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THECTARDIS AVALONENSIS: A NEW EDIACARAN FOSSIL FROM THE MISTAKEN POINT BIOTA, NEWFOUNDLAND

MATTHEW E. CLAPHAM,[1,2] GUY M. NARBONNE,[1] JAMES G. GEHLING,[1,3] CAROLYN GREENTREE,[4] AND MICHAEL M. ANDERSON[5]

[1]Department of Geological Sciences, Queen's University, Kingston, Ontario K7L 3N6, Canada, [2]Present address: Department of Earth Sciences, University of Southern California, Los Angeles 90089, <clapham@usc.edu>, [3]Present address: South Australian Museum, Division of Natural Science, North Terrace, Adelaide, South Australia 5000, [4]1–249 Macdonnell Street, Kingston, Ontario K7L 4C4, Canada, and [5]53 Sterling Crescent, St. John's, Newfoundland A1A 4J9, Canada

ABSTRACT—The Neoproterozoic Ediacara biota at Mistaken Point contains the oldest diverse Ediacaran assemblages and is one of the few known deepwater localities, yet the biota is dominated by endemic forms, nearly all of which remain undescribed. *Thectardis avalonensis* new genus and species, one of these endemic forms, is a cm-scale triangular fossil with a raised rim and a featureless-to-faintly-segmented central depression. More than 200 specimens occur on two bedding plane surfaces: the 565 Ma E surface and the 575 Ma Pigeon Cove surface, nearly 2,000 m lower in the succession. Morphological and taphonomic data suggest that the organism was an elongate cone that may have lived as a suspension-feeding ''mat sticker'' with its pointed base inserted into the microbially bound sediment. If true, *Thectardis* n. gen. would be the tallest-known mat sticker, reaching a maximum height of over 15 cm. Specimens display little ontogenetic change in length:width ratio, suggesting that *Thectardis* grew uniformly by incremental addition of material to its distal end. Morphological differences between specimens at two well-separated stratigraphic levels may have resulted from evolutionary or ecophenotypic variation.

INTRODUCTION

DISTINCTIVE EDIACARA-TYPE megafossils were first reported from the Mistaken Point area of southeastern Newfoundland more than 30 years ago (Anderson and Misra, 1968; Misra, 1969); subsequent work has suggested that the ''Mistaken Point biota'' may include as many as 20–30 taxa (Anderson and Conway Morris, 1982; Landing et al., 1988; Narbonne et al., 2001). Mistaken Point (Fig. 1) is one of the most important Ediacaran fossil localities because it contains the oldest-known diverse Ediacaran fossil assemblages (Martin et al., 2000; Bowring et al., 2003; Narbonne and Gehling, 2003) and records one of the few Neoproterozoic deepwater slope biotas (Misra, 1971; Narbonne et al., 2001; Wood et al., 2003). In addition, the occurrence of the fossils as untransported census populations beneath beds of volcanic ash (Seilacher, 1992; Narbonne, 1998) provides perhaps the best opportunity anywhere to study the ecology of the Ediacara biota (e.g., Seilacher, 1999; Clapham and Narbonne, 2002; Clapham et al., 2003). Although the Mistaken Point biota contains several cosmopolitan taxa (e.g., *Aspidella* Billings, 1872; *Charniodiscus* Ford, 1958; and *Charnia* Ford, 1958) and some forms also known from Charnwood Forest, England (e.g., *Bradgatia* Boynton and Ford, 1995 and *Ivesia* Boynton and Ford, 1995), the majority of fossils are endemic and remain undescribed, hindering evolutionary and ecological comparisons with other Ediacaran localities. With the exception of the recently named trilobate form *Triforillonia costellae* Gehling et al., 2000 and the new frondose species *Charnia wardi* Narbonne and Gehling, 2003, all endemic forms have been referred to in the literature using informal but consistently applied names (e.g., ''spindles,'' ''pectinates;'' see Waggoner, 1999). This paper describes one of these forms, *Thectardis avalonensis* n. gen. and sp., previously referred to as ''triangles'' (Narbonne et al., 2001; Clapham and Narbonne, 2002; Clapham et al., 2003; Narbonne and Gehling, 2003).

SYSTEMATIC PALEONTOLOGY

Genus THECTARDIS new genus

Type species.—*Thectardis avalonensis* new species, by monotypy.

Diagnosis.—As per species.

Etymology.—From the Greek ''thektos'' (sharp-pointed) and ''ardis'' (arrowhead), in reference to the pointed triangular shape of the fossil.

THECTARDIS AVALONENSIS new species
Figures 2.1–2.6, 4.1–4.4, 5

Diagnosis.—A cm-scale imprint in the shape of a triangle, with a prominent raised margin and an interior that is featureless or exhibits faint transverse markings.

Description.—All specimens are preserved as slightly raised impressions on upper bedding surfaces (positive epirelief). The holotype (Fig. 2.1) is an elongate triangular-shaped fossil 90 mm long and 30 mm wide at the triangle base, with a prominent 5–7 mm-wide raised margin that tapers towards the apex. The featureless interior has the same texture as the surrounding bedding surface. Other specimens range in length from 26 to 165 mm and in width from 24 to 96 mm (Fig. 3) after the effects of tectonic shortening have been removed (see Wood et al., 2003 for methodology). Specimens from Mistaken Point tend to be narrower for a given length than those from Pigeon Cove (Fig. 3); most have length:width ratios of 2–3.5 (mean 2.59, $n = 53$), whereas the length:width ratio of Pigeon Cove forms typically ranges between 1 and 2.5 (mean 1.81, $n = 136$). All display a prominent raised margin (e.g., Fig. 2.1–2.6); some also have a completely raised central area (Fig. 2.2, 2.3), others have a depressed center (Fig. 2.1, 2.5), and some are intermediate, partially depressed forms (Fig. 2.6). Mistaken Point forms display straight margins, whereas the edges of many Pigeon Cove specimens tend to curve inwards apically, giving them a more bullet-shaped appearance. Most have a featureless interior, although some display one or two transverse ridges (Fig. 2.1), either continuous or discontinuous, at varying distances from the apex. One specimen (Fig. 4.3, 4.4) has a central longitudinal ridge that decreases in width from 20 mm wide at the base toward the apex, disappearing 20 mm from the apex. This specimen also bears a deformation in the margin near the apex where the fossil overlaps a holdfast disc belonging to an unidentified frondose form. Several other specimens overlap underlying recumbent organisms (Fig. 4.1, 4.2) or smaller frondose taxa (Fig. 2.3).

Etymology.—For the Avalon Peninsula, Newfoundland, where all known specimens occur.

Types.—The 205 known field specimens of *Thectardis avalonensis* occur in the Mistaken Point Ecological Reserve and thus

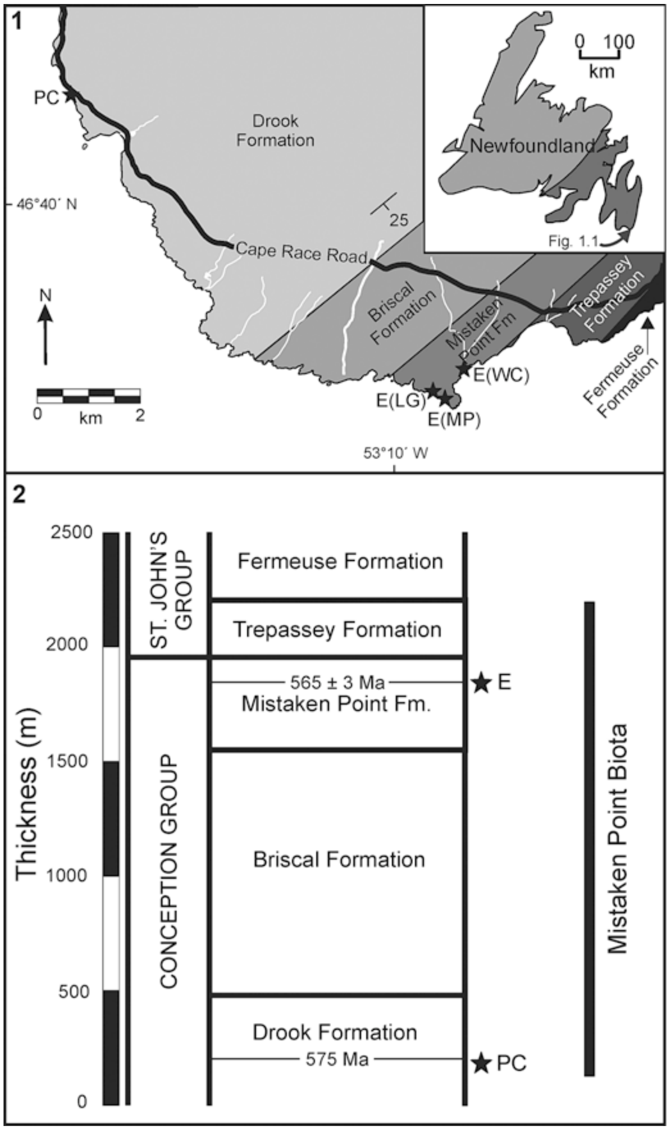

FIGURE 1—*1*, Map showing location of Mistaken Point (Avalon Terrane is shaded in inset) and fossil surfaces with specimens of *Thectardis avalonensis* n. gen. and sp. PC is Pigeon Cove surface, E(LG) is ''E surface'' at Laurentian Gulch, E(MP) is ''E surface'' at Mistaken Point, E(WC) is ''E surface'' at Watern Cove; *2*, stratigraphic section showing location of fossil-bearing surfaces relative to stratigraphic extent of Mistaken Point biota and position of dated volcanic ash beds. Upper ash bed date is from Benus (1988); lower ash bed date is from Bowring et al. (2003).

are amenable to study but protected from collection. All specimens were photographed and latex molds were made of critical material. A single previously collected specimen curated at the Royal Ontario Museum, Toronto (ROM 38632, Fig. 2.1), from the terminal Neoproterozoic (Ediacaran) Pigeon Cove surface (ca. 575 Ma; Bowring et al., 2003), upper Drook Formation (Fig. 1), is herein selected as the holotype of *Thectardis avalonensis*.

Occurrence.—*Thectardis avalonensis* occurs at two stratigraphic levels separated by nearly 2,000 m of strata (Fig. 1). A surface in the upper Drook Formation at Pigeon Cove (Fig. 2.4) contains 140 specimens comprising 58 percent of all fossils on the surface; associated fossils on this surface include *Ivesia lobata* Boynton and Ford, 1995 and *Charnia masoni* Ford, 1958 (Clapham et al., 2003; Narbonne and Gehling, 2003). An ash bed in the upper Drook Formation has yielded an age of 575 Ma (Bowring et al., 2003). The classic ''E surface'' in the upper Mistaken Point Formation at Mistaken Point, Watern Cove, and Laurentian Gulch contains 65 specimens comprising $<$1 percent of the fossils on the surface; this surface contains a diverse Ediacaran assemblage consisting of at least 12 species of spindlelike, bush-shaped, and frondose taxa (Narbonne et al., 2001; Clapham et al., 2003). Volcanic ash covering the E surface has been dated at 565 $\pm$ 3 Ma (Benus, 1988).

Discussion.—Specimens of *Thectardis* n. gen. have a simple, angular geometric shape, and the relatively consistent down-current flaring raises the possibility that *Thectardis* may represent a current scour mark or flute cast. However, the suite of morphological and taphonomic features associated with the specimens is not consistent with an inorganic origin and confirm the biogenicity of *Thectardis*. The presence of a raised rim with a central depression in these triangles is not easily reconciled with simply physical processes, although the raised triangular shape is vaguely similar to that of bedform features such as setulfs (Friedman and Sanders, 1974). However, those structures typically form in noncohesive sands, not cohesive mud like at Mistaken Point, and decrease in relief toward the flared end, unlike the uniform height of *Thectardis*. *Thectardis* also only occurs on bedding planes in association with rich assemblages of Ediacaran fossils, including cosmopolitan taxa such as *Charnia* and *Charniodiscus*. In addition, the overlapping relationship between *Thectardis* and other fossils (Figs. 2.3, 4.1, 4.2) is inconsistent with a bedform origin for the triangular shapes, as are specimens of *Thectardis* that point at right angles or even in the opposite sense to the current direction (Figs. 2.4, 6).

Most specimens (e.g., Fig. 2.1–2.6) preserve a record of the top surface of the organism, produced when the mantling volcanic ash layer was cast from below by the underlying siltstone (Seilacher, 1992; Gehling, 1999; Narbonne et al., 2001). Transverse bars developed in some specimens may represent primary internal structures but their infrequent preservation and inconsistent morphology suggest that they more likely record folding and deformation of the three-dimensional body during collapse. The outer covering behaved in a strong, semirigid fashion, as implied by its high-relief preservation, although the deformation of felled *Thectardis* over frond holdfasts (Fig. 4.3, 4.4) suggests that the body material also possessed at least some flexibility.

The original three-dimensional body shape of *Thectardis* is not obvious from its typical preservation as bedding-plane impressions. The simplest reconstruction of the triangular imprint suggests that *Thectardis* may have been a thin two-sided sheet; however, it is difficult to envisage how an organism with a sheetlike morphology could have functioned in the aphotic environments preserved at Mistaken Point. Additionally, a flat sheetlike morphology would allow preservation of overlying organisms (which would also be molded by the ash if they fell flat)—a relationship which is not observed (e.g., Fig. 4.3, 4.4). *Thectardis* may have had a conical body (Fig. 5), the simplest three-dimensional form and one most similar to shapes observed in many living and fossil groups. The prominent and uniform outer margins observed on all specimens could have been produced by bowing near the edges of the collapsed specimen if the tissue material was partially stiff, as suggested by its high-relief preservation yet flexible deformation. During collapse, central regions would compact fully; however, regions near the rim, in close proximity to the folded edge of semirigid body material, could not collapse to a flat surface. The resulting impression, produced by felling and collapse of a partially stiff conical body, would display raised ridges with a

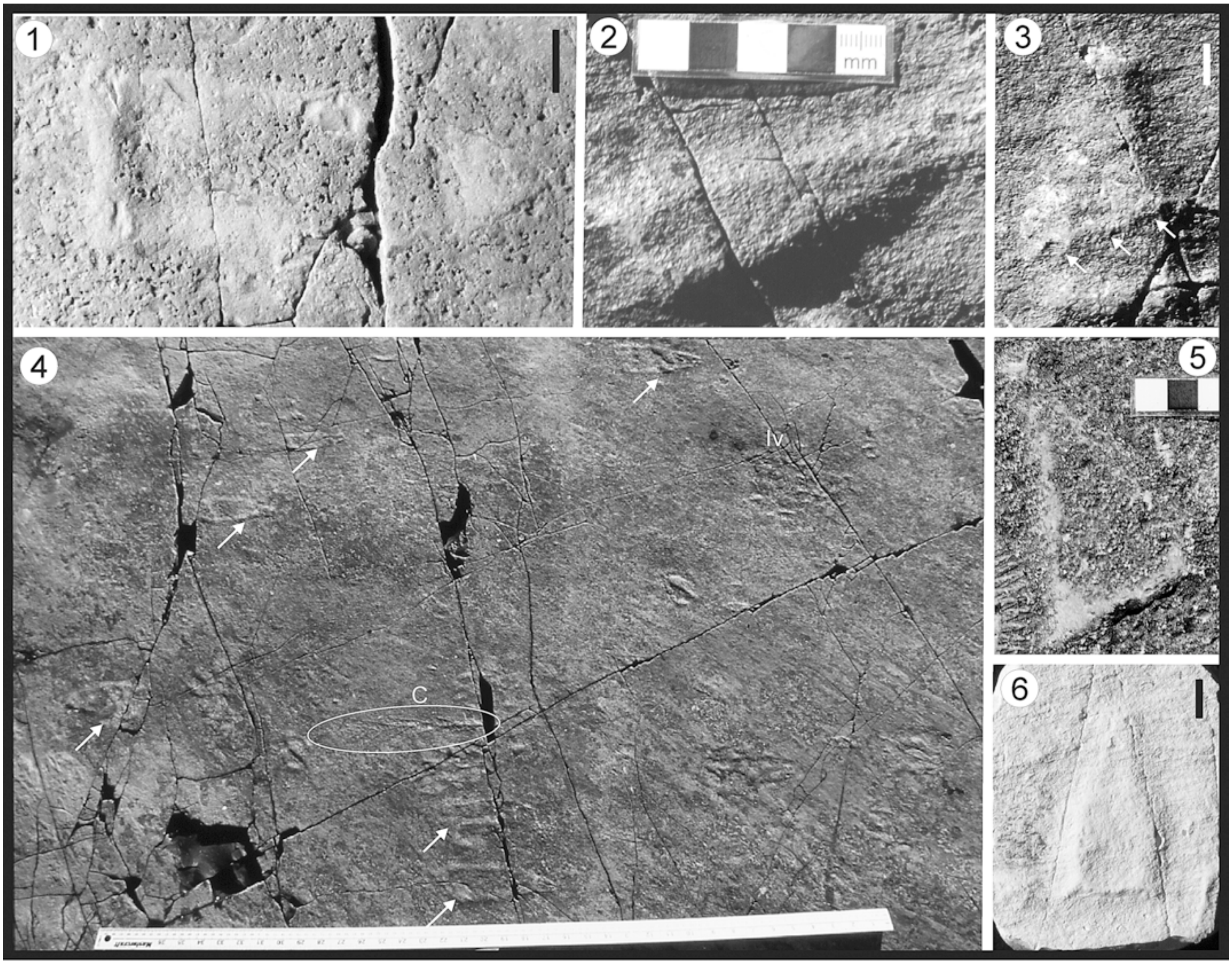

FIGURE 2—*Thectardis avalonensis* n. gen. and sp. *1,* Holotype ROM38632 from Pigeon Cove surface, showing raised rim and depressed center (scale bar is 1 cm); *2,* fully raised specimen from E surface at Mistaken Point; *3,* fully raised specimen from E surface at Mistaken Point (scale bar is 1 cm), felled overtop small *Charniodiscus* Ford, 1958 specimen (arrowed); *4,* field photograph of part of the Pigeon Cove surface showing oriented specimens of *Thectardis* n. gen. (arrowed) with *Charnia* Ford, 1958 (circled and indicated by letter C) and *Ivesia* Boynton and Ford, 1995 (Iv); *5,* specimen with raised rim and ash-infilled center from E surface at Watern Cove; *6,* plaster cast of fully raised specimen from E surface at Mistaken Point (scale bar is 1 cm).

sharp outer edge grading inward to a flat central area. One specimen displays a central longitudinal ridge (Fig. 4.3, 4.4) that could instead have formed from collapse and composite molding of a three-sided pyramid; however, this shape is not able to account for other morphologic features. Complete collapse of a pyramidal body should result in four or five longitudinal ridges produced by buckling of the sides, whereas if the body was not collapsed it would project into the overlying sediment, preventing molding by the ash layer and subsequent casting from below. This shape may also result in more pronounced margins near the apex where the three edges join; however, the opposite relationship is observed in most specimens, where the relief of marginal ridges increases away from the apex. In addition, felling of the neighboring frondose organism (holdfast in Fig. 4.3, 4.4) over the fallen *Thectardis* specimen adds significant uncertainty regarding the biological significance of the longitudinal ridge. Thus, a conical body constructed of semirigid but still partially flexible material remains the most likely three-dimensional shape for *Thectardis* (Fig. 5). There are few constraints on the material properties or morphology of the upper face of the organism, which is not directly preserved in the specimens; however, collapse of the conical body would have been mechanically easier if the upper face was not covered by an organic membrane. The presence of an open upper face would be consistent with a suspension-feeding lifestyle, which may be suggested by the striking similarities between Mistaken Point community structure and the structure of Phanerozoic and modern suspension-feeding animal communities (Clapham and Narbonne, 2002).

Specimens of *Thectardis* display a consistent preferred orientation (measured from triangle apex to triangle base) on both surfaces, colinear with the known frondose taxa (e.g., *Charniodiscus*, *Charnia*) from the same surface (Figs. 2.4, 6). The unimodal orientations of other frondose taxa were caused by felling in a unidirectional current, in contrast to the random orientation of

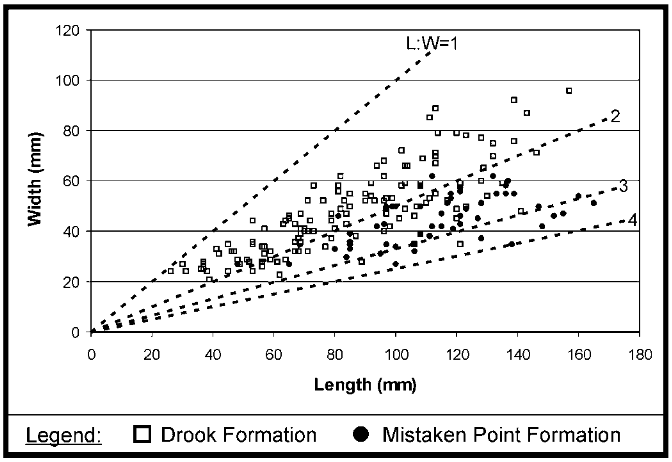

FIGURE 3—Quantitative paleontology of *Thectardis avalonensis* n. gen. and sp. Graph plots width versus length; dashed lines indicate constant length:width ratios. Specimens from the PC surface (Drook Formation) are indicated by open squares; specimens from the E surface (Mistaken Point Formation) are shown by solid circles.

recumbent taxa such as ''spindles'' (Seilacher, 1999; Wood et al., 2003). The unimodal felling direction of *Thectardis* implies that it also lived upright, with its pointed base tethered to the sea bottom (Fig. 5). An upright life position is also supported by observed superpositional relationships on the E surface, where specimens of *Thectardis* were felled on top of recumbent ''spindles,'' bushlike *Bradgatia* (e.g., Fig. 4.1, 4.2), or over smaller frondose organisms such as *Charniodiscus* (e.g., Fig. 2.3) and ''dusters.''

This unusual upright life position, with no visible attachment structure, is shared by other Neoproterozoic and Early Cambrian organisms that are interpreted as requiring firm, mat-bound substrates to support their bodies in an upright position (Seilacher, 1999). The presence of fine-scale crinkly laminations and pustular surface texture (''old elephant skin'') at Mistaken Point (e.g., Fig. 2.2, 2.3; Wood et al., 2003, fig. 10) implies that the sediment surface was stabilized by microbial mats, providing the firm substrate required by many Neoproterozoic organisms for attachment (Gehling, 1999; Wood et al., 2003). *Thectardis* may have attached directly to the sediment surface, although it does not have the discoidal holdfast structure typical of other upright Ediacaran fronds (e.g., Jenkins and Gehling, 1978; Clapham and Narbonne, 2002; Narbonne and Gehling, 2003). It is also possible that *Thectardis* used an unpreserved thin filament to tether itself to the seafloor, rather than a holdfast disc. However, the morphology of

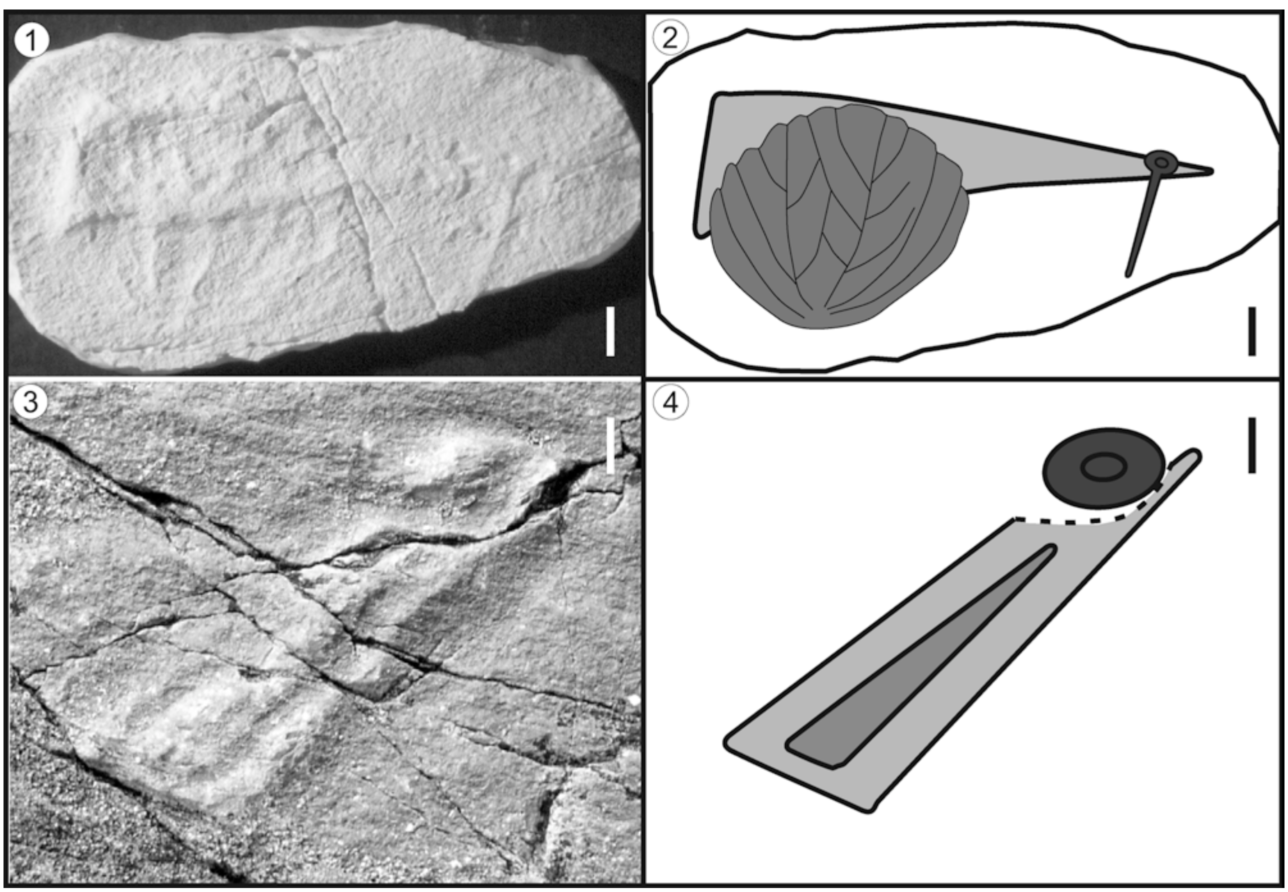

FIGURE 4—*Thectardis avalonensis* n. gen. and sp. *1,* Plaster cast of specimen showing overlapping relationship with *Bradgatia* Boynton and Ford, 1995; *2,* interpreted line drawing of specimen shown in *1*. *Thectardis* n. gen. specimen (light gray) overlaps *Bradgatia* (gray) and a small frond holdfast and stem (dark gray); *3,* field photograph of specimen displaying central longitudinal ridge; *4,* interpreted line drawing of specimen shown in *3*. *Thectardis* n. gen. (light gray) was felled over the holdfast (dark gray) of a frondose organism that subsequently fell on top of the *Thectardis* n. gen. specimen, producing the central impression (shown in gray). All scale bars 1 cm.

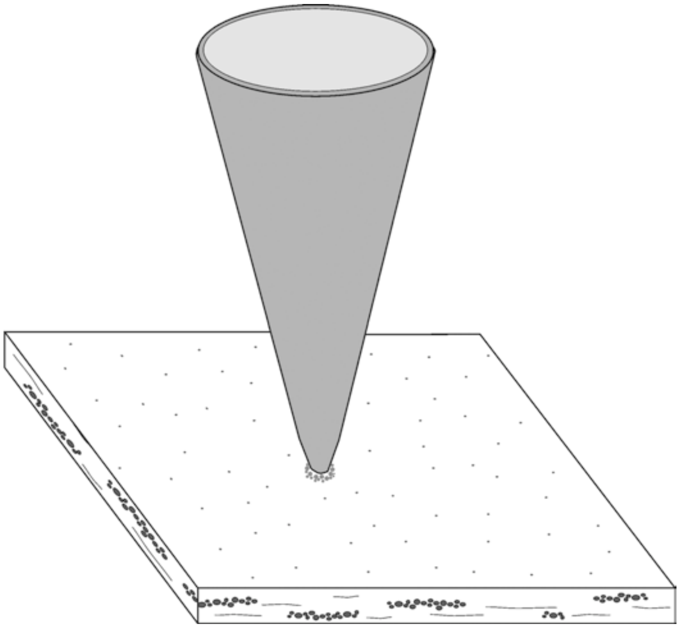

FIGURE 5—Reconstruction of *Thectardis avalonensis* n. gen. and sp. in interpreted life position.

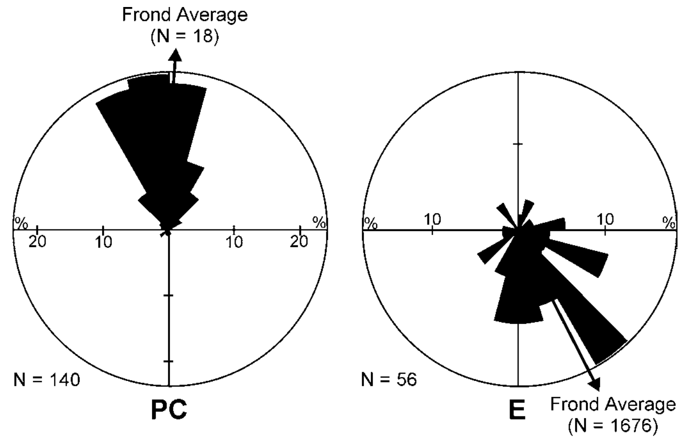

FIGURE 6—Rose diagrams of the orientations of *Thectardis avalonensis* n. gen. and sp. specimens on two bedding planes (PC and E). N = number of specimens in each diagram. Arrow indicates mean azimuth of other oriented frondose taxa on each surface.

Thectardis, especially its pointed base, is instead strongly reminiscent of Neoproterozoic and Early Cambrian ''mat sticker'' organisms (Seilacher, 1999; Dornbos and Bottjer, 2000), suggesting that it may have lived with its base inserted into the mat-bound sediment.

In contrast to *Thectardis*, which reached heights of greater than 15 cm, most other mat stickers, such as helicoplacoid echinoderms, were no more than 5–7 cm tall (Durham, 1993; Dornbos and Bottjer, 2000). This height disparity may reflect a lack of predation and bioturbation affecting the Neoproterozoic *Thectardis* and/or adaptation to different environmental conditions. Helicoplacoids lived in storm-influenced shallow water environments (Dornbos and Bottjer, 2000) where wave turbulence may have prevented them from reaching significant height above the substrate. The lower-energy deep slope environment at Mistaken Point, influenced by a contour-parallel current but located well below storm wave base (Narbonne et al., 2001; Wood et al., 2003), would have permitted *Thectardis* to grow taller than shallow water mat stickers.

Quantitative measurements of *Thectardis* specimens from both surfaces show that growth pattern was relatively consistent throughout ontogeny (Fig. 3). The length:width ratio did not change during growth, suggesting that *Thectardis* likely grew by addition of material to its distal end, or less likely, by uniform scaling of its soft body. Although growth pattern was consistent during ontogeny, the length:width ratio differed significantly between specimens from the PC and E surfaces (Mann-Whitney U-test; $U = 6{,}516.5$, $df = 189$, $P < 0.001$). Specimens from the PC surface tended to have a smaller length:width ratio than specimens from the E surface (Fig. 3). These growth differences may reflect an evolutionary adaptation by the E surface *Thectardis*, minimizing the projected surface area exposed to the current at a given height and enhancing stability in the contour current regime. Alternatively, the narrower morphology may have been an ecophenotypic response if contour current flow was faster in the E surface community.

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