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BROMALITES FROM THE SOOM SHALE LAGERSTÄTTE (UPPER ORDOVICIAN) OF SOUTH AFRICA: PALAEOECOLOGICAL AND PALAEOBIOLOGICAL IMPLICATIONS

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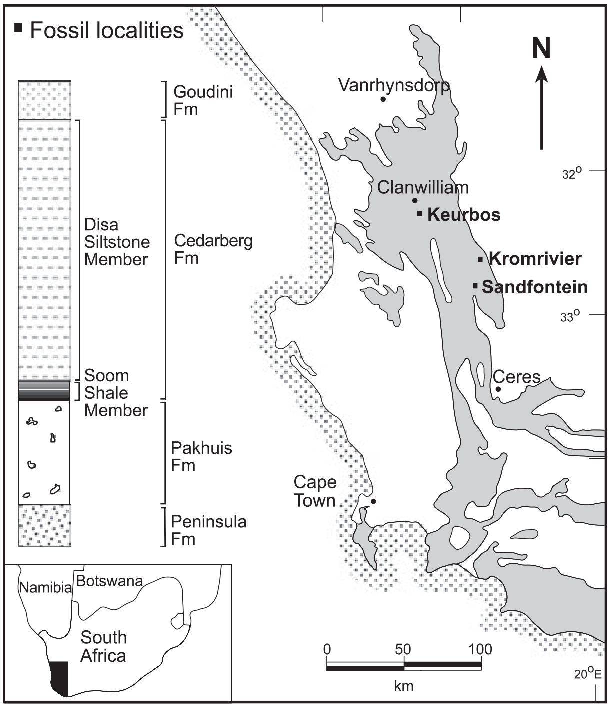
Abstract: Bromalites from the Soom Shale are allocated to five main categories on the basis of shape, content and internal structure: those containing broken conodont elements; those containing brachiopod fragments; corrugated/spiral forms; coiled coprolites and wrinkled coprolites. It is impossible to allocate specific bromalites to the organisms that formed them, but the occurrence of crushed discinoid valves in several specimens demonstrates that an effective durophagous predator was present in the Soom Shale community. The presence of fragmented elements of conodonts in other specimens provides direct evidence of tiering within the predatory trophic level in the Soom Shale. Conodonts, other agnathan vertebrates, orthoconic cephalopods and eurypterids are all possible contenders for producing most of the bromalites recorded, but there may have been unrecorded large predators in the community.

Key words: bromalites, coprolites, Soom Shale, Ordovician, South Africa, palaeoecology, palaeobiology.

THE Soom Shale Lagerstätte, of Late Ordovician age, crops out in the Cedarberg mountain range, to the north of Cape Town, South Africa (Text-fig. 1). The horizon has attracted considerable palaeontological interest because it provides a rare example of soft-tissue preservation of Ordovician fossils (Aldridge *et al.* 1994, 2001). The biota is quite diverse, with soft and hard tissues uniquely preserved through replacement by illite with alunite group minerals, frequently to a high degree of fidelity (Gabbott 1998; Gabbott *et al.* 2001). Several papers have now been published that describe elements of this biota, principally conodonts (e.g. Aldridge *et al.* 1995; Gabbott *et al.* 1995), naraoiid arthropods (Fortey and Theron 1995), eurypterids (Braddy *et al.* 1995, 1999), chitinozoans (Gabbott *et al.* 1998), orthocones with encrusting brachiopods and cornulitids (Gabbott 1999) and myodocopid ostracodes (Gabbott *et al.* 2003). Several taxa remain to be described, including some enigmatic soft-bodied forms. The deposit also contains a variety of bromalitic material, which we document and discuss in this contribution.

The term bromalite covers all fossilized remains engendered from the digestive tracts of animals, and includes regurgitalites (ejected from the oral cavity), cololites (*in situ* intestinal contents), gastrolites (fossilized stomach contents) and true coprolites (fossilized faeces) (Hunt 1992; Hunt *et al.* 1994; Northwood 2005). It is not usually possible to relate particular bromalites to their producer, although the nature of the associated fauna and the anatomy of living analogues can provide constraints. As well as being of interest in their own right, bromalites can also supply valuable evidence for assessing palaeoecological interactions and for the reconstruction of ancient food webs.

The Soom Shale, in preserving skeletonized and soft-bodied animals, provides an exceptional window into an Ordovician palaeocommunity. In this context, the bromalites from the shale assume a particular interest, as they can provide direct evidence of interrelationships within the community. Several of the specimens contain identifiable prey material, showing that a range of organisms served as food for higher carnivores or scavengers. The environment in which the Soom Shale was deposited is unusual, reflecting quiet, probably shallow and cool, marine waters with periodic anoxia, in which nektonic and nektobenthic organisms were apparently dominant. The



TEXT-FIG. 1. Map of the south-west region of the Western Cape Province, showing the outcrop area of the Table Mountain Group (shaded) and the bromalite-bearing fossil localities. Stratigraphic log showing the position of the Soom Shale Member in the local Ordovician–Silurian succession; only the upper part of the Peninsula Formation is shown; to scale, Soom Shale Member 10 m thick.

bromalites form an important link in the process of reconstruction of this unique Ordovician ecosystem. In addition, the Soom Shale bromalites provide direct evidence relating to the early Palaeozoic evolution of predatory behaviour.

GEOLOGICAL BACKGROUND

Stratigraphy

The Soom Shale Member is the lower unit of the Cedarberg Formation, the only argillaceous component of the dominantly arenaceous Table Mountain Group (Theron and Thamm 1990; Text-fig. 1). The dark grey, thinly laminated Soom Shale, which rarely exceeds 15 m in thickness, overlies the glaciogenic Pakhuis Formation and underlies the coarser, buff-coloured Disa Siltstone Member. The Soom Shale has been dated by the presence of the trilobite *Mucronaspis olini* (Temple, 1952), which indicates a late Ashgill (Rawtheyan–Hirnantian) age (Cocks and Fortey 1986; Theron *et al.* 1990).

Palaeogeography and palaeoenvironment

During the Late Ordovician, South Africa was a part of the supercontinent Gondwana and was strongly affected by the Hirnantian glaciation. The Soom Shale Member has been interpreted as the very fine clastic outwash from the retreating ice sheets of the latest Ordovician climatic amelioration (Theron and Thamm 1990). The deposition was in waters of very low energy, which were probably shallow, although there is little direct evidence of depth. The presence through the deposit of stenohaline organisms such as conodonts and cephalopods indicates that open marine conditions prevailed for much of the time. The finely parallel-laminated, non-bioturbated nature of the deposit and the results of geochemical analyses of the sediment show that the bottom waters were dominantly anoxic-euxinic (Gabbott 1998). However, there were periods in which the lowest waters became oxygenated, as shown by the colonization of orthocone conches by epibionts while they lay on the sea floor (Gabbott 1999). Geochemical evidence for oxygenation has also been found in some sediment samples, which are characterized by low degrees of pyritization and low molybdenum levels (Gabbott 1998).

THE SOOM SHALE BIOTA

This unique Ordovician Lagerstätte preserves both entirely soft-bodied organisms and also some animals which possess biomineralized parts. The fauna is distributed randomly throughout the deposit, from less than 1 m above the basal boundary with the Pakhuis Formation probably to the upper boundary with the Disa Siltstone Member (Aldridge *et al.* 1994).

Conodonts are particularly noteworthy for their relative abundance, the unusually large size of the elements (up to 22 mm), the presence of numerous complete feeding apparatuses and the preservation of soft tissues (Theron *et al.* 1990; Aldridge and Theron 1993; Aldridge *et al.* 1995; Gabbott *et al.* 1995). All specimens reported in the literature to date belong to a single species, the prioniodontid *Promissum pulchrum* Kovács-Endrödy, *in* Theron and Kovács-Endrödy 1986; this taxon strongly dominates the conodont fauna, although a few undescribed apparatuses of at least one other species have now been collected.

Other nektonic organisms include an undescribed jawless vertebrate, more than 50 mm long, with similarities to the Silurian *Jamoytius*. Orthoconic cephalopods are fairly common, reaching at least 220 mm in length. They are often encrusted by discinoid brachiopods and more infrequently by cornulitids (Gabbott 1999); a single specimen also has attached rhynchonellids. Isolated discinoids and rhynchonellids also occur in the sediment, and there are rare specimens of *Lingula* or a closely related genus. Myodocopid ostracodes have most commonly been found in association with orthocone conches, although a few isolated specimens occur (Gabbott 1999; Gabbott *et al.* 2003).

Other arthropods are represented by eurypterids, naraoiid trilobites and the dalmanitid trilobite *Mucronaspis*; there are also rare undescribed carapaces and appendages belonging to additional arthropod taxa. The eurypterids, assigned to the species *Onychopterella augusti* Braddy *et al.*, 1995, are interpreted as nektobenthic predators/scavengers (Braddy *et al.* 1995). Specimens reach at least 70 mm in length and preserve cuticular exoskeletons, sensory chelicerae, locomotory appendages and occasionally the spiral alimentary tract and gill lamellae (Braddy *et al.* 1995, 1999). The uncalcified *Soomaspis*, assigned to the family Naraoiidae, is fairly common, but preserved appendages or soft tissues have not been found (Fortey and Theron 1995); specimens range in size up to at least 30 mm. *Mucronaspis* is known only from Buffel's Dome near Ceres (Moore and Marchant 1981; Cocks and Fortey 1986), some 50 km away from the nearest sites that have produced fossils with preserved soft tissues.

The presence of polychaete worms is revealed by several complete scolecodont apparatuses, some clusters of elements and a number of isolated elements (Gabbott *et al.* 1998 and subsequent finds) although no body fossils have yet been discovered. Modern polychaetes have a wide range of life modes, from burrowing to free-floating; the lack of burrows in the Soom Shale suggests that the fossil specimens most likely lived on or above the sea floor.

There are several enigmatic fossils of unknown affinity in the fauna. Some of these completely lack biomineralized tissues and may reach large sizes; the biggest found to date is a segmented organism more than 400 mm in length. Another, *Siphonacis parva* (Kovács-Endrödy, 1986), is represented only by scattered organic-walled spines; these were originally regarded as plants, but have also been considered to be metazoan sclerites (Chesselet 1992).

Algal ribbons and swirls cover many of the bedding planes and it is possible that surfaces were bound by microbial mats. Palynological processing has also produced microplanktonic cysts, primitive plant spores (Gray *et al.* 1986) and chitinozoans (Cramer *et al.* 1974). Chitinozoans are also visible on some bedding surfaces as scattered individuals, chains and aggregates; a few of the chains and clusters are associated with organic envelopes (Gabbott *et al.* 1998).

MATERIAL

The bromalites are mostly preserved as isolated specimens on bedding planes or sometimes in association with scatters of organic-walled spines (*S. parva*). Occasionally they are found in the presence of other faunal elements, for example conodont apparatuses, chitinozoan masses and chitinozoan chains. In total, more than 100 bromalite specimens, mostly represented by part and counterpart (designated a and b), have been collected. The majority of the specimens are from the locality at the farm of Keurbos, near Clanwilliam, with a few from Kromrivier and Sandfontein (Text-fig. 1). At Keurbos, bromalite specimens are found throughout the exposure of the Soom Shale and do not appear to be concentrated at any levels. The repository of the specimens is the Geological Survey of South Africa (GSSA) and all specimens bear the numbers of that organisation.

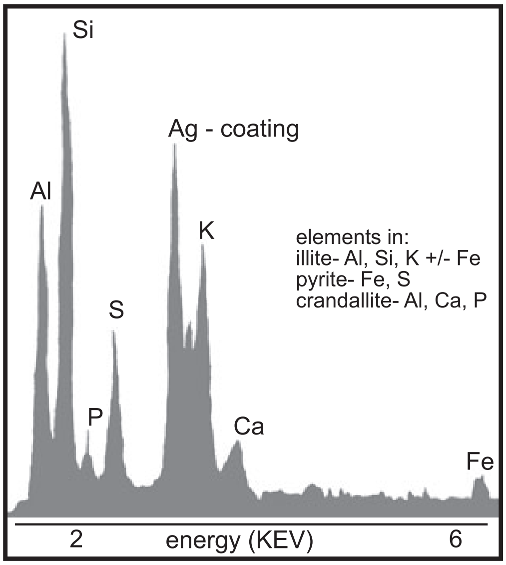
Preparation

The bromalites are set in a silty/muddy matrix that has weathered to a pale grey to orange/brown. Sediment partially obscures some specimens and sediment infills commonly highlight surface relief. Some specimens were prepared to remove this extraneous sediment from the bromalite surface and margins using a fine gramophone needle in an Eclipse pin-vice: for example, specimens C771b and C489a and b. A few specimens were broken during collection, transport or preparation. These have been glued together with a solution of paraloid diluted with butanone. The specimens are generally soft and friable, and are not easy to section, but one of the more robust specimens (C2042) has been impregnated with araldite and thin-sectioned transversely to reveal additional details of internal structure.

THE BROMALITE SPECIMENS

The bromalites vary in size, shape, content and internal structure. These characteristics permit subdivision of the bromalites into different categories. However, different sizes and shapes are not necessarily indicative of different creators; a single species is capable of producing faecal material of various morphologies, as exemplified by numerous living organisms. There may have been some modification of internal structure patterns during diagenesis and weathering, and chemical composition will also have been influenced by secondary mineralization. Therefore, form and content have been selected as the main criteria for grouping the bromalites.

The bromalites have been assigned to five groups on these criteria. Using content, three groups are distin-



TEXT-FIG. 2. A typical energy-dispersive X-ray (EDX) trace obtained from both specimens C544 and C755.

guished: bromalites containing conodont elements, those containing discinoid fragments and those containing fine sediment and organic matter; the last group is further divided based on shape and structure into corrugated/spiral, coiled and wrinkled. Some specimens that are questionably bromalitic fall outside these categories. Some workers consider that a formal nomenclature and classification should be applied to bromalites, but we concur with those (e.g. Chin in Hunt *et al.* 1994) who feel that a binomial nomenclature is inappropriate.

The majority of the bromalite specimens are three-dimensional and now appear to be composed mainly of clay minerals. Analysis of two specimens (C554, C755) using the energy-dispersive X-ray facility (EDX) on a scanning electron microscope produced peaks consistent with a composition of clay minerals plus some calcium phosphate or crandallite (Text-fig. 2). Most specimens lack identifiable prey or other food contents, but a few contain broken conodont elements and a larger number contain crushed brachiopod valves. Rarely, *Siphonacis* spines are evident.

Bromalites containing conodont elements

There are two main types of bromalite that contain conodont elements, either compact clusters or dispersed scatters. Both are infrequently found; in all, six compact clusters and four scatters have been collected. All the conodont elements in the bromalites appear to come from the *Promissum* apparatus.

The compact form is exemplified by specimens C815 (13 mm long, 5·5 mm wide; Pl. 1, fig. 1) and C882 (11 mm long, 4 mm wide; Pl. 1, fig. 2). Each specimen comprises a compact collection of broken elements with no clear preferred orientation. The elements are preserved without any kind of enclosing matrix and there is no definite margin separating them from the surrounding sediment. The majority of elements are present as broken portions of processes, with the longest fragment being 5·5 mm in C815 and 4 mm in C882. However, both figured specimens contain fragments of ramiform S and M elements in which the cusp and proximal portions of processes are evident; there are also one or two identifiable P elements. It is not possible in any of the specimens to demonstrate that a complete single apparatus is represented in the fragmentary material, although this is a possibility.

The four examples of scatters comprise randomly dispersed, highly broken conodont elements; some process fragments are very short, with only two or three denticles. Again, most fragments are of processes from ramiform elements, although proximal portions of S elements with identifiable cusps do occur and one or two P elements are recognizable. As with the more compact clusters, it is not possible to demonstrate that a single complete apparatus is represented in any of the scatters. The longest fragment in each specimen is about 3 mm. The elements are spread out across the bedding plane with no obvious connection, matrix or outline. Specimen C616 (Pl. 1, fig. 3) exhibits a roughly elongate shape (19 mm long, 7 mm wide) as does the coprolite specimen among the conodont apparatuses and chitinozoan masses on C946 (see Gabbott *et al.* 1998, fig. 6) and unfigured specimen C1627. Contrastingly, specimen C1025 (Pl. 1, fig. 4) has

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EXPLANATION OF PLATE 1

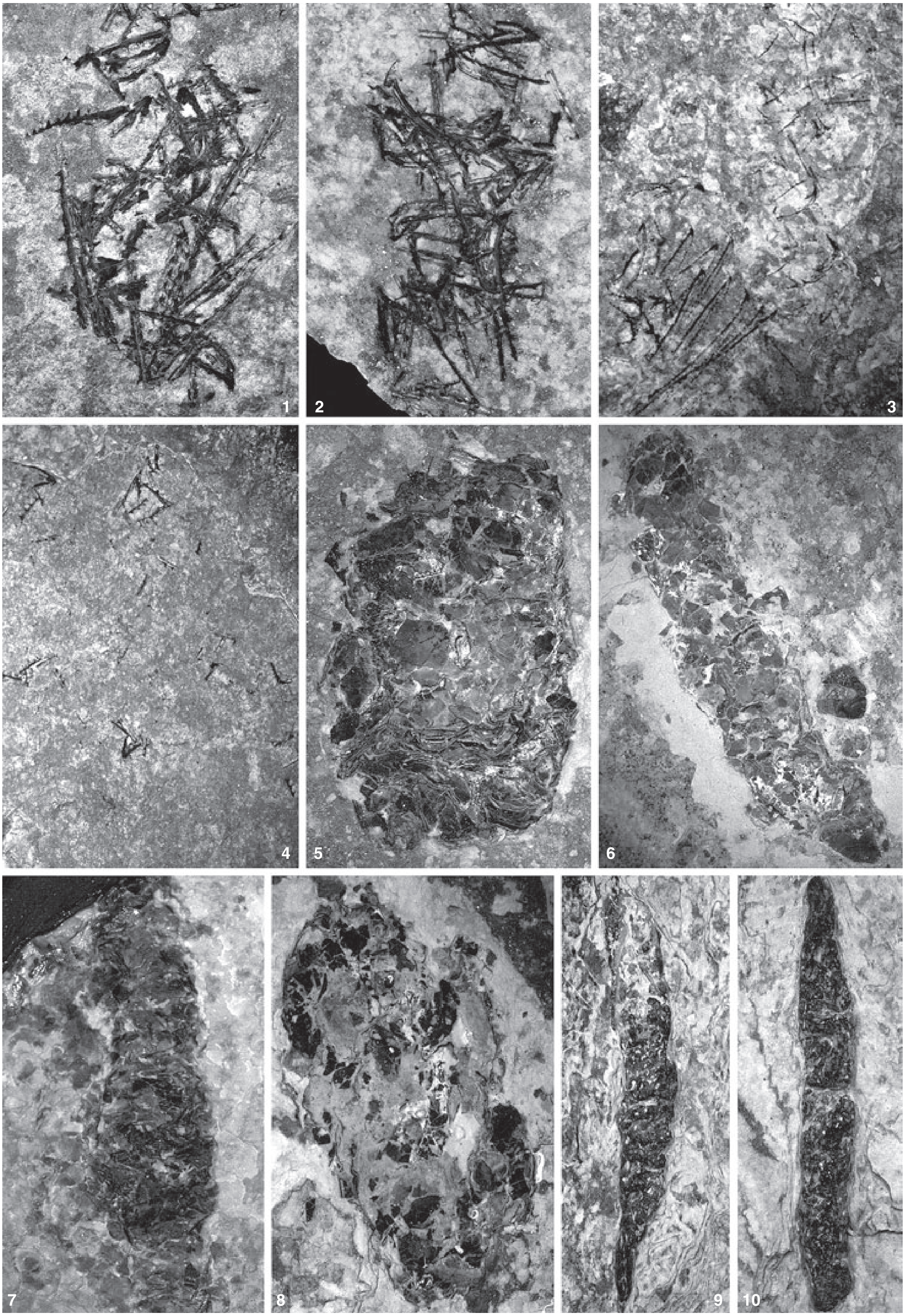
Figs 1–4. Bromalites containing conodont elements. 1, specimen C815a; × 7·2. 2, specimen C882a; × 9·5. 3, specimen C616a; × 5. 4, specimen C1025b; × 3·4.

Figs 5–8. Bromalites containing crushed discinoid fragments. 5, specimen C525b; × 8·2. 6, specimen C799b; × 2·7. 7, specimen C929; × 3·5. 8, specimen C927b; × 5·3.

Figs 9–10. Bromalites showing a spiral morphology. 9, specimen C443; × 2·2. 10, specimen C554; × 3·3.

All specimens from the Upper Ordovician (Ashgill) Soom Shale, Keurbos Farm near Clanwilliam, Western Cape Province, South Africa.

PLATE 1



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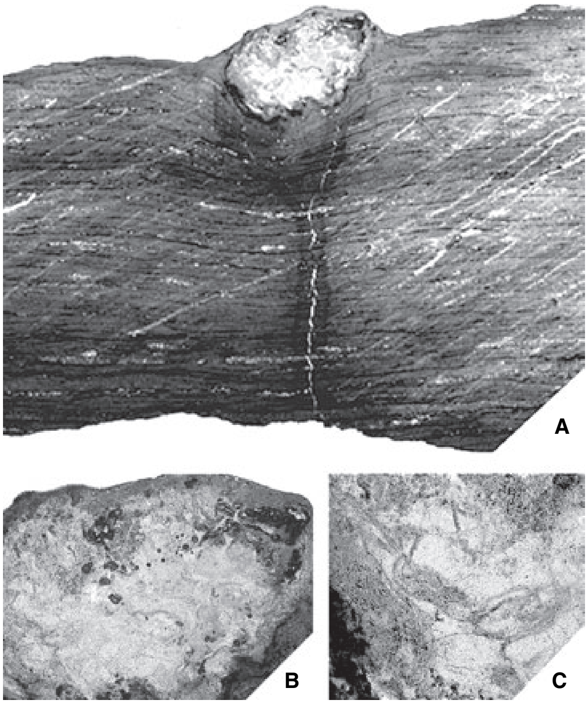
no obvious shape, with the elements much more widely distributed (25 × 16 mm).

Bromalites containing discinoid fragments

A significant proportion of the bromalitic material is composed of broken and compacted shell fragments of discinoid, and occasionally trematid, brachiopods. These specimens range from very densely packed masses of shell material to bromalites that contain shell fragments but are essentially sediment dominated. The densely packed forms are most numerous. Subrectangular specimens of this type vary in length: specimen C525 (Pl. 1, fig. 5) is 8·5 mm long, whereas C799 (Pl. 1, fig. 6) is 25 mm, but all are of similar width, from 4·5 mm to 6 mm. They are composed of numerous crushed shell fragments in various orientations, sometimes flat and compressed, sometimes forming transverse layers. The fragments are commonly dark grey/black and exhibit growth lines. Some are pale yellow/brown and lacking in ornament, probably representing inner layers of the valves. All of these bromalites have definite margins and are preserved in three dimensions with a very rough and uneven surface texture. Specimen C525 (Pl. 1, fig. 5) is typical, purely comprising compacted brachiopod valves without any sedimentary matrix. Specimen C799 (Pl. 1, fig. 6) contains some evidence of a pale, fine-grained sedimentary matrix and is associated on the bedding plane with two complete discinoid specimens and a chitinozoan mass. Specimen C929 (Pl. 1, fig. 7) is largely similar, but broadens at one end, where it is less consolidated and contains some sedimentary matrix. The shell debris also extends laterally, dominantly to one side, into a scatter of unconsolidated shell fragments. This debris was presumably once part of the bromalite but has been moved, possibly by current action, to fan out from one side of the consolidated mass. A few specimens contain more sediment (e.g. C944) and some are sediment-dominated with a scatter of shell fragments, for example C927 (Pl. 1, fig. 8); these specimens still display well-defined margins.



TEXT-FIG. 3. Transverse thin section of a corrugated bromalite; specimen C2042 from the Soom Shale Member at Keurbos, near Clanwilliam, Western Cape Province, South Africa. A, showing the relationship of the bromalite (top) to the laminations in the shale; × 7. B, showing the mottled internal structure of the bromalite; × 16. C, detail of the lower left portion, showing the fibrous structure within the darker areas; × 32.

Corrugated/spiral bromalites

Some bromalite specimens exhibit a distinctive corrugated morphology, possibly a loose spiral. The best preserved example, specimen C443 (Pl. 1, fig. 9), is 28 mm long and 4 mm at its widest point, showing distinct tapering at one end; at the other end it passes into a dark organic film. These elongate bromalites are grey or black in colour and are preserved in three dimensions. The specimens are composed of sediment with fine fragments, apparently organic.

EXPLANATION OF PLATE 2

Fig. 1. Spiral bromalite, specimen C492; × 2·2.

Figs 2–3. Coiled coprolites. 2, specimen C879i; × 7·3. 3, specimen C668; × 7.

Fig. 4. Uncategorized bromalite, specimen C771b; × 5·6.

Figs 5–8. Wrinkled coprolites. 5, specimen C755; × 6·9. 6, specimen C880; × 5. 7, specimen C854b, coprolite with associated *Siphonacis* spines; × 8·9. 8, specimen C505b (see also Text-fig. 4); × 4·8.

Fig. 9. Possible bromalite, specimen C465b; × 3·4.

All specimens from the Upper Ordovician (Ashgill) Soom Shale, Keurbos Farm near Clanwilliam, Western Cape Province, South Africa.

PLATE 2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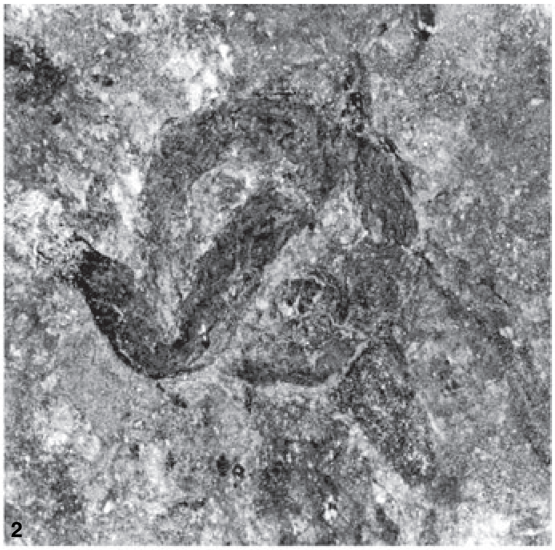
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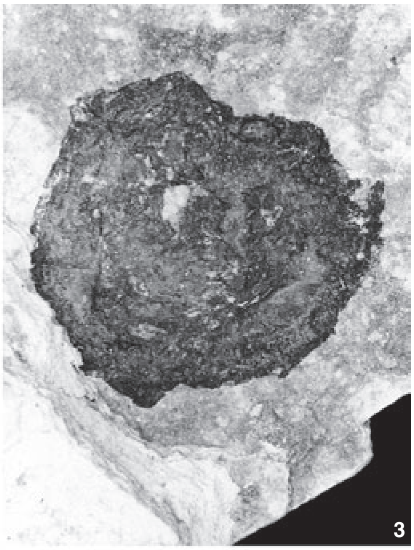
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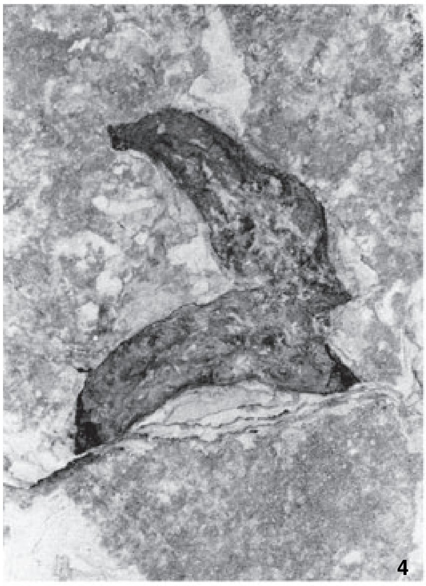
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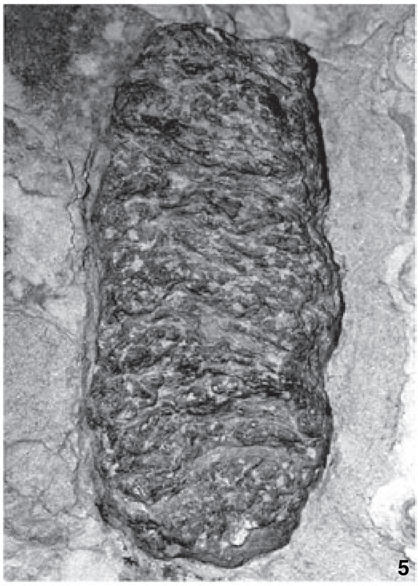
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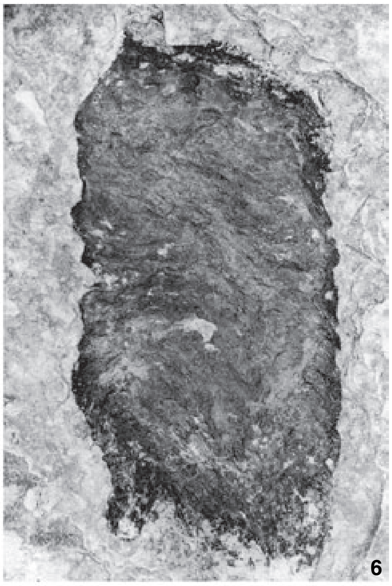
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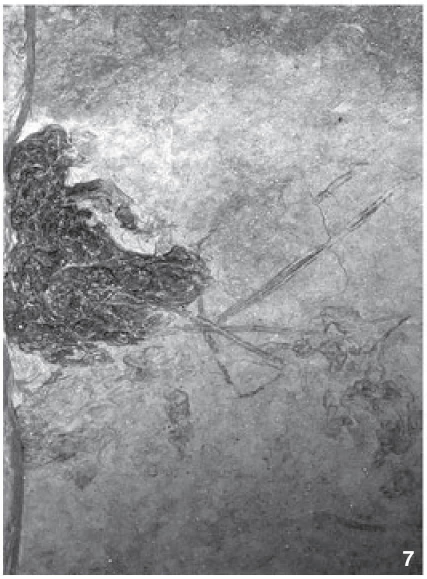
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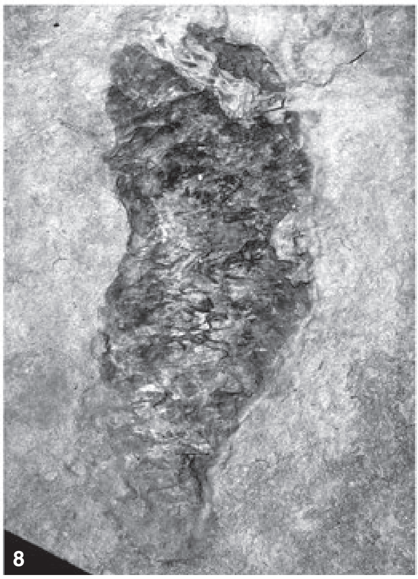
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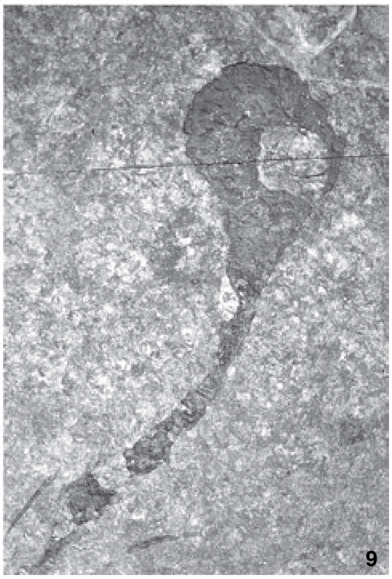
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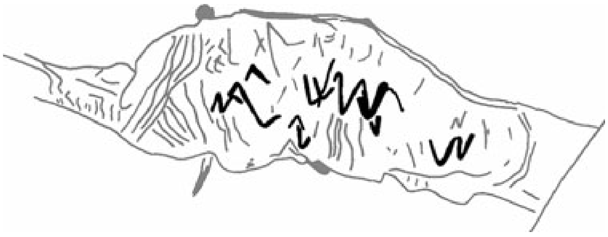
The internal structure is characterized by a series of transverse ridges, which are sometimes prominent. Specimen C443 exhibits four definite, and possibly up to seven, ridges of approximately 1 mm width; this specimen also contains an identifiable *Siphonacis* spine. Specimen C554 (Pl. 1, fig. 10) shows similar morphology and dimensions although internal structure is less prominent. The specimen is 17 mm long and 3 mm wide with indistinct ridges 0·5 mm wide. Rare specimens appear as an elongate spiral 'ripple' in the rock, for example C492 (Pl. 2, fig. 1). None of the bromalites in the Soom Shale shows evidence of internal scroll structures such as those described and attributed to early agnathan vertebrates by Gilmore (1992). Transverse sectioning of one corrugated specimen (C2042; Text-fig. 3) reveals only an irregular mottling, with the darker areas exhibiting a fibrous texture.

Coiled coprolites

There is a small group of coprolites consisting of elongate faecal material that has been deposited in a circular, coil-like pattern. This is well illustrated by specimen C879i (Pl. 2, fig. 2). The width of the coprolite material forming the coil is 1·5 mm, and the coil is 6 mm in overall diameter. The material is dark grey/black in colour, without recognizable fossil fragments, lacks any major internal structure or folding, but has a slightly rough relief. The coprolite has a definite outline, with one end of the coil terminating abruptly, as if broken. Two other specimens, C879ii and C668 (Pl. 2, fig. 3), show similar internal features but have a slightly different external morphology. These two specimens exhibit very compact coils with the successive layers lying upon each other, completely obscuring the underlying sediment, unlike in C879i. These coils are very difficult to distinguish but some portions of the coil are visible. They also have slightly more relief than C879i, but their dimensions are closely similar; the overall diameter of C879ii is 5·5 mm and that of C668 (Pl. 2, fig. 3) is 6·5 mm. Another specimen, C771 (Pl. 2, fig. 4), exhibits apparent faecal material that appears identical in composition, thickness and dimensions to the coiled forms. However, the morphology of this specimen is different, consisting of two elongate structures seemingly joined at one end. These two structures have definite outlines, picked out in places by a blackened margin, and show strong three-dimensional relief.

Wrinkled coprolites



TEXT-FIG. 4. A camera lucida drawing of specimen C505 (see also Pl. 2, fig. 8), showing a number of zigzag marks (in black) that cross the rugose fabric of the coprolite; × 3·6.

Many of the bromalites are composed of fine organic and/or sedimentary material and show a rugose internal structure. The material is dark grey or black in colour and is heavily wrinkled, forming a series of linear to gently curved transverse ridges and furrows within the coprolite fabric, as illustrated by specimens C755 (Pl. 2, fig. 5) and C880 (Pl. 2, fig. 6). There are many elongate forms of this coprolite type, up to 23 mm in length and 7 mm in width. Several specimens have been included in this category on the basis of their internal structure, although they may have a variety of shapes. For example, C854 (Pl. 2, fig. 7) is a black coprolite with a rugose internal structure, but its shape is irregular and globular, 9·5 mm long and 7·5 mm wide; it is associated on the bedding surface with scattered specimens of *Siphonacis*. Specimen C505 (Pl. 2, fig. 8) is elongate in shape and has internal wrinkling, but also displays an unusual pattern comprising a series of regular zigzag scratch-like marks that cross the rugose fabric of the coprolite but are not present on the surrounding sediment (Text-fig. 4). These marks are enigmatic; they appear to reflect an internal layering within the specimen, but this is not regular or pervasive. An alternative speculative explanation might be that they represent a grazing trace of an organism that once fed on this organic material. There are no clear modern or other analogues for coprophagy producing this kind of zigzag pattern, but sinuous surface traces that may have been produced by grazing invertebrates are known in a number of fossil coprolites (e.g. Northwood 2005, p. 60).

The coprolites in this group display a variation in colour probably resulting from differing degrees of weathering and iron oxidation. Although most of the coprolites are preserved as dark grey to black material, some have a distinctive yellow-brown staining.

AFFINITIES OF THE BROMALITES

Bromalites containing conodont elements

The compact, pellet-like clusters of fragmented conodont elements are tentatively interpreted as regurgitalites rather than coprolites. The elements in specimens C815

(Pl. 1, fig. 1) and C882 (Pl. 1, fig. 2), although broken, are preserved as relatively long sections of processes or with the cusp and proximal ends of the processes intact. The 'pellets' have no sharp outline or internal matrix, possibly indicating that the elements were deposited as isolated hard parts enclosed by an insubstantial, unpreservable medium, such as salivary or gastric secretions. These specimens could represent the regurgitate produced by an animal that has ingested the whole conodont animal, yet only digested its soft tissues, resorting to regurgitating the hard, partially fragmented, oral/pharyngeal apparatus. Such selective feeding behaviour has been reported in extant hagfishes (*Myxine glutinosa*), which rapidly eat the soft tissues, from liver to muscles, of their prey before discarding the skin and backbones (Hardisty 1979).

The dispersed scatters, such as C616 (Pl. 1, fig. 3) and C1025 (Pl. 1, fig. 4), also lack any kind of binding matrix or definite outline. However, the elements are very much more fragmented (*c.* 3 mm maximum length), indicating a greater degree of processing before they were discarded. This may be the result of mastication before regurgitation or may indicate that the elements were broken up in the mouth of a predator prior to passing through a gut.

The organism(s) responsible for producing these specimens must have been active predators on the nektonic conodont animals, or scavengers from carrion floating in the water column or lying upon the substrate. The conodonts would have made attractive prey, being primarily soft bodied, with just the elements of the oral/pharyngeal apparatus mineralized by calcium phosphate. Those in the Soom Shale probably reached more than 400 mm in length, with the apparatus typically occupying only about 10–15 mm (Gabbott *et al.* 1995). Several known animals high in the Soom Shale trophic web may have been capable of predation on the conodonts, including the orthoconic cephalopods, the eurypterids and the larger enigmatic soft-bodied organisms. Conodont predation by soft-bodied animals is known from the example of *Typhloesus wellsi* (Melton and Scott, 1973) from the Carboniferous Bear Gulch Limestone of Montana, which has gut contents dominated by conodont elements (see Conway Morris 1990). It may also be possible to consider the conodonts themselves as producers of these bromalites. Functional analysis of the apparatus architecture indicates that *Promissum* was a macrophagous organism with a complex array of movable mouthparts that operated as grasping and food-processing teeth (Aldridge *et al.* 1995). There is also evidence from surface microwear on elements of the apparatus that many conodont taxa were macrophagous (Purnell 1995), so the conodont animals in the Soom Shale might have been cannibalistic. However, there are constraints posed by the ability of one feeding apparatus to accommodate another and it may be that only juvenile conodonts could have been the prey of members of their own species. There is certainly no direct evidence to suggest that these conodont fragments, either coprolites or regurgitalites, were produced by predatory conodont animals, nor can they be directly linked with any other of the candidate predators. It is also possible that these bromalites were produced by as yet undiscovered larger predators in the Soom Shale community.

Bromalites containing brachiopod fragments

These bromalites are of particular interest, as the highly fragmented nature of the shells demonstrates that the attacks on the brachiopods were unquestionably lethal. Previous reports of predation on Early Palaeozoic brachiopods do not generally relate to highly fractured material, and valves commonly show repair after sustaining injury (Alexander 1986). In the example reported by Alexander (1986), highly fragmented 'brachiopod hash' was commonly produced through abiotic, mechanical means, but the well-defined masses with internally layered structures found in the Soom Shale are clearly not mechanically produced shell hashes. Furthermore, it is extremely unlikely that mechanically fragmented shell material was subsequently ingested by the bromalite producer, as the Soom Shale was deposited under extremely low energy conditions and no bedding planes containing brachiopod shell hash have been found. Therefore, we conclude that a member of the Soom Shale community had the capacity to crush and thoroughly fragment brachiopod shells.

It is quite possible that the range of discinoid-bearing bromalites, from those that are densely packed to those that contain a substantial sedimentary matrix, were all produced by the same type of animal. The differences in the density and packing of the shell fragments may be due to food availability at the time of feeding (i.e. whether or not the diet was exclusively discinoid), or possibly attributable to the length of time that the undigested material was stored in the gut before excretion. For example, specimen C525 (Pl. 1, fig. 5) is composed entirely of very densely compacted shell fragments, probably representative of several individual shells, suggesting that they had been accumulating in the organism's digestive tract for some time. Conversely, specimens such as C927 (Pl. 1, fig. 8), which contain substantial amounts of sedimentary material, may have been excreted rapidly after soft part digestion or may have been initially ingested as a mixture of shell material and sedimentary debris.

Present-day predators on brachiopods include starfish, crustaceans, gastropods and fish (Mauzey *et al.* 1968; Vermeij 1987). Of these, starfish and gastropods are not known from the Soom Shale. Other organisms with hard parts originally composed of calcite (trilobites, rhynchonellid brachiopods) and aragonite (orthocones) are preserved in the shale, suggesting that neither starfish nor gastropods were members of the living community. Moreover, starfish are not known to crush and fragment their prey in the process of ingestion (Vermeij 1987). Fossil evidence of fish predation on brachiopods includes the recognition of shell fragments in the stomachs of chondrichthyans (Moy-Thomas and Miles 1971) and, more indirectly, the attribution of tetrahedral indentations on Carboniferous brachiopods from Utah to the bites of shell-crushing sharks (Alexander 1981). In an unusual example from the Upper Ordovician of the USA, nautiloids were implicated in brachiopod durophagy through the presence of an embedded rhyncholite-like crushing element, similar in morphology to the calcified rhyncholites of Mesozoic–Recent nautiloids, in a brachiopod valve (Alexander 1986).

Any organism that produced the bromalites described here must have possessed hard mouth parts, or other processing appendages, that enabled it to crush the resistant discinoid shells into small fragments. The possible candidates known to date from the Soom Shale are the orthoconic cephalopods, conodonts and eurypterids.

Discinoid specimens are found in large numbers on orthocone conches and also as clusters and isolated specimens in the sediment. Size distribution analyses show that Soom Shale orthocones were colonized by discinoids both *in vivo* and post-mortem, when the conch lay on the sea bed and may have formed a benthic island (Gabbott 1999). The specimens that are not directly associated with orthocones may have fallen from floating conches, but it is also possible that some individuals survived on the sea bed in times of bottom-water oxygenation. However, the high concentrations of the discinoids in many of the bromalites suggest that the predator most probably gathered them from the rich pickings on living or dead orthocone shells rather than from scattered specimens on the substrate.

For the orthoconic cephalopods to have preyed on the living discinoids they must either have removed encrusting animals from the conches of other individuals or have reached backwards with their tentacles to scrape specimens from their own conch. Four orthocone specimens in the Soom Shale have been described with preserved radulae (Gabbott 1999), but there are no clear mandibles. Beaks (mandibles) are only very rarely preserved in fossil orthoceratoids; only two examples have been recorded so far, from the Silurian (Zakharov and Lominadze 1983) and from the late Mississippian Bear Gulch Limestone (Mapes 1987), but these specimens lack preserved radulae. Comparison of the Soom orthocones with Recent *Nautilus* and with ammonite reconstructions (Lehmann 1981), however, led Gabbott (1999) to suggest that the bulbous masses associated with the radulae in some of the specimens may be evidence of beaks. This suggests that the Soom cephalopods may have had hard mouth parts that were capable of crushing the discinoid valves, although there is no evidence that these beaks were biomineralized. The rhyncholite-like structure reported by Alexander (1986; see above) provides possible evidence of brachiopod predation by Ordovician nautiloids, but in this case the brachiopod shells were not highly fractured.

All recent cephalopods are known to be predatory carnivores, either benthic or nektonic hunters, feeding upon crustaceans, fish and molluscs (Boucaud-Camou and Boucher-Rodoni 1983). Similarly, the jaws and radulae of fossil cephalopods indicate that these animals were generally carnivorous (Lehmann 1988). The food that they ingest must be broken into small enough pieces to pass along the oesophagus without damaging the brain that surrounds it and is located posteriorly to the buccal mass (Nixon 1988). All these characteristics of the cephalopods and their known feeding habits indicate that they could have been predators upon the discinoids, crushing their valves and ingesting them as small fragments. Certainly, the beak of *Nautilus* is capable of inflicting severe damage to durable tissues; *Nautilus* can shear chicken bones (Griffin 1900), mollusc shells (Saunders *et al.* 1978) and lobster moults (Ward and Wicksten 1980).

Conodonts provide another possible candidate for producing these bromalites. They were nektonic, predatory organisms that could have removed the discinoids from the conches while the cephalopods were in the water column or could have picked up specimens from the surfaces of conches lying on the substrate. Conodonts had hard grasping mouthparts, and microwear studies of pectiniform elements (Purnell 1995) have indicated that these were used to crush food items. However, it is unlikely that conodont elements, even the large ones of *Promissum*, were robust enough to crush the heavily mineralized brachiopod shells, especially to the degree exhibited in the bromalitic material.

Eurypterids are also contenders. There is no direct evidence, in the form of gut contents, for the eurypterid diet, but indirect evidence, by extrapolation of information gained from Silurian specimens (Selden 1984), suggests predatory habits. There is certainly evidence that some other Early Palaeozoic arthropods were durophagous carnivores, particularly from the record of crushed eodiscoid trilobites in the gut of a Middle Cambrian *Fuxianhuia*-like arthropod from Kaili, South China (Zhu *et al.* 2004). Eurypterids appear to have been actively swimming carnivores with stereoscopic vision. Possible eurypterid coprolites from the Ordovician of Ohio

(Caster and Kjellesvig-Waering 1964) contain fragments of trilobite cuticle and of other eurypterid species. The animals appear to have been able to gather prey using their fore-limbs and to transfer it to their mouths for mastication. A distant relative of eurypterids, the horseshoe crab, is known to use its gnathobases to grind up bivalves (Turner *et al.* 1948). However, the eurypterid specimens recovered so far from the Soom Shale are too small to have coped with discinoids. In one specimen the spiral valve of the anterior alimentary canal is preserved, and is only a couple of millimetres in maximum diameter (Braddy *et al.* 1995). Thus, it seems improbable that these eurypterids would have been able to pass the discinoid coprolites, which can reach up to 6 mm in width, without considerable distension of the gut. Alternatively, there may be eurypterids of much larger proportions in the deposit that as yet have not been discovered.

Interestingly, round masses of fragmented skeletal material from the Middle Cambrian Spence Shale of Utah were identified as coprolites by Conway Morris and Robison (1988), and attributed either to very large *Anomalocaris* individuals or to an unidentified very large predator. The masses are 25–45 mm across and contain skeletal material of trilobites, echinoderms and lingulate brachiopods. The shape of these masses is less clearly bromalitic than that of the Soom Shale specimens, but there is a general comparability. The enigmatic soft-bodied fossils known to date from the Soom Shale, although sometimes large and with some *Anomalocaris*-like features, lack the substantial hard mouth parts necessary to break the discinoids as represented in the bromalitic material. These discinoid-bearing bromalites, as with all the bromalites considered here, could, of course, originate from some as yet undiscovered organism in the deposit.

The occlusive forces required to fracture brachiopod shells have been the subject of preliminary experiments, which have demonstrated that biconvex shells can withstand considerably greater pressures than those with concave or planar valves (Beale *et al.* 1983). Discinoids are biconvex with several shell layers and it appears that, whatever organism was crushing and ingesting the brachiopod shells, it was a formidable durophage. Occasional brachiopod specimens with damaged growth lines suggestive of healed injuries have been recognized in the Soom Shale, but their rarity relative to the discinoid-bearing bromalites suggests a high rate of successful predation.

Corrugated/spiral bromalites

Spiral coprolites are well documented throughout the geological record, for example from the Lower Permian shales of Kansas (Williams 1972) and from the Lias of Lyme Regis, Dorset, UK (Häntzschel *et al.* 1968). However, they are usually affiliated with vertebrates, in particular sharks that possess spiral valves such as *Acrodus* and *Hybodus* (Williams 1972). Spiral faecal pellets are known from many modern fish, for example the African lungfish *Protopterus*, whose coprolites are tightly spiralled when first deposited, but tend to uncoil slightly after 24 h in water (Williams 1972). Tightly spiralled, scroll coprolites have also been reported from the Silurian of Ireland, where they have been attributed to early agnathan vertebrates belonging to the Anaspida and Thelodontii (Gilmore 1992). However, the spirals exhibited by our material are not tight scrolls, but open, elongate spirals in which each whorl lies adjacent to its predecessor.

The only vertebrates described to date from the Soom Shale are the conodonts, and there is no evidence that they had a spiral intestine and produced such coprolites. Purely in terms of size (*c.* 28 mm long, *c.* 1 mm thick), however, the coprolites could feasibly have been produced by a conodont animal. Perhaps a more serious vertebrate contender is the undescribed *Jamoytius*-like agnathan, now known from nine specimens from the Soom Shale; several authors have allied *Jamoytius* to the anaspids (e.g. Donoghue *et al.* 2000), which have been implicated by Gilmore (1992) as possible generators of spiral coprolites. Of course, there may have been other early vertebrate taxa in the Soom Shale that have not yet been found as fossils; arandaspids are known from the Ordovician of Australia, Bolivia and Argentina (see Elliott *et al.* 1991; Janvier 1996; Smith *et al.* 2002) and might be expected in other parts of Gondwana, including Africa.

The eurypterids are the only organisms in the deposit that are definitely known to possess a partially spiralled gut. Coprolites that are thought to belong to eurypterids have been described from the Hagshaw Hills Silurian inlier of Scotland as 'unstructured masses of disarticulated agnathan fragments' (Selden 1984, p. 46). This indicates that some eurypterid faecal material is far from being a tightly coiled pellet, more an undifferentiated mass. However, the anatomical evidence supports eurypterids as candidates for the producers of the corrugated or spiral bromalites in the Soom Shale.

Other organisms such as trilobites, orthocones and soft-bodied enigmatica could all potentially have produced these bromalites, but again there is no direct evidence to link a spiral faecal morphology to any of these taxa.

One bromalite specimen, C492 (Pl. 2, fig. 1), is less clearly preserved in the rock, resembling an elongate ripple. This may simply be poorly preserved faecal material or may alternatively represent the traces of the alimentary canal (cololite) of a fossil organism that has otherwise not been preserved. There is direct evidence that preservation of three-dimensional gut traces does occur in the Soom

Shale. A single, as yet undescribed specimen of an enigmatic soft-bodied animal (C1180) contains apparent gut contents preserved as an elongate, three-dimensional, gently corrugated cololite. Preservation of soft tissues in the Soom Shale appears to be patchy, and it is possible that other specimens assigned to the corrugated/spiral bromalite category represent gut contents, with the rest of the animal unpreserved. Another possibility is that gut-fills of this type might represent the replacement of mid-gut glands by clay minerals. Butterfield (2002) showed that the three-dimensional axial structure commonly preserved in the Burgess Shale arthropod *Leanchoilia* was not ingested sediment but phosphatized, biserally repeated mid-gut glands. Other, less corrugated and more equivocally bromalitic specimens from the Soom Shale (e.g. C465; Pl. 2, fig. 9) might also represent preserved alimentary tracts, but specimens suitable for thin-sectioning would be required to test this.

Coiled coprolites

The original type of food ingested to produce these coprolites is indeterminable, although it was presumably soft and easily digestible as no hard parts are present in the faecal material. The specimens have been compacted and were probably much more pronounced three-dimensional structures when initially deposited. They may have been produced by the same organism(s) as the corrugated/spiral bromalites under different feeding, depositional or preservational conditions, as their width, colour and consistency are closely similar. Conodonts, other agnathans, orthocones, eurypterids, trilobites and soft-bodied metazoans are therefore possible candidates for producing these coprolites. In addition, consumers lower in the food chain, such as polychaete worms, may have grazed upon algal debris and fine sediments to produce these coprolites of undifferentiated fine organic material.

Wrinkled coprolites

The shape of coprolites in this group varies from ellipsoidal pellet-like forms, such as C755 (Pl. 2, fig. 5), to more irregular specimens such as C854 (Pl. 2, fig. 7). These variations may be attributable to differences in food availability, in the nature of the food ingested or in the amount of time that the coprolite was stored in the gut prior to excretion. For example, if the food were plentiful and passed through the digestive tract rapidly, then the subsequent coprolite would presumably be less dense and compact than those produced from long-term accumulation of food in the gut. The composition, texture and nature of the material are similar enough to suggest that, although in various morphs, these coprolites might have been produced by the same type of organism. As with the corrugated/spiral and coiled forms these wrinkled coprolites are composed of fine, dark organic material of indeterminable origin. Therefore, the size and shape of the coprolites are the main indicators as to which organisms were capable of producing them. The width of these coprolites is on average *c.* 7 mm, indicating that the organism producing them must have been relatively large or possessed a widely distendable alimentary canal. The naraoiids, eurypterids, polychaetes and *Jamoytius*-like agnathan vertebrates would seem too small to be capable of producing such large coprolites, with the conodonts, large soft-bodied metazoans and possibly the orthoconic cephalopods seemingly more likely candidates.

It is also possible that some of these bromalites, particularly those with an organized internal structure (e.g. C505; Pl. 2, fig. 8; Text-fig. 4), might not be coprolites at all, but cololites representing gut infills or replacements.

DISCUSSION

This investigation of bromalites from the Soom Shale of South Africa has revealed a number of different forms. In total, five distinct types of bromalite have been discriminated, in addition to a number of equivocally bromalitic specimens. The bromalites provide indisputable evidence that something in the Soom Shale community was eating brachiopods and that something was preying on conodonts. The fragmented brachiopod shells present in some specimens show that durophages, and probably morphologically specialized shell breakers, were active by the Late Ordovician. The presence of fragmented elements of conodonts, themselves predators/scavengers, in excreted or regurgitated material also provides direct evidence of tiering within the predatory trophic level in the Soom Shale. There are other records of probable coprolitic aggregates of conodont elements in Ordovician deposits (e.g. Tolmacheva 1996; Tolmacheva and Purnell 2002; Stewart and Nicoll 2003), indicating that these primitive vertebrates were falling prey to other organisms by the Early Ordovician. However, in none of the other reported coprolites are the elements fragmented to the degree seen in the Soom specimens.

The preserved Soom Shale palaeocommunity has a high representation of secondary and tertiary consumers, primarily conodonts, orthoconic cephalopods and eurypterids, and these taxa are all contenders for producing most of the bromalites recorded. Further field and laboratory research may identify more of the primary consumers and producers of this marine ecosystem that must have been present in order to support the higher trophic forms. The bromalites may be further understood and their origins more accurately determined by biological modelling using modern analogues. For example, directed studies of the biological waste produced by hagfishes and lampreys may help to constrain interpretations involving the conodonts and other agnathans, and modern cephalopods may serve as a proxy for the orthoconic forms.

However, there is some doubt that the taxa found to date can adequately account for the production of all the bromalites recognized. The bromalites made up of crushed brachiopod valves, in particular, seem too large to have been produced by eurypterids and orthocones of the maximum size known in the Soom Shale. If we use linear extrapolation from the sizes of known conodont animals and their apparatuses, then conodonts in the Soom Shale may have reached 1 m, easily large enough to produce any of the bromalites we have collected. However, their elements, although designed for grasping and crushing (Aldridge *et al.* 1995; Purnell 1995), are sharp-tipped and could not plausibly have crushed the discinoid shells to the fragmentary state seen in the bromalites. As discussed above, there may well have been large predators in the Soom Shale community that we have yet to discover.

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