The last meal of the Late Ordovician mollusc 'Helminthochiton' thraivensis Reed, 1911, from the Lady Burn Starfish Beds, southwest Scotland.

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The last meal of the Late Ordovician mollusc '*Helminthochiton*' *thraivensis* Reed, 1911, from the Lady Burn Starfish Beds, southwest Scotland

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An exceptional specimen of the Late Ordovician mollusc '*Helminthochiton*' *thraivensis* Reed, from the Katian of the Lady Burn Starfish Beds, southwest Scotland, preserves gut contents that include nine pelmatozoan ossicles. These are interpreted as including two nodal and five internodal columnals, and two radice ossicles from the attachment structure. The stem was cyclocyclic and heteromorphic, possibly N212. Radice ossicles were wider than the height of nodals, so radice scars must have encroached onto the latera of adjacent internodals. These features were compared with the 26 known pelmatozoan taxa from the Lady Burn Starfish Beds. Paracrinoids (one species) and glyptocystitid rhombiferans (six species) were discounted as prey because of their cemented attachment, and incorrect columnal morphology and lack of attachment, respectively. Of 19 species of crinoids, eight are discounted in which the column is pentagonal, tetragonal or unknown. Of the remaining 11 species, only the monobathrid camerate *Macrostylocrinus cirrifer* Ramsbottom satisfies all criteria for identification of the prey, including heteromorphy and radice scars encroaching adjacent internodals. Copyright © 2010 John Wiley & Sons, Ltd.

1. INTRODUCTION

Recognising the occurrence and nature of ancient interactions between organisms has been, historically, a field littered with at least as much unsupported speculation as hard fact. Speculation can be based on strong data—mammal X occurs in the same bed as grass Y and dental analysis supports the herbivory of one upon the other (Janis, 1990). Speculation can also be wild—the dinosaurs went extinct because the emergent mammals ate all of their eggs (critiqued by Bakker, 1986, pp. 425–444). Much better than speculation is the analysis of actual specimens preserving intimate biotic interactions, associations that Boucot (1990, p. 9) referred to his Category 1 behaviour: '[The] select minority of examples where the evidence is incontrovertible, and even purists will find little to quibble about. I have sometimes referred to these examples as 'frozen' behavior.' Such specimens are some of the most exciting fossils known

(see Boucot, 1990, for examples), but they are also rare in most groups.

One group in which interactions with other organisms may be well displayed are the echinoderms which can preserve growth deformities, particularly stereomic overgrowths, in response to the unwelcome attentions of encrusting, embedding and boring invertebrates. Commonly a steromic reaction is associated with a trace fossil, such as *Oichnus* Bromley (for example, Eckert, 1988), so the nature of the organism infesting the echinoderm is conjectural. More rarely a skeletonized invertebrate is preserved in intimate contact, such as the tabulate coral *Cladochonus* sp., which attached to and subsequently was overgrown by the columns of Mississippian crinoids (Donovan and Lewis, 1999). These interactions were obviously slow and took some time to develop, measureable in weeks, months or more. Other interactions were much faster and occurred in minutes. One such 'fast' association is the subject of this paper.

Donovan *et al.* (2010) documented the gut contents of an articulated (but mouldic) specimen of the Late Ordovician (Katian) chiton '*Helminthochiton*' *thraivensis* Reed, 1911.

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Unexpectedly, large, identifiable elements in the gut are columnals of pelmatozoan echinoderms, probably crinoids. Living chitons are commonly regarded as grazers, but many extant species are carnivorous, at least in part. Some are specialized ambush predators (McLean, 1962). The unique specimen of '*H.*' *thraivensis* extends evidence of chiton carnivory back to the Ordovician and records a unique association; no modern chitons are known to be crinoidivorous.

Donovan *et al*. (2010) considered that this association was more likely to involve scavenging or predation rather than detrivory; these arguments are extended herein. However, the principal purpose of the present communication is to improve on the original determination of the identity of the prey organism. Donovan *et al*. (2010) favoured the prey being a stalked crinoid. Herein, we attempt to reconstruct the column preserved in the gut of this unique specimen and determine its identity.

2. LOCALITY AND HORIZON

The type locality for '*H.*' *thraivensis* is the Lady Burn Starfish Beds of Threave Glen, Girvan district, Ayrshire (=Strathclyde), southwest Scotland [NGR NS 250 038] (Figure 1), which form part of the Drummuck Subgroup, South Threave Formation, Farden Member of the Craighead Inlier (Harper, 1982a, b; Rushton and Owen, 1999). These beds are Upper Ordovician, Ashgill, Katian (=Cincinnatian, Richmondian in terms of the North American succession; Rawtheyan in terms of the British succession; Ingham *in* Fortey *et al*., 2000, figure 24). Ingham (1978) and Harper
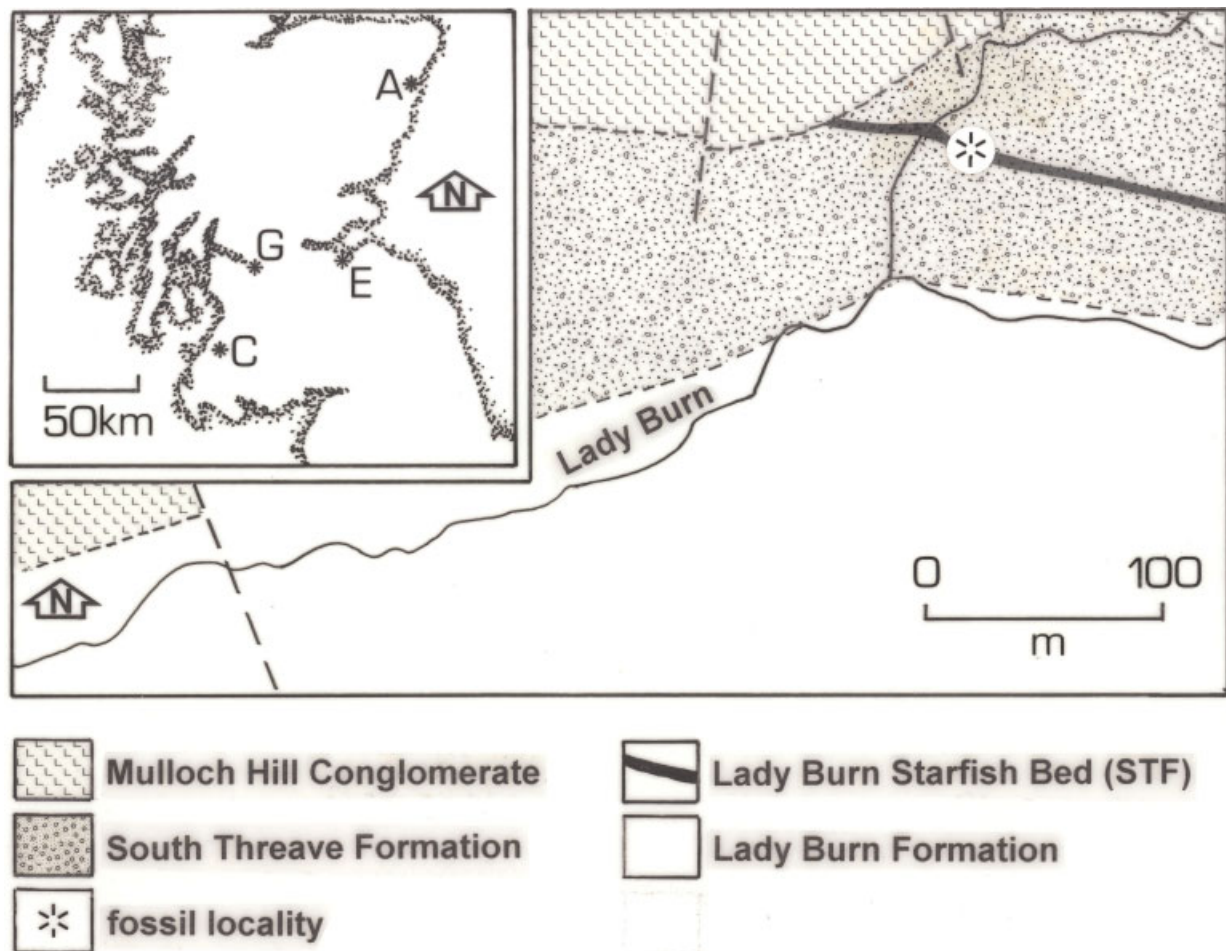
Figure 1. Geological map of the area east of South Threave farmhouse in the Craighead Inlier, Girvan, Ayrshire (after Donovan *et al*., 2010, figure 1; simplified after Harper, 1982b, figure 11). The asterix (*) marks the position of the exposure of the Lady Burn Starfish Beds. Correlation: Lady Burn and (overlying) South Threave formations, Rawtheyan (Ashgill, Ordovician); Mulloch Hill Conglomerate Formation, Rhuddanian (Llandovery, Silurian); contact unconformable. Note that the Lady Burn Starfish Beds are in the South Threave Formation, not the Lady Burn Formation. The inset shows the position of the main map in southwest Scotland (=C). Key: A = Aberdeen; C = Craighead Inlier, near Girvan; E = Edinburgh; G = Glasgow.

(1979, 1982a, 2001) have argued convincingly that the Lady Burn Starfish Beds represent a deeper water, downslope setting in a steep, narrow shelf/slope preserving an allochthonous faunal assemblage, perhaps reminiscent of the setting of Neogene shell beds on isolated islands in tectonically active settings (Donovan, 2002). This superseded the earlier interpretation of Goldring and Stephenson (1972) that this was a shallow water, parautochthonous accumulation. Although it is difficult to interpret which faunal elements were allochthonous and which autochthonous, the Lady Burn Starfish Beds nevertheless provide a glimpse of echinoderm diversity immediately prior to the end Ordovician extinctions (Donovan, 1989b, 1992c).

The Lady Burn Starfish Beds preserve complete specimens of invertebrates with complex skeletons, such as trilobites (Owen and Ingham, 1996). It is the most important echinoderm locality in the British Ordovician, and includes articulated crinoids, glyptocystitid rhombiferans, paracrinoid ossicles, asteroids, ophiuroids, echinoids, bothriocidaroids, cyclocystoids, edrioasteroids, solutes and cornutes (Donovan *et al.*, 1996; Jefferies, 1996). It is the first three groups that are of particular interest to the present study (Tables 1 and 2). These are discussed in detail below, along with certain other, less plausible 'victims'.

3. MATERIALS AND METHODS

(Based on Donovan *et al.*, 2010, pp. 935–936.) The specimen (BMNH G47258; Figure 2) is a syntype of the primitive chiton '*Helminthochiton*' *thraivensis* Reed; this taxon is currently the subject of a formal taxonomic revision (M.D.S. and J.D.S., research in progress) and Reed's binomen is retained herein for convenience only. BMNH G47258 was imaged using the Metris X-Tek HMX-ST high-resolution X-ray MicroTomography (XMT) scanner housed in the Natural History Museum, London (Ketcham and Carlson, 2001; Sutton, 2008). Scans were conducted with a current of 200 mA, voltage of 225 kv, 0.17 s exposure, tungsten reflection target and a 1 mm copper filter. Voxel

Table 1. Pelmatozoans (excluding crinoids) from the Lady Burn Starfish Bed, near Girvan, southwest Scotland (compiled from Paul, 1965, 1973–1997; Regnéll and Paul, 1981; Donovan *et al.*, 1996)

RHOMBIFERA (glyptocystitids)
    Acanthalepis jamesii M'Coy, 1846
    Homocystites constrictus (Bather, 1913)
    Homocystites beggi Regnéll and Paul, 1981
    Pleurocystites foriolus (Bather, 1913)
    Pygecystis quadrata (Bather, 1913)
    Pygecystis procera (Bather, 1913)
PARACRINOIDS
    Comarocystites sp. or *Sinclairocystis* sp. *in* Paul, 1965

Table 2. Crinoids from the Lady Burn Starfish Bed, near Girvan, southwest Scotland (compiled from given references and Donovan, 1989b; Brower, 1995)

Subclass DISPARIDA
    Westheadocrinus girvanensis Donovan, 1989a
    Serendipocrinus lamonti Donovan, 1992b
    Eocicerocrinus sevastopuloi Donovan, 1989a
    Anulocrinus thraivensis Ramsbottom, 1961
    Cremacrinus drummuckensis (Ramsbottom, 1961)
    Claviculacrinus scoticus Donovan, 1989a
Subclass CLADIDA
    Euspirocrinus girvanensis Donovan, 1992a
    Porocrinus scoticus Ramsbottom, 1961
    Plicodendrocrinus collapsus (Donovan, 1992a)
    Plicodendrocrinus granditubus (Ramsbottom, 1961)
    Cupulocrinus drummuckensis Kolata, 1975
    Cupulocrinus heterobrachialis Ramsbottom, 1961
    Protaxocrinus girvanensis Ramsbottom, 1961
Subclass CAMERATA
  Order MONOBATHRIDA
    Xenocrinus multiramus Ramsbottom, 1961
    Xenocrinus breviformis Brower, 1974
    Macrostylocrinus cirrifer Ramsbottom, 1961
  Order DIPLOBATHRIDA
    Eodimerocrinites littlewoodi Donovan *in* Donovan & Gilmour, 2003
    Diabolocrinus sp. *in* Ramsbottom, 1961
    diplobathrid(?) indet. *in* Brower, 1974

size is 32 microns; the reconstructed volume is $1202 \times 1118 \times 847$ voxels. Three-dimensional reconstructions were produced using the custom SPIERS software suite, implementing the isosurface-based reconstruction approach described by Sutton *et al.* (2001) augmented by an interactive OpenGL-based rendering package. Prior to three-dimensional imaging the specimen was digitally prepared to remove extraneous 'noise' such as unrelated fossil fragments, to identify each valve of the chiton and to differentiate these from gut contents.

Specimens figured and discussed herein are in the collections of the Natural History Museum, London (BMNH), the British Geological Survey, Edinburgh (BGS GSE) and the Hunterian Museum, Glasgow (HM).

4. DESCRIPTION OF OSSICLES IN GUT

High resolution XMT imagery of BMNH E47258 has revealed a curved, linear arrangement of shelly debris that lies inside and follows the curvature of the chiton dorsum (Donovan *et al.*, 2010, figure 3). This debris includes nine disc-like structures which were referred to therein as Ossicles 1 to 9. Each of the ossicles is a low disc, approximately circular to elliptical in outline with a central,

Figure 2. The Natural History Museum, London (BMNH) G47258, a syntype of '*Helminthochiton*' *thraivensis* Reed, 1911 (after Donovan *et al.*, 2010, figure 2). Scale in mm. This figure is available in colour online at wileyonlinelibrary.com/journal/gj

rounded to irregularly ovate perforation (=lumen) and a low latus (Donovan *et al.*, 2010, p. 936).

Figure 3 illustrates all of the columnals in the gut of BMNH G47258, ordered from posterior (Ossicle 1) to anterior (9) relative to the chiton valve series. Four columnals have a narrow, rounded lumen (1, 6, 7, 9); four have a broader, rounded lumen (3, 4, 5, 8); and one is misshapen, perhaps ellipsoidal triangular (2). Three columnals are elliptical in outline (2, 3, 5) and the others are all rounded. All columnals are low, the highest being Ossicles 4 and 8.

With this melange of morphological features, our assumption that the nine ossicles represent one species may appear at least superficially speculative. However, it must be assumed that the nine ossicles have been variously modified by solution and etching in the chiton gut. That dissolution has occurred is demonstrated best by Ossicle 2. No crinoid had or has a lumen this shape and in this slightly eccentric position. Crinoids with triangular lumina are known from the Upper Ordovician, but these are invariably in the centre of the articular facet and are either equilateral or, at least, bilaterally symmetrical (see, for example,
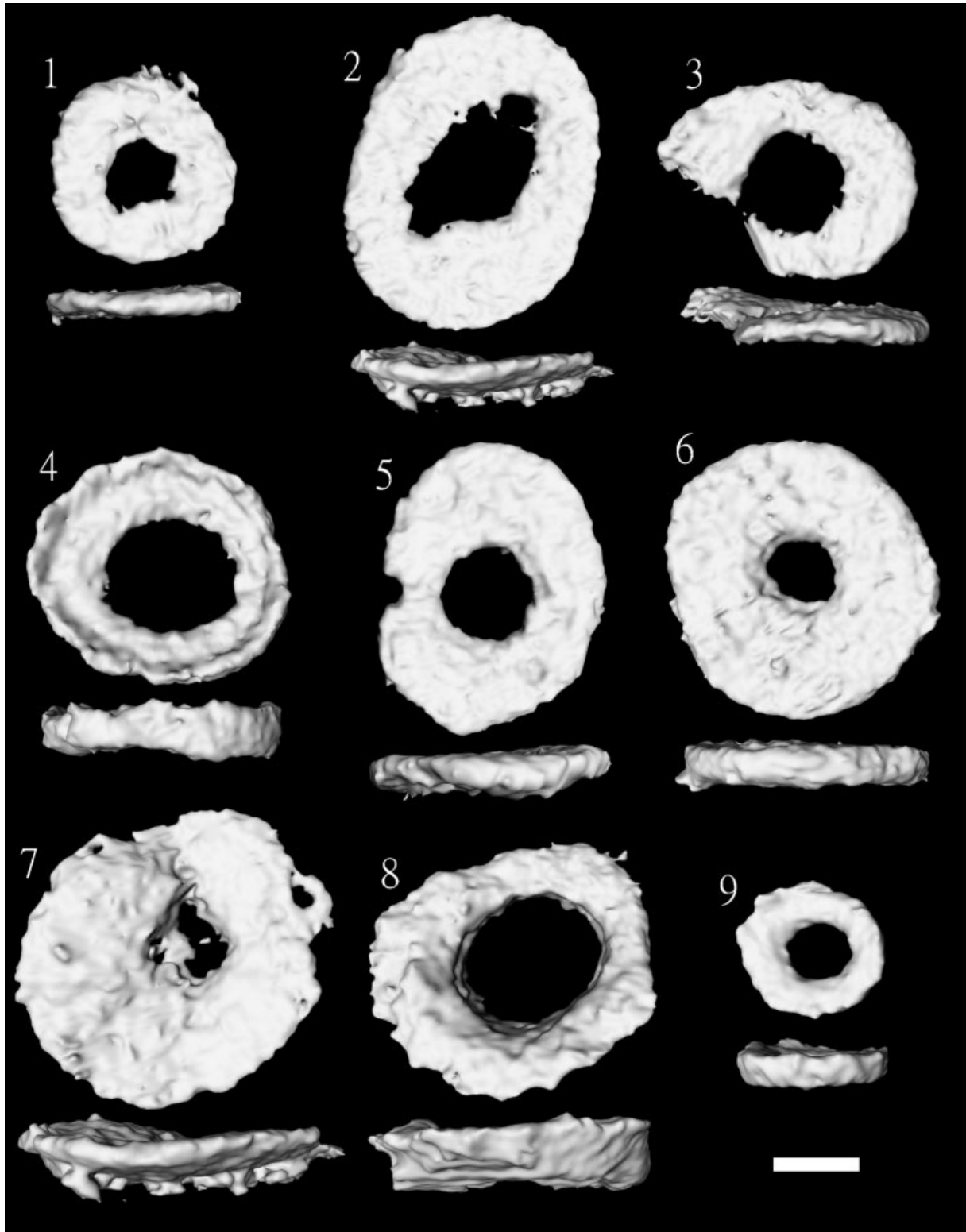
Figure 3. High-resolution X-ray microtomography images of crinoid columnals in the gut of 'Helminthochiton' thraivensis Reed, BMNH G47258. Ossicles 1–9 are in the sequence that they appear in the gut (Donovan et al., 2010, figure 3), numbered from posterior to anterior relative to the chiton valve series. Key: 4, 8 = nodals; 2, 3, 5, 6, 7 = internodals and 1, 9 = radice ossicles. Scale bar represents 2 mm.

Donovan, 1986a, b, 1989a; Titus, 1989). The only possible exception, a small ossicle with a V-shaped rather than truly triangular lumen, is probably a radice ossicle (Donovan, 1989a, p. 92, text-figure 33E, pl. 9, figures 2, 3). Dissolution is not unexpected as modern chitons have gut environments that are acidic (Fretter, 1937; Greenfield, 1972, p. 42).

It is relevant at this point to revisit the question of detritivory versus predation or scavenging. Accepting that the nine, etched ossicles came from one crinoid column, could they not have been eaten with other detritus from the sea floor? It is apparent that if the column had completely disarticulated, then it would suggest selective feeding on dead crinoid ossicles from a single species, yet with no nutritional value to the chiton; we reject this suggestion outright. More likely, the chiton might have ingested a disarticulated pluricolumnal before rotting of the collagenous ligaments that bound the columnals together. However, we now know that disarticulated lengths of modern crinoid columns can remain alive for over a year after being detached from the crown and more proximal stalk (Donovan and Pawson, 1998; Oji and Amemiya, 1998). So, ingestion of a pluricolumnal, even though disarticulated from the column, must be considered either scavenging or predation depending upon whether it was recently dead or still alive. It may also be relevant to note that disarticulated columnals and pluricolumnals are uncommon in the Lady Burn Starfish Beds. Further, the possibility cannot be discounted that this pluricolumnal was ingested after a predatory attack on an elevated stalked crinoid, perhaps on an individual with a recumbent dististele.

Perhaps significantly, this crinoid debris is accompanied by other bits of invertebrate debris. It seems improbable that a predatory chiton would be able to hit fast animals like trilobites. If an ambush predator (the only way it is likely to have caught a trilobite), why is it eating sessile prey such as crinoids? This perhaps lends weight to an interpretation of '*H.*' *thraivensis* as a scavenger rather than a predator.

From the ossicles illustrated in Figure 3, it is determined that the crinoid had a cyclocyclic, heteromorphic column, with nodals highest (Ossicles 4, 8) and internodals lower (2, 3, 5, 6, 7). Ossicles of noticeably small diameter (1, 9) may have been internal internodal columnals, that is, lacking an external expression, but, somewhat more likely, were radice ossicles, that is, part of the 'root'. Thus, there are two nodals, five internodals and two radice ossicles. This association of columnals that came from one stem demonstrates that the chiton must have ingested an intact pluricolumnal that subsequently disarticulated in the gut. This suggests that the noditaxis may have been something like N212 (notation of Webster, 1974; Figure 4 herein). Latera appear to be approximately planar, but no more so than the articular facets, neither being well preserved. The latter would imply that the crinoid lacked a symplectial articulation which we consider highly unlikely (Donovan, 1990). There is good evidence of a sloping claustrum (5?, 6, 8) and perhaps a raised rim to the circumference of the articular facet in nodals (4, 8?).

A speculative reconstruction of the gross morphology of the ingested column is given in Figure 4. For comparison with pelmatozoans of the Lady Burn Starfish Beds, the
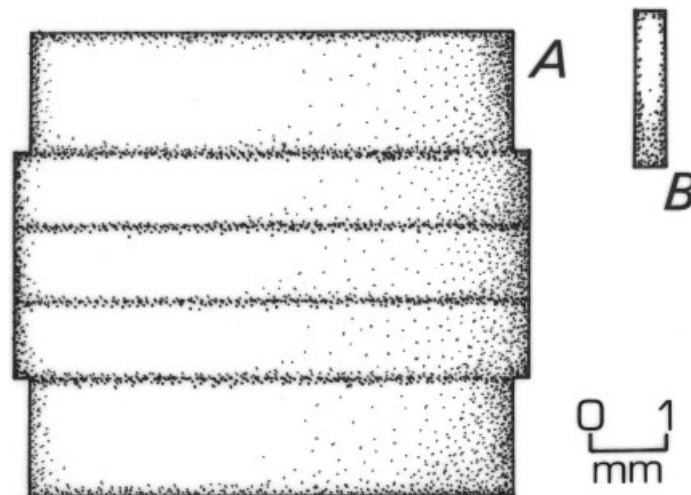

Figure 4. Coarse reconstruction of the gross features of the pluricolumnal (**A**) and a radicular ossicle (**B**) of the prey pelmatozoan, based on measurements taken from Figure 3. Measurements used are nodal diameter = 6.4 mm (ossicle 8); nodal height = 1.6 mm (8); internodal diameter = 6.8 mm (7); internodal height = 1.0 mm (6); radice ossicle diameter = 2.1 mm (1) and radice ossicle height = 0.4 mm (9). As some dissolution has occurred, the measurements probably underestimate the true dimensions of these ossicles. In particular, the maximum diameters of nodals and internodals are close; it is only very rarely that an internodal would have a greater diameter than a nodal. Note that the radicular ossicle is wider than a nodal columnal is tall; therefore, the radice scar must have encroached on the lateral of adjacent internodals.

important morphological features are those apparent in external view. This is because the fossil pelmatozoans are preserved as external moulds and studied as latex casts; features of the axial canal and articular facet are largely unknown.

For clarity, the echinoderm that yielded these ossicles will be referred to below as the prey pelmatozoan.

5. THE LADY BURN STARFISH BEDS AND THEIR STALKED ECHINODERMS

The following review considers the geometry of the column in all pelmatozoans from the Lady Burn Starfish Beds. These notes should be used in conjunction with Tables 1 and 2.

5.1. Non-crinoid pelmatozoans (Table 1)

The non-crinoid pelmatozoans of the Lady Burn Starfish Beds include one paracrinoid and six species of glyptocystitid rhombiferan cystoid (Table 1). Paracrinoids at Lady Burn are only known from disarticulated thecal plates left in open nomenclature (Paul, 1965), although other species are known from elsewhere with more complete specimens. For example, the column of *Comarocystites punctatus* Billings, from the Upper Ordovician Hull Formation of Quebec (Trenton Group = Caradoc; Fortey *et al*., 2000, figure 34), '... is cylindrical, with no evidence of pentamerism either exteriorly or interiorly. The ... columnals are very thin, alternating in thickness, about 20 occurring in a length of six millimetres in the column attached to that Billings type-specimen which retains the arm. This column has a diameter of four millimeters. The surface of the column is ornamented by minute granules, seven in a width of one millimeter, arranged quincuncially, in diagonal intersecting rows. The lumen equals one-fourth of the diameter of the column. The flat surfaces of the columnals are striated radially' (Foerste, 1916, p. 89; Figure 5 herein). This column thus sounds similar to that of the prey pelmatozoan, although the attachment is by a distal cemented disc, not radices (Figure 5).

The glyptocystitid rhombiferans from the Lady Burn Starfish Beds (Table 1) are all known from complete specimens preserving at least part of the proxistele (Paul, 1984; Donovan *et al*., 1996). The columns of glyptocystitids are well known and consistent in gross morphology, the broad, but tapering, heteromorphic proxistele grading into a slender dististele more like a string of beads (e.g., Paul, 1968, 1984). It is the columnals of the proxistele that holds the greatest similarity with the prey pelmatozoan, although this is superficial. Glyptocystids invariably have a broad axial canal, much wider than in any columnal in Figure 3 (for

Figure 5. The paracrinoid *Comarocystites punctatus* Billings, 1854 (after Foerste, 1916, pl. 5). Specimen in the collection of the Canadian Museum of Nature (formerly the Victoria Memorial Museum), Ottawa. Specimen about 210 mm in height.

example, compare with Paul, 1968, text-figures 1, 2, pl. 112, figures 6, 7; 1984, text-figure 51). Also, there is no evidence for any of these glyptocystitds having a radicular attachment; indeed, some or all were unattached as adults or younger (Paul, 1967, 1968).

5.2. Other 'stalked' echinoderms

For completeness, two other non-crinoid echinoderm groups with 'stalks' are mentioned, although they are morphologically very different from the predicted prey organism. The pyrgocystid edrioasteroid *Pyrgocystis grayae* Bather, 1915, has a straight peduncle consisting of numerous circlets of imbricate plates that could not be confused with a holomeric columnal (Donovan *et al.*, 1996, pl. 52, figures 4, 5). Somewhat more diverse are the carpoids, including two species of solute and two species of cornute (Jefferies, 1996). The tails of these taxa are multiplated with at least two ossicles forming each 'circlet' (Jefferies, 1984) and are thus different from those of the prey pelmatozoan.
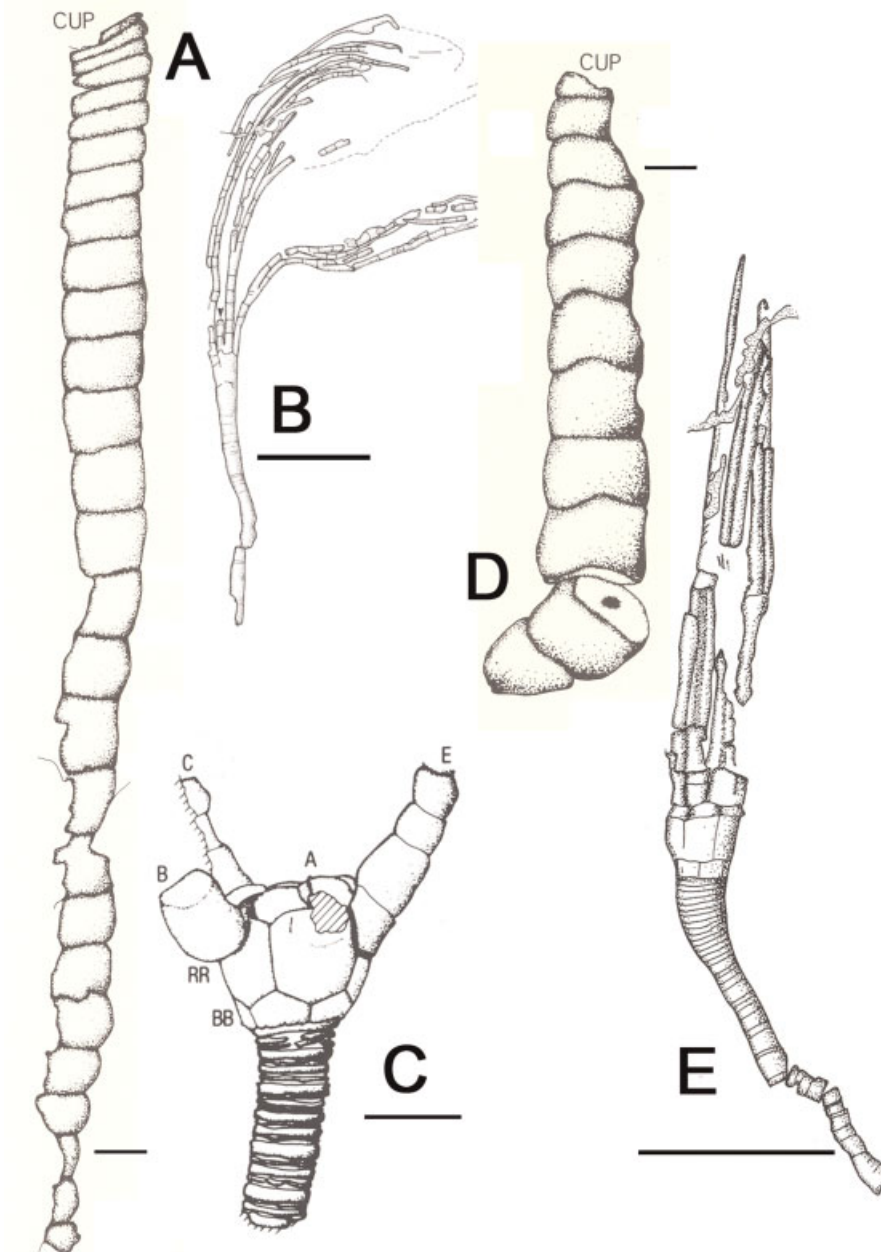

Figure 6. Disparid crinoids from the Lady Burn Starfish Beds, Girvan, southwest Scotland (Upper Ordovician). (**A**) *Anulocrinus thraivensis* Ramsbottom, paratype, BMNH E47311, column (after Donovan, 1986a, text-figure 13A). Scale bar represents 1 mm. (**B**) *Claviculacrinus scoticus* Donovan, holotype, BMNH E47316a, crown and proximal column (after Donovan, 1989a, text-figure 28A). (**C**) *Serendipocrinus lamonti* Donovan, holotype, HM E3951/a, crown and proximal column (after Donovan, 1992b, figure 2a). (**D**) *Cremacrinus drummuckensis* (Ramsbottom), BMNH E67923a, column (after Donovan, 1986a, text-figure 13C). Scale bar represents 1 mm. (**E**) *Eocicerocrinus sevastopuloi* Donovan, holotype, BMNH E51633a, crown and proximal column (after Donovan, 1989a, text-figure 24A). All camera lucida drawings of latex casts taken from natural moulds. Scale bars represent 5 mm unless stated otherwise.

5.3. Crinoids (Table 2)

Nineteen species of crinoid are known from the Lady Burn Starfish Beds, including two in open nomenclature. The column is unknown in the cladid *Euspirocrinus girvanensis* Donovan and the diplobathrid *Diabolocrinus* sp., but examination of the columns of members of the same genera suggests no close match. These species will not be considered further.

Some taxa can be discounted easily because of the angular external geometry of their column. For example, the monobathrid camerate *Xenocrinus* S.A. Miller, represented by two species (Table 2), is unusual in having a column of tetragonal section (Donovan *et al.*, 1995, figures 2E, F). The two species of *Plicodendrocrinus* Brower have pentastellate columns. The disparid *Westheadocrinus girvanensis* Donovan has a rounded pentagonal column in which the range of columnal heights is more extreme than in the prey pelmatozoan. The cladid *Cupulocrinus heterobrachialis* Ramsbottom has a column that is pentastellate proximally trending to pentagonal in section more distally.

Further, all but one of the remaining five species of disparid can easily be shown to differ from the prey pelmatozoan, even though they have columns with circular sections (Figure 6). *Anulocrinus thraivensis* Ramsbottom and *Cremacrinus drummuckensis* (Ramsbottom) both have typical calceocrinid columns consisting of high, barrel-shaped columnals except immediately beneath the cup. Both the gracile species, *Eocicerocrinus sevastopuloi* Donovan and *Claviculacrinus scoticus* Donovan, have columns that are too slender to be the prey pelmatozoan. *Eocicerocrinus sevastopuloi* has a homeomorphic column, while that of *C. scoticus* may be more rounded pentagonal in section. Only *Serendipocrinus lamonti* Donovan has a moderately broad, heteromorphic proximal column composed of low columnals.

Of the remaining seven possible victims of the attentions of '*H.*' *thraivensis*, three are cladids (Figure 7). *Cupulocrinus drummuckensis* Kolata has a cylindrical column that tends towards homeomorphy distally (that is, closer to the seafloor). *Protaxocrinus girvanensis* Ramsbottom has low columnals proximally, but more distally they are higher and
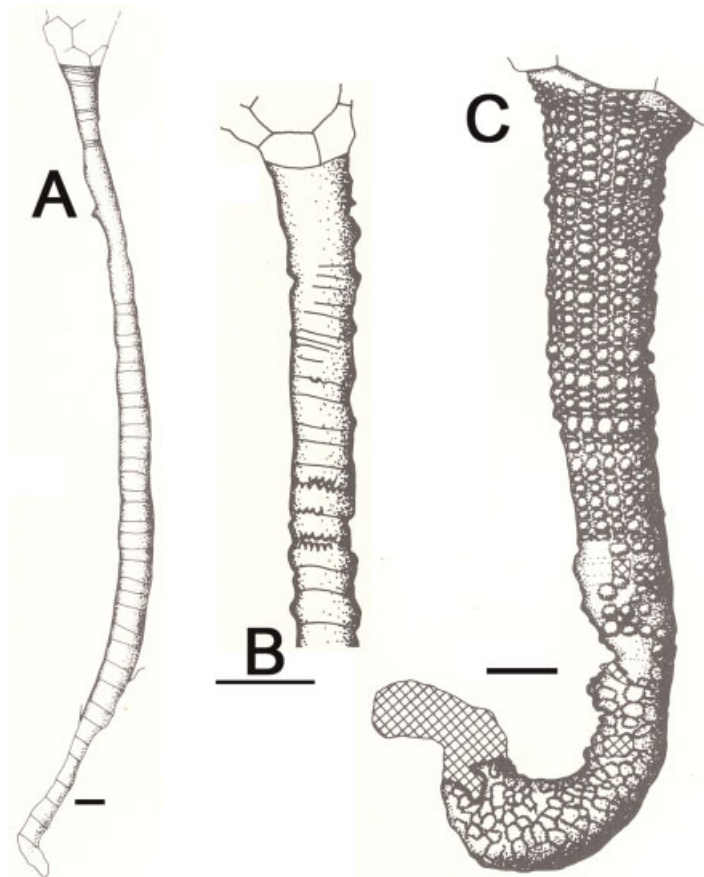

Figure 7. Cladid crinoids from the Lady Burn Starfish Beds, Girvan, southwest Scotland (Upper Ordovician). (**A**) *Cupulocrinus drummuckensis* Kolata, holotype, BMNH E47313a, column (after Donovan, 1986a, text-figure 13J). (**B**) *Protaxocrinus girvanensis* Ramsbottom, BMNH E67934, column (after Donovan, 1986a, text-figure 16C). (**C**) *Porocrinus scoticus* Ramsbottom, holotype, BMNH E47331, proximal column (after Donovan, 1986a, text-figure 13M). All camera lucida drawings of latex casts taken from natural moulds. Scale bars represent 1 mm.
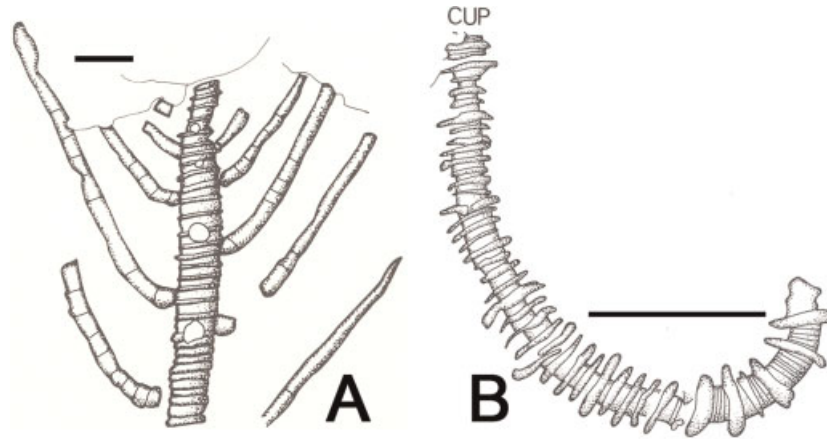
Figure 8. Camerate crinoids from the Lady Burn Starfish Beds, Girvan, southwest Scotland (Upper Ordovician). (**A**) Monobathrid *Macrostylocrinus cirrifer* Ramsbottom, paratype, HM 3599a, proximal column (after Donovan, 1986a, text-figure 17L). Scale bar represents 1 mm. (**B**) Diplobathrid(?) indet., HM E3580b, column (after Donovan, 1989a, text-figure 25C). Scale bar represents 5 mm. All camera lucida drawings of latex casts taken from natural moulds.

of more constant diameter. *Porocrinus scoticus* Ramsbottom has a column that is strongly heteromorphic with a distinct external sculpture of columns of 'warts', no evidence for which is preserved in the prey pelmatozoan. All three species must be considered possible, but not highly likely.

Of the remaining species–*Serendipocrinus lamonti* Donovan (Figure 6C), *Macrostylocrinus cirrifer* Ramsbottom (Figure 8A), *Eodimerocrinites littlewoodi* Donovan (Figure 9) and diplobathrid(?) indet. (Figure 8B)–all have heteromorphic columns in which the differentiation between nodals and internodals is at least dependent upon columnal height. All are thus possible solutions to the question of identity of the victim of '*H.*' *thraivensis*, but only one of the crinoids from Lady Burn has abundant radices preserved associated with the column and that is *Macrostylocrinus cirrifer*. Most notably, the radices of *M. cirrifer* are wider than the height of the nodal ossicles (Figure 8A; see also Brower, 1973, text-figure 19B-D) and encroach on the adjacent internodals, as determined for the prey pelmatozoan (Figures 3, 4). This is a feature more common in crinoids of the Late Palaeozoic and is otherwise rare in the Ordovician. All available evidence therefore suggests that *Macrostylocrinus cirrifer* Ramsbottom was the most probably prey organism for '*Helminthochiton*' *thraivensis* Reed.

6. DISCUSSION

The most complete description of the stem of *Macrostylocrinus cirrifer* is in Donovan (1986a, p. 47): 'Articular facet not seen. Stem circular in section and cylindrical, with no taper away from the cup. Column heteromorphic, ?N1 or ?N212, although sutures between columnals are difficult

to see. Nodals are taller than internodals. Latera planar (nodals) or convex (internodals). [Radices] developed in the proximal region of the stem, curving towards the crown and increasing in length towards the distal part of the column. [Radices] are arranged in spiral clusters, but not whorls, with a cycle occupying 6 to 17 columnals (Brower, 1973, p. 370). [Radice] scars always appear to cross plate boundaries'' (for other descriptions, see Ramsbottom, 1961, pp. 20–21, pl. 6, figures 6–13; Brower, 1973, pp. 363–371, pls 64, 65, text-figures 16, 17, 19). The descriptions of Donovan and others match well the description of the prey pelmatozoan built up above.

One criticism of the assessment made herein must be that crinoid attachment structures are a rare component of the fauna of the Lady Burn Starfish Beds. Crinoids are preserved in beautiful detail from about the mid-column up, but distal attachments are almost unknown. It is probable that the crinoids were swept up in a submarine mass flow deposit which either broke the columns or, more probably, induced the crinoids to autotomize (Wilkie, 2001) the more distal stem. The one notable exception from Lady Burn is a distal radicular dendritic attachment, known only from counterpart wax squeezes (BMNH E21582a, b) and attached to a pentameric dististele (Donovan, 1986a, p. 61, text-figure 20M). This is not conspecific with the gut contents of '*H.*' *thraivensis*. Further, our analysis has restricted the possible prey pelmatozoan to one of four known crinoid species out of 26 pelmatozoans (Tables 1 and 2); that evidence points most strongly to one species is more than coincidental.

It is not surprising that we have been able to reach this solution. The morphology of the crinoid column can be as distinct as, say, the ribs on a brachiopod valve or trilobite pygidium. In the British Ordovician trilobites and brachiopods have received the focussed attention of morphologists
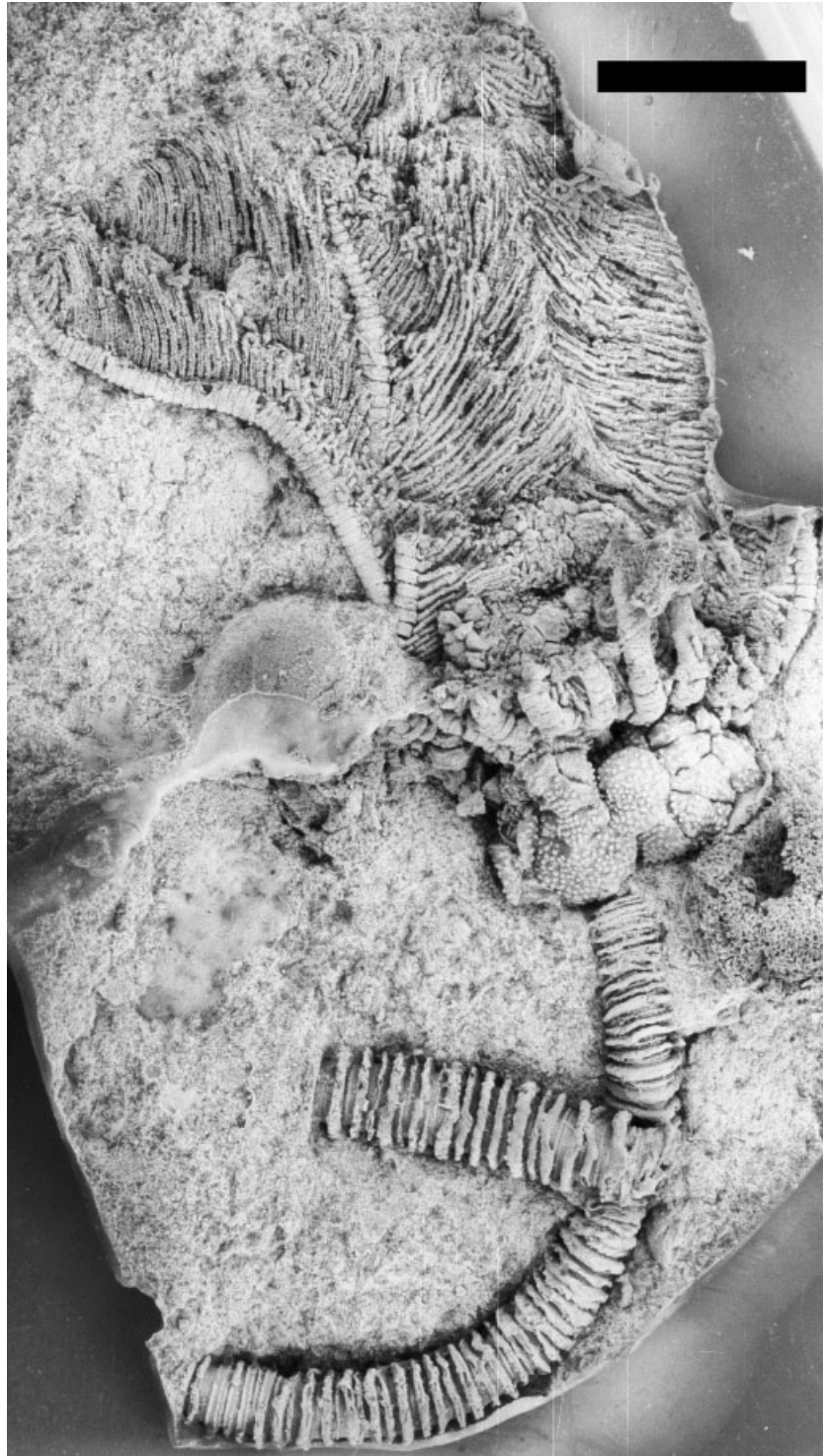
Figure 9. Diplobathrid camerate crinoid *Eodimerocrinites littlewoodi* Donovan, holotype, BGS GSE 15124 + 15128 (after Donovan and Gilmour, 2003, figure 2C), from the Lady Burn Starfish Beds, Girvan, southwest Scotland (Upper Ordovician). Anterior view, A ray slightly left of centre, crown and column. Latex cast taken from a natural mould and whitened with ammonium chloride. Scale bar represents 10 mm.

for over 150 years. The study of the coeval crinoids really only dates back to Ramsbottom (1961) and, even now, there remain few who have studied them in detail, but a lack of firsthand knowledge should not be mistaken for a scarcity of morphological detail.

We conclude that the Late Ordovocian mollusc 'Helminthochiton' thraivensis was a crinoidivorous scavenger or predator that fed on a species with a holomeric, heteromorphic stem bearing radices. The most probable prey was the monobathrid camerate crinoid *Macrostylocrinus cirrifer* Ramsbottom. This is an early association of invertebrates that is known with unusual precision, but remains unique. However, reassessment of similarly well preserved members of the Ordovician vagile benthos using similar technology to that employed herein may lead to the discovery of equally unexpected interactions.

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