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Author: Savazzi, Enrico

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The early Cambrian Eophyton toolmark and its producer

ENRICO SAVAZZI

School of Geosciences, Building 28, Monash University, Victoria 3800, Australia and Hagelgränd 8, Uppsala 75646, Sweden (e-mail: enrico73@savazzi.net)

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Abstract. Eophyton toolmarks from the early Cambrian Mickwitzia Sandstone of Sweden were examined to assess the characteristics of the Eophyton producer. Based on these observations, the producer is inferred to be an organism carrying a large, neutrally buoyant frond-like structure or crown of tentacles that acted as a sail in water currents. Attached to this sail, possibly via a stalk, was a smaller structure with a diameter ranging between 3 and at least 100 mm, weighted with sediment contained in its interior and/or adhering to its exterior. This weighted anchor plowed the Eophyton furrow while the organism was dragged by water currents, probably in connection with storm events. The anchor was roughly discoidal in shape, with a perimeter that carried small tubercle-like projections and a few deep folds, and was sufficiently flexible to sag against the bottom under its own weight. Psammocorals have been proposed in the literature as possible Eophyton producers. Among the psammocorals from the Mickwitzia Sandstone, *Protolyellia* can be dismissed as an Eophyton producer, while *Spatangopsis* cannot be firmly excluded but does not fulfill all morphological requirements. Remaining possibilities are an, as yet, unknown psammocoral with a non-cemented sand skeleton, an actinian-like cnidarian, a seaweed or a kelp-like alga.

Key words: Cambrian, Eophyton, Mickwitzia Sandstone, Sweden, toolmark

Introduction

The Mickwitzia Sandstone (Holm, 1901) of the early Cambrian in the province of Västergötland, southern-central Sweden, contains a varied fauna and ichnofauna, including *Spatangopsis* and *Protolyellia*, generally regarded as psammocorals in the modern literature (see Seilacher, 1992; Seilacher and Goldring, 1996; Savazzi, 2007, 2012), trace fossils (e.g. Jensen, 1997, Rydell *et al.*, 2001; Hoffmann and Rudolph, 2011), wrinkle structures, *Kinneyia*-type blisters, elephant-skin textures and sand chips, currently interpreted as related to microbial biomats (Seilacher, 2007; Savazzi, 2007, fig. 3a, b; see also Pflueger and Gresse, 1996; Mei *et al.*, 2007; Gerdes, 2007; Porada and Bouougri, 2007). Fragmentary, apparently quilted structures were interpreted as vendobionts (Savazzi, 2012). Possible psammosponges and other problematic structures of likely biogenic origin are also present (author's personal observation).

The sediment is siliciclastic, often poorly sorted and thickly bedded, and the environment of the Mickwitzia Sandstone is interpreted as relatively shallow water exposed to waves, currents and periodic storm activity (e.g. Seilacher, 1992; Jensen, 1997). Some of the beds of the Mickwitzia Sandstone at the localities of Lugnås and Kinnekulle in Västergötland contain abundant *Eophyton linneanum* Torell, 1868, preserved in hyporelief. Eophyton is a striated rod-like structure preserved on sandstone soles (Figure 1), and was originally interpreted as a body fossil or an impression of a plant (e.g. Torell, 1868, 1870). The nature of Eophyton from the Mickwitzia Sandstone as a trace fossil or toolmark has been recognized since the late 19th century (e.g. Nathorst, 1881; Dawson, 1888). It is currently regarded as a toolmark (e.g. Jensen, 1997). For this reason, in the present paper Eophyton is not regarded as a taxon or ichnotaxon, and therefore not italicized, except when discussing earlier literature that uses the binomial *E. linneanum*.

Typically, body fossils are not found on the same bed surfaces as Eophyton. The Mickwitzia Sandstone contains no fossils that can unquestionably be identified as the producers of the Eophyton toolmarks, although psammocorals (e.g. Seilacher, 1999) or intraclasts (Jensen, 1997) have been suggested as possible candidates.

The present paper examines the morphology of Eophyton in an attempt to place constraints on the size, shape and physical characteristics of its producer, and

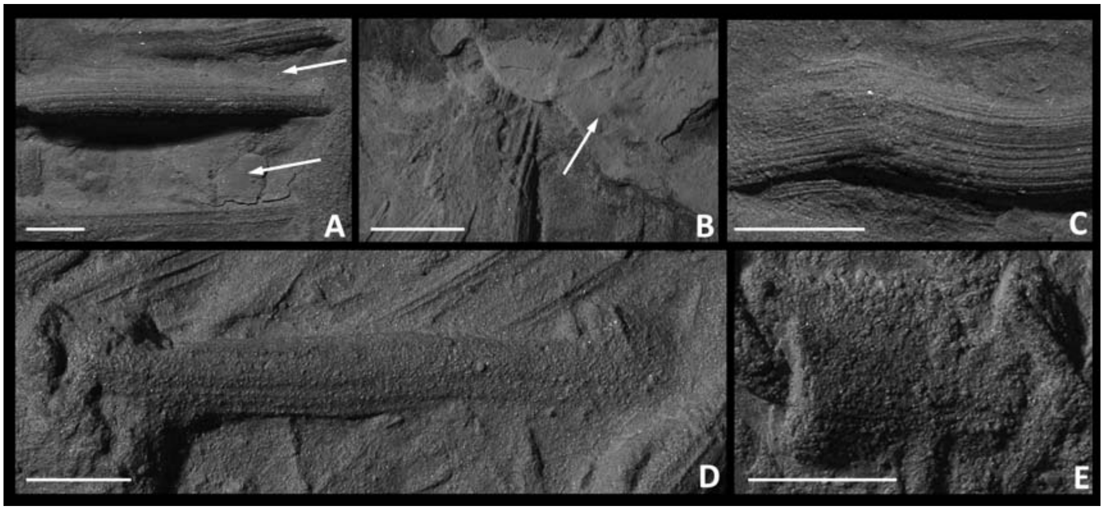

Figure 1. Eophyton from Lugnås, Sweden. **A,** specimen X.129. Arrows point to fragments of muddy sediment from the epirelief bed between Eophyton furrows. **B,** specimen X.154. Arrow points to a portion of the epirelief bed still adherent to the hyporelief surface. **C,** Furrow showing a sharp change in direction and a more gentle curve. **D,** specimen displaying a few large clasts, both on the hyporelief furrow and surrounding sediment. **E,** part of specimen X.150. Eophyton devoid of fine detail due to a large amount of coarse clasts. Scale bars represent 10 mm.

therefore on its possible nature. Toolmarks from other ages and localities, partly comparable to Eophyton from the Mickwitzia Sandstone, are briefly discussed below. The present study, however, concentrates on Eophyton from the Mickwitzia Sandstone.

Materials and methods

Several slabs covered with Eophyton from the early Cambrian Mickwitzia Sandstone of localities of the Västergötland province of southern-central Sweden, stored in the collections of the Swedish Museum of Natural History, Stockholm, Sweden, were examined and photographed for this study. Inventory numbers, if available, are indicated in the figure captions. Modelling clay was used to create temporary casts of individual Eophyton, in order to observe the amount of convexity of the hyporelief in cross-section.

Terminology

In the present paper, the term *furrow* is applied to a single instance of Eophyton preserved in hyporelief on a slab. This term is used as a way to avoid other established terms that may imply a nature as a trace fossil, toolmark or abiological feature. The terms *length* and *longitudinal* are applied to a direction of the furrow parallel to its surface grooves. In most cases, the length is the major dimension of an Eophyton furrow. *Width* and *transversal* refer to a direction perpendicular to the length of the furrow and parallel to the surface of the slab. *Cross-section* refers to a section through the furrow in a plane perpendicular to its length. The cross-section of a furrow can often be observed where a furrow is mutilated at the edge of a slab.

The *sides*, or *lateral* portions of a furrow are the portion closest to the surrounding bedding plane along the furrow width, while the *median* portion is located at the center of the furrow width.

The *extremities* of a furrow mark the positions where the furrow producer started or ended its plowing action.

The object or organism that caused the formation of Eophyton furrows is referred to as its *producer.* This term implies neither a specific nature of the producer, nor an active versus passive mechanism of production.

The *perimeter* of an Eophyton producer is the surface of the producer that plowed the furrow by displacing sediment. As a first approximation, the portion of perimeter of the producer that was buried in sediment while plowing a furrow has the same cross-section as the freshly produced furrow.

Observations

Preservation and sediment

The slabs containing Eophyton furrows in hyporelief available for this study consist of hard, medium- to coarse-grained siliciclastic sandstone. No instance of Eophyton preserved in epirelief was available. Some of

Figure 2. Eophyton slabs from Lugnås, Sweden. **A,** specimen X.143, originally illustrated by Jensen (1997), figure 11A; **B,** specimen X.150. Scale bars represent 20 mm.

the Eophyton slabs seem to have been prepared by removing adhering fine-grained sediment, possibly with the help of a solvent, while others have been cleaned by weathering.

Fragments of the sediment directly underlying the Eophyton beds are sometimes preserved, and attached to the hyporelief surface (arrows in Figure 1A, B). In most cases, the bed underlying the Eophyton surface apparently consisted of silt (Figure 1A). In one instance (Figure 1B), the underlying sediment consists of a thinly bedded, very fine-grained siliciclastic sandstone, much more friable than the overlaying hyporelief bed and unlikely to survive mechanical separation from the latter. The exposed surface of this layer, originally located 3–4 mm below the Eophyton surface, displays reworking by infaunal trace fossils but no obvious deformation induced by the process that created the Eophyton furrows.

The amount of surface detail displayed by individual furrows is variable. Some of the furrows are preserved in relatively fine detail (e.g. Figure 1C), while others display a coarse-grained surface where little detail is visible (e.g. Figure 1D, E). The latter surfaces, in particular, often display coarse-grained quartzite clasts, reaching 2–3 mm in diameter, mixed with a more abundant, finer sand fraction. The larger quartzite clasts often stand out in relief on the slab surface. This may be a result of selective erosion of finer-grained material from the slab surface (either during preparation or as a result of weathering). Alternatively, these larger clasts may have settled directly onto the underlying, fine-grained bed, and, being essentially incompressible, were pressed into this softer material during sediment compaction.

General morphology and size

Furrow width within individual Eophyton instances usually remains constant along the length, but varies considerably among different furrows, even on the same bedding plane (e.g. Figure 2). In the material available for this study, width ranges from approximately 3 mm to over 100 mm. Most of the furrows have widths between approximately 10 and 20 mm.

As most instances are mutilated at both ends along the edges of a slab, their actual lengths are unknown. The longest furrow among the material available for this study is in excess of 250 mm and is mutilated at both

Figure 3. Schematic cross-sections of examples of Eophyton furrows (A–C).

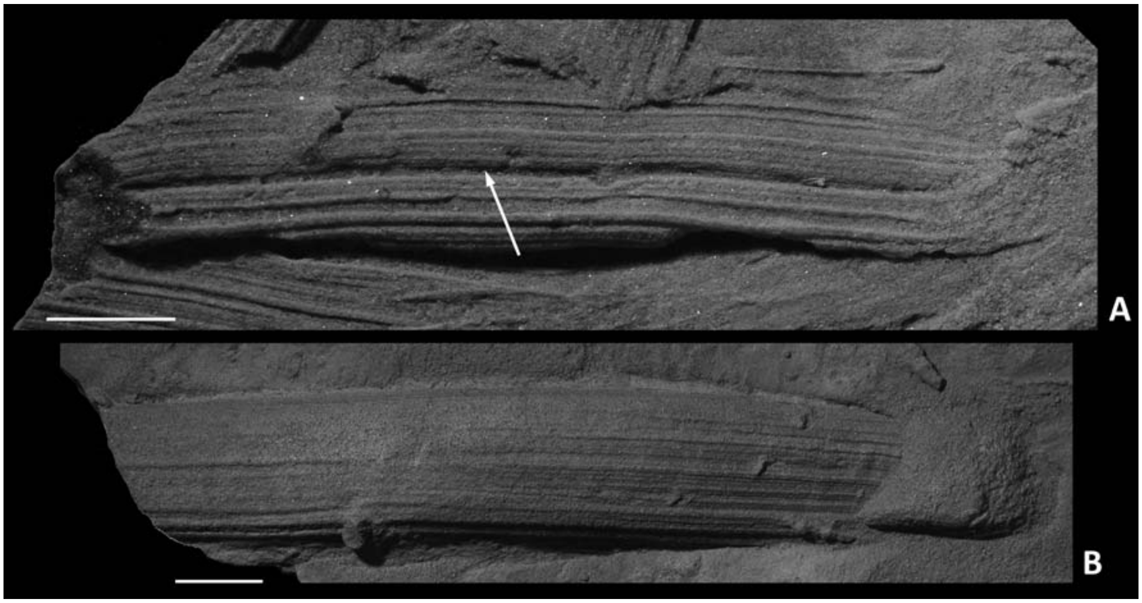

Figure 4. Eophyton from Lugnås, Sweden. **A,** specimen X.154. Arrow points to a major groove. **B,** specimen showing changes in strength of some of the minor grooves along the length of the furrow. Scale bars represent 10 mm.

edges of the slab. As a rule, the length of a furrow exceeds its width.

Most furrows are approximately straight, but a few display substantial changes in direction. The latter instances are described in detail below.

Cross-sectional geometry

The Eophyton furrows, as preserved in hyporelief, are invariably raised from the bedding surface (Figure 2). The cross-section is quite variable and ranges from distinctly convex to approximately flat, or in some cases slightly concave, in its median region. The curvature radius of the furrow surface (as measured in cross-section) is often shortest in the lateral regions of the furrow, while the median portion is less convex (i.e., has a higher curvature radius; Figure 3A–C).

Surface detail

The surface of Eophyton displays grooves and ridges of varying depth and width, typically parallel to the length of the furrow. Within an individual furrow, two types of grooves are usually present:

- Major grooves, running along the bottom of a broad and shallow V-shaped depression of the hyporelief furrow surface (arrow in Figure 4A). Some instances of Eophyton, however, display no obvious major groove (e.g. Figure 4B). Typically, from one to three major grooves are visible across the furrow width, regardless of the absolute width of the furrow (Figures 4A, 5A, B). Major grooves seem to be spaced at broad, roughly constant reciprocal intervals across the width of individual furrows.
- Minor grooves, shallower and much more numerous than the major grooves (all instances in Figures 4, 5). Minor grooves are spread across the whole surface of the furrow. Their depth, width and reciprocal spacing are variable.

Individual grooves usually can be followed along the entire preserved length, but sometimes a groove gradually changes in width and depth along the furrow length.

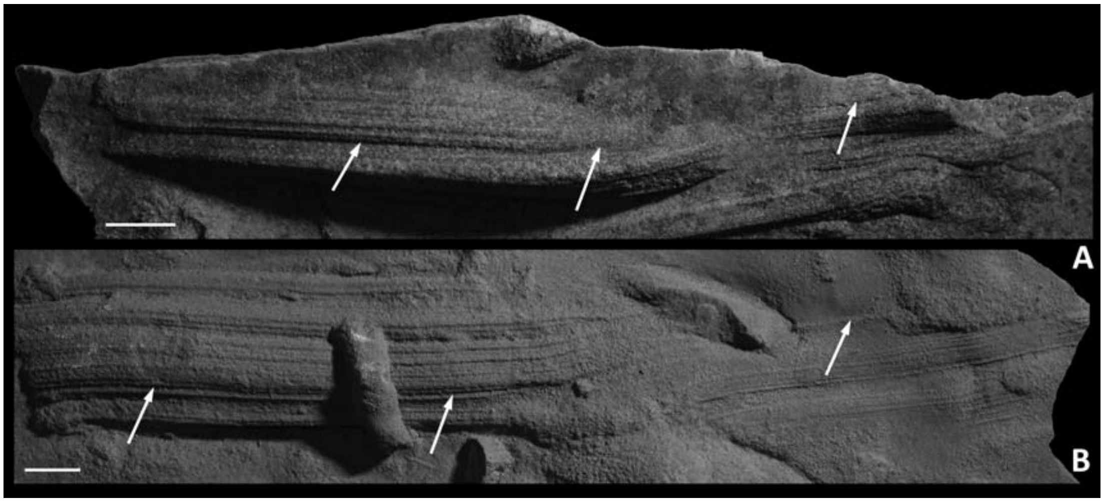

Figure 5. **A, B,** Eophyton twisting about their longitudinal axes, from Lugnås, Sweden. Arrows on each specimen point to successive positions along the same major groove. Scale bars represent 10 mm.

This is true of both major and minor grooves.

In rare cases, a portion of the furrow twists about its length (Figure 5A, B). In both of the illustrated examples, it can be arbitrarily assumed that the direction of movement of the producer was from left to right. The amount of twisting was sufficient to move one of the major grooves (arrows) from a position on the median region to a lateral position, and to cause another major groove, originally lifted above the sediment surface, to appear along the opposite side of the furrow (lowermost in the Figure 5A, B). The furrow in Figure 5A has a laterally asymmetrical cross-section. The instance in Figure 5B markedly decreases in convexity and groove strength from left to right.

A few instances of Eophyton display an apparent widening, or “splitting open” of a major groove (arrows in Figure 6), accompanied by a corresponding increase in furrow width. In these cases, new minor grooves may be seen in the space between the diverging margins of the major groove (in particular, see Figure 6C).

Sometimes, ridges located between adjacent grooves seem to carry a row of very small pits regularly spaced along the length of the furrow. However, close examination shows this to be an artifact caused by the alignment of uniformly sized sediment particles along ridges of the hyporelief surface. Eophyton preserved in poorly sorted sediment lack these features. Eophyton furrows lack larger, periodically repeated features along the furrow length (e.g. leg marks, peristaltic waves), as well as on the surrounding sediment surfaces. Sets of shallow, parallel scratch marks are frequently observed on the bedding plane of Eophyton slabs, and grade into typical Eophyton (leftmost portion of Figure 7A, B).

Furrow orientation

No statistical study of the orientation of Eophyton furrows was attempted, and the original orientation of the available slabs was not recorded on the material. Qualitative observations suggest that, within each slab, Eophyton furrows may be preferentially oriented along one or two directions (e.g. Figure 2). However, examples of furrows crossing each other at virtually any angle are available.

Morphology of furrow extremities

Despite the fact that most furrows are mutilated at the edges of slabs, several instances of preserved extremities were found. These extremities can be classified into three, somewhat intergrading types.

- Gradual (about thirty observed instances; e.g. leftmost portion of Figure 7A, B; rightmost portion of Figure 7C). Width and/or depth decrease gradually toward the extremity over a distance of up to a few centimeters. The reciprocal spacing of furrow grooves remains instead constant, and their arrangement remains parallel. This is the most common type of furrow extremity.
- Abrupt (about twelve observed instances; e.g. Figure 7D–H). The furrow keeps a constant width up to its extremity and ends abruptly, without gradually reducing its width or depth. The extremity of this type of furrow can be a roughly straight edge, per-

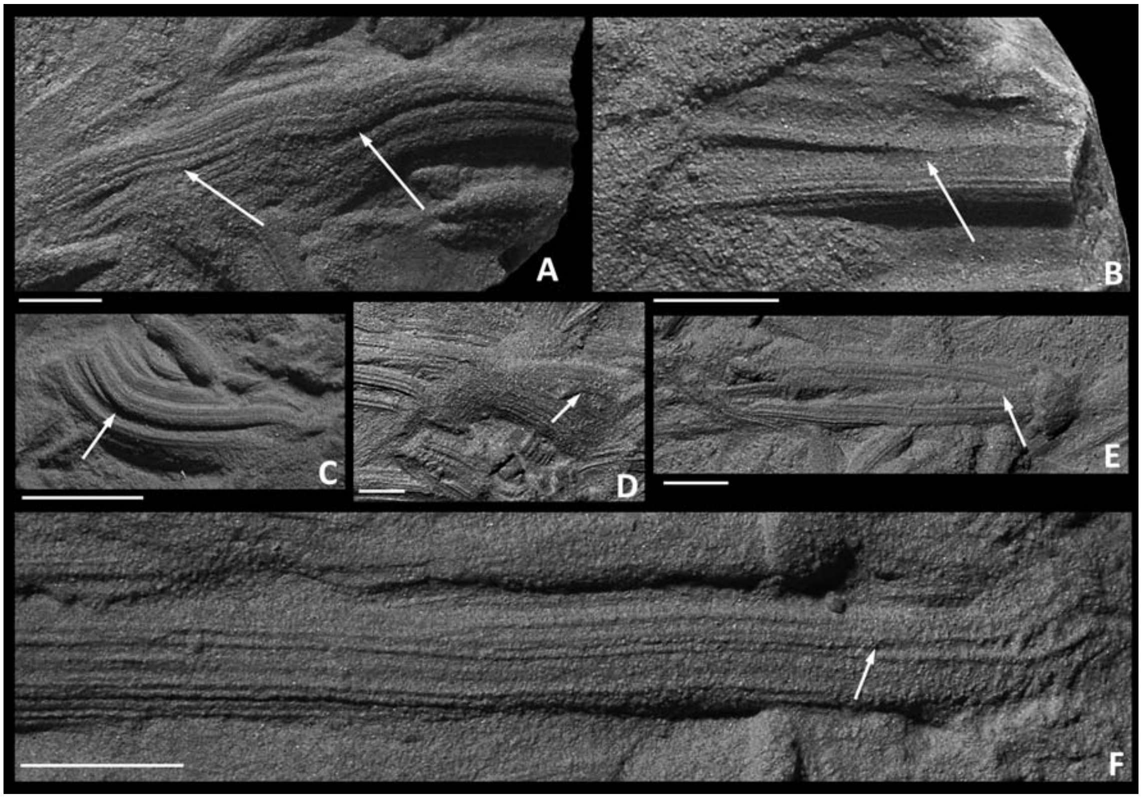

Figure 6. Eophyton displaying a major groove gradually changing in width along the furrow length (arrows), from Lugnås (A, B, D–F) and Kinnekulle (C), Sweden. **D** and **F,** specimen X.147. Scale bars indicate 10 mm.

pendicular or oblique to the length of the furrow (Figure 7E–H), or less frequently an irregular or zigzag line (Figure 7D).

- Capped (eight observed instances; e.g. Figure 7G–L). This is an abrupt extremity of the furrow as described above, albeit in hyporelief it carries an additional, convex "cap" adjacent to the furrow extremity, often separated from this extremity by a groove. The cap displays no surface markings corresponding to the grooves on the adjacent furrow. The width of the cap is approximately equal to, or slightly higher than, the width of the furrow. The sediment constituting the cap is of the same type that fills the Eophyton furrow in hyporelief.

Short furrows with both extremities preserved were observed (e.g. Figure 7A–C). A gradual extremity can be associated with an opposite extremity of any type, including gradual. An abrupt extremity is associated with either another abrupt extremity or (more commonly) with a gradual extremity. A capped extremity is only associated with a gradual or abrupt extremity at the opposite end of the same furrow (e.g. Figure 7J–L).

In some cases, minor grooves become more distinct at an abrupt extremity of the furrow (Figure 7B, H). A single instance of capped extremity (Figure 7I) seems to display the impression of a row of tubercle-like structures in a narrow transversal band between the furrow extremity and its cap.

In a few cases (Figure 7F, J–L), the sediment infilling an abrupt extremity, a capped extremity or its cap seems to have broken into sand chips and dislocated slightly.

Curved furrows

Minor changes in direction within an individual Eophyton furrow are common (e.g. Figure 8A, B). In some cases, it is difficult to decide whether a track apparently displaying a sharp curve (Figure 8C, D) is a genuine feature, or an artifact caused by different furrows accidentally superposed at one of their extremities. Nonetheless, two clearly bent furrows were observed (Figure 8E, F). In one case (Figure 8E) the curve is so sharp that the furrow partly overlapped itself. In the other case (Figure 8F) the furrow curves approximately 90°, and continues faintly at its lower-right end in Figure 8F,

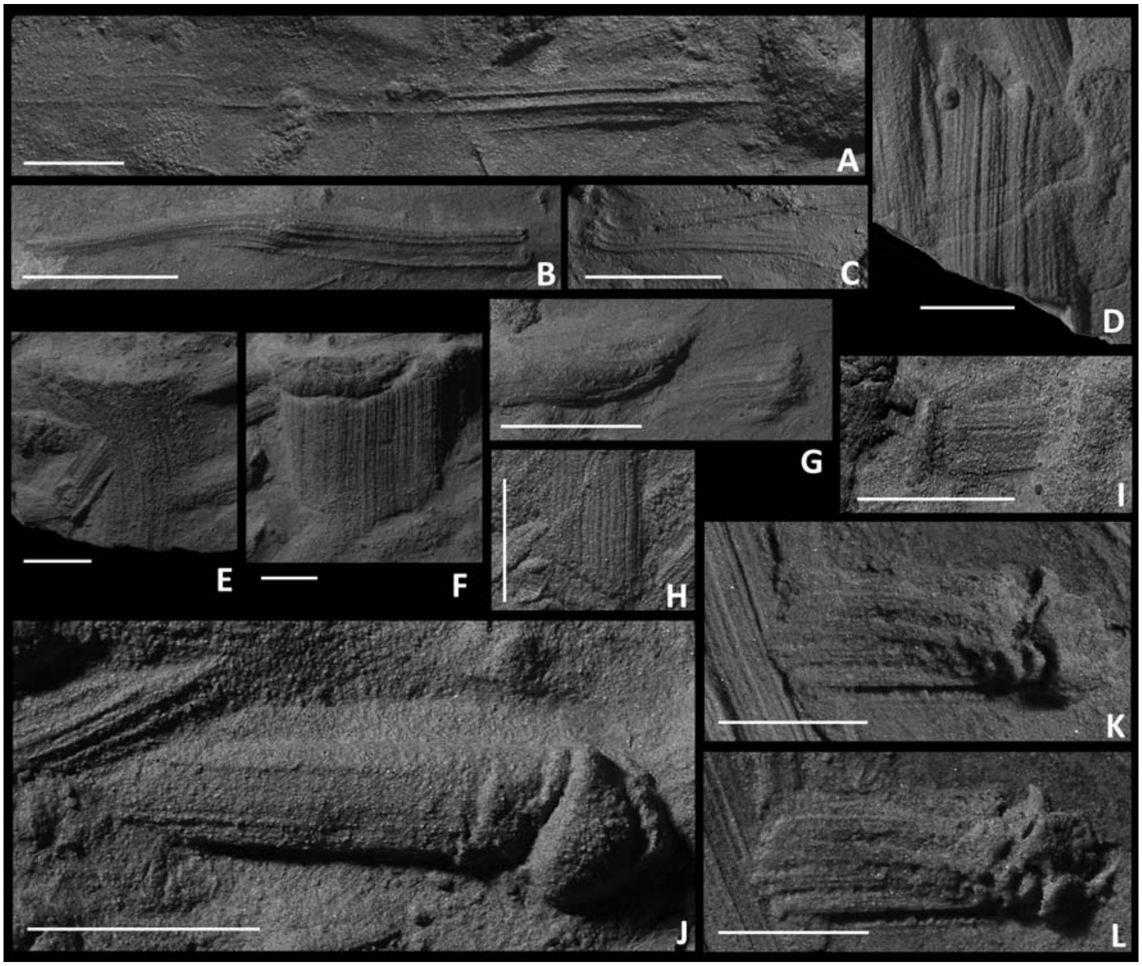

Figure 7. Eophyton displaying the morphology of furrow extremities, from Lugnås. **A,** gradual extremities at both ends, especially on the left. **B,** gradual (left) and abrupt (right) extremities. At the right end, an earlier and shallower furrow continues in the same direction. **C,** abrupt ends (left), apparently of two partly superposed furrows. **D,** abrupt end with a jagged outline (uppermost). **E, F,** abrupt ends (uppermost), specimen X.129. The hyporelief sediment at the end of the furrow in F has fragmented into a large sand chip. **G,** two abrupt ends of irregular shapes. **H,** abrupt extremity (lowermost) showing impressions of possible tubercles at its very end. **I,** capped end (left) apparently showing impression of a transversal row of possible tubercles. **J,** capped end, specimen x143. **K, L,** specimen X.154 illuminated from different directions, which results in surface detail being highlighted in dramatically different ways. The cap has apparently fragmented into sand chips. Scale bars represent 10 mm.

performing an additional 90° turn.

Cross-cutting Eophyton furrows

Observations confirm the fact, repeatedly noted or illustrated in the literature (e.g. Linnarson, 1869, pl. 8), that when two Eophyton furrows cross each other, the overlapping region of one of them is completely erased by the other.

Interaction with other structures

In the specimens available for this study, Eophyton furrows evidently modified by trace fossils are common. For instance, some specimens are cross-cut by small vertical burrows (Figures 4B, 7D) or a horizontal burrow (Figure 5B).

A large Eophyton that apparently plowed away the topmost portion of a small, buried individual of *Spatangopsis* is available among the material. This specimen was illustrated and discussed by Savazzi (2012, fig. 2D).

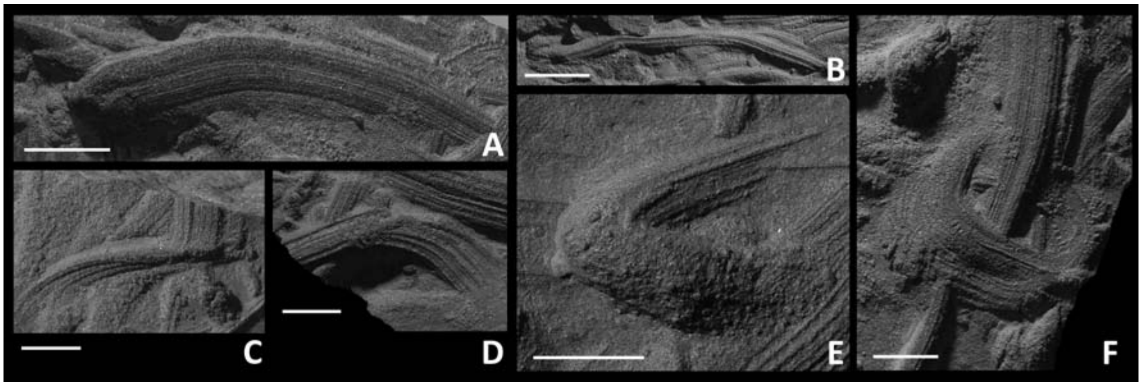

Figure 8. Eophyton furrows displaying changes in direction, from Lugnås (A, C–E) and Kinnekulle (B). **C–D,** specimen X.143; **E,** specimen X.147. **F,** specimen X.150. Scale bars represent 10 mm.

Discussion

Problems of interpretation

During the examination of Eophyton furrows, it became evident that some of the available specimens are difficult to interpret. In particular, the high density of Eophyton furrows on most of the available slabs increases the likelihood that an apparently single furrow is actually the result of a second furrow producer retracing a preexisting one and modifying it, extending the length of a preexisting furrow, or following a path parallel and adjacent to another furrow.

In this study, the writer decided to apply caution in interpreting instances of furrows that display unusual characteristics, and to exclude from the following discussion the cases most likely to be artifacts of the type described above. However, a degree of uncertainty remains. This uncertainty makes it impossible, for instance, to state an exact number of occurrences of each type of furrow extremity, since a few examples of each type cannot be conclusively identified as either genuine or artifacts caused by crowding and/or sediment reworking.

If a future study of Eophyton should be undertaken, it may be desirable to obtain fresh material, especially from beds that do not display a high density of Eophyton and trace fossils. This should lower the frequency of closely adjacent or superposed Eophyton and trace fossils, thereby reducing the likelihood of misleading artifacts.

It is quite possible that the Eophyton slabs available for this study do not represent the typical frequency of furrows on the Eophyton beds, and that they are a biased selection from horizons carrying an unusually high number of furrows. In a comparable example of collecting bias, Linnarsson (1869, pls. 7–9) established the species *Eophyton torelli* on Eophyton furrows unusually heavily modified by subsequent trace fossils. This accidentally increased the resemblance of Eophyton to bud-carrying fossils of higher plants (which could be the very reason why these specimens were selected among less visually striking ones by Linnarson). There can be little doubt that *E. torelli* is the same toolmark as *E. linneanum* Torell, 1868.

Active movement versus passive transportation

There are no serially repeated marks (e.g. leg scratches) along Eophyton furrows and the surrounding sediment. This suggests a passive transportation of the Eophyton producer by water currents while plowing its furrow. Therefore, these observations confirm the interpretation of Eophyton as a toolmark (e.g. Jensen, 1997).

Shallow parallel scratch marks found on Eophyton beds sometimes grade into typical Eophyton (Figure 7A). The switching between the two types of toolmark was likely caused by changes in current speed and/or sediment cohesiveness.

Sediment properties at the time of furrow production

The Eophyton furrows were produced in silt or fine-grained siliciclastic sand mixed with silt (Figure 1A, B). This sediment was sufficiently cohesive to preserve Eophyton furrows for some time despite the presence of water currents, as shown by the abundance of Eophyton criss-crossing each other on the same surface (Figure 2) and by the apparent lack of erosion of the earliest of these furrows (which can be distinguished from subsequent ones based on cross-cutting relationship). There is no evidence of surrounding sediment collapsing into Eophyton furrows.

A cohesivity of this sediment comparable to mud or

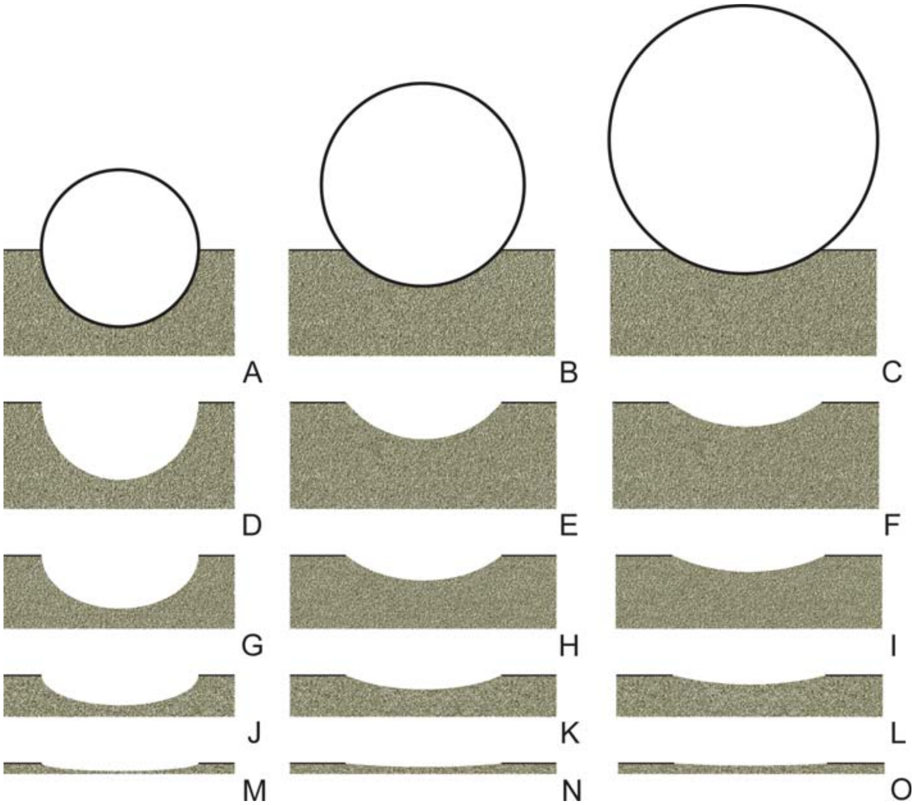

Figure 9. Idealized cross-sections of Eophyton furrow producers (A–C), their furrows in non-compacted sediment (D–F), and the same furrows after compaction by 30% (G–I), 60% (J–L) and 90% (M–O).

soft clay seems likely. This would have offered a relatively high resistance to plowing and would have slowed the movement of the furrow producer relative to the water current.

In a few instances (Figure 7F, J–L), part of the coarse sediment infilling a furrow extremity or its cap seems to have broken into sand chips and slightly dislocated, leaving open cracks. This seems to imply that the sediment of the epirelief bed was subjected to a modest amount of plastic flow during compaction, while the material of the hyporelief bed was more cohesive and tended to fragment into chips, rather than deforming in a plastic way during the early phases of diagenesis.

A significant amount of sediment must have been displaced during the formation of an Eophyton furrow. However, the surrounding bed surfaces show no evidence of loose sediment heaped around the furrow edges, or of swelling of the surface of the bedding plane around the furrow caused by plastic flow. It is possible that sediment loosened by the plowing action of the Eophyton producer lost its cohesivity and was carried away by the same water currents that were dragging the producer.

The coarser sandy sediment infilling the Eophyton furrows was likely deposited in a single event on each Eophyton bedding plane, perhaps in connection with a storm event, and protected the furrows from erosion. Its coarse sandy texture does not allow the preservation of very small surface detail of the furrow.

It is possible that the presence of a mud or clay fraction in the sediment on the epirelief bedding plane caused it to adhere to the surface of the Eophyton producer. Individual adhering sand clasts, however, were probably too small to explain the consistent pattern of ridges and grooves on the surface of Eophyton. It is more likely that the Eophyton grooves were produced by a genuine relief of the furrow producer (e.g. papillae, setae or tubercles).

Factors affecting the furrow cross-section

The cross-sectional geometry of Eophyton furrows is affected by a number of factors, which include the geometry of the Eophyton producer as well as synsedimentary and diagenetic phenomena. In particular, a significant amount of sediment compaction would alter the original cross-section of Eophyton furrows. It is therefore necessary to assess these factors.

Figure 9A–C shows a comparison between three theoretical instances of Eophyton producers of different absolute sizes. For simplicity, the figure shows the cross-section of the producers as circular. The smallest producer (Figure 9A) is shown plowing a furrow while half submerged below the bedding plane. The larger producers (Figure 9B, C) plowed their furrow with proportionally lesser fractions of their diameter submerged into the sediment. Although the furrow width is the same in these examples, their curvature radius and depth are obviously different (Figure 9D–F). It can be expected that different sediment properties of the epirelief bed and current speeds would have resulted in furrows with different proportional depths, and therefore different curvature radiuses.

Sand, which is a major component of the Eophyton furrow, is subjected to low amounts of compaction (up to about 10% according to Nichols, 1999, p. 279, 397). Simple, small infaunal burrows in the Eophyton beds (e.g. center-left in Figures 4B and 5B) typically display a roughly circular cross-section in their vertical as well as horizontal portions, consistent with a low amount of sediment compaction.

A uniform sediment compaction can be modelled by applying a corresponding deformation along the vertical axis to the theoretical model discussed above. This simple model ignores the possibility of plastic flow and different compressibility of portions of the bed. A compression by 30% perpendicular to the bedding plane transforms the cross-section of the theoretical Eophyton furrows from arcs of circles (Figure 9D–F) to arcs of ellipses (Figure 9G–I). The curvature radius of the furrow cross-section decreases in the lateral portions of the furrow and increases in its median portion. A compression of 60% (Figure 9J–L) and 90% (Figure 8M–O) of the same furrows was also modelled. The cross-section of the models compacted by 60%–90% is comparable to the actual cross-sections of Eophyton furrows (Figure 3A–C). However, such a high compaction is not feasible in siliceous sand. Thus, a more realistic interpretation is that the flat median regions observed in many Eophyton furrows are genuine features, and that the Eophyton producer was flexible and flattened against the substrate. This flattening of the median region persisted, in some cases, even when the furrow producer rolled about its longitudinal axis (Figure 5B), and was likely a result of the producer sagging against the bottom sediment under its own weight, like a rubber balloon filled with loose sediment rather than a rigid body. The producer is no longer an intraclast as inferred by Jensen (1997). The longitudinal grooves, instead, remain strong even in these flat regions, and likely were produced by stiffer superficial structures of this “balloon”. The observed tendency of the sediment of the hyporelief bed to fragment, rather than flowing in a plastic way (Figure 7F, K, L), makes it unlikely that the instances of Eophyton with flat median regions were caused by plastic flow of the hyporelief beds.

Size and specific gravity of the Eophyton producer

The depth of Eophyton furrows into the epirelief bedding plane is often substantial, implying that the furrow producer displaced a significant amount of sediment while plowing. Thus, this portion of the Eophyton producer must have had a specific gravity higher than sea water, and probably comparable to the surrounding sediment.

The largest observed width is approximately 100 mm, and this furrow is mutilated along its sides. Since the diameter of the Eophyton producer, in principle, can exceed the furrow width (see Figure 9B, C), this furrow instance only sets a lowest limit for the diameter of its producer. It is entirely possible that the largest Eophyton producers reached a higher diameter.

Surface relief of the producer

The furrows that display an axial rolling of the producer (Figure 5A, B) suggest that the surface relief of the producer was uniformly distributed around its whole perimeter, but none of the observed furrows shows a complete axial revolution of its producer. Major grooves also appear to have been produced by a small number of folds, or introversions (perhaps 3 to 6), distributed around the perimeter of the producer. The instances of Eophyton displaying a major groove opening (or closing, since it is not possible to decide the direction of movement) during the production of the furrow (Figure 5A–F) show that at least some of the major grooves correspond to deep folds in a flexible structure, and that the walls of these folds carried the same type of relief as the rest of the perimeter of the producer.

Furrow extremities

One of the problems in interpreting the different types of Eophyton extremities is deciding whether a given instance of an extremity is the start or end of a furrow in a chronologic sense, i.e., the point where the Eophyton producer initially settled onto the sediment surface and started plowing, or was lifted away from the sediment after plowing a furrow.

Gradual extremities are obviously caused by the producer gradually switching its behavior between being dragged along the bottom and being water-borne. This type of extremity lacks telltale signs to distinguish whether a given extremity marks the chronologic start or end of a furrow. It seems likely that both events would produce essentially the same results, as shown by instances with gradual extremities at both ends (e.g. Figures 1D, 7A, B).

It is uncertain whether abrupt extremities represent the chronologic start or end of a furrow. It is conceivable that an Eophyton producer transported in mid-water by a strong current could fall to the bottom when the current slowed, thus becoming partly embedded in the sediment and producing an abrupt start of a furrow. It is also possible that a producer plowing a furrow could be lifted off the sediment by a sudden increase in current speed, thus leaving an abrupt extremity at the end of the furrow.

The cap associated with an extremity was originally a depression in the sediment, often separated from the adjacent Eophyton furrow by a shallow ridge. Both the furrow and its cap were filled at the same time and with the same sediment. The cap could be the impression of an integral part of the Eophyton producer, the impression of a lump of sediment adhering to the producer, or a partly collapsed cavity in the epirelief surface as discussed below. None of the available caps displays surface detail. In particular, none of the caps displays the same type of grooves present on Eophyton furrows.

The rightmost extremity in Figure 4B could also be a capped one. The cap was apparently located slightly underneath the Eophyton furrow and cut by the latter. This implies that the Eophyton furrow was produced after (in a chronologic sense) the cap itself. In this specific case, the unusual “cap” might instead be an unrelated trace fossil cut by Eophyton.

No furrow carrying capped extremities at both ends was observed. Since capped extremities are the least frequent type of furrow extremity, even assuming they could be produced at both start and end of a furrow, it is statistically unlikely to find two such extremities in the same furrow. Therefore, it cannot be stated with certainty that capped extremities were produced only at the chronologic end (or start) of a furrow.

It is tentatively proposed that a cap (assuming it to be a genuine part of the Eophyton furrow and not an allochronous feature) is a partly collapsed cavity in the sediment left when a producer slightly buried in the sediment was uprooted by water movements and started to produce a furrow. In this interpretation, the featureless surface of the cap can be explained as a result of surrounding epirelief sediment collapsing into the cavity. Since the epirelief bedding plane and its underlying sediment in correspondence of a cap is not available, it is impossible to tell the depth of this cavity, and whether this semi-infaunal position of the producer was caused by active burrowing or passively, by fine sediment settling around the producer in an interval between storm events.

Mode of furrow production

The arrangement of grooves on the surface of Eophyton is typically parallel to the furrow direction, and individual grooves normally can be followed for the whole preserved length of a furrow. This suggests that the producer usually plowed its furrow while remaining in a constant orientation, and did not roll like a wheel on the sediment surface. On the other hand, a ball-shaped object dragged along the bottom by water currents would display a strong tendency to cartwheel (i.e., to roll about an axis perpendicular to the direction of movement and parallel to the surface of the sediment), rather than plowing a furrow without rolling. An elongated object also tends to roll on the sediment in a comparable way, albeit with its major axis perpendicular to the current direction (author’s personal observation).

The type of rolling described above would produce the equivalent of a tire track on mud. This type of furrow usually displays a negative, three-dimensional impression of the tire surface in excellent relief. In the fossil record, roll marks of this type were left, for instance, by the keels of empty, current-transported ammonite shells (albeit in this case, with an alternating motion between rolling and skipping/sliding; e.g. Seilacher, 2007, p. 161, 164, 212). Plowing, instead, only leaves a furrow with a cross-section that matches the widest cross-section of its producer.

Shape and physical properties of the Eophyton producer

There is an apparent inconsistency between the type of sediment in which Eophyton furrows were produced (a silt, or a mixture of fine-grained sand and silt) and the fact that the Eophyton producer (with a maximum width of at least 10 cm) must have been sufficiently heavy to plow a furrow in this sediment, thus requiring water currents strong enough to provide a sufficient traction. A current capable of dragging such an object across the sediment surface should be more than sufficient to deeply scour fine-grained sediment.

To solve this inconsistency, it is necessary to assume that the Eophyton producer consisted of a heavy portion, acting like an anchor plowing the furrow, and a larger portion, of lower specific gravity or neutrally buoyant, that acted like a sail or parasail, dragging the anchor along the bottom. This model implies a biological nature of the Eophyton producer, and provides the following advantages:

- A large sail can drag a heavy anchor even when currents and waves are relatively weak and unlikely to erode the sediment (see also Kudrass, 1974; Frey and Dashtgard, 2012; and discussion below).
- A sail tethered to an anchor prevents the anchor

from cartwheeling along the bottom.

- Grooves on the surface of Eophyton are continuous even while the furrow is executing a sharp turn. This is consistent with the furrow producer being tethered to a pulling sail, and therefore always pointing in a direction parallel to the direction of movement.
- Rotation of a tethered anchor about an axis parallel to the direction of movement remains possible, as displayed by a few instances of Eophyton furrows twisting about their length.

Instances of Eophyton furrows displaying a sharp turn (Figure 8E, F, and possibly Figure 8C) indicate that the object plowing the furrow was very short along its direction of movement. Its shape was roughly discoidal, since a sausage-shaped object elongated in the direction of movement would not allow turns with such a short radius. Abrupt extremities are also compatible with a discoidal anchor (Figure 7B, C, E, F, H). Some of the instances of abrupt extremities, however, suggest a more irregular shape of the producer (Figure 7D, G), e.g. a flexible disc with portions of its perimeter bending backwards while being dragged against the sediment.

The above evidence is insufficient to decide among the following alternatives:

- Whether the sail was directly attached to the anchor, or via a stalk, column or pedicle.
- Whether the sail was a crown of tentacles, a *Charnia*-like frond, a kelp-like thallus with fronds (and possibly gas-filled vescicles to increase its buoyancy, like in Recent kelp), or other comparable structures.

Incidentally, an elongated stalk would make it possible for two or more furrow producers to become tangled together, thus producing some of the observed furrow features (e.g. Figure 6A–F). In this case, some of the major grooves might represent the zone of reciprocal contact between separate producers with tangled stalks, rather than a fold in the perimeter of an anchor. Multiple tangled individuals could also explain the type of zigzagging abrupt furrow extremity shown in Figure 7D.

The inferred presence of sediment weighting the anchor suggests that the Eophyton producer was sessile, and either immobile or capable only of limited active righting and/or shallow burrowing. The high size variability of the Eophyton producer is compatible with different explanations, e.g.:

- Populations of the Eophyton organism contained individuals of widely varying sizes, representing different growth stages.
- The Eophyton organism was colonial or modular, and the different furrow sizes reflect the variable size of colonies or clusters.
- The Eophyton organism was fragile and easily broke apart during storm events and/or transportation. Fragmentation took place along prebuilt lines of mechanical weakness, and resulted in each fragment consisting of a sail, an anchor and a connecting stalk.

Psammocorals as Eophyton producers

The psammocorals *Protolyellia princeps* Torell, 1870 and *Spatangopsis costata* Torell, 1870 are found in the Mickwitzia Sandstone. The latter species is sometimes found in proximity to Eophyton (albeit not on the same bedding surfaces: Savazzi, 2012, fig. 2D). It is therefore reasonable to ask whether either species may have been the Eophyton producer, as suggested by Seilacher (1994).

The general morphology and adaptations of the producer inferred in the preceding section are consistent with those of psammocorals. These organisms possessed a combination of weighted anchor (in the form of an internal cemented sand button), stalk-like structure (preserved in *Protolyellia*; Savazzi, 2007, and inferred as possible in *Spatangopsis*; Savazzi, 2012) and a crown of tentacles or a suspension-feeding apparatus (inferred in both genera; Savazzi, 2007, 2012). *Protolyellia* also possessed an external sand-encrusted epithelium (Savazzi, 2007).

The anchor of soft tissues containing the sand button of *Protolyellia* apparently had a diameter only slightly larger than the button itself, as proved by concentrations of closely packed individuals that most likely were alive when buried (Seilacher, 1992; Seilacher and Goldring, 1996).

A living *Protolyellia*, with the feeding apparatus acting as a sail and the weighted bottom of the body dragged along the sediment surface by currents, would have produced a furrow reflecting the circular outline of the sand button. The shape of the button would have allowed both sudden changes in the direction of the furrow and abrupt furrow extremities comparable to those observed in Eophyton. The wrinkles on the sand-encrusted epithelium (Savazzi, 2007, fig. 1) could conceivably have produced grooves on the furrow surface. However, the perimeter of the anchor containing the sand button, because of the modest thickness of its soft tissues, necessarily behaved as a solid object, and could not sag against the sediment surface. For the same reason, the perimeter was unlikely to possess folds sufficiently deep to split open to reveal an extensive internal structure (Figure 6C).

The external appearance of living *Spatangopsis* is somewhat uncertain. The peripheral region of the “arms” on the upper surface of its star-shaped button probably were exposed when the organism contracted (Savazzi, 2012), as likely during passive transportation. The outermost ends of these arms would have projected from the perimeter of the organism, and should have left deep grooves (i.e., hyporelief ridges) in some Eophyton furrows. However, such ridges are not observed.

Even after removing possible artifacts, some instances of major grooves splitting open to reveal minor grooves within (Figure 6C) seem to be a genuine feature. Thus, major grooves appear to be a position where the epithelium of the furrow producer was folded inwards. In *Spatangopsis*, the grooves that contained the arms of the sand button in relaxed specimens could have produced comparable features, but only after the distal portion of the arms of the sand button broke off. The arms of the *Spatangopsis* sand button lack a relief pattern matching the Eophyton minor grooves observed within opened major grooves (Figure 6C).

In conclusion, it is not likely that Eophyton was produced by either *Protolyellia* or *Spatangopsis*. No other psammocorals are known from this formation. Although it remains possible that an as yet unknown psammocoral is the producer of Eophyton, it is likely that a psammocoral common enough to produce the abundant Eophyton furrows, by now, would have been observed in the Mickwitzia Formation.

Other sediment-weighted organisms

To accommodate the apparent sagging of the furrow producer against the bottom sediment, the weighted anchor can be reconstructed as containing loose sediment, rather than a button of cemented sand. It is also possible that this sediment was contained within multiple internal diverticula, rather than a single cavity. This would have allowed the anchor to remain flexible enough to sag against the sediment and to allow major grooves to open.

As an alternative, a large number of clasts could have adhered to the external epithelium (as seen in the wrinkled epithelium of *Protolyellia*; Savazzi, 2007). In this case, a weight sufficient to plow furrows of a depth consistent with Eophyton would seem to require numerous, deep folds that substantially increased the surface of the epithelium available for this function. It is unlikely that a small number of folds (each corresponding to a major groove in the Eophyton furrow) could suffice, unless each of these folds was further folded internally in a fractal pattern.

A non-cemented sand button, especially if distributed among multiple internal cavities, would be very unlikely to be preserved. After decay of the soft tissues, it could have collapsed into an unrecognizable heap of sediment particles even if rapidly buried. Given the abundance of sand chips, burrows filled with coarse sediment and other comparable structures in the Mickwitzia Sandstone, the likelihood of small concentrations of sediment particles being recognizable as soft sand skeletons of a psammocoral-like organism is very low, and this hypothesis is therefore unlikely to be supported by evidence.

A more conservative hypothesis, including sand-weighted actinian-type cnidarians, seaweeds and kelp attached to an anchor, remains possible, but also in this case it should be very difficult to find direct evidence. The benthic transportation of pebbles attached to the holdfasts of Recent kelp and seaweed by waves and currents was discussed by Kudrass (1974), Frey and Dashtgard (2012), and references therein. Dragging of these pebbles along the bottom by waves is possible when the wet weight of the algae acting as a sail approaches or exceeds one-third of the weight of the pebble (Kudrass, 1974). Dragging by waves or unidirectional currents takes place at water speeds roughly one order of magnitude lower than necessary to transport similarly sized pebbles devoid of algae (Frey and Dashtgard, 2012). Large kelp can transport boulders weighting up to 100 kg in strong waves (Smith and Bayliss-Smith, 1998). Although the size and nature of the sail certainly affects its dragging efficiency, these findings show that the idea of Eophyton being produced by a sail-and-anchor organism transported by current or wave action of moderate strength is physically feasible.

Eophyton from other ages and localities

Haines (1997) described linear and curvilinear toolmarks from northern Australia, dated approximately 1,750 Ma, morphologically similar to Eophyton as described in this paper but much narrower (4 mm maximum width). Haines (1997) interpreted these toolmarks as made by algal strands passively dragged against fine-grained sediment. The illustrated material shows gentle changes in direction of the toolmarks, but neither clearly identifiable sharp turns, nor abrupt/capped extremities. Therefore, the producer of these toolmarks may have been an elongated, flexible strand as suggested by Haines (1977), rather than a disc-shaped object as inferred in this paper for Eophyton from the Mickwitzia Sandstone.

A strand origin for the Australian toolmarks is also consistent with their often discontinuous appearance (Haines, 1997, fig. 2B), which suggest that portions of the producer remained lifted from the surface of the substrate. Thus, the producer was likely of lower specific gravity than the Eophyton producer from the Mickwitzia Sandstone. Therefore, in spite of the partly comparable morphology, these early Australian toolmarks likely had a different type of producer than Eophyton as inferred in this paper.

Eophyton-like toolmarks are recorded from a number of other ages and localities (e.g. see the discussion in

Jensen, 1997, and the summary and illustrations in Hoffmann and Rudolph, 2011). Several of these examples obviously differ from Eophyton from the Mickwitzia Sandstone, and likely had a different type of producer.

Conclusions

At the time of Eophyton toolmark production, the seafloor sediment consisted of silt or a mixture of silt and fine-grained siliciclastic sand. The Eophyton producer was passively dragged along the seafloor by currents or waves and plowed the Eophyton furrows. Subsequently, the furrows were filled and covered in a single event by a mixture of silt and coarser siliciclastic sand, possibly in connection with a storm.

Based on the morphology of the furrows, a number of characteristics of the Eophyton producer were inferred:

- The portion of the Eophyton producer plowing the furrow was short in the direction of movement and wide in a perpendicular direction, thus allowing the furrow to take sharp turns. This portion of the Eophyton producer probably was roughly discoidal, flexible and sagged against the sediment under its own weight. Its perimeter carried small knobs or papillae and typically a few deep folds, which occasionally opened or closed while plowing a furrow.
- In a few instances, furrows abruptly changed direction, but the orientation of the furrow producer remained parallel to its direction of movement. This is the behavior typically displayed by an object being dragged by a tether.
- The depth of the furrow suggests that the furrow-plowing portion of the Eophyton producer was heavy. The lack of significant current scour on the Eophyton beds is not consistent with the fact that a strong current is required to drag a heavy, relatively large object that partly sinks into the bottom sediment. This inconsistency can be solved by assuming that the Eophyton producer was an organism consisting of a sediment-weighted anchor and a frond-like apparatus or set of tentacles acting as a sail in the presence of water movements, possibly joined by a stalk or column.

The psammocorals *Spatangopsis* and *Protolyellia* from the same formation are not likely to be the Eophyton producer. The anchor of the latter probably contained loose sediment rather than a cemented sand skeleton comparable to the sand button of psammocorals. Alternatively, this anchor was weighted by sediment adhering to its external epithelium. A cnidarian, seaweed or kelp-like nature of the Eophyton producer is also possible.

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