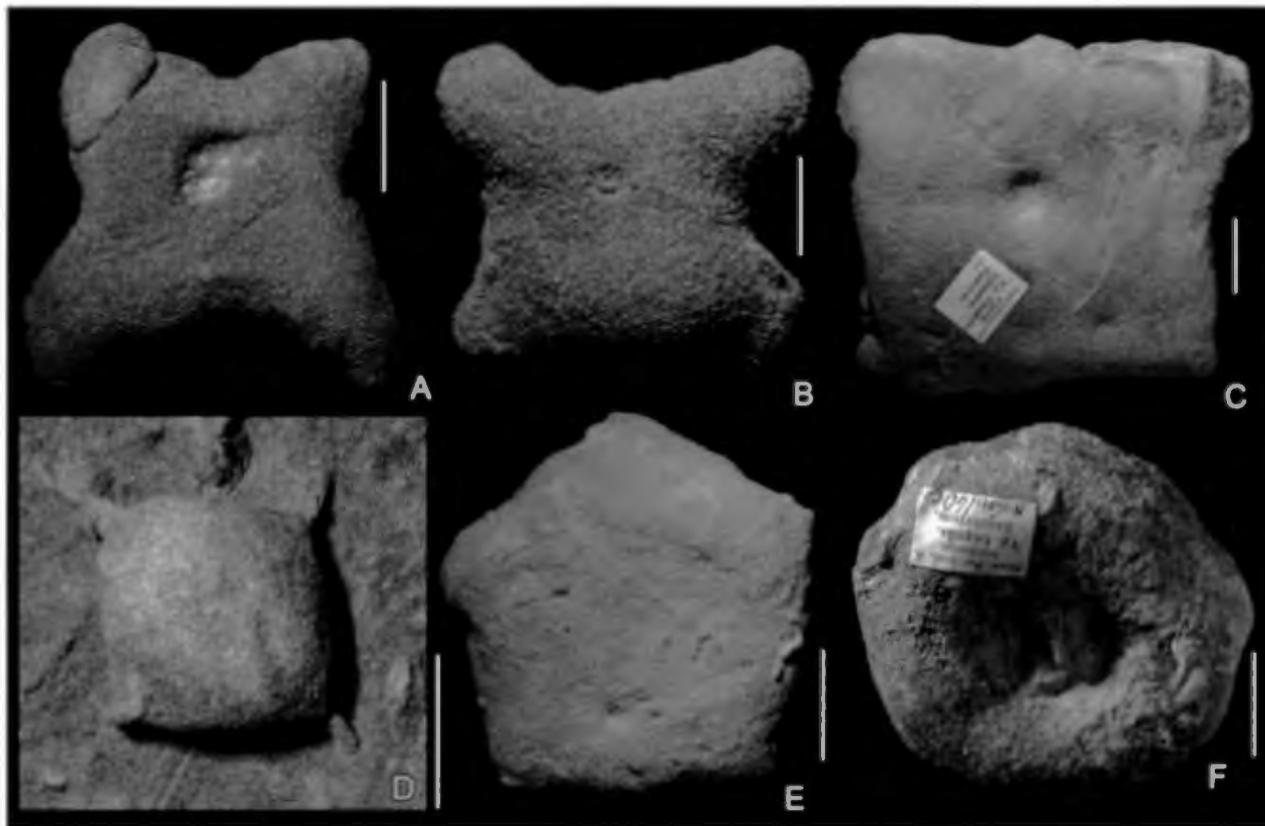
Figure 2. Ventral surface of *Spatangopsis costata*. Four-rayed (**A–D**) and five-rayed (**E–F**) specimens. Note the variable development of the ventral dimple. Lugnås (A–B, E–F) and Kinnekulle (C–D), Vestrogothia, Sweden (F: Cn 160C). Scale bars represent 20 mm.

or *valleys*, in the outline of the sand button, in correspondence to the center of each sector (Figure 1A–B). Within the skinny morphotype, the thickness of the rays is much variable (Figure 1A–B). The specimen in Figure 1C displays shallow valleys in three sectors, but the remaining sector seems to display an incipient cheek (unless this is a taphonomic artifact caused by compaction and/or reworking by ichnofossils). The two morphotypes appear to grade into each other. The specimen in Figure 1A is an extreme case of the skinny morphotype, and partly conforms to the diagnostic characters of *S. alata* (Seilacher in Seilacher and Goldring, 1996), albeit it lacks the distinctive growth lines of this species and therefore is regarded herein as *S. costata*.

The ventral surface (Figure 2) is smooth. The rounded depression often present at the center of the ventral surface (Figure 2A–C) is called *dimple* (Seilacher and Goldring, 1996). The dimple is of variable diameter and depth, and may be totally absent (Figure 2D–E). Figure 2F shows an extremely large dimple, which may be the result of post-mortem reworking by burrowing organisms.

Figure 3B shows an unusual, sharp ridge around the periphery of the button. Since this specimen also displays an evident reworking by burrowing organisms, it is likely that the peripheral ridge is a taphonomic artifact caused by partial compaction and collapse of a button that had already turned into loose sediment.

Morphology and preservation

Large specimens of *S. costata* in museum collections are typically isolated from their matrix. The specimens in Figures 1–3 (with the exception of Figure 2D, which is unusual in being preserved in hyporelief) are typical of this type of material.

Small specimens of *S. costata* embedded in the matrix at the top of bedding planes are available among the studied material (Figure 4). Some of the specimens of this type are weathered, but their outlines clearly stand out from the surrounding matrix (Figure 4A). Other specimens are better preserved in three-dimensional relief (Figure 4B–C).
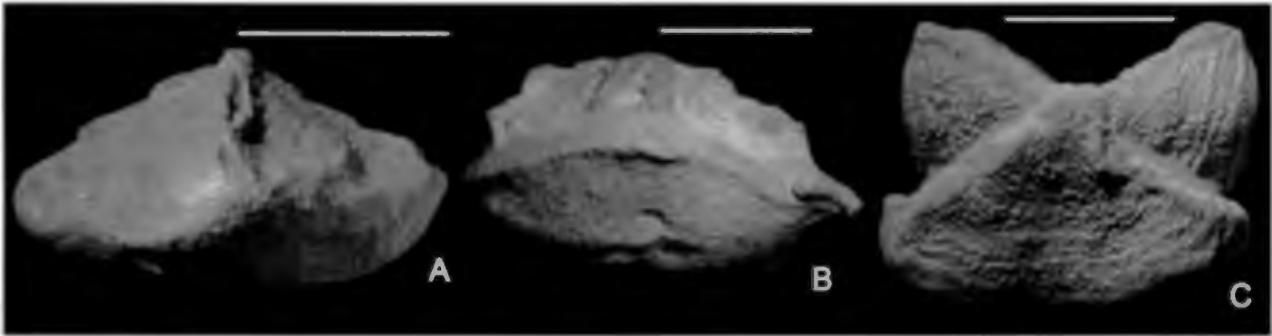
Figure 3. Lateral views of *Spatangopsis costata*. **A,** typical aspect of a slightly irregular specimen; **B,** an unusual specimen with a sharp ridge along its periphery and evident reworking by ichnofossils; **C,** a compactionally deformed specimen, probably buried in an oblique orientation, with coarse growth lines. Scale bars represent 20 mm.
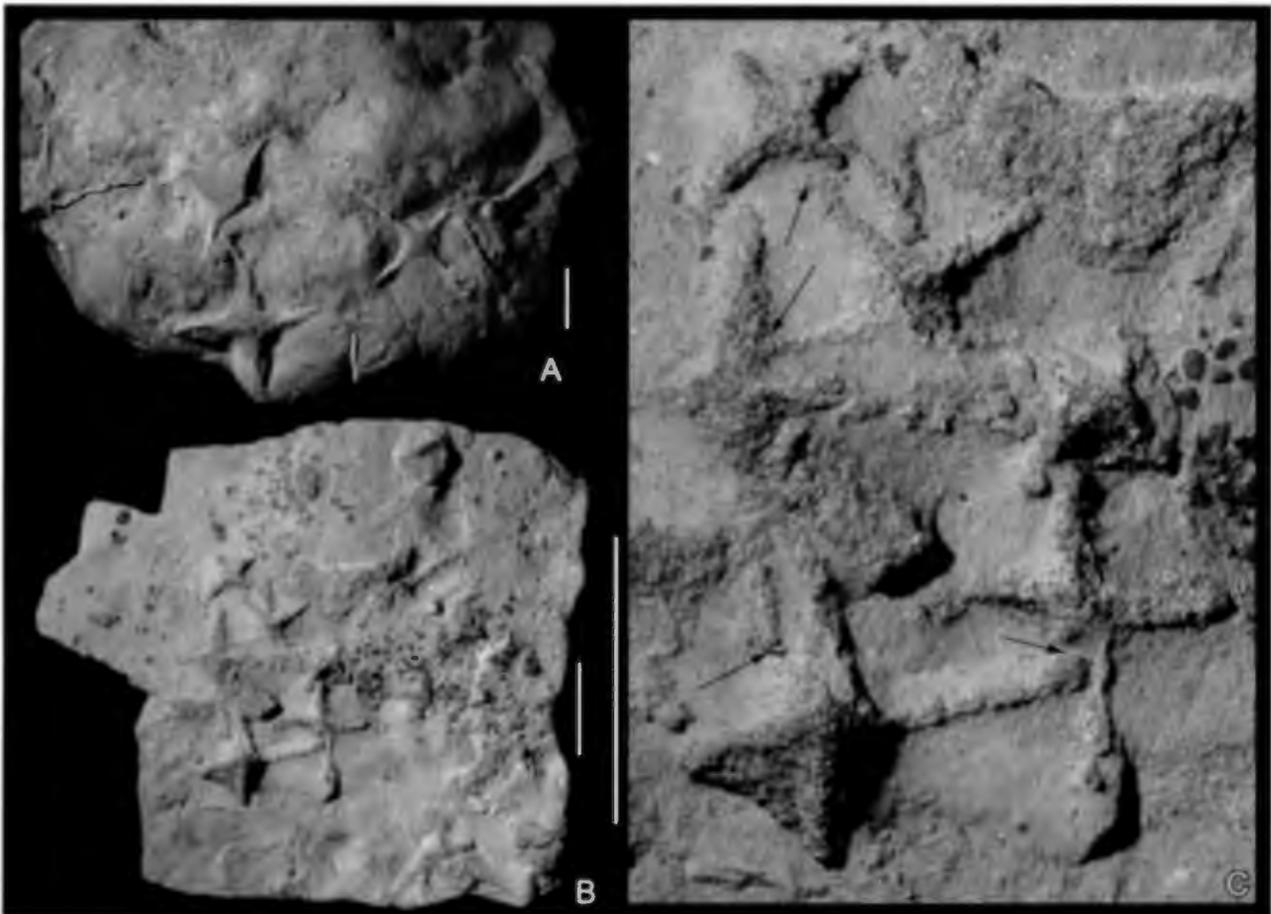

Figure 4. Slabs containing *Spatangopsis costata*. **A,** from Kinnekulle, Vestrogothia, Sweden; **B, C,** from Lugnås, Vestrogothia, Sweden. Scale bars represent 10 mm.

The slab in Figure 4B–C shows individuals embedded at slightly different depths into the bedding plane. The following observations can be made on this slab:

- As noted by Seilacher (1992), adjacent individuals of *S. costata* never penetrate each other. The observed behavior is expected of body fossils, while ichnofossils and synsedimentary structures commonly penetrate and modify earlier structures of the same types.
- The rays extend for a substantial distance from the perimeter of the body. In some cases (e.g. most individuals in Figure 4A; lowermost portion of Figure 4C), each ray extends for a total length from the center exceeding twice the diameter of the central body of the button. This is in stark contrast with larger specimens isolated from the matrix, in which the rays project from the perimeter of the main button, and above its dorsal surface, only by a few millimeters.
- Individuals are packed closely together, with the extremities of the rays abutting and slightly overlapping portions of the neighboring sand buttons. This occurrence is compatible with a process of storm- or current-induced sorting and accumulation of sessile organisms, which is generally assumed as being involved in the typical taphonomy of these organisms (Seilacher, 1992; Buss and Seilacher, 1994; Seilacher and Goldring, 1996). The organisms, unless quickly buried, may have survived this type of transportation event, thanks to the passive righting encouraged by the heavy sand button located lowermost within their soft parts. This type of occurrence, however, is also compatible with a process of gradual crowding, in which individuals encroach onto neighboring ones during growth.

A large, five-rayed specimen of *S. costata*, partly embedded in sediment (Figure 5), sheds additional light on the morphology of the *S. costata* organism and on the preservation of its button. This specimen is characterized by a very long ray, extending outward from the perimeter of the central sand button for a distance approaching the diameter of the central button (Figure 5A). Thus, assuming that all rays were equally developed, the total diameter of the button, and therefore of the organism, was approximately three times the diameter of the central button as normally preserved in large specimens. As a result, the morphology of this specimen was quite similar to the small individuals of Figure 4.

It should be noted that specimens with mostly or entirely preserved rays are illustrated in the literature (Nathorst, 1881, pl. 4, figures 1, 3) and this character was recognized by Jensen (1997). However, these observations apparently were not incorporated in subsequent reconstructions of *Spatangopsis* as a psammocoral

(Seilacher, 1992; Buss and Seilacher, 1994; Seilacher and Goldring, 1996), which only show the sand button as normally preserved, *i.e.*, with mutilated rays.

The specimen in Figure 2D conforms to the same geometry, although its rays are only partly preserved. The dorsal portion of this sand button (facing away from the observer in the figure) appears to have been planed off by a large passing object that left a toolmark with parallel ridges (probably *Eophyton*) and destroyed the dorsal surface of the button and the projecting portions of the rays. This type of preservation implies that the sand button of this specimen consisted of loose particles at the time (see also above). Jensen (1997, figure 12D) illustrated a similarly preserved, five-rayed specimen.

It is likely that the rays of individuals of geometry similar to the one described above, during post-mortem transportation prior to final burial, as well as weathering and/or mechanical extraction of fossils from the matrix, would largely break off, producing the commonly observed morphology with rays projecting by only a few millimeters above the dorsal surface of the button. In fact, the irregular appearance of the topmost ridge of large portions of the rays in most specimens (e.g. Figure 1 C–F) does suggest a mechanical fracturing. The causes and mode of fracturing of the rays are discussed below.

The writer regards the above specimens as sufficient evidence that the rays of *S. costata* normally did extend far beyond the outline of the central sand button. The question remains, whether the soft parts were shaped like a thin envelope that replicated the outline of the button and its rays (thereby imparting a star-shape to the perimeter of the organism), or as a thick mass that surrounded the skeleton, giving the organism a circular or slightly polygonal perimeter.

The latter question is answered by the specimen in Figure 5. The bottom of the slab displays a distinct impression bearing numerous coarse radial ribs (Figure 5B). This impression, incompletely preserved, is centered directly beneath the button (as evidenced by the radial relief pattern of the impression). The impression extends from the center of the button to a distance comparable to the total length of the single preserved ray. This ribbed impression was produced by a structure that extended uninterrupted between adjacent rays of the *S. costata* organism. Its apparent outline is roughly circular, and does not visibly reflect the radiate geometry of the button. This surface sloped uniformly upwards from the center to its periphery.

From the preserved portion, which represents roughly one-quarter of the structure, it is possible to infer the presence of approximately 30 ribs around its whole perimeter. Adjacent ribs are rather irregularly spaced (roughly 10–20 mm) and approximately constant in
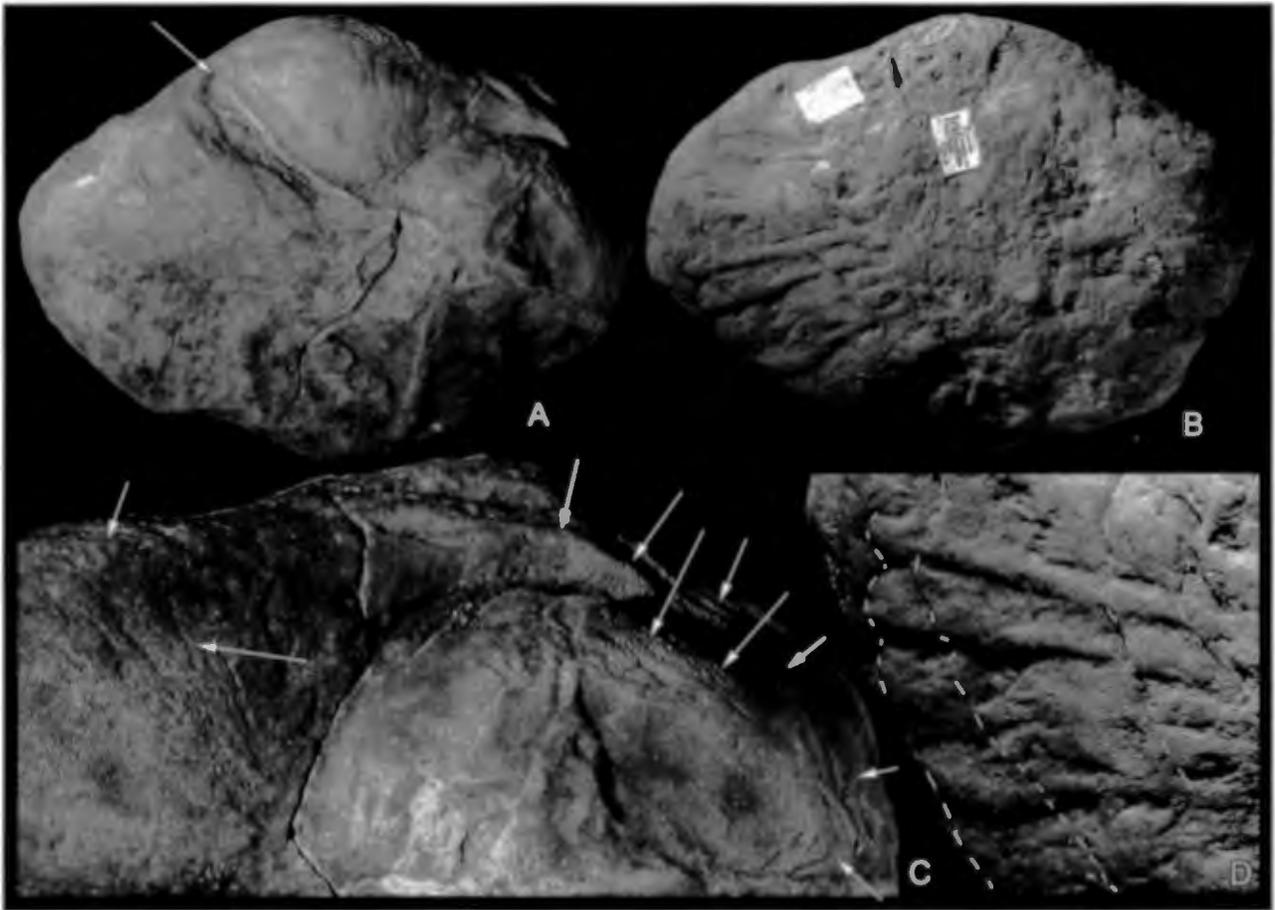
Figure 5. Specimen of *Spatangopsis costata* embedded in life position in sediment (NRM X3238a and b). **A**, dorsal surface (the arrow points to the extremity of one of the rays); **B**, impression of soft parts surrounding and enclosing the ventral region of the sand button (which is embedded in the sediment and not visible); **C**, detail of fine sediment layering (arrows) surrounding the dorsal region of the sand button; **D**, magnified portion of impression of ventral soft parts, showing radial ridges and layering (white dashes are added to emphasize the edges of sediment layers). Scale bars represent 15 mm.

thickness along the perimeter (roughly 5–7 mm). There is no evidence of ribs branching along their length.

The undersurface of the slab, in the region immediately below the ventral surface of the button in the original sedimentational orientation, displays an unsorted texture with coarse clasts mixed with fine ones (Figure 5B). This suggests that this part of the slab was probably located close to the bottom of a storm bed. The coarse clasts likely represent the material first deposited near the end of the storm event, with finer clasts being deposited afterwards, as the waves and/or currents subsided. The mixing of fine and coarse clasts, together with the lack of an impression directly below the center of the button, suggests that the coarse clasts were biogenically reworked from the bottom of the bed and mixed with subsequently deposited, much finer sediment. In the absence of other

traces of bioturbation in this area, active burrowing by the *S. costata* organism in an upward direction may well be the cause of this reworking.

The sand button of this individual is surrounded by finely layered sediment undisturbed by bioturbation (Figure 5C). This explains the presence of a fully preserved ray (the other rays were probably preserved, but subsequently destroyed by weathering of the fossil) and confirms the idea that the specimen is preserved *in situ*, rather than after storm transportation/concentration as typical of this species.

The ribbed impression under the button displays at least three thin successive layers, emphasized by weathering (Figure 5D). The rib pattern is exactly replicated from layer to layer, indicating that the structure that left the impression periodically moved upward, likely in

response to slow fouling by sedimentation. These layers are, therefore, analogous to the spreiten or back-fillings often produced by burrowing organisms under similar circumstances, and may be regarded as an example of the ichnotaxon Equilibrichnia (e.g. Bromley, 1990; Seilacher, 2007).

The slab of this specimen was evidently glued together after being broken in its middle. Since the laminations visible on the exterior of the block are well highlighted by weathering and, typically, freshly broken surfaces of this type display little or no visible bedding structures, it is doubtful that a visual observation of the broken surface would reveal any additional detail. For this reason, it was not attempted to separate the two glued portions.

Seilacher and Goldring (1996, figure 10A) published drawings of comparable impressions of soft parts, located underneath and around specimens of *S. costata* preserved on a ripple-mark surface as storm accumulations of individuals. Because of the different type of preservation, the soft-part impressions inspected by the above authors are not detailed and do not display recognizable spreiten, leading the authors to interpret the imprints as produced by a fringe of stiff tentacles, rather than a continuous ribbed surface. However, there is little reason to doubt that also these impressions were produced by the same type of ribbed surface shown in Figure 5B, D. Significantly, these specimens, in which the sand button was obviously surrounded by soft tissues at the time of burial, display mutilated rays as typical of the preservation of *S. costata*.

The above evidence strongly suggests that the specimen of Figure 5 represents an individual of *S. costata* preserved in life position on, or slightly buried within, a bed of fine-grained sediment that deposited slowly and gradually, during an uninterrupted hiatus between storm events. This is in contrast to the typical preservation of *S. costata* as storm accumulations (above references and discussion).

The almost universal orientation of transported and accumulated specimens with the dorsal side uppermost (above references) strongly suggests that the organisms were alive at the time, or at least that the button was surrounded by soft tissues and located near the bottom of the organism. Passive reorientation would not be possible, or would be less consistent than observed, in sand buttons separated from the soft parts. Therefore, the mutilation of the rays, always observed in large transported individuals, likely occurred already during the transportation of living organisms. In turn, this implies that the rays were likely housed in grooves or slots of soft tissues that directly communicated with the surrounding environment and allowed the ray fragments to escape. It is even possible that, as a response to storm transporta-

tion, the soft tissues of *S. costata* strongly contracted (as typical of certain soft-bodied invertebrates, e.g. actinians) and partially exposed the rays to the surrounding environment. Any preserved, isolated fragments of the rays are likely to pass unnoticed among the abundant sand-chips present in these beds (see above).

The present observations strongly support Seilacher's (1992) interpretation of the sand button of S. *costata* as a weighted internal anchor that stabilized the organism against waves and currents, and additionally facilitated its passive righting after accidental disturbances caused by storms. The writer sees no reason to suggest changes in this respect to Seilacher's "rock-in-a-sock" functional paradigm.

Growth

Numerous specimens of *S. costata* display coarse grooves and ridges on the dorsal surface of the button, roughly parallel to each other and unconformable with respect to the direction of the rays (Figure 3C). These relief features are always interrupted by rays, but it is often possible to follow individual grooves/ridges across rays and through most or all sectors of the specimen. As discussed by Seilacher, these features correspond to an internal layering of the button clasts, and are therefore analogous to growth lines, or growth increments, in accretionary skeletons. These growth increments allow one to infer that the button grew by addition of material on its perimeter and ventral surface. This is the same growth pattern displayed by the sand button of *Protolyellia* (Seilacher, 1992; Seilacher and Goldring, 1996; Savazzi, 2007).

Seilacher (1992) and Seilacher and Goldring (1996) hypothesized that sediment particles in both genera could be phagocitized and brought to the button chamber directly through the epithelia and tissues of the organism. While this mechanism cannot be conclusively proved or disproved, a more conservative alternative of ingestion through openings in the organism is equally compatible with the observed morphology. In particular, the central dorsal boss of *Protolyellia* and the dorsal edges of the rays in *Spatangopsis* are natural candidates for the location of such a connection.

In *Protolyellia*, the fine layer of particles on the dorsal button surface and its honeycomb relief pattern were interpreted by Seilacher (1992) as a genuine characteristic of the button. In turn, this made a transportation of coarse particles from the central dorsal boss to the ventral region of the button, *i.e.*, passing above the fine-grained honeycomb layer, unlikely. This objection was removed by Savazzi's (2007) finding that the honeycomb layer is allocthonous in life, and its typical preservation attached to the sand button a taphonomic artifact. Thus, both

genera could conceivably collect sand particles through one or more openings in direct communication with the external environment, and the buttons of *Protolyellia* and *Spatangopsis* apparently grew in the same fashion.

In the context of this mode of growth of the *S. costata* button, the ventral dimple can be interpreted either as the impression of a boss present at the bottom of the button chamber, or as a region into which sediment particles simply were not carried, thus causing the formation of a dimple even in the absence of a corresponding relief of the chamber bottom. The sometimes irregular shape of the dimple is consistent with the latter alternative. Seilacher and Goldring (1996, figure 10E–G) illustrated specimens of *S. costata* with lobes and furrows on the ventral surface, strongly suggesting an uneven transportation of particles fanning out from a few points on the periphery of the button, rather than being uniformly transported downward and inward from the whole periphery as typical. Such specimens are not present among the material available to the writer.

Since the volume of the dimple is usually a minor portion of the button volume, the formation of a dimple did not substantially reduce the weight of the button and wasted only little space inside the button chamber (with the possible exception of the extremely large dimple in Figure 2F, which may, at least in part, be a taphonomic artifact). Occasional specimens (e.g. Figure 2E) seem to display small multiple dimples, but their nature as a genuine feature is questionable.

The dorsal and peripheral surfaces of the button, in the best preserved specimens, often display a somewhat knobby surface, with individual "lumps" larger than the clast size. This is especially visible where "growth lines" are observed (e.g. Figure 3C). The exact significance of this character is not clear, but it appears to be a genuine feature rather than a preservational artifact, and its occurrence together with coarse growth lines may reflect a poorer control by the organism on the accretion of the button in these regions than on the ventral surface, which is typically smoother.

Affinities of *Spatangopsis costata*

Seilacher (in Seilacher and Goldring, 1996) included four species in the genus *Spatangopsis*:

- *S. costata* Torell, 1870, from the Mickwitzia Sandstone of Lugnås, Sweden.
- *S. alata* Seilacher, 1996 (in Seilacher and Goldring, 1996, from the Mickwitzia Sandstone of Lugnås, Sweden). This species is usually tetrameral and its sand button consists mostly of narrow arms, without a distinct central body. In general perimeter outline, *S. alata* is not unlike the specimen of *S. costata* in Figure 1F. The latter specimen, however, lacks the

prominent, subhorizontal irregular ridges present on the arms of *S. alata*. Among the material available for the current study, no specimens can be unequivocally referred to *S. alata*.

- *S. scotica* Seilacher, 1996 (in Seilacher and Goldring, 1996), from the Lower Cambrian Pipe Rock of Scotland. *S. scotica* was originally described as an unnamed body fossil by Campbell and Paul (1983). It is similar in general shape to specimens of *S. costata* with a rounded outline, but *S. scotica* appears to be always pentameral and a thin discontinuity (possibly marking the position of soft tissues or an organic membrane) runs radially through the center of each ray.
- *S. mongolica* Seilacher, 1996 (in Seilacher and Goldring, 1996), from the Lower Cambrian of Bayan Gol, Mongolia. This species is only known from hyporelief casts, rather than complete sand buttons. It had a large ventral dimple and a number of rays variable from five to seven (judging from published illustrations).

All species of *Spatangopsis* share a radiate symmetry. It seems likely that *S. costata* and *S. alata* are closely related.

The presence of a longitudinal soft-tissue septum penetrating along the top of each ray in *S. scotica*, hypothesized by Seilacher and Goldring (1996), sets this species apart from the two preceding ones, and is difficult to reconcile with the above reconstruction of the rays of *S. costata* being housed in soft-tissue slots that opened into the external environment. Alternatively, the observed, septum-like median discontinuity of the internal structure of the rays in this species may be a fabricational feature caused by accretion along both sides of the ray, rather than a cast of a septum. It is also possible that the discontinuity represents a region of different composition of the button (e.g. consisting largely of organic cement rather than sediment). It may also be noted that occasional specimens of *S. costata* display possible median discontinuities along their rays (Figure 3A; Seilacher and Goldring, 1996, figure 10D–E).

The affinities of *S. mongolica* are uncertain, since no sand button was found. Seilacher and Goldring (1996, figure 7C) illustrated a specimen of *P. benderi* from the Upper Ordovician of Jordan with five apparent rays on its dorsal surface. Other specimens of this species lack rays. Since this species also seems to lack the honeycomb layer characteristic of *P. princeps* (see above), the exact affinities of *P. benderi* with other psammocorals may be questionable.

The conservative reconstruction of *Spatangopsis* is that of a primitive actinian, or actinian-like polyp, with a sand button housed in a specialized cavity of the body

(above references). In spite of the additional evidence on the morphology and biology of *S. costata* provided by the present study, the affinities of *Spatangopsis* remain difficult to ascertain.

In view of the fact that the rays are typically mutilated in specimens of *S. costata* that were transported with the button still surrounded by soft tissues (see above), a reconstruction of *S. costata* with the button housed deep within a specialized diverticulum located at the bottom of the gut cavity, by analogy with Savazzi's (2007) reconstruction of *P. princeps*, is not consistent with the evidence. The close proximity of the *S. costata* rays with the external environment along their entire length leaves little or no space available, in the soft tissues above the button, for a central gut comparable with that of a modern actinian or polyp. Although the cavity housing the button in *S. costata* may have evolved from a gut similar to the one in modern coelenterates and the one hypothesized in *P. princeps*, it may have entirely lost its digestive function in *S. costata*, and the digestive process may have been carried out by other structures. Thus, *S. costata* may not be closely related to *Protolyellia*, and their similarities may, at least in part, be due to functional convergence of the button as a weighted anchor.

As an alternative hypothesis to the polyp paradigm, *S.costata* could have been a colonial organism with a central body (probably representing a modified polyp or zooid) carrying numerous, smaller feeding individuals on its dorsal surface. This type of organization would have freed the central individual from the necessity of keeping a functional gut, and allowed it to specialize entirely as a supporting and anchoring structure. Individuals specialized for different functions, as well as sharing of food resources, neural signaling and other functions among colony individuals, are common among modern colonial invertebrates, including cnidarians (e.g. Shelton, 1975).

A third possibility is that *S. costata* was a specialized, late representative of the frond-bearing Ediacaran organisms that include *Charnia*, *Bradgatia* and comparable taxa that adhered to biomat-consolidated soft sediments with a discoidal holdfast (e.g. see discussion and references in Fedonkin *et al.*, 2007). In this context, *S. costata* would differ from these organisms in being equipped with a weighted anchor instead of a disk holdfast. This adaptation should be seen within the context of the strong reduction in the availability of biomats as a substrate suitable for anchoring, which most likely was the driving force toward the evolution of alternative weighted holdfasts in psammocorals (e.g. Seilacher, 1992; Savazzi, 2007).

The rays in *S. costata*, which meet at the center of the dorsal surface, suggest that this species did not possess a single frond projecting from the center of the anchor,
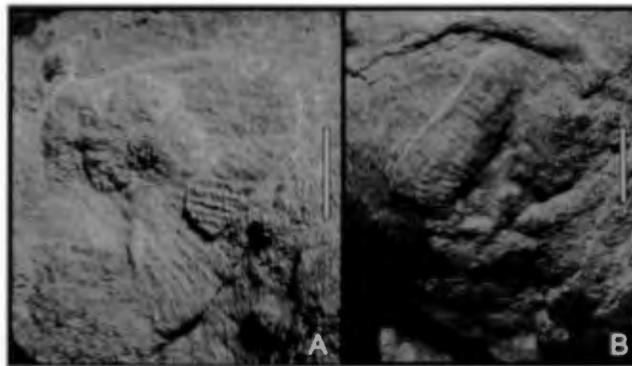

Figure 6. Ediacara-type quilted structures, herein interpreted as possible fronds constituting the feeding apparatus of *S. costata*. **A,** from Kinnekulle; **B,** from Lugnås (NRM Cn 257). Scale bars represent 10 mm.

but more likely multiple fronds (*i.e.*, at least one per sector). In this context, a possible alternative body plan to an individual organism is that the button of *S. costata* was surrounded by multiple individuals or modules, each constituting a sector of the organism (*i.e.*, a ring-like arrangement of individuals/modules geometrically not unlike the Recent colonial tunicate *Botryllus*; pers. obs.). Thus, the observed variable number of rays and the occasionally nonuniform size of the sectors in *S. costata* could reflect the variable number and development of individuals/modules constituting such an organism.

Jensen (1997, figure 13D) published a tantalizing picture of a slab bearing multiple impressions of chevron-shaped structures that could represent multiple fronds of a single organism or colony, and may be a candidate for the *S. costata* feeding apparatus discussed above. The impressions were apparently left by the distal regions of multiple structures of very similar sizes and shapes, and suggest, but do not prove, that they were physically tied together. The slab is fragmentary, and does not include a sand button.

Further fragments of the same, or comparable, structures are shown by Jensen (1997, figure 11B). Figure 6 shows two such structures. Figure 6A is obviously the same type of structure illustrated in Jensen's figure 11B, and provides additional information: a portion of the ribbed structure is folded on itself along a straight line, showing that (1) the structure was flexible, and (2) that its appearance is identical on both sides. Figure 6B is the most complete example of this type of chevron structure known to the writer.

Common to these structures is that they are apparently preserved as fine-grained infillings of mechanical impressions in hyporelief, frequently (albeit not always)

in close proximity to large trace fossils, suggesting that the structure was forcibly shoved into soft sediment. Such an event is likely to leave a mechanical impression even in the lack of preservable tissues. Their surface displays fine, regular and subparallel ribs, herein interpreted as representing the walls between adjacent cavities of a quilted structure, typical of the vendobiont body plans common in the Ediacaran (e.g. Seilacher, 1992; Buss and Seilacher, 1994; Fedonkin *et al.*, 2007) and known to have survived into the Early Cambrian (Antcliffe and Brasier, 2007, and references therein). These internal walls apparently resisted collapse better than the outer walls of the quilts, and the relief is consequently inverted.

As a result of the above discussion, the writer feels that the interpretation of *S. costata* as a solitary polyp or primitive actinian should be regarded as questionable, and less likely than the alternatives proposed above. Like *P. princeps* (see Savazzi, 2007), *S. costata* displays no evidence of mesenteria, and therefore was, at most, only loosely related to modern cnidarians, and quite possibly unrelated.

Conclusion

The sand button of *S. costata*, in life, consisted of a central body carrying a number of dorsal rays that projected sideways from the perimeter of the central body, commonly reaching a total diameter in excess of three times the diameter of the central body. This was true of small and large individuals (or colonies) alike.

Storm and current transportation of living *S. costata* resulted in the fragmentation and mutilation of the rays, fragments of which apparently detached from the button. Together with further fragmentation as a result of mechanical extraction or weathering of fossil specimens, this resulted in the typical appearance of isolated *S. costata* buttons, in which the rays usually project only a short distance above and around the central portion of the button. This implies that the rays were housed within shallow slots of soft tissues that communicated directly with the external environment, through which ray fragments could escape. It is also possible that contraction of the soft tissues during transportation largely exposed the button rays, making them even more vulnerable to damage.

A large specimen of *S. costata*, preserved *in situ*, displays an incompletely preserved, roughly circular, radially ribbed impression of the soft parts underneath the button. This surface extended from the center to a radius roughly three times the radius of the central portion of the button. A lone, preserved ray projects from the button by an equivalent distance. Thus, the soft parts of *S. costata* had a roughly circular peripheral outline with a total diameter roughly three times the diameter of the central button portion.

A conservative reconstruction of *S. costata* as an individual actinian or polyp is not convincing, since the close proximity of the rays to the external environment leaves little or no space available for a central coelenterate-type gut. It appears more likely that *S. costata* was a colonial organism with one large polyp/zooid specialized as a platform and anchor, carrying smaller feeding individuals on its dorsal surface. Alternatively, *S. costata* may have been a descendant of frond-bearing sessile Ediacaran life forms that evolved a weighted anchor in place of an adhesion disc, which was no longer a viable anchor because of the strong reduction in the availability of soft-bottom biomats in the Early Cambrian compared to the Late Proterozoic. In this case, however, the body of *S. costata* likely was modular and supported multiple fronds (possibly, one per sector) rather than a single frond. Jensen (1997, figure 13D) published an illustration of a slab carrying several, closely-spaced problematic impressions that may represent this type of multiple frond.

The general adaptive value of the sand button of *S. costata* as a weighted anchor that stabilized a sessile organism and favored its passive righting by water movements is confirmed by this study.

Acknowledgements

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