# SYSTEMATICS, TAPHONOMY AND PALAEOECOLOGY OF SELECTED INVERTEBRATES FROM THE LATE ORDOVICIAN SOOM SHALE LAGERSTÄTTE, SOUTH AFRICA

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by

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# ABSTRACT

The diversity of the Late Ordovician Soom Shale Lagerstätte ecosystem is increased by the identification of three new species. The arthropod *Caryocaris cedarbergensis* n. sp. is described, extending the geographical, ecological and temporal range of the family Caryocarididae and providing the first evidence of a zooplanktonic constituent to the Soom Shale biota. The scolecodont species *Xanioprion*? n. sp. is distinguished, based on poor material, and the species *Synaptogenys rietvleiensis* n. gen., n. sp. is described, providing the first documented scolecodont fauna from South Africa and the first apparatus based taxonomic study of specimens from palaeocontinental Gondwana.

Two new soft-bodied organisms, which would both have had an extremely low preservation potential, are added to the Soom Shale ecosystem. A scyphozoan medusoid exhibits features that can be related to those observed in modern scyphozoans and is the second zooplanktonic organism identified in the Soom Shale ecosystem. A xenusiid lobopodian, showing features homologous to those of other Palaeozoic marine lobopodians, is the first definite marine lobopodian to be described outside of the Cambrian and adds a rare benthic component to the Soom Shale ecosystem.

The recognition of three new types of arthropod, comprising large carapaces of unknown affinities, a possible nektonic specimen and a nektonic predatory specimen, increases the diversity of arthropods in the Soom Shale ecosystem, and confirms the arthropods as the most diverse fauna from the Soom Shale community.

The identification of fibrous clay mineral coatings, which could be a result of diagenetic or metamorphic growth, complicates the current models for the taphonomy of the Soom Shale. An additional preservation mechanism, pyrite mineralization, occurs along with clay and alunite replacement, organic films and late stage fibrous clay growth.

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And Finally….. Thanks to Dave. I love you.

# Chapter 1

# INTRODUCTION

THE Soom Shale Konservat Lagerstätte (site of exceptional fossil preservation) is a Late Ordovician deposit located in the Cedarberg Mountains, north of Cape Town (Fig. 1.1). An exceptionally preserved soft-bodied fauna has been recovered from several localities (Gabbott *et al.* 1995; Gabbott 1998; Aldridge *et al.* 2001), most notably conodonts (Aldridge and Theron 1993; Gabbott *et al.* 1995), eurypterids (Braddy *et al.* 1995, 1999) and enigmatic fossils. Compared with the Cambrian System, the Ordovician has few known Konservat Lagerstätten and of these the Soom Shale records the greatest number of taxa and the highest fidelity preservation of decay-prone tissues, principally as clay mineral replacements. The Soom Shale also represents a rare cold-water community (Theron and Thamm 1990; Aldridge *et al.* 1994; Gabbott 1998; Aldridge *et al.* 2001), and has been interpreted as a post-glacial transgressive deposit (Sutcliffe *et al.* 2000; Young *et al.* 2004). The unusual temporal, geographical and ecological setting may all have contributed to the evolution and preservation of the unique specimens found at this site.

## THE GEOLOGY OF THE TABLE MOUNTAIN GROUP

The Soom Shale Member, a 10–15m thick unit, is the lower member of the Cedarberg Formation, which occurs towards the top of the Table Mountain Group in South Africa (Fig. 1.2). The Table Mountain Group was deposited during the Cambrian, through the Ordovician and into the Silurian (Cocks and Fortey 1986; Hiller 1992). The sediments were derived from a cratonic source to the North. Hiller (1992) suggested that the very mature nature of the sediments indicates that they were deposited in the relatively stable tectonic conditions of a slowly subsiding shelf. The group consists of clastic sediments and rests unconformably on eroded Proterozoic metasediments and granitic intrusives of the Cape Granite Suite, which have been dated radiometrically at 632–517 Ma (Hiller 1992). The Table Mountain Group is divided into three parts, based on the extent of outcrop and lithology. The lower part includes

the Piekenier, Graafwater and Peninsula Formations, totalling over 3000 m in thickness. These are mainly shallow marine sediments without body fossils but rich in trace fossils. The middle part consists of the glaciogenic Pakhuis Tillite Formation (up to 150 m in thickness) and the overlying argillaceous Cedarberg Formation (up to 120 m in thickness), which contains vertebrate and invertebrate body fossils. The Nardouw Subgroup constitutes the upper part of the Table Mountain Group, and is a quartzite unit, over 1000 m thick with some trace fossils (Rust 1973, 1977; Cocks and Fortey 1986) (Fig. 1.2).
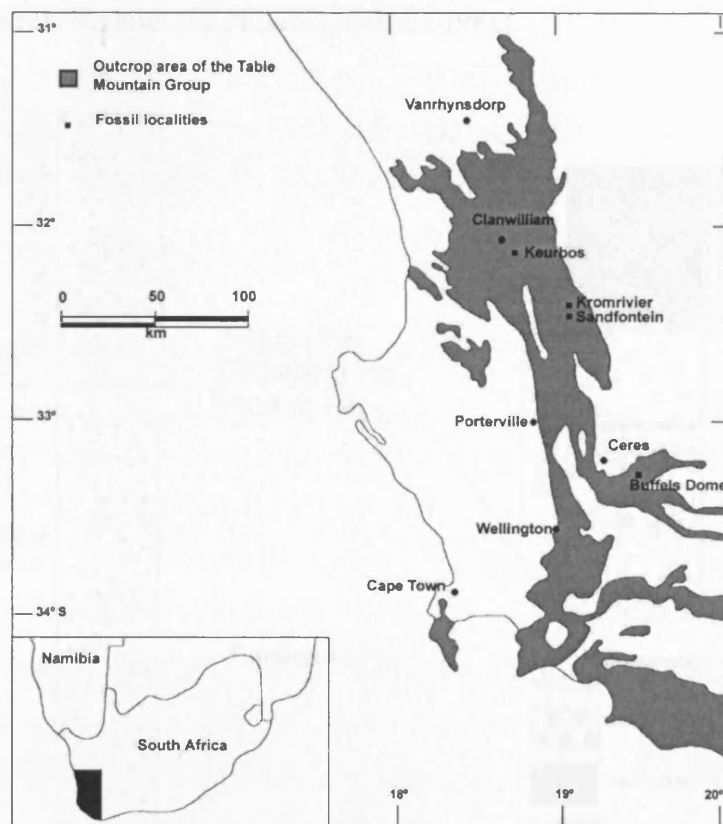


**Figure 1.1.** The distribution of the Table Mountain Group in southwestern South Africa showing the location of the fossiliferous outcrops of the Soom Shale (from Gabbott *et al.* 2003).

*The Piekenier Formation*

The Piekenier Formation is the oldest unit of the Table Mountain Group and is estimated to be late Cambrian or early Ordovician in age based on sedimentation rates (Rust 1967, 1981; Hiller 1992). The base of the formation rests unconformably on the metamorphosed Cape Granite suite and the unit is geographically confined to the Western Cape (Hiller 1992). The

formation consists of coarse clastics and oligomictic conglomerates containing many exotic pebbles. Towards the southeast these pass into a thick (900 m) sequence of coarse-grained supermature sandstones (Hiller 1992). The palaeoenvironment has been interpreted as a braided river plain, with a marked facies zonation possibly representing the area where the river went into the sea creating a fan-delta or a braid delta (Hiller 1992). Overall, the Piekenier Formation is thought to represent a tongue shaped clastic apron, which invaded the newly formed Table Mountain Basin from the northwest (Rust 1981). The provenance area for the sediment is considered to be the Atlantic highland, which was intermittently active as a source of sediment throughout the Palaeozoic (Rust 1981).
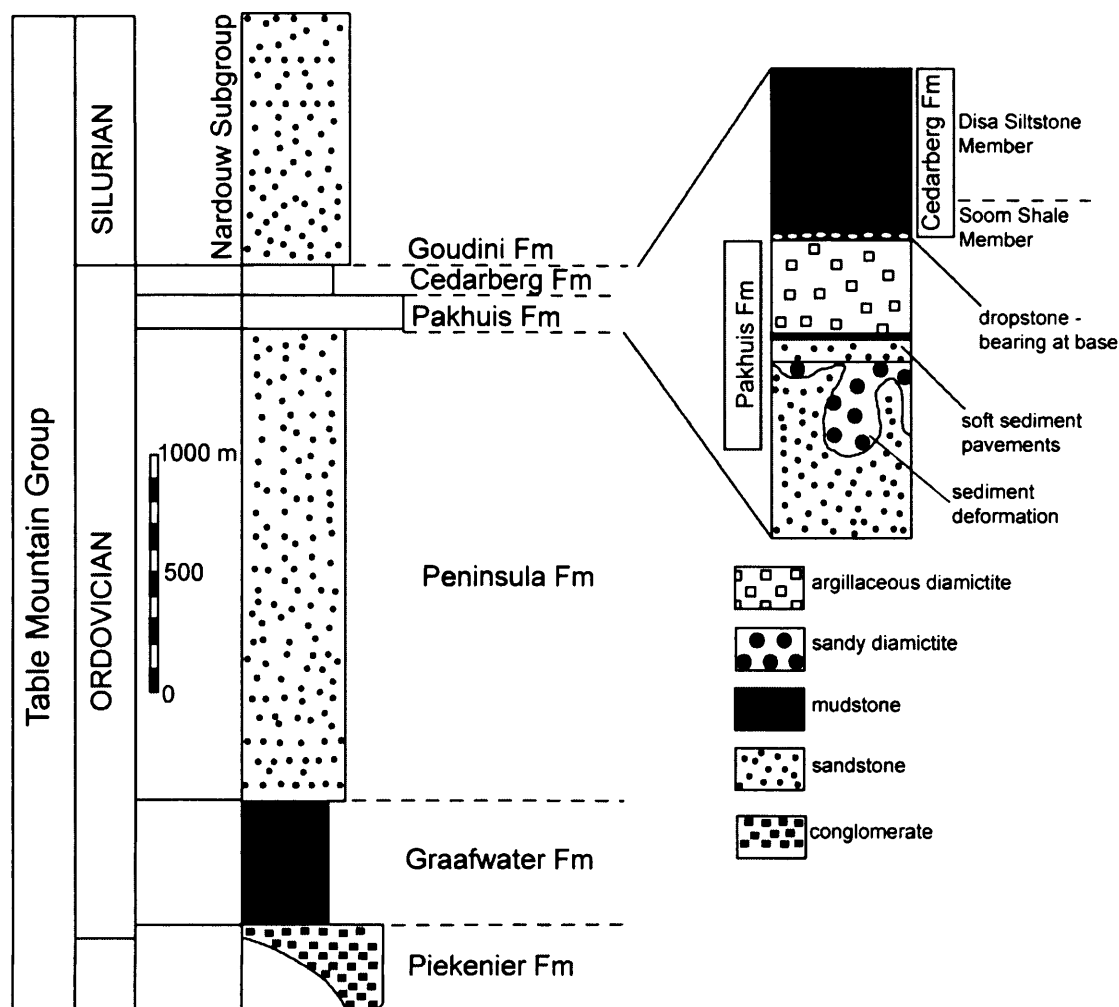


**Figure 1.2.** Generalised stratigraphy of the Table Mountain Group, showing the position of the formations mentioned in the text. Expanded column (not to scale) shows the stratigraphic relationships between the Pakhuis and Cedarberg formations, and the position of the Soom Shale and Disa Siltstone members (modified from Young *et al.* 2004; after Theron and Thamm 1990).

*The Graafwater Formation*

The Graafwater Formation overlies the Piekenier Formation conformably and marks a dramatic change from a high-energy environment in the basin to a low energy tidal flat situation (Rust 1981). It consists of thin interbedded fine-grained quartz arenites and reddish siltstones or mudstones and, in the north, basal members of the unit contain conglomerate horizons. The formation is of variable thickness; it is in excess of 300 m thick along the basin axis and thins towards the margins. Trace fossils have been found including *Skolithos*, *Cruziana*, *Helminthoida* and *Scolicia*, giving the formation an Early Ordovician date (Anderson 1975; Rust 1981, Hiller 1992). Sedimentary structures identified include herringbone cross-stratification, reactivation surfaces and fining-upwards cycles, which can be indicators of a tidal environment but have been reported from fluvial environments (Hiller 1992).

*The Peninsula Formation*

The Peninsula Formation consists of supermature arenaceous sediments and contains the bulk of Ordovician sediments in South Africa. The formation consists of pure quartz sandstone that has been transformed by burial and dynamic metamorphism to metaquartzite (Hiller 1992) and is generally unfossiliferous, although it does show a variety of trace fossils at certain horizons. These indicate a possible Arenig–Llanvirn age (Hiller 1992). It has been suggested that the Peninsula Formation was deposited in a major braided fluvial floodplain system that prograded into a marine environment in the southwest (Hiller 1992). Alternatively it could represent a prograding braided fluvial system that was subjected to periodic minor marine transgressions (Hiller 1992). It has also been considered that the formation reflects extensive marine reworking of sediments on a broad, stable shelf in a barrier beach or shallow shelf setting (Gray *et al.* 1986). The upper part of the formation is thought to show a regressive cycle coupled with a glacio-eustatic fall in sea level, which accompanied the extensive Late Ordovician Gondwana glaciation. In the closing stages of Peninsula Formation sedimentation, glaciogenic deposits were being reworked by coastal processes (Gray *et al.* 1986).

*The Pakhuis Tillite Formation*

The Pakhuis Tillite Formation overlies the Peninsula Formation disconformably in the Western Cape and consists predominantly of glaciogenic sediments ranging from true tillite through diamictite, sandstone and shale. It represents a unique incursion of texturally immature sediments within the mature sediments of the Table Mountain Group (Rust 1981; Theron and Thamm 1990; Young *et al.* 2004). It is a thin formation (with a maximum thickness of 120 m), and can be traced over distance of 300 km in a north-south direction and for 300 km east of Cape Town (Hiller 1992). It has been suggested that the glaciogenic rocks formed at or near to sea level (Young *et al.* 2004). The formation has been interpreted as being deposited under the influence of a major glacial episode that affected the southern Gondwanan continents at the time. Evidence of glacial pavements can be seen on the upper surface of the underlying Peninsula Formation (Aldridge *et al.* 1994).

*The Cedarberg Formation*

The Cedarberg Formation, of which the Soom Shale is the lower member and the Disa Siltstone the upper member, constitutes the only significant fine-grained unit within the Lower Palaeozoic arenaceous Table Mountain Group (Rust 1981). The formation is laterally persistent, rarely more than 120 m thick, and as it occurs within predominantly arenaceous rocks it forms a distinctive marker horizon (Gray *et al.* 1986).

*The Soom Shale Member*. The Soom Shale Member can be followed from the northwest extremity of the Cape Basin southwards to the Cape Town area and east to Port Elizabeth. It crops out as a recessive level throughout the Cedarberg Mountains north of Cape Town, and is highly deformed in the region east of Cape Town (Aldridge *et al.* 2001). This unit provides the only datable fossils in the entire Table Mountain Group, with the fauna indicating a late Ashgill (Rawtheyan or Hirnantian) age (Cocks *et al.* 1970; Cocks and Fortey 1986; Theron *et al.* 1990). The Soom Shale is thought to be a post glacial transgressive unit (Sutcliffe *et al.* 2000; Young *et al.* 2004) as it overlies tillites of the glaciogenic Pakhuis Formation, thus sequence stratigraphy constrains the age of the unit to an interval possibly equivalent to the *persculptus* graptolite zone of the Hirnantian.

Fossiliferous exposures of the Soom Shale occur at Keurbos (18°58'E, 32°15'S) near Clanwilliam (Fig. 1.3), Kromrivier (19°17'E, 32°32'S) (Fig. 1.4A, B), Swartleikloof

(19°11'E, 32°32'S) and at Sandfontein (19°14'E, 32°40'S) (Fig. 1.4A, C), 52 km SSE from Clanwilliam. Fossils have also been discovered at Buffels Dome (19°50'E, 33°30'S) (Moore and Marchant 1981) (Fig. 1.1). The material in this project came from Sandfontein, Kromrivier and Keurbos.
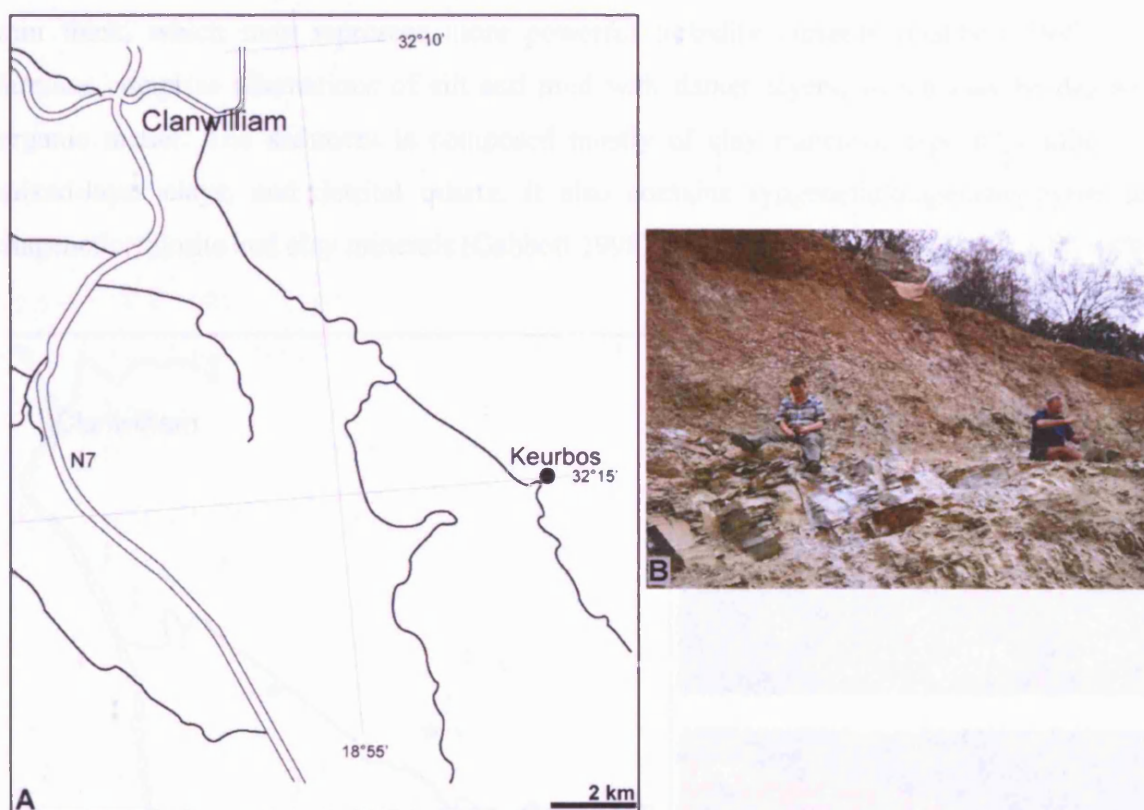


**Figure 1.3**. The Soom Shale collecting site at Keurbos **A**. Detailed location (base map from Cedarberg Map, issued by the directorate of Forestry, Pretoria, South Africa), for general location see Fig. 1.1. **B**. Sample collection at Keurbos.

The Soom Shale Member consists of a laminated micaceous mudrock 10-15 m in thickness with sporadic dropstone layers, which are occasionally present in the lower part of the member and indicate the possibility of periodic ice-coverage (Theron and Thamm 1990). Mud and silt laminae are normally less than 1 mm thick, rarely up to 10 mm. The layers are laterally persistent and undisturbed by penetrative bioturbation or current activity indicating dominantly quiet water conditions (Theron and Thamm 1990; Gabbott *et al*. 2003). Geochemical analyses of the sediment indicate that bottom and pore waters were anoxic and at times euxinic (Gabbott 1999). The results from the geochemical study of Young *et al*. (2004) show that anoxia was greatest at the base of the Soom Shale Member and decreased

towards the top. It is thought that the sediments were deposited by the settling of fine detritus from suspension in a brackish to marine water body; possibly in a shallow partially ice bound embayment (Aldridge *et al*. 1994). Laminations represent intercalations of sediment deposited by distal turbidity currents, which had lost nearly all of their energy, and hemipelagites. Occasional perturbation of varve deposition is shown by thicker homogenous beds up to 10 mm thick, which may represent more powerful turbidity currents (Gabbott 1999). The laminae comprise alternations of silt and mud with darker layers, which may be degraded organic matter. The sediment is composed mostly of clay minerals, especially illites and mixed-layer clays, and detrital quartz. It also contains syngenetic/diagenetic pyrite and diagenetic chlorite and clay minerals (Gabbott 1998).
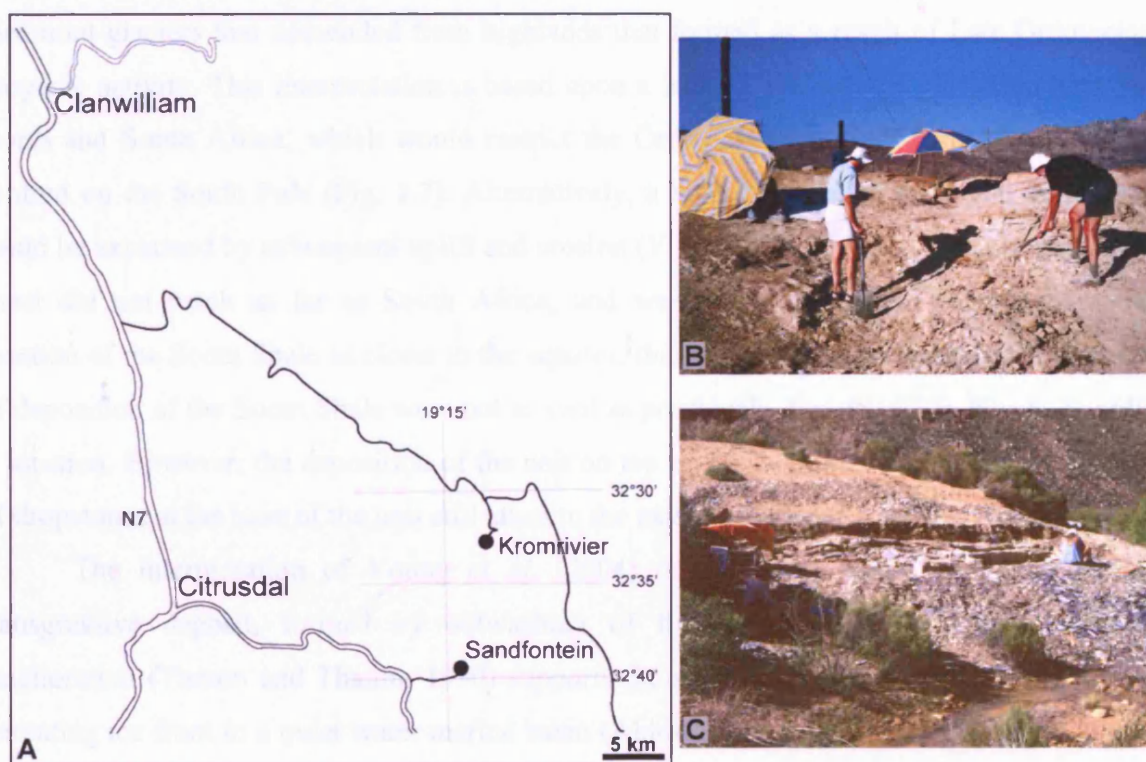


**Figure 1.4.** The Soom Shale collecting sites at Kromrivier and Sandfontein A. Detailed location (base map from Cedarberg Map, issued by the directorate of Forestry, Pretoria, South Africa), for general location see Fig. 1.1. B. Sample collection at Kromrivier. C. Sample collection at Sandfontein.

The location of the Soom Shale depositional basin has been suggested as approximately 60° S (Gabbott *et al*. 1995; Gabbott 1998; Aldridge *et al*. 2001); however, the tip of South Africa has been placed at between about 30° S and 45° S by several continental

reconstructions for the Late Ordovician (Fig. 1.5) (Beuf *et al.* 1971; Smith 1997; Sutcliffe *et al.* 2000; Cocks and Torsvik 2002; Fortey and Cocks 2003; Young *et al.* 2004). The contact of the Soom Shale with the underlying glacial Pakhuis Tillite has been described as gradational by Theron and Thamm (1990) and this has been used to suggest that the Soom Shale was deposited under the influence of glacial conditions. It has been suggested that the Late Ordovician ice sheet radiated outward from central Africa and was large and continuous (Beuf *et al.* 1971; Deynoux 1985; Sutcliffe *et al.* 2000) (Fig. 1.6), possibly extending up to 30° S (Scotese *et al.* 1999; Evans 2003; Le Heron *et al.* 2005). However, glacial conditions in the Late Ordovician may have been characterised by the synchronous growth of separate ice centres (Blanpied *et al.* 2000; Ghienne 2003; Le Heron *et al.* 2005). Young *et al.* (2004) suggested that glacial conditions in South Africa might have been partly derived from piedmont glaciers that descended from highlands that formed as a result of Late Ordovician orogenic activity. This interpretation is based upon a lack of evidence of glaciation between North and South Africa, which would restrict the Ordovician ice sheet to northern Africa, centred on the South Pole (Fig. 1.7). Alternatively, a lack of evidence of glacial conditions could be explained by subsequent uplift and erosion (Young *et al.* 2004). If the continental ice sheet did not reach as far as South Africa, and we accept the current palaeogeographic location of the Soom Shale as closer to the equator, this may mean that conditions at the time of deposition of the Soom Shale were not as cool as previously thought, when based on a 60° S location. However, the deposition of the unit on top of the Pakhuis Tillite and the presence of dropstones at the base of the unit still attest to the existence of cold water.

The interpretation of Young *et al.* (2004) of the Soom Shale as a post glacial transgressive deposit, formed by outwashing of fine-grained material during climatic amelioration (Theron and Thamm 1990) supports the suggestion that it formed close to the retreating ice front in a quiet water marine basin (Aldridge *et al.* 1994; Aldridge *et al.* 2001). It has been inferred that bottom waters in the Soom Shale basin were quite cool given its glacial associations (Gabbott 1998). Water depth was unlikely to have been great as the basin was in an intracratonic setting and the Soom Shale is bounded by the subaerial tillites below, and the shallow marine Disa Siltstones above. A likely depth of 100 m may have existed over the majority of the basin unless microbial mats bound the sediment or the sea surface was ice covered (Gabbott 1999).
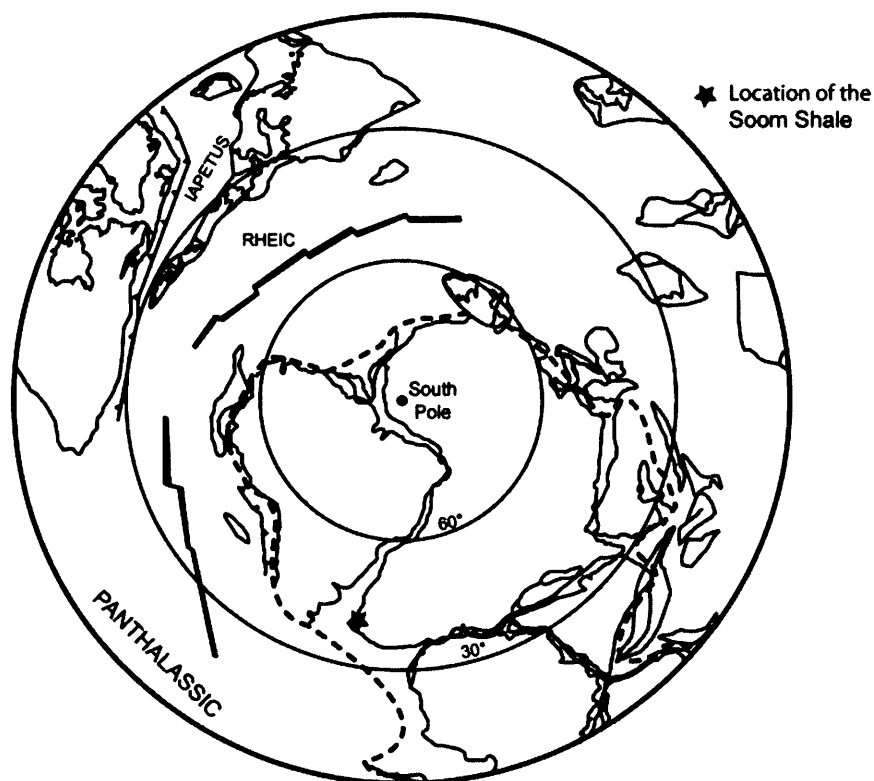
**Figure 1.5.** A global reconstruction for the end of the Ordovician/beginning of the Silurian (440 Ma), with the location of the Soom Shale Lagerstätte (reconstruction from Fortey and Cocks 2003; modified from Cocks and Torsvik 2002).

The sediment is thought to have undergone burial anchimetamorphism temperatures of at least 200°C because of the black colour of palynomorphs and chitinozoans that have been found in the Soom Shale (Cramer *et al.* 1974). In places this metamorphism has transformed the shale and siltstone into a sheared slate, destroying primary internal features. Soom Shale siltstones and mudstones are black when fresh, but have been subject to Neogene weathering that in most places has changed the rock from the original black colour, still seen at Sandfontein, to grey/orange seen at Keurbos and Kromrivier (Gabbott 1998). At Kromrivier the rock is more weathered.
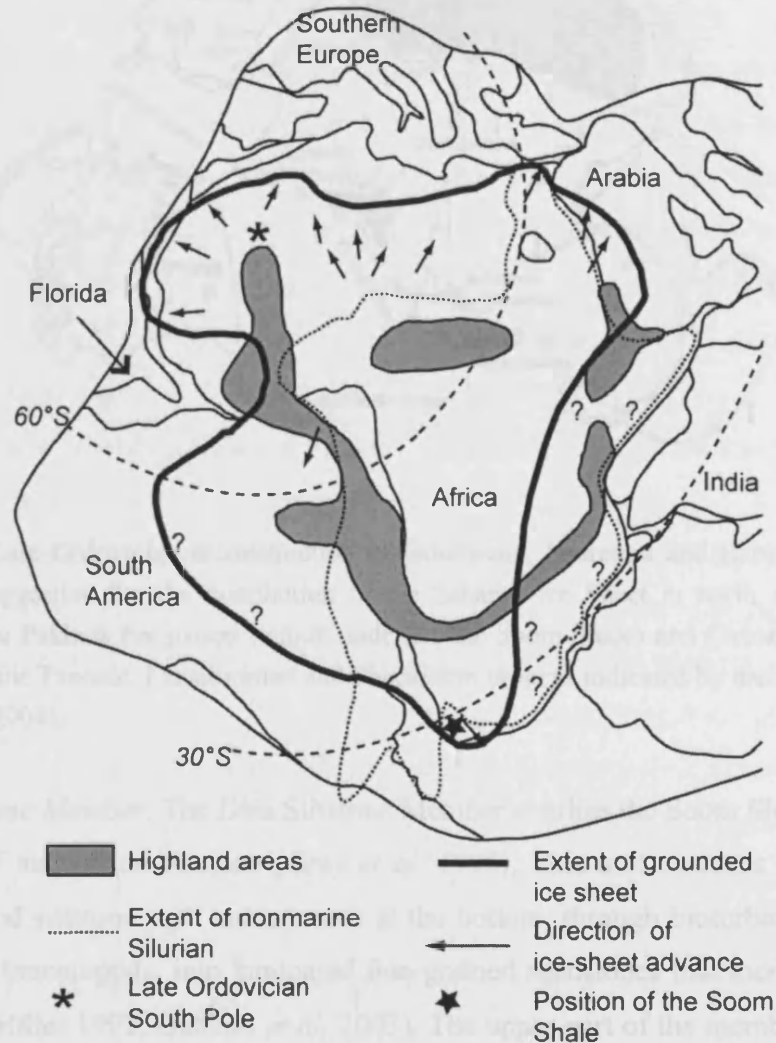
**Figure 1.6.** Late Ordovician palaeogeographical reconstruction of West Gondwana, with the location of the Soom Shale and an interpretation of the approximate extent of grounded ice sheet (Beuf *et al.* 1971; Vaslet 1990; Scotese *et al.* 1999) (modified from Sutcliffe *et al.* 2000).
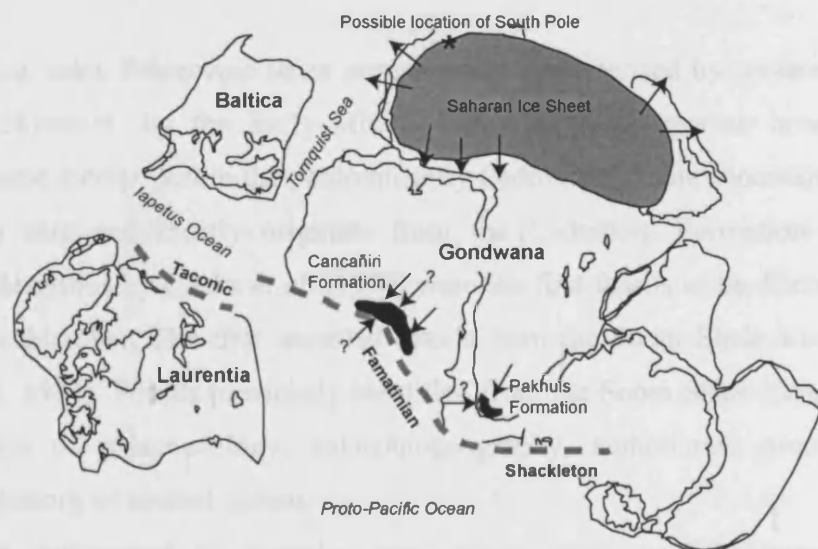
**Figure 1.7.** Late Ordovician reconstruction of Gondwana, Laurentia and Baltica to show an alternative suggestion for the distribution of the Saharan Ice Sheet in north Africa and the location of the Pakhuis Formation (which underlies the Soom Shale) and Cancañiri Formation in relation to the Taconic, Famatininian and Shackleton orogens indicated by dashed lines (from Young *et al.* 2004).

*The Disa Siltstone Member.* The Disa Siltstone Member overlies the Soom Shale Member and is composed of micaceous siltstone (Gray *et al.* 1986). This unit coarsens upwards from a grey fine-grained siltstone with shale lenses at the bottom, through bioturbated siltstone and mudstone with brachiopods, into laminated fine-grained sandstones that increase upwards in bed thickness (Hiller 1992; Gabbott *et al.* 2003). The upper part of the member is of variable lithology. In the central part of the member, between Porterville and just south of Wellington, Cape Province, is a 10m thick band containing a shelly fauna, known as the Brachiopod Zone (Cocks and Fortey 1986), which is markedly bioturbated and fossiliferous. A suggested age for the unit of latest Ordovician (Hirnantian) to Silurian has been made based on fossils such as *Heterorthina* and *Heterorthella* (Cocks and Fortey 1986). The Disa siltstone consists of fine-grained sandstone or silty mudstone of variable thickness (~10 m) (Gray *et al.* 1986). The coarser sediments of the Disa Siltstone Member record further melting and retreat of the ice sheet with wave and current activity gradually increasing in importance (Aldridge *et al.* 1994). The Cedarberg Formation grades upwards into the Goudini Formation, which is part of the Nardouw Subgroup, where conditions appear to have returned to those prevailing during the deposition of the Peninsula Formation (Hiller 1992).

## FOSSILS OF THE SOOM SHALE

In South Africa, early Palaeozoic strata are generally characterised by containing no or very few fossils. However, by the Early–Middle Devonian fossil marine invertebrates were plentiful (Boucot 1999). Within the predominantly Ordovician Table Mountain Group fossils are relatively rare and mostly originate from the Cedarberg Formation (Hiller 1992); brachiopods described by Cocks *et al.* (1970) were the first fossils to be discovered from the Disa Siltstone Member. The first recorded fossils from the Soom Shale were chitinozoans (Cramer *et al.* 1974). Fossils previously identified from the Soom Shale have contributed to the knowledge of palaeoecology, palaeobiogeography, taphonomic processes and the evolutionary history of several groups.

Fossils interpreted as vascular land plants, with a dichotomously branching morphology were described by Kovács-Endrödy (1986). However, they were subsequently reinterpreted by Theron *et al.* (1990) as conodont bedding plane assemblages. Throughout the exposure at Keurbos conodonts are found as isolated elements and as bedding plane assemblages and they are often associated with lobate structures anterior of the apparatus, which have been interpreted as the sclerotic cartilages surrounding the eyes (Aldridge and Theron 1993). Most of the conodonts have been assigned to the prioniodontid species *Promissum pulchrum* Kovács-Endrödy, 1986 (Theron *et al.* 1990). The apparatuses are large compared to most other conodonts, with single elements up to 20 mm in length.

A conodont specimen with a preserved trunk has been discovered from Sandfontein (Gabbott *et al.* 1995); this is the third locality in the world in which such fossils have been found. The specimen has exceptionally preserved trunk musculature, a feeding apparatus and eyes. The entire length of the animal, of which only the anterior 110 mm is present on the slab, was estimated at approximately 400 mm, and at the time was thought to show the earliest fibrous muscle tissue preserved in the vertebrate fossil record (Gabbott *et al.* 1995). *Promissum* is considered to be a representative of a cold-water Gondwanan lineage that survived the Late Ordovician extinction event, and it may have given rise to the radiation of the Pterospathodontidae in warmer Llandovery seas (Theron *et al.* 1990). Specimens of a naked agnathan have also been discovered (Aldridge *et al.* 2001; Aldridge and Purnell 2005).

Arthropods from the Soom Shale include trilobites, naraoiids, eurypterids and ostracods. The trilobites have been identified as *Mucronaspis olini* Temple, 1952 and were found near the base of the unit at Buffels Dome, near Worcester in the Cape Province (Moore and Marchant 1981). The material includes two imperfect dorsal exoskeletons, a large

cephalon and other fragmentary articulated specimens (Cocks and Fortey 1986). The arthropod *Soomaspis splendida* Fortey and Theron, 1994 was also described from the Soom Member and was included with the primitive and uncalcified trilobites in the family Naraoiidae.

A new genus and species of ostracod was described by Gabbott *et al.* (2003) from the Keurbos locality in the Soom Shale Member. *Myodoprimigenia fistuca* Gabbott, Siveter, Aldridge and Theron, 2003 is the earliest and only Ordovician occurrence of the superorder Myodocopa. The myodocopes were found in association with orthoconic cephalopods, suggesting that they fed on cephalopod carrion as nektobenthic scavengers. This extended the possible evidence of a scavenging lifestyle in ostracods back by 200 million years (Gabbott *et al.* 2003). The shells of the ostracods were interpreted as thin, lightly mineralized and flexible, with microstructures resulting from *in vivo* calcification processes. This microstructure is closely comparable to that of Silurian myodocopes, supporting evidence that the fossils are a sister group to the Upper Silurian 'cyprinid' myodocopes and allied forms (Gabbott *et al.* 2003). Gabbott *et al.* (2003) noted that many of the ostracods had co-joined valves and suggested that these delicate fossils would have been disarticulated had transport occurred.

Eurypterids have been described from the Keurbos and Kromrivier exposures of the Soom Shale Member. Specimens have been assigned to *Onychopterella augusti* Braddy, Aldridge and Theron, 1995. Some are very well preserved, with muscles, respiratory structures and gut traces evident. The discovery of *Onychopterella augusti* in the Soom Shale Member extended the temporal range of the genus into the Late Ordovician, and recorded its first occurrence in Gondwana (Braddy *et al.* 1995). One specimen has lamellate book gills preserved, which provides a synapomorphy that supports a sister group relationship between eurypterids and scorpions (Braddy *et al.* 1999).

Molluscs from the Soom Shale include orthoconic cephalopods, which have been found at Keurbos. The orthocones have been severely dissolved and compacted and cannot be identified to any taxonomic level. The siphuncle is not preserved in any of the specimens and septa are rare and poorly preserved. However, some of the specimens have a radula showing teeth with simple curved morphology, which taper to a point in the direction of the centre of the radula (Gabbott 1999). Other molluscs found in the Soom Shale Member at Buffels Dome include three incomplete specimens of a trilobed bellerophontid monoplacophoran belonging to the family Sinuitidae (Cocks and Fortey 1986), which have been tentatively identified as *Bucanella* sp.. Also five specimens of infaunal deposit feeding nuculanacean bivalves from this site have been attributed to *Concavodonta* (Cocks and Fortey 1986).

Discinoid brachiopods and rhynchonellids occur as epibionts associated with orthocones, and as isolated specimens in the sediment at all localities (Gabbott 1999; Aldridge *et al.* 2006). A few specimens of small (up to 5 mm) lingulate brachiopods have also been found (Aldridge *et al.* 1994).

Small spore tetrads have been found from the Soom Shale Member at Swartleikloof (near Kromrivier) (Cocks and Fortey 1986; Gray *et al.* 1986). The spore tetrads have not been found in association with any plant megafossils. Phytoplankton has also been recognised in the form of leiospheres, sphaeromorphs and spherical bodies with smooth-walled or rarely granular or microechinate surfaces (Gray *et al.* 1986). The spherical bodies have been attributed to the Prasinophyta, a group of green algae variously included within, or separated from, the Chlorophyta, which have a modern distribution in marine, brackish and freshwater environments (Tappan 1980; Gray *et al.* 1986). Palynomorphs from the Soom Shale have been extensively coalified and degraded (Gray *et al.* 1986).

Isolated individuals of chitinozoans have been identified from the base of the Soom Shale at Swartleikloof. These include *Ancyrochitina merga* Jenkins, 1970, *Conochitina oelandica* Eisenack, 1955, *Ancyrochitina* spp., *Cyathochitina dispar* Benoit and Taugourdeau, 1961, *Desmochitina minor* Eisenack, 1931, *Desmochitina* spp. and *Hoegisphaera* spp. (Cramer *et al.* 1974). Chitinozoans have also been found from Keurbos and Sandfontein on bedding planes as scattered individuals, in linked chains, in aggregated masses and with associated organic envelopes. On the basis of size, at least two morphological groups have been identified, one with a vesicle width of 0.16–0.35 mm and the other with a width of 0.05–0.11 mm. The general morphology of the specimens and the presence of a carina led Gabbott *et al.* (1998) to suggest that they may belong to the genus *Cyathochitina*.

Carbonaceous compressions of small, randomly orientated pointed axes have been recorded from the Soom Shale. These were originally described by Kovács-Endrody (1986) as the remains of a non-vascular land plant and were given the designation *Eohostimella parva*. Subsequently, Chesselet (1992) reinterpreted these structures as possible disarticulated remains of a problematic Ordovician metazoan. Therefore, they were renamed as *Siphonacis parva* (Kovács-Endrody, 1986). These fossils have been found from Keurbos, where they occur as isolated individuals or in pairs and dense scatters occur on some bedding planes. Chesselet (1992) stated that the proximal end appears incomplete and torn in some specimens of *Siphonacis*, but in a few specimens the two axes are joined at the base. This was interpreted to be evidence that they are part of a larger organism. They commonly appear in association with assemblages of *Promissum pulchrum*, but their affinities remain unknown. There are also

many soft-bodied forms with unknown affinities, which have yet to be identified (Aldridge *et al.* 2001).

Several different types of bromalite have been identified from the deposit, and the presence of crushed discinoid valves in several specimens demonstrates that an effective durophagous predator was present in the Soom Shale community and the presence of conodont elements in some specimens provides evidence that there was tiering within the predatory trophic level (Aldridge *et al.* 2006).

TAPHONOMY

Specimens of *Promissum pulchrum* from the Soom Shale are generally preserved as internal and external moulds. Phosphate has been leached or replaced by clay minerals, sometimes giving a pale green appearance (Theron *et al.* 1990). At the time of discovery, the conodont animal specimen exhibited the earliest fibrous muscle tissue preserved in the vertebrate fossil record (Gabbott *et al.* 1995). Soft tissues of the *Promissum pulchrum* specimen from Sandfontein are preserved as illite and mixed-layer clay minerals (Gabbott *et al.* 1995). Some of the eye capsules are preserved as flattened, black remains of sclerotized tissues and others are partially or completely mineralized by a silvery white mineral, which Gabbott (1998) suggested is illite.

Specimens of the trilobite *Mucronaspis olini* and most specimens of the naraoiid *Soomaspis splendida* occur as internal and external moulds, mostly with no trace of the original exoskeleton (Moore and Marchant 1981; Cocks and Fortey 1986; Fortey and Theron 1994; Gabbott 1998). The holotype of *S. splendida* (C453) shows some cuticle preservation anterior to the cephalic margin (Fortey and Theron 1994). Most of the eurypterids in the Soom Shale are also preserved as internal and external moulds. A few have preserved exoskeletal material present, which has been replaced by clays and alunite group minerals (Gabbott 1998). In some specimens, traces of internal soft tissues, which are rarely preserved, have been identified. These include muscular tissue associated with the appendages and telson, respiratory structures (areas of the branchial chambers and lamellate gills) and an apparently spiral valve in the anterior part of the alimentary canal (Braddy *et al.* 1995, 1999).

Ostracods in the Soom Shale have been preserved through early diagenetic mineralization by clay minerals (Gabbott *et al.* 2003). Some of the specimens are very faint, and in others only the outline of the valve or valves and wrinkles in the valves are evident, appearing dark grey in colour. Several specimens have an entire carapace preserved in dark

grey or orange and yellow. In these specimens, exfoliation of mineral layers sometimes occurs, exposing folded cuticle below. Analysed dark grey specimens have an illitic composition (Gabbott *et al.* 2003).

Orthocones are preserved as internal, external or composite moulds. The original aragonite has been completely lost (Gabbott 1999). Some of the specimens contain radulae in their body chambers, preserved as external moulds. Some of the orthocones retain relief and lack fracture patterns, and these were probably infilled prior to compaction. Some have little relief and have longitudinal fracture patterns in the body chamber and chaotic fracture patterns in the phragmocone produced by crushing. Other specimens have body chambers that are nearly completely flat with longitudinal wrinkles and phragmocones that are severely flattened (Gabbott 1998).

Discinoids are the most abundant brachiopods in the Soom Shale, internal and external moulds co-occur and some also retain a high proportion of shell material, particularly on the external surface (Gabbott 1998). On the internal surface of some of the valves, growth lines are clearly distinguishable, and externally fila are apparent on some specimens. There are a few specimens that have preserved material in the area of muscle scars, which may be the remains of soft tissue. Trematid brachiopods are less common. The specimens occur isolated in the sediment or associated with the orthocones. When isolated in the sediment, the trematids are dominantly mouldic, although some shell material is preserved on a few specimens. Details of growth lines can be seen. Specimens that occur on or in the vicinity of the orthocones are generally very poorly preserved (Gabbott 1998).

Bromalite specimens from the Soom Shale are generally preserved in three dimensions. They are mainly composed of clay minerals, plus some calcium phosphate or crandallite (Aldridge *et al.* 2006).

Chitinozoans from the Soom Shale show two preservation styles. The first is where the original organic walls are entirely replaced by illite and/or muscovite minerals. This is found predominantly at Sandfontein (Gabbott *et al.* 1998). The second style of preservation is where the central portion of the chitinozoan is mouldic, with no illite or muscovite replacement. Diagenetic recrystallisation has obliterated any internal features of the chitinozoa.

Spores and acritarchs are highly resistant to microbial decay and inorganic degradation. They are dark brown to black, indicating considerable thermal alteration, and are probably composed of altered sporopollenin (Gabbott 1998). Specimens of *Siphonacis parva* are preserved as carbonaceous compressions (Kovács-Endrody 1986; Chesselet 1992).

The modes of preservation of the Soom Shale fossils highlighted above indicate that the most labile tissues (for example muscle tissue) were replaced by authigenic clay minerals, which now have illitic composition (Gabbott *et al.* 2001). The more recalcitrant tissues (for example spores, acritarchs and chitinozoans) are preserved as altered organic material plus clay minerals (Gabbott 1998; Gabbott *et al.* 1998; Gabbott *et al.* 2001). Alunite also replaces parts of fossils in the Soom Shale (for example some of the eurypterid exoskeletal material) (Gabbott 1998), but it is currently unknown whether these areas have a particular histology or decay profile. Prevalent anoxic-euxinic bottom waters may have restricted scavengers, cool temperatures would have retarded the decay rate (Gabbott 1998) and these factors combined with low pH conditions would have promoted the preservation of soft tissues. Gabbott (1998) suggested that in the presence of cations, organic substrates would have had an affinity for colloidal clay minerals and may have acted as templates, controlling the adsorption of clay minerals which eventually replaced them. In Gabbott *et al.* (2001) it was suggested that labile tissues were replaced rapidly after death by authigenic clay minerals, which now have an illitic composition. However, this model has been questioned by Butterfield *et al.* (2007 p. 542) who stated that the 'claims of primary aluminosilicate permineralization in the Soom Shale Lagerstätte (Gabbott *et al.* 2001) are undermined by the pervasive, demonstrably late-stage aluminosilification of the whole biota'.

There is no evidence to suggest that fossil specimens underwent significant lateral transport before preservation as many have remained articulated. For example, valves of some of the brachiopods are conjoined, bedding plane assemblages of conodont apparatuses are intact and epibionts remain attached to orthocone carcasses. It is probable that disarticulation of these fossils would have occurred under transport (Gabbott 1998). The preservation of soft tissues, such as muscle fibres, in some organisms also suggests that specimens have not undergone significant transport. During a period of transport, it is likely that these tissues would have undergone a higher degree of decay (Gabbott 1998). Organisms from the Soom Shale can show differing types of preservation, dependent on their anatomy but also dependent on their location. For example, illite and muscovite recrystallisation at Keurbos is generally less extensive than at Sandfontein (Gabbott *et al.* 1998).

## THE ORDOVICIAN: PALAEONTOLOGICAL CONTEXT

### *The Ordovician radiation*

The Ordovician radiation was one of the most extensive intervals of diversification in the history of life (Miller 1997) (Fig. 1.8) and can be recognised at a wide spectrum of taxonomic levels from species to class (Owen and Crame 2002). It was characterised by a three to fourfold increase in the number of marine animal families and genera worldwide (Sepkoski 1993, 1997; Miller and Foote 1996; Miller 1997). There was a massive hike in biodiversity (Sepkoski 1981) matched by an increase in the biocomplexity of marine life (Droser and Sheehan 1997). The period was an unusually dynamic time in the Earth's physical history (Miller 1997); the biogeographical pattern associated with the radiation of individual clades reflects a complex combination of plate distribution, sedimentary environment, sea level rise and glaciation (Owen and Crame 2002). The radiation commenced during the middle Ordovician and continued into the late Ordovician, prior to the end Ordovician extinction event. Therefore, the Ordovician radiation occurred over a time span of approximately 25 Myr (Sepkoski 1995; Harper 2006). Many new taxa evolved during the Ordovician, and there is the potential for these organisms to be discovered in the Soom Shale Lagerstätte.
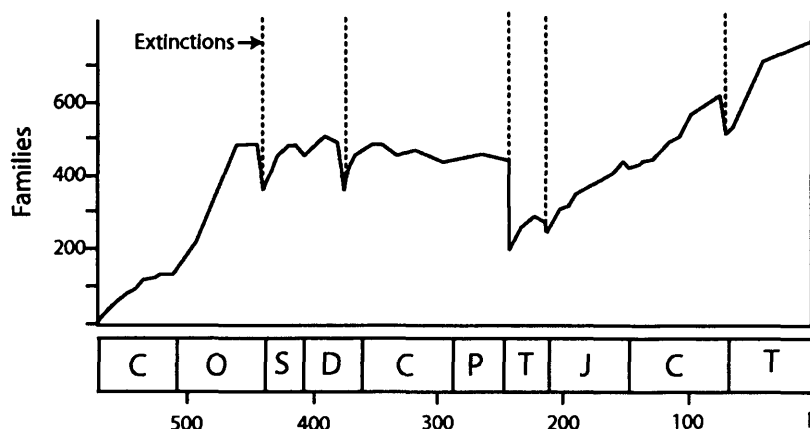


**Figure 1.8.** Biodiversity curve highlighting the large and rapid increase in biodiversity, which can be seen in the Early-Middle Ordovician, and the extinction event at the end of the Ordovician period (from Sepkoski 1993; modified by Sheehan 1996; Harper 2006).

*Other exceptionally preserved Ordovician fossils*

Occurrences of Konservat Lagerstätten in the Ordovician are rare, but there have been several documented occurrences of exceptional preservation (Fig. 1.9). One of the oldest exceptionally preserved Ordovician organisms is an arthropod described from the Tremadoc of England. This has a pair of annulated, uniramous, probable frontal appendages (Siveter *et al.* 1995). The fossil represents the third microfossil arthropod with preserved soft integument from the Ordovician, the others being of Tremadoc age from Öland (Andres 1989) and Newfoundland (Roy and Fåhræus 1989).

In the Arenig (Early Ordovician) mudstones to fine sandstones of the Upper Fezouata Formation of Morocco, benthic organisms are preserved essentially *in situ* (Van Roy *et al.* 2004). Exceptionally preserved organisms from this unit include articulated specimens of sponges, probable annelids, a possible planarian, a cheloniellid arthropod, a *Tremaglaspis*-like arthropod, large bivalved arthropod carapaces, an articulated plumulitid machaeridian, a tuboid graptolite and *Clonograptus* preserving soft tissues (Van Roy *et al.* 2004).

Another site of exceptional preservation is in the basal Caradoc mudstones of the Llanfawr Quarries, Llandrindod, Powys, Wales (Botting 2004). At this site an abundant sponge collection represents the most diverse fine-sediment sponge fauna recorded from the British Palaeozoic. Graptoloids and chitinozoans are also found (Botting 2004). Some sponge specimens are preserved with organic or pyritic films representing soft tissue and most have high-fidelity preservation of spicule external moulds (Botting 2004).

The Middle Ordovician vertebrate and invertebrate fauna of the Winneshiek Lagerstätte is preserved as soft body tissues, impressions and 3-dimensional body fossils (H. Liu *et al.* 2006). The fossils were discovered from the St. Peter Sandstone in Northeast Iowa and include conodonts, which are a dominant component of the fauna, with some occurring as bedding plane assemblages (H. Liu *et al.* 2005, 2006). A variety of other fossils are preserved including jawless ostracoderm fish, early eurypterids, phyllocarids, linguloid brachiopods plus vermiform and other indeterminate fossil forms. The preservation of soft tissues and organic matter from this site indicates limited benthic oxygenation. The environment of deposition is thought to have been a shallow brackish to marine estuarine embayment (H. Liu *et al.* 2006).

The Late Ordovician Beecher's Trilobite Bed of New York State, USA is known for the exceptional preservation of trilobites with appendages and other soft tissues preserved in pyrite (Briggs *et al.* 1991*a*). The exceptional preservation was a result of the rapid burial of the carcasses in a sediment low in other metabolizable organic matter, but with a high

concentration of iron reactive towards $H_2S$. The conditions limited sulphate reduction in the enclosing sediments; there was sufficient sulphate to allow the decay of the most metabolizable parts of the organism and reactive iron to trap $H_2S$ efficiently at the decay site (Briggs *et al.* 1991 *a*).

There are two Late Ordovician (Richmomdian) shoreline biotas from Manitoba, Canada, one of which, along with other taxa, has well preserved cnidarian medusae (jellyfish) (Young *et al.* 2006). Rare macrofaunal elements at William Lake site include eurypterids, xiphosurids, ostracods, bivalves, several kinds of problematic fossil and conodonts. At the Churchill site, the biota includes dasycladacean green algae, eurypterids, xiphosurids, linguloid brachiopods, and a variety of problematica and conodonts. The Churchill macrofossils are preserved by pyrite, by dolomite, as carbonised films, or as unmineralized organic material.

A Moroccan deposit has been described that yields numerous specimens of problematic soft-bodied metazoans preserved in coarse sandstones (Samuelsson *et al.* 2001). The locality is estimated to be of Late Ordovician (Rawtheyan) age and Samuelsson *et al.* (2001) stated that the finds show that Ediacara-like coarse-clastic preservation did not completely vanish with the onset of the Phanerozoic. The deposit contains one of the oldest known paropsonemids (a problematic group), possibly some of the youngest protoyelloids (largely Early Cambrian problematica) and aglaspidids.

The Soom Shale Lagerstätte is the youngest site (Hirnantian) of soft-tissue preservation; the biota includes a mixture of organisms and problematic putative fossils like many of the other Ordovician areas of exceptional preservation. However, a greater number of taxa are currently recorded from the Soom Shale than from any other Ordovician Lagerstätten. A variety of taphonomic modes were involved in the preservation of the fossils, similar to the Manitoba Lagerstätten. However, in the Soom Shale, the replication of internal anatomy is more extensive than the preservation of external features, and many of the fossils now have a clay mineral composition (Gabbott 1998; Gabbott *et al.* 2001). The Soom Shale Lagerstätte is also unusual because of its glacially influenced cold-water setting (Aldridge *et al.* 1994).

*The end Ordovician extinction*

It is estimated that approximately 22% of all families became extinct in the Late Ordovician (Brenchley 1990), making it one of the largest episodes of mass extinction (Raup and

Sepkoski 1982) (Fig. 1.8). The occurrence of glaciation during the Late Ordovician (Hirnantian) has been related to a complex series of events that produced the end Ordovician mass extinctions (Owen and Crame 2002). There were two pulses of extinction (Sheehan 2001). The first is attributed to global cooling (Hallam and Wignall 1999), a consequence of the onset of the Ordovician glaciation which began before the Hirnantian Stage (Sheehan 2001). The glaciation resulted in a regression that occurred immediately after the extinction event (Hallam and Wignall 1999). Due to this regression, marine strata of the succeeding Hirnantian are of very limited geographical extent. The second extinction pulse closely coincides with end to the glaciation (Sheehan 2001) and transgression, and the spread of oxygen-deficient bottom waters (Hallam and Wignall 1999). It has been interpreted that the Soom Shale was deposited during the Hirnantian transgression (Sutcliffe *et al*. 2000; Young *et al*. 2004), after the melting of glaciers responsible for the deposition of the underlying Pakhuis formation; thus the Soom Shale was deposited at a time when many taxa were declining in numbers, or had become extinct.

| ABSOLUTE AGES (Ma) | SYSTEM | GLOBAL SERIES | BRITISH SERIES | GLOBAL STAGES |
|---|---|---|---|---|
| 443.7 | | | | |
| 445.6 | | | ASHGILL | HIRNANTIAN |
| | | UPPER | | KATIAN |
| 455.8 | ORDOVICIAN | | CARADOC | |
| 460.9 | | | | SANDBIAN |
| | | MIDDLE | LLANVIRN | DARRIWILIAN |
| 468.1 | | | | Third Stage |
| 471.8 | | | ARENIG | |
| | | | | FLOIAN |
| 478.6 | | LOWER | | |
| | | | TREMADOC | TREMADOCIAN |
| 488.3 | | | | |

- Soom Shale Lagerstätte, South Africa, Hirnantian
- Coarse clastic preservation Morocco, Upper Ordovician
- William Lake and Churchill Lagerstätten, Manitoba, Upper Ordovician
- Beecher's Trilobite Bed, New York State, Caradoc
- Llanfawr Quarries mudstones, Wales, Basal Caradoc
- Winneshiek Lagerstätte, Iowa, Middle Ordovician
- Fezouata Fm, Morocco, Arenig
- Arthropods from UK, Öland and Newfoundland, Tremadoc

**Figure 1.9.** The Ordovician timescale (from the International Subcommission on Ordovician Stratigraphy, ICS, IUGS, 2006; http://www.ordovician.cn) with the position of occurrences of exceptional preservation throughout the period marked.

## AIMS AND OBJECTIVES

Many fossils from the Soom Shale Lagerstätte are termed 'enigmatic' as they are difficult to identify. This is because they represent parts of organisms or because they do not belong to currently identified groups. Another reason is that the preservation style makes them hard to assign to groups easily; many of the systematic characters of fossils are external and because Soom Shale specimens preserve mostly labile, internal anatomy, comparison with other species can be difficult. These fossils form the material for this study. Some non-enigmatic organisms are also studied that have not been described before, for example, the scolecodonts.

*Overall aim of the Project*:

To enhance our understanding of the diversity of the Soom Shale ecosystem.

*Objectives*:

1. To document unpublished organisms from the Soom Shale Lagerstätte
2. To assess their biological affinities
3. To place the fossils within a taxonomic framework
4. To study the taphonomy of the fossils to give further information on the organisms, and to try to identify and understand the taphonomic pathways that have led to the preservation of the Soom Shale fossils.

## ORGANISATION OF THESIS

The following chapters present new results and interpretations. They have been prepared in a format suitable for submission as papers for specific journals, and follow the instructions to authors for that journal.

*Chapter 2 – Taphonomy and palaeoecology of a Late Ordovician caryocaridid from the Soom Shale Lagerstätte, South Africa.*

The chapter is a multi-author paper; my contribution was undertaking the taxonomic, taphonomic and palaeoecological studies and producing the manuscript. S. E. Gabbott provided assistance with the taphonomic study and along with R. J. Aldridge provided feedback on the manuscript. The chapter addresses a previously undescribed species of arthropod from the Soom Shale. The taphonomy of the specimens is investigated, the diversity and evolutionary history of the group is extended and a hypothesis for the palaeoecology of the group is outlined. The ecological range of organisms from the Soom Shale is extended. The paper was accepted for publication in the journal *Palaeogeography, Palaeoclimatology, Palaeoecology*, in April 2007 (Appendix vii).

*Chapter 3 – A Late Ordovician medusoid from the Soom Shale Lagerstätte, South Africa.*

The chapter is written as a paper for the journal *Palaeontology*. A circular structure previously unidentified in the Soom Shale fauna is described and its preservation is outlined. A hypothesis is proposed that the structure is a scyphozoan medusoid and it is compared with abiological structures and circular organisms before this hypothesis is accepted as the best available.

*Chapter 4 - Late Ordovician scolecodont apparatuses from the Soom Shale Lagerstätte, South Africa.*

The chapter is written as a paper for the *Journal of Micropalaeontology*. Two scolecodont groups are identified, increasing the diversity of the Soom Shale ecosystem. The preservation of the fossils is outlined. Implications for the evolutionary history of one of the groups are discussed. The geographical range of scolecodonts is increased. The possible palaeoecology of the group is highlighted, and their possible affinities to chitinozoans are discussed.

*Chapter 5 - An Ordovician xenusiid lobopodian from the Soom Shale Lagerstätte, South Africa.*

The chapter is written as a paper for the journal *Palaeontology*. A new soft-bodied organism is described as a xenusiid lobopodian, and its mode of preservation is outlined. The new organism is discussed in the context of the evolutionary history and palaeoecology of the lobopodians as well as the palaeoecology of the Soom Shale.

*Chapter 6 – New arthropods from the Soom Shale Lagerstätte, Late Ordovician, South Africa.*

The chapter is written as a paper for the journal *Palaeontology*. The arthropods are the most diverse phylum in the Soom Shale fauna. To this group, three new types are added and described. The preservation of the specimens is outlined and the possible modes of life of the new animals are discussed.

*Chapter 7 – The Biota of the Soom Shale: Palaeoecological and Taphonomic Syntheses, Conclusions and Future Work.*

The chapter is formatted in accordance with the instructions for authors for the journal *Palaeontology*. The components of the Soom Shale ecosystem are outlined, an assessment of the palaeoecology of the fauna is made and a synthesis of the taphonomy of the Soom Shale provided. These conclusions are based on previous studies and on evidence presented in this thesis. Overall conclusions from this thesis are drawn, and suggestions for future work are made.

<div align="right">

# Chapter 2

</div>

# Taphonomy and palaeoecology of a Late Ordovician caryocaridid arthropod from the Soom Shale Lagerstätte, South Africa

## Abstract

A new species of caryocaridid is reported from the Late Ordovician of South Africa. The fossils show a complex, multi-layered structure that may represent exceptional preservation of the original arthropod exo-, endo- and epicuticle. Alternatively, the layered structure may comprise the carapace, with a mineralized cast of the internal void and a layer of fibrous illite external to the carapace. The genesis of the fibrous illite is important as it demonstrates that not all fibrous textures associated with fossils in the Soom Shale, and perhaps other Lagerstätten, can be interpreted as mineralized muscle tissue.

*Caryocaris cedarbergensis* n. sp. extends the geographical, ecological and temporal range of the family and provides the first evidence of a zooplanktonic constituent to the Soom Shale biota. The genus most likely represents a cool-adapted mesopelagic group during the Early–Middle Ordovician, which inhabited an epipelagic cold-water shelf environment during the Late Ordovician.

## 1. Introduction

The Soom Shale Konservat Lagerstätte (site of exceptional fossil preservation) contains several taxa displaying exceptional preservation of soft parts, most notably conodonts (Aldridge and Theron, 1993; Gabbott et al., 1995), eurypterids (Braddy et al., 1995, 1999) and enigmatic fossils. Compared with the Cambrian System, the Ordovician has few known Konservat Lagerstätten and of these the Soom Shale records the greatest number of taxa and the highest fidelity preservation of decay-prone tissues, principally as clay mineral replacements. Other occurrences of exceptional preservation in the Ordovician are the Late Ordovician Beecher's Trilobite Bed of New York State, USA, known for trilobites with

appendages and other soft tissues preserved in pyrite (Briggs et al., 1991a); the basal Caradoc mudstones of the Llanfawr Quarries, Llandrindod, Powys, Wales, which preserve an abundance of graptoloids, chitinozoans and sponges in pyrite (Botting, 2004); the Middle Ordovician Winneshiek Lagerstätte from the St. Peter Sandstone in Northeast Iowa which includes conodont apparatuses and a variety of other fossils (including caryocaridids) preserved with associated soft tissue impressions (H. Liu et al., 2005, 2006); an arthropod described from the Tremadoc of England with preserved appendages (Siveter et al., 1995); and two Late Ordovician shoreline biotas from Manitoba, Canada, one of which, along with other taxa, has well preserved cnidarian medusae (jellyfish) (Young et al., 2006).

The caryocaridids have been placed within the Class Malacostraca Latreille, 1806, and the Subclass Phyllocarida Packard, 1879; though there is currently no soft-tissue preservation of the head appendages to confirm their crustacean affinities. They were originally placed in the Family Ceratiocarididae Salter, 1860, by Salter (1863), but were established in their own family, the Caryocarididae by Racheboeuf et al. (2000). The caryocaridids attained their highest diversity and numerical abundance during the Arenig and Llanvirn (Early–Middle Ordovician) (Vannier et al., 2003). Previously, the family was known to range from the Tremadoc to the Early Caradoc (Braddy et al., 2004), when it was thought that they became extinct. They form a recurrent component of graptolite-bearing black, outer-shelf shales (Vannier et al., 2003, Braddy et al., 2004).

Here we report the occurrence of caryocaridids from the Soom Shale Lagerstätte; these specimens occur approximately 10 myrs after the hitherto youngest caryocaridids from the early Caradoc of South America (Bulman, 1931; Vannier et al., 2003). The fossils are very rare, as only two specimens have been discovered in fifteen years of collecting. We also comment on the mode of preservation and palaeoecological significance of this new discovery.

*1.1. Stratigraphy and Sedimentology*

The Cedarberg Formation, of which the Soom Shale is the lower member and the Disa Siltstone the upper member, constitutes the only significant fine-grained unit within the Lower Palaeozoic arenaceous Table Mountain Group (Rust, 1981), outcrops of which are found in the Western Cape, South Africa (Fig. 2.1). The Cedarberg Formation contains the only datable fossils within the entire sequence; these have indicated a late Ashgill (Rawtheyan or Hirnantian) age (Cocks et al., 1970; Cocks and Fortey, 1986; Theron et al., 1990). Sutcliffe

et al. (2000) and Young et al. (2004) interpreted the Soom Shale as a postglacial transgressive deposit resulting from the demise of the Late Ordovician glaciers, as it directly overlies tillites of the glaciogenic Pakhuis Formation, thus representing an interval that is possibly equivalent to the *persculptus* graptolite zone of the Hirnantian.

The Soom Shale comprises laminated mud and siltstone and is 10–15 m in thickness. Soom Shale siltstones and mudstones are black when fresh, for example at Sandfontein, but weather to a pale grey colour in surface exposures at Keurbos (Gabbott, 1998). The black colour of palynomorphs and chitinozoans indicates that the sediment has undergone burial anchimetamorphism to temperatures of at least 200°C (Cramer et al., 1974; Gabbott et al., 2003). The laminae comprise alternations of silt and mud with darker layers, which may be degraded organic matter. The sediment is composed mostly of clay minerals, especially illites and mixed-layer clays, and detrital quartz. It also contains syngenetic/diagenetic pyrite and diagenetic chlorite and clay minerals (Gabbott, 1998).



**Fig. 2.1.** The location of the Soom Shale sites at Keurbos and Sandfontein, from which the caryocaridid fossils were collected (from Gabbott et al., 2003).

*1.2. Palaeogeography and Palaeoenvironment*

Previously, the basin in which Soom Shale was deposited was thought to be located at approximately 60° S (Gabbott et al., 1995; Gabbott 1998; Aldridge et al., 2001); however, several continental reconstructions for the Late Ordovician have placed the tip of South Africa at between about 30° and 45° S (Fig. 2.2) (Beuf et al., 1971; Smith, 1997; Sutcliffe et al., 2000; Cocks and Torsvik, 2002; Fortey and Cocks, 2003; Young et al., 2004). The Soom Shale is a postglacial transgressive unit (Sutcliffe et al., 2000; Young et al., 2004), with dropstones recorded from the base of the member. This indicates a cold-water setting.
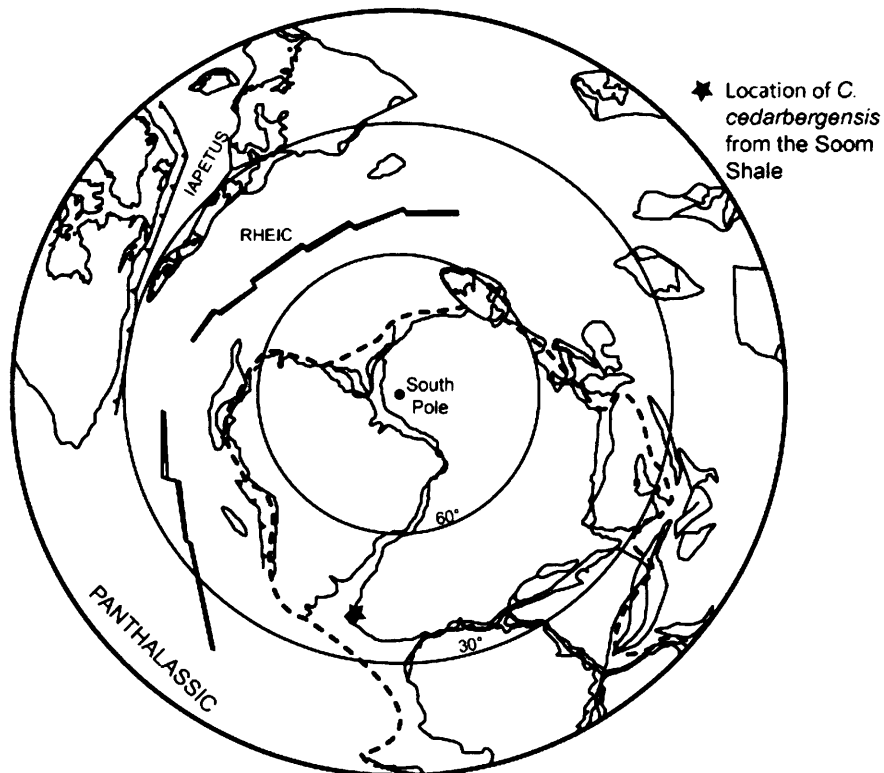


**Fig. 2.2.** A global reconstruction for the end of the Ordovician/beginning of the Silurian (440 Ma), with the location of *C. cedarbergensis* from the Soom Shale Lagerstätte (reconstruction from Fortey and Cocks, 2003 modified from Cocks and Torsvik, 2002).

The depositional setting is thought to have been in a quiet water basin close to a retreating ice front (Theron and Thamm, 1990); water depth is unknown but was unlikely to have been great as the basin was in an intracratonic setting and the Soom Shale is bounded by subaerial tillites below and shallow marine siltstones above (Gabbott, 1999). On the basis of the lack of sedimentary structures, Gabbott (1999) suggested a water depth of at least 100 m,

although she cautioned that it could be much shallower if microbial mats bound the sediment or if the sea surface was ice covered. This would represent an inner shelf setting. However, the water depth in the Soom Shale is imprecisely defined and not supported by a detailed sedimentological analysis. The laminated fine-grained nature of the Soom Shale might represent the outwashing of material during climatic amelioration and ice-sheet retreat (Theron and Thamm, 1990). Dominantly quiet water conditions in the Soom Shale lithology are indicated by a lack of flow-induced sedimentary structures and the taphonomy of the fossils. The Soom Shale sediment was largely anoxic; geochemical analyses indicate that euxinic bottom waters prevailed at times (Gabbott, 1998). In some areas metamorphism has transformed the shale and siltstone into a sheared slate, destroying primary internal features (Aldridge et al., 1994).

### 1.3. Palaeontology

To date, taxa found from the Soom Shale include conodonts (Theron et al., 1990; Aldridge and Theron, 1993; Gabbott et al., 1995), myodocopid ostracods (Gabbott et al., 2003), eurypterids (Braddy et al., 1995) and naraoiids (Fortey and Theron, 1994). Also present are chitinozoans (Cramer et al., 1974; Gabbott et al., 1998), marine phytoplankton (Gray et al., 1986), brachiopods (Aldridge et al., 1994), orthoconic cephalopods (Gabbott, 1999) and trilobites (Moore and Marchant, 1981), which are organisms indicative of a marine setting. The soft tissues of many taxa are preserved through replacement by illite, sometimes with alunite group minerals, frequently to a high degree of fidelity (Gabbott, 1998; Gabbott et al., 2001). Most notable is the preservation of conodont myomeres and eye muscles (Gabbott et al., 1995), and muscle tissue and gill tracts in eurypterid specimens (Braddy et al., 1995, 1999).

### 2. Materials and Methods

The repository of the two specimens used in this study is the Council of Geosciences of South Africa, Bellville. Specimen C1971 is from Keurbos Quarry (18°58'E, 32°16'S) near Clanwilliam, and specimen C1587 is from Sandfontein (19°14'E, 32°40'S), 52 km from Clanwilliam, South Africa (Fig. 2.1). The fossils were studied using an optical microscope, drawn with the aid of a camera lucida, and photographed using a digital camera (Nikon E995). Photography and elemental analysis was carried out using a Hitachi S-3600N

Scanning Electron Microscope with an Oxford Instrument Energy Dispersive X-ray facility (SEM EDX). For SEM EDX analysis uncoated material was placed in partial vacuum at 15 Kv. Elemental mapping was used to show the relative abundance of elements in different areas of the fossils and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) of the fossil to be determined, from different parts of the two specimens and from the sediment.

## 3. Systematic Palaeontology

Phylum ARTHROPODA Siebold and Stannius, 1845.

Family CARYOCARIDIDAE Racheboeuf, Vannier and Ortega, 2000.

Genus *Caryocaris* Salter, 1863

*Type species*: *Caryocaris wrightii* Salter, 1863 from the Skiddaw Group (Arenig).

*Diagnosis*: 'Elongated carapace with both dorsal and ventral convex margins (when seen in lateral view). No rostral plate. Pointed anterior end expressed as a prominent horn-like rostrum. Short anterodorsal spine. Posterior margin straight to oblique, typically fringed with a row of minute secondary spinules. Indented posteroventral margin (one to several spinules). Narrow ridge and/or shallow furrow running parallel to ventral margin. Very thin, flimsy, weakly or uncalcified carapace.' (after Racheboeuf et al., 2000, pp. 322–323).

Species *Caryocaris cedarbergensis* n. sp.

*Holotype:* C1971, 1 complete carapace C1971b from Keurbos, with broken counterpart C1971a.

*Type locality*: Keurbos Quarry, near Clanwilliam, South Africa (18°58'E, 32°16'S).

*Type horizon*: Soom Shale Member, Cedarberg Formation, Table Mountain Group, Late Ordovician (Hirnantian).

*Derivation of name*: After the Cedarberg Mountains, South Africa.

*Other Material*: One complete carapace C1587a from Sandfontein (19°14'E, 32°40'S), with half counterpart C1587b. Neither of the specimens has preserved abdominal segments, telson or furcal rami.

*Diagnosis*: *Caryocaris* with almost vertical anterior and posterior margins, a short, pronounced horn-like rostrum anteriorly, and a smooth posterior margin, without spines, spinules or combs.

*Description*: Carapace length of holotype 17.6 mm (16 mm C1587), elongate. Maximum height of valve 6.1 mm (5.5 mm C1587), greatest height of valve just anterior to mid-length. Height of posterior of valve less than that of anterior. Dorsal margin of carapace moderately convex. A pronounced horn-like rostrum, 2 mm long on both specimens, is directed anteriorly. Anterior margin below the rostrum angled at almost 90° to dorsal and ventral margins. Ventral margin moderately convex, similar to dorsal margin. Along the ventral border is a clear and pronounced doublure, which has a uniform width of 0.5 mm. Posterior margin of carapace strongly angled at almost 90° to dorsal and ventral margins, with no spinules, fringe dorsal spines or ventral spines. Posterodorsal margin terminates at a point (Fig. 2.3).
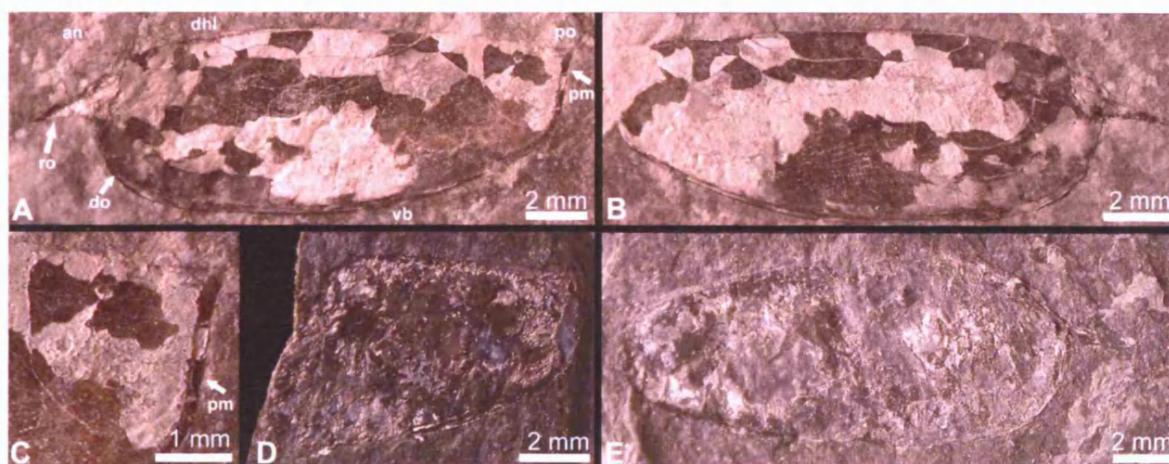


**Fig. 2.3.** The two specimens of *Caryocaris cedarbergensis* n. sp. **A.** and **B.** part and counterpart, respectively, of C1971, **C.** enlargement of smooth posterior margin of C1971. **D.** and **E.** counterpart and part of C1587. Principal morphological features of the composite moulds are shown on A and C. **an** = anterior, **po** = posterior, **dhl** = dorsal hinge line, **pm** = posterior margin, **ro** = rostrum, **do** = doublure, **vb** = ventral border. Scale bars = 2 mm, except in C = 1 mm.

*Remarks*: The overall shape of the carapace and the presence of the long process identified as the anterodorsal horn-like rostrum place this specimen within the genus *Caryocaris*. Previously described caryocaridids range in length from approximately 8.6–25.5 mm (Fig.

2.4); at 17. 6 mm, *C. cedarbergensis* falls within this range. *Caryocaris cedarbergensis* differs from the type species *Caryocaris wrightii* Salter, 1863, *C. raymondi* Ruedemann, 1934 and *C. acuta* Bulman, 1931 by having a prominent rostrum. It also differs from *C. wrightii* and *C. raymondi* by possessing a smooth posterior margin without spines, spinules, bristles, teeth or a fine comb (Fig. 2.4). Although *C. acuta* does have a smooth posterior margin, it exhibits dorsal and ventral margins that are nearly parallel, unlike the curved margins of the new species.



**Fig. 2.4.** Carapace outlines of members of the genus *Caryocaris*. **A.** and **B**: *C. wrightii* Salter, 1863 and *C. subula* Chlupáč, 1970 from the Llanvirn of Bohemia (after Chlupáč, 1970). **C**: *C. delicatus* Racheboeuf et al., 2000 from the Llanvirn of Argentina (from Racheboeuf et al., 2000). **D**: *C. stewarti* Jell, 1980 from the middle Tremadoc of Australia (after Jell, 1980). **E**: *C. zhejiangensis* Shen, 1986 from the Lower Ordovician of SE China (from Shen, 1986). **F**: *C.* cf. *monodon* (Gurley, 1896) from the Middle Ordovician of Norway (from Størmer, 1937). **G**: *C. curvilata* Gurley, 1896 from the Arenig/Llanvirn of Alaska (from Churkin, 1966). **H**: *C. acuta* Bulman, 1931 from the Caradoc of Peru (from Bulman, 1931). **I**: *C. raymondi* Ruedemann, 1934 from the Middle Ordovician (Caradoc) of North America (from Ruedemann, 1934). **J**: *C. scanicus* Moberg and Segerberg, 1906 from the Tremadoc of Scania (from Moberg and Segerberg, 1906). **K**: *Caryocaris cedarbergensis* n. sp. from the Hirnantian of South Africa. Scale bars = 5 mm.

The remaining described species of the genus *Caryocaris* all have prominent rostra, also described as anterodorsal spines or carapace horns (Fig. 2.4). *C. scanicus* Moberg and Segerberg, 1906 and *C. zhejiangensis* Shen, 1986 have rostra that are longer in relation to the size of the carapace than that of *C. cedarbergensis*. *C. scanicus* also has a posterior dorsal margin that ends in an elongate point (Moberg and Segerberg, 1906) and *C. zhejiangensis* has a spinose posterior margin (Fig. 2.4). *C. stewarti* Jell, 1980, *C. monodon* Gurley, 1896, *C. delicatus* Racheboeuf et al., 2000, and *C. subula* Chlupáč, 1970, all differ from *C. cedarbergensis* by exhibiting spines, spinules, fringes and/or combs on the posterior margin. *C. subula* and *C. delicatus* also both possess oblique posterior margins (Fig. 2.4). *C. curvilata* Gurley, 1896 exhibits a similar carapace morphology to *C. cedarbergensis*, but differs by having a carapace horn slightly closer to the dorsal margin, and by having a spinose posterior margin (Fig. 2.4).

## 4. Taphonomy

Both of the specimens of *Caryocaris cedarbergensis* show a layered structure, each layer defined by a distinct mineralogical composition (Fig. 2.5). Six preserved layers on C1587 are interpreted as representing two valves each composed of three layers. Four preserved layers on C1971 may represent two valves each composed of two layers. In specimen C1587 each valve exhibits illite as the outside layer, carbon as the middle layer and alunite as the inner layer (Fig. 2.5A); and in C1971 each valve exhibits illite as the outside layer and alunite as the inner layer (Fig. 2.5B).

Enrichment in the elements Si, Al and K (Figs. 2.6C–E, K; 2.7B–D, L; 2.8C–E, J) is consistent with the presence of the clay mineral illite ($KAl_3Si_3O_{10}(OH)_2$) identified from the Soom Shale by Gabbott (1998). This illite has a fibrous habit distinct from the detrital illite in the host sediment. Enrichment in P, S, K, Al and Ca relative to other areas of the carapace and the matrix (Figs. 2.6F, G, I; 2.7E–H, J; 2.8F–I) is accounted for by the presence of minerals in the alunite solid solution series, e.g. crandallite ($CaAl_3(PO_4)_2(OH)_5.H_2O$) or alunite ($KAl_3(SO_4)_2(OH)_6$) also identified from the Soom Shale by Gabbott (1998). The carapace of C1587 also has a very distinct dark layer, between the illite and alunite layers, enriched in carbon relative to the rest of the carapace and the matrix (Figs. 2.6H, J; 2.7I, K), but also showing a clay mineral signature (Figs. 2.6J; 2.7K). This carbon-rich layer is sheet-like and in some areas it shows brittle cracking features (Fig. 2.6B layer J, Fig. 2.7A layer K).

**Fig. 2.5.** Schematic diagram to show the composition and structure of the *Caryocaris* fossils from the Soom Shale. **A**. diagrammatic representation explaining the way in which specimen C1587 has split revealing different parts of the layered structure in the part and counterpart of the fossil. Due to the transgressive nature of the split through the fossil, in places on both the part and counterpart all six layers may be seen, whereas at others only the underlying or overlying sediment is seen. **B**. diagrammatic representation explaining the way in which specimen C1971 has split revealing the layered structure in the part and counterpart of the fossil. The split is more planar, and on both part and counterpart the illite layer lies underneath the alunite layer. Therefore, the alunite layer must have originally lain on the inside and the illite layer on the outside of the fossil.

Vannier et al. (2003) suggested that the carapaces of the caryocaridids consist of three mineralized layers that may represent the typical cuticular structure of crustaceans (the epi-, exo- and endocuticle). The innermost endocuticle is the most labile layer (least decay resistant) because the fibrous chitin-protein matrix, from which it is made, has a much coarser structure (Raabe et al., 2005). In life, the exocuticle (middle layer) is protein rich and rigid due to the very fine woven structure of the fibrous chitin-protein matrix, which gives it a

greater hardness and stiffness (Raabe et al., 2005). In the Crustacea the exocuticle is stiffened further by calcium carbonate (Addadi et al., 2003). The thin external waxy layer of the cuticle, the epicuticle, is intermediate in hardness between the exocuticle and endocuticle (Raabe et al., 2005).
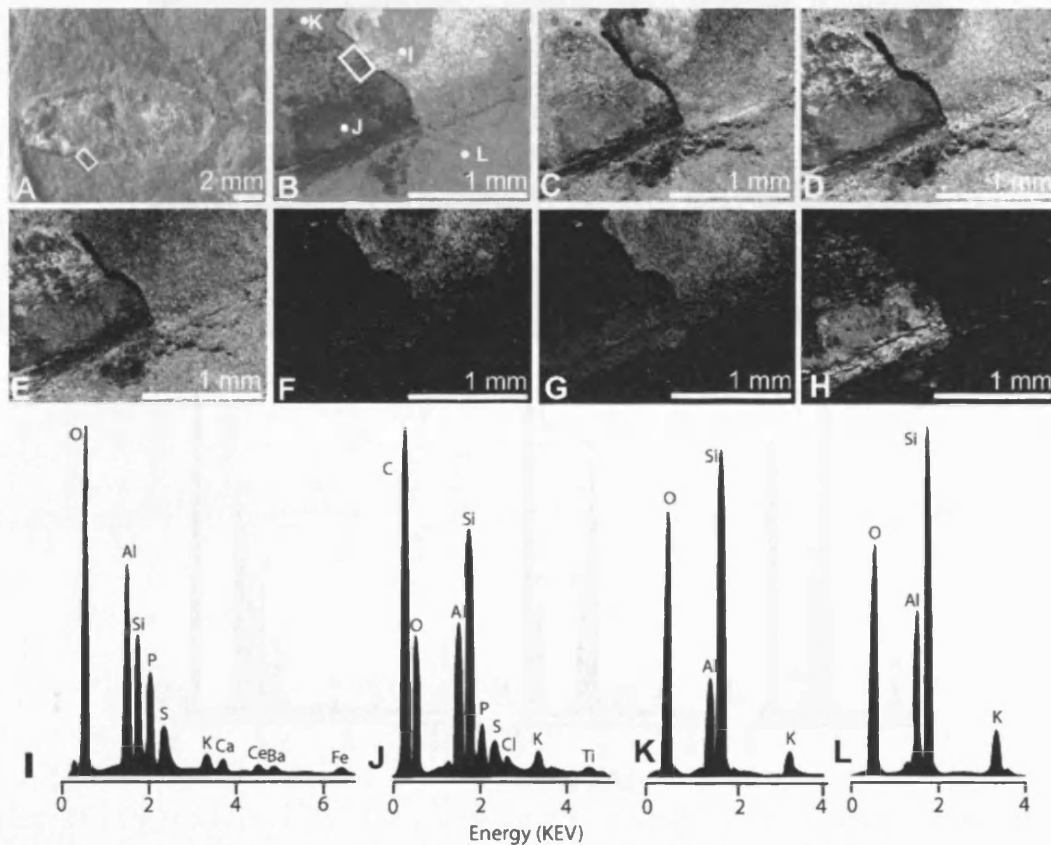


Fig. 2.6. A. C1587a, with area of SEM analysis (shown in B–H) indicated by the box. B. back scattered electron image of boxed area shown in A. The square box on B indicates the location for analytical results shown in Fig. 2.7, and the spots labelled I–L denote the positions of the EDX traces I–L. C.–H. element maps where light areas indicate a relative high abundance of each element. C. silica. D. aluminium. E. potassium. F. phosphorus. G. sulphur. H. carbon. An analysis for calcium showed no areas of enhanced concentration. I. EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite, $CaAl_3$ $(PO_4)_2(OH)_5.H_2O$; elemental peaks of S, Ce, Ba and Fe are indicative of other alunite-group minerals. J. Peaks indicate the presence of carbon and clay mineral/alunite mineral mixture. K. Peaks in Al, Si and K indicate the presence of illite. L. EDX trace indicates an illite signature for the host sediment.

**Fig. 2.7.** SEM analysis of C1587a, enlargement of area indicated by box on Fig. 2.6B. **A.** back scattered electron image showing patch of cracked carbon (K) with fibrous illite in between (L). The layer with an alunite composition (J) overlies this. Spots labelled J–L denote the positions of the EDX traces J–L. **B.–I.** element maps where light areas indicate a relative high abundance of each element. **B.** silica. **C.** aluminium. **D.** potassium. **E.** phosphorus. **F.** sulphur. **G.** calcium. **H.** iron. **I.** carbon. **J.** EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite $CaAl_3$ $(PO_4)$ $_2(OH)_5.H_2O$; elemental peaks of S and Ce are indicative of other alunite-group minerals. **K.** peaks indicate the presence of carbon and clay mineral/alunite mineral mixture. **L.** peaks in Al, Si and K indicate the presence of illite.

**Fig. 2.8. A.** C1971b, with area of SEM analysis indicated by white box. **B.** back scattered electron image of boxed area, letters denote the position of EDX traces I–K, dhl = dorsal hinge line of carapace. **C.–H.** element maps and **I.–K.** EDX traces for the three layers of carapace. **C.** silica. **D.** aluminium. **E.** potassium. **F.** phosphorus. **G.** sulphur. **H.** calcium. An analysis for carbon showed no areas of enhanced concentration. **I.** EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite $CaAl_3$ $(PO_4)$ $_2(OH)_5.H_2O$; elemental peak of S is indicative of other alunite-group minerals. **J.** Peaks in Al, Si and K indicate the presence of illite. **K.** EDX trace indicates an illite signature for the host sediment.
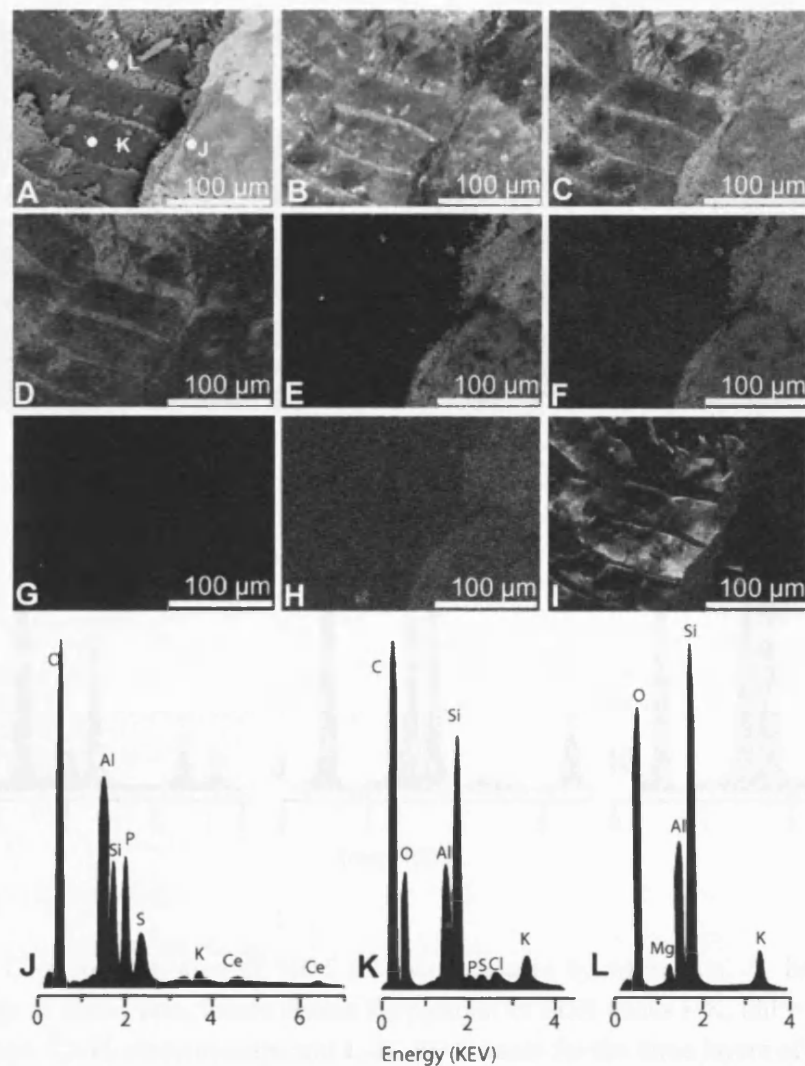
The current taphonomic model for Soom Shale fossils (Gabbott, 1998; Gabbott et al., 2001) indicates that the most labile tissues are replaced by clay minerals such as illite, and more recalcitrant tissues are preserved as carbon. It is currently unknown whether alunite replaces tissues with a particular histology or decay profile. The illite layer occurs on the exterior of the valves and so cannot represent the labile inner endocuticle. The illite layer most probably represents the outer epicuticle, intermediate in hardness, the carbon the recalcitrant exocuticle and the alunite the labile inner endocuticle. Another alternative is that the illite could be an overgrowth on the outside of the fossil, rather than replacing or

replicating a layer. In this scenario carbon represents the fossil carapace, and alunite has infilled the internal void. However, this is difficult to test in the case of C1971, where there is no preserved carbon layer. It is therefore necessary to consider the origin of the illite layer.



**Fig. 2.9.** Fibrous illite on specimen C1971. **A.** the layer on the right hand side (labelled 1) is composed of minerals in the alunite solid solution series; the layer on the left hand side (labelled 2) is composed of aligned fibrous illite. **B.** shows fibrous illite, which can sometimes occur in tufts.

The illite layer shows a fibrous habit on both specimens and on each the shiny white fibrous illite has the same orientation over the majority of the fossil (Fig. 2.9A), although in places it occurs in tufts (Fig. 2.9B). Some fibres have been measured at approximately 2 μm in diameter and 50 μm in length (n=20). They do not appear to show any ultrastructure such as banding. There are several possibilities to account for the fibrous habit of the illite; we consider these scenarios below.

1. Illite or a dioctahedral precursor (*see discussion in* Gabbott et al., 2001) could have replicated fibrous muscle tissue. This has been described from eurypterids (Braddy et al., 1995), and a conodont (Gabbott et al., 1995) from the Soom Shale. However, it is unlikely for the *Caryocaris* specimens because the fibres are not confined to any particular morphological features or areas of the carapace where muscle blocks would be expected. Additionally, there is no evidence remaining of any internal structures such as appendages to which the muscle fibres would be attached, the fibres do not show the fibril bundles or banding that characterize muscle tissue in the conodont specimen (Gabbott et al., 1995), and the preserved fibres occur on the exterior of the valve.

2. The fibrous illite may have grown in pore spaces surrounding the fossil during diagenesis of the sediment, such as in examples of 'authigenic' mineral growth in sandstone reservoirs (Bjørlykke, 1998). 'Authigenic' illite in these cases refer to diagenetic reactions

that usually occur at over 100°C (Wilkinson and Haszeldine, 2002). Therefore, to avoid confusion we propose that the growth of 'authigenic' clay minerals in voids, such as those that occur in reservoir rocks should be termed diagenetic growth. Only growth of clay minerals on the seafloor, or immediately after burial, when ambient seawater temperatures prevail, should be termed authigenic growth. There is a strong substrate control upon fibrous diagenetic illite formation, which occurs almost exclusively upon substrates that have a similar molecular surface configuration to illite so that the interfacial energy between the growing nucleus and the substrate is minimized (Wilkinson and Haszeldine, 2002). Nucleation control and rapid growth are the causes of the fibrous morphology of the crystals (Mullin, 1961; Wilkinson and Haszeldine, 2002). The Soom Shale sediment contains detrital illite (Gabbott et al., 2001), which may have provided some of the necessary chemical conditions for the nucleation of fibrous diagenetic illite. Fibrous or lath habits may have become further aligned upon compaction of the rock. Diagenetic illite with a fibrous habit precipitating on, or replacing a layer of, the *Caryocaris* carapaces cannot be discounted.

3. The fibrous illite may have grown authigenically on the sea floor or immediately after burial so that illite (or a dioctahedral precursor) either replaced a layer or layers of the carapace, or formed on a template of the organic material on the surface of the fossil. The fibrous morphology could be a result of the rapid growth necessary for authigenic illite to do this before the organic material decayed completely. Authigenic illite growth is uncommon below around 100°C (Wilkinson and Haszeldine, 2002) but there are reports of precipitation at temperatures as low as 40–50°C (Harper et al., 1995; Ziegler and Longstaffe, 2000), and there is considerable debate as to whether illite can form at temperatures of less than 40°C (Šrodoń and Eberl, 1984; Šrodoń, 1999; Wilson, 1999; Gilg et al., 2003). Gabbott et al. (2001) recognized that kinetic factors at low temperatures could prohibit direct illite growth, and suggested the initial precipitation of a dioctahedral phase, which was later illitized. Gabbott et al. (2001) also suggested that partial decay of organisms produced high $K^+:H^+$ activity ratios surrounding the Soom Shale fossils. This coupled with bacterial mediation, recently demonstrated by Tuck et al. (2006) to induce rapid clay formation, could have overcome kinetic factors and lowered the temperature necessary for authigenic illite formation.

4. The fibrous illite on the *Caryocaris* carapaces may have been a result of metamorphism. The Soom Shale sediment probably underwent burial anchimetamorphism temperatures of at least 200°C (Cramer et al., 1974; Gabbott et al., 2003), the upper end of the scale for diagenetic illite formation at around 100–200°C (Bjørlykke, 1998; Wilkinson and

Haszeldine 2002) and the lower end of the metamorphically formed illite zone at around 200–350°C (Sherlock et al., 2003). Therefore, non-fibrous illite that formed authigenically on the fossils could have been rendered fibrous during metamorphism, or fibrous illite could have formed directly during burial metamorphism. Fibrous phyllosilicates can form in association with fossils in strain shadows, where the fossils have acted as rigid bodies. However, these surround and do not cover the fossil (Sherlock et al., 2003).

It has been indicated that clay minerals can form on organic fossils through metamorphism independent of strain (Page et al., 2006). This occurs as a consequence of temperature dependent phyllosilicate-organic interactions, with the expulsion of volatiles in maturation and/or graphitisation leading to the precipitation of white mica on the most labile matter present. Clay minerals can become aligned if strain has subsequently developed (Page et al., 2006). Therefore, white mica is always associated with the most organic carbon-rich matter present (Page et al., 2006). This would explain the fibrous illite and carbon layers in C1587 but not in C1971 where there is no evidence of carbon, although there is a large proportion of fibrous illite. A higher degree of weathering could have led to the removal of carbon in this case, leaving just fibrous metamorphic phyllosilicate. However, there are carbon films known from other fossils from this locality, such as carbonized conodont eye capsules and many features of an undescribed naked agnathan, suggesting that carbon can survive the weathering.

Whilst replacement of muscle fibres by illite can be refuted, the growth of fibrous illite as an authigenic, diagenetic or metamorphic mineral cannot, as the temperatures at which illite forms are all possible in the history of the Soom Shale. In any event, it is unlikely that the fibrous habit of the illite reflects original tissue histology in these specimens. This serves as a cautionary note to palaeontologists trying to interpret soft tissues in the fossil record, particularly from Lagerstätten, and suggests that there is a need to re-assess other occurrences of fibrous illite in Soom Shale specimens, especially in the conodont myomeres and the conodont eyes.

## 5. Palaeoecology

Caryocaridids have the morphological characteristics (carapace design and ultrastructure, abdominal morphology) of midwater active swimmers that are also recognized in Recent planktonic crustaceans (Vannier et al., 2003). Other members of the Soom Shale biota described to date are dominantly nektonic and nektobenthic organisms, such as

conodonts, naked agnathans, orthoconic cephalopods, eurypterids, naraoiids and trilobites (Aldridge et al., 2001). Myodocopid ostracods have been interpreted as nektobenthic based on their morphology and association with cephalopod carcasses (Gabbott et al., 2003). Phytoplankton has also been recognized (Gabbott et al., 2003). These new specimens of *Caryocaris* provide the first record of a zooplanktonic life habit in the Soom Shale.

All occurrences of *Caryocaris*, other than those in the Soom Shale, are associated with graptolites, indicating that caryocaridids were a cosmopolitan constituent of the Ordovician plankton. To date, no graptolites have been found from the Soom Shale Lagerstätte; although the presence of stenohaline organisms such as conodonts and cephalopods indicates that open marine conditions prevailed for much of the time (Theron et al., 1990). The absence of graptolites may reflect non-preservation, although this is unlikely given the recalcitrance of graptolite periderm (Crowther, 1981). The nadir of graptolite diversity was in the Late Ordovician *extraordinarius* and *persculptus* zones, when the total world graptolite fauna consisted of only a few genera (Brenchley, 1990), and there was a low abundance of graptolites in high latitude environments (Lüning et al., 2000; Zalasiewicz, 2001). It is possible that graptolites were not present because there were none remaining at the time that were adapted to the palaeoenvironmental conditions of the Soom Shale. The presence of *Caryocaris* without graptolites in the Soom Shale might be an indication that *Caryocaris* could tolerate a wider range of palaeoenvironments than the graptolites.

Caryocaridids were cosmopolitan, and have been found previously from the major palaeo-plates of Gondwana, Laurentia, Avalonia, Perunica, Baltica and South China within a broad transequatorial latitudinal distribution (75° S–20° N) from the Tremadoc to Early Caradoc (Vannier et al., 2003) (Fig. 2.10). Specimens from the margins of Gondwana have been recorded from Australia (from the Tremadoc and Arenig) and South America, including the oldest (from the Tremadoc) and what were hitherto thought to be the youngest occurrences (from the early Caradoc) (Vannier et al., 2003). The Soom Shale specimens constitute the first record of Caryocarididae from the South African margin of Gondwana (Fig. 2.2) as well as the youngest occurrence yet recorded. The Soom Shale was deposited in the Hirnantian (446–444 Ma), and thus the new species extends the range of this family by at least ten million years. The two specimens also provide the only evidence of *Caryocaris* during an icehouse environment, in a possible inner shelf setting, in a Lagerstätte thought to contain an unusual cold-water community (Aldridge et al., 2001). The lack of recorded caryocaridids in the Silurian suggests that they disappeared towards the end of the Ordovician extinction event.

Vannier et al. (2003) stated that the exact bathymetrical range of caryocaridids within the water column cannot be inferred from fossil evidence. Here we present the hypothesis that the genus *Caryocaris* most likely represents a cool-adapted, stenothermic, mesopelagic group during the Early–Middle Ordovician, and inhabited an epipelagic cold-water shelf environment during the Late Ordovician. The evidence for the Early–Middle Ordovician caryocaridids being mesopelagic stenothermic organisms is the wide distribution of the caryocaridids at that time. Present day cool-adapted stenothermic groups are known to have very wide distributions, from shallow depths in the cold waters of the Arctic and Antarctic, to deep waters across the globe including equatorial regions, where the waters are cold due to thermal stratification (Lalli and Parsons, 1995).

There is geological and recent evidence that some lineages, which dominantly occur in open ocean mesopelagic habitats, include more primitive or more derived species than those found in epipelagic settings on the continental shelf. These modes of derivation are known as polar submergence or emergence and examples of both are found in different isopod species at the present day (Brandt, 1992). Stratigraphic parsimony and the cold-water shelf setting of the Soom Shale fit with emergence in cold water being responsible for the occurrence of *Caryocaris* in the Soom Shale. The restricted presence of *C. cedarbergensis* in the Soom Shale indicates that the genus inhabited a cold-water inner shelf setting in the Hirnantian, and thus a change to an epipelagic habitat had occurred.

This hypothesis could be disputed if transport of the carapaces had occurred. The two specimens consist only of carapaces with no tail-pieces, suggesting that transport has disrupted the skeleton. However, there is no evidence to suggest that any significant lateral transport of other Soom Shale specimens took place before they reached the sea floor, as fossils such as conodont assemblages remain fully articulated, fossils remain randomly aligned, epibenthic brachiopods remain attached to orthocones and soft tissues, which would have decayed during prolonged floating, are preserved in several organisms (Gabbott, 1998). Therefore, assuming similar hydrodynamic properties, significant transport may be discounted.
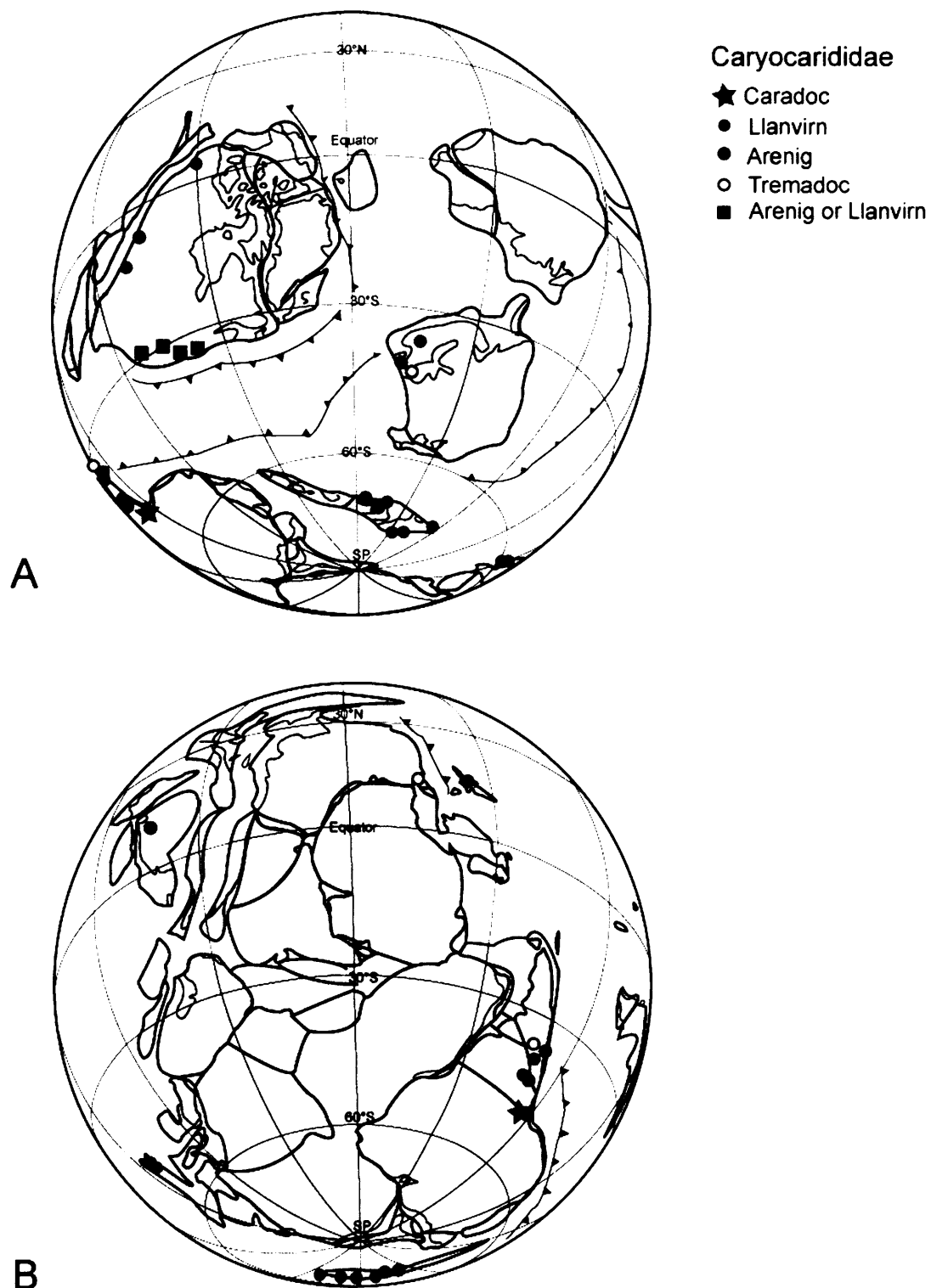
**Fig. 2.10.** Caryocaridid occurrence plotted on global maps for the Early Ordovician (Arenig; ca. 480 Ma), centred on the North Iapetus Ocean (A) and on the Gondwanan supercontinent (B) (Modified from Vannier et al., 2003. Continental distribution as given by Cocks, 2001; modified from C. R. Scotese PaleoGIS for Arcview package).

The hypothesis could also be refuted if there were evidence for the genus being epipelagic throughout the Ordovician. In this scenario, the broad distribution of *Caryocaris* during the greenhouse climate of the Early–Middle Ordovician and the presence of the genus in the Late Ordovician in an icehouse climate would indicate that it was a eurythermic organism. However, in the Hirnantian the genus is currently only known from a cold-water setting; if it could tolerate a wide range of temperatures other Late Ordovician occurrences would be expected. Other Late Ordovician occurrences would also be expected if the genus followed cold-water bodies globally throughout its history, in the mesopelagic and epipelagic realm. Any discovery of Hirnantian caryocaridids in warm water and/or open ocean environments would necessitate reconsideration of our hypothesis, as would any evidence that the Soom Shale environment itself was warm-water rather than cold-water or that it represents a deeper water setting.

## 6. Conclusions

1) Caryocaridids from the Soom Shale either show the typical structure of crustacean cuticle, consisting of three layers, the epi-, exo- and endocuticle, or preserve the carapace with a filled internal void and an outer layer of fibrous illite that could be authigenic, diagenetic or a metamorphic overgrowth.

2) Not all material of a fibrous nature within fossils from the Soom Shale Konservat Lagerstätte is muscle tissue.

3) The caryocaridids range from the Tremadoc to the termination of the Ordovician.

4) The ecological diversity of the unusual cold-water community of the Soom Shale has been extended to include a new zooplanktonic organism, the first known from this Lagerstätte.

5) It is hypothesized that *Caryocaris* is a cool-adapted stenothermic genus that inhabited the mesopelagic realm during the Early–Middle Ordovician greenhouse phase, and that *C. cedarbergensis* is an epipelagic representative present in cold near-surface water during an icehouse phase.

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**Chapter 3**

</div>

# A LATE ORDOVICIAN MEDUSOID FROM THE SOOM SHALE LAGERSTÄTTE, SOUTH AFRICA

**Abstract:** A round structure, preserved by clay minerals, is described from the Late Ordovician Soom Shale Lagerstätte. It is hypothesised that the structure represents a scyphozoan medusoid. To test this hypothesis inorganic modes of formation that have previously been mistaken for jellyfish remains, such as fluid escape and nodule growth, are considered and ultimately refuted. Biological modes of origin, such as trace fossils and taxonomically enigmatic organisms, are also discounted due to morphological differences. The specimen exhibits many features that can be related to those observed in modern scyphozoans and thus the specimen is accepted as a fossil scyphozoan. The discovery of a soft-bodied pelagic organism confirms that the Soom Shale provides a rare window into Late Ordovician marine life, in what was probably a cold-water Gondwana setting and demonstrates that organisms with an extremely low preservation potential are represented in this Konservat Lagerstätte. The medusoid and a recently described caryocaridid represent the only known zooplankton in the Soom Shale community, which is dominated by benthic and nektobenthic organisms.

THE Soom Shale is a Late Ordovician deposit famous for exceptionally preserved fossils (e.g. Aldridge and Theron 1993; Gabbott *et al.* 1995; Braddy *et al.* 1995, 1999). The Soom Shale community consists of invertebrates, early vertebrates and algae. Of particular interest are a number of arthropod taxa (Moore and Marchant 1981; Fortey and Theron 1994; Braddy *et al.* 1995, 1999; Gabbott *et al.* 2003; Whittle *et al.* 2007), conodonts (Theron *et al.* 1990; Aldridge and Theron 1993; Gabbott *et al.* 1995), agnathans (Aldridge *et al.* 2001), brachiopods (Aldridge *et al.* 1994), orthoconic cephalopods (Gabbott 1999) and enigmatica (Aldridge *et al.* 2001). Many of the fossils exhibit soft part preservation, which can include muscle tissue (Gabbott *et al.* 1995). It is thought that authigenic replication of the fossils through replacement by clays with associated alunite group minerals has led to this preservation, sometimes with a high degree of fidelity (Gabbott 1998; Gabbott *et al.* 2001). This

investigation focuses on a single circular specimen preserved with some relief from the Soom Shale. After comparison with many circular pseudofossils and with other organisms the fossil is interpreted to be a scyphozoan medusoid.

GEOLOGICAL SETTING

The Soom Shale, a horizon approximately 10–15 m thick situated in the Cedarberg Mountains, South Africa was deposited under marine conditions in a dominantly quiet water environment, where bottom waters may have been quite cool (Gabbott 1998). The laminated fine-grained lithology shows very little evidence of current activity or bioturbation (Gabbott *et al.* 2003), possibly related to the largely anoxic environment of deposition, where euxinic bottom waters prevailed at times (Gabbott 1998; Gabbott *et al.* 2003). A water depth of at least 100 m has been suggested, although it could be much shallower if microbial mats bound the sediment or if the sea surface was ice covered (Gabbott 1999). The palaeogeographical setting is thought to be a quiet water basin close to a retreating ice front, in an intracratonic setting. The laminated fine-grained nature of the Soom Shale is thought to represent the outwashing of material during climatic amelioration and ice-sheet retreat (Theron and Thamm 1990).

MATERIALS AND METHODS

The specimen (C1376) consists of a part and counterpart, and was collected from the Soom Shale Member at Kromrivier (19°11'E, 32° 32'S), situated in the Cedarberg Mountains, near to the town of Citrusdal, South Africa; the repository is in the collections of the Council of Geosciences of South Africa, Belville. The specimen was studied using an optical microscope, drawn with the aid of a camera lucida, and photographed using a digital camera (Cannon EOS 5D), after being whitened with ammonium chloride. A Hitachi S-3600N Scanning Electron Microscope with an Oxford Instrument Energy Dispersive X-ray facility (SEM EDX) was used to photograph and analyse the specimen, with the uncoated specimen placed in partial vacuum at 15 Kv. Elemental mapping was used to show the relative abundance of chemical elements in different areas of the specimen and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) to be determined, from different areas on the specimen and from the sediment.

RESULTS

*Description.* The specimen shows positive relief on the part and negative relief on the counterpart. The overall shape of C1376 is ovoid, with a short diameter of 13.54 mm and a long diameter of 16.15 mm (Fig. 3.1A, B). The specimen has a distinct central portion, which exhibits a greater relief than the rest of the structure and accounts for forty to fifty percent of the diameter of the structure (Fig. 3.1A, B). In this area there are four large raised domes and these show the maximum relief in the disc at approximately 1–2 mm in height. Extending from the margin of the central portion to the outer margin of the specimen is a set of fine radiating linear structures, which occur all round the disc (Fig. 3.1A, C). The presence of a concentric ring close to the edge of the fossil is indicated in two places. There is a distinct outer margin, which is entire (Fig. 3.1A, B). At least one other subcircular structure has been found in the Soom Shale; this may not be biological in origin as it is completely flattened and shows no clear internal features (see Appendix ii).
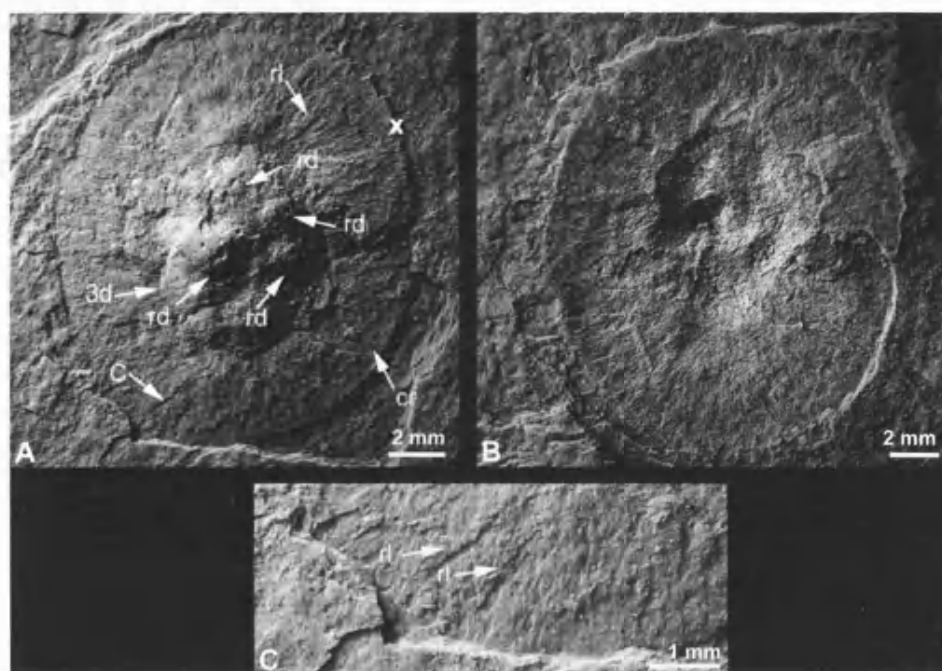


**Figure 3.1.** The specimen C1376. **A.** and **B.** Part and counterpart, respectively. Labels **3d** = the margin of the elevated central portion of the structure; **rd** = raised domes, seen at the centre of the structure; **rl** = radiating lines; **cr** = possible concentric ring, seen towards the margin of the structure in some areas; **C** = location of enlargement shown in C. **X** = location of SEM photographs in Fig. 3.3. **C.** Labels **rl** highlight some of the radiating lines.

*Preservation.* The specimen exhibits a similar clay mineral composition to the surrounding sediment, suggesting that it may be an impression (Fig. 3.2). However, the mineral texture of the specimen is distinct from that of the host sediment (Fig. 3.3). The surface of the host sediment is pitted (Fig. 3.3C), a texture observed frequently in the Soom Shale sediment at a magnification of x450 and greater. There are raised sinuous lines (Fig. 3.4A) in the elevated central area of the fossil (the area labelled as 3d in Fig. 3.1A); in between these lines are circular patches, which are seen clearly under backscatter on the SEM because they have a more iron rich composition than the surrounding area and the sediment (Fig. 3.4D, E).
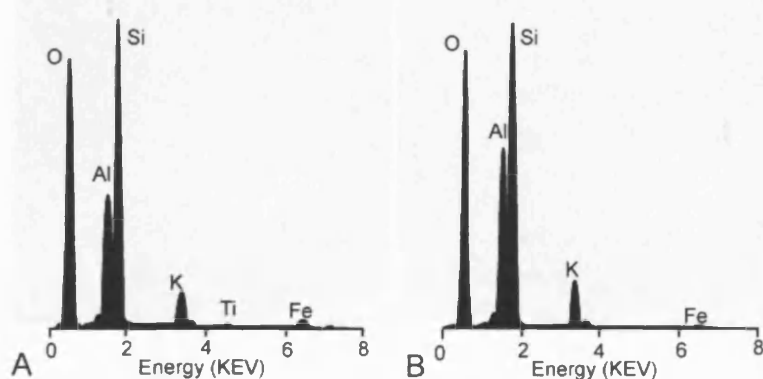


**Figure 3.2.** Comparison of EDX traces from **A.** Specimen C1376 and **B.** Sediment. Both exhibit a clay mineral signature.
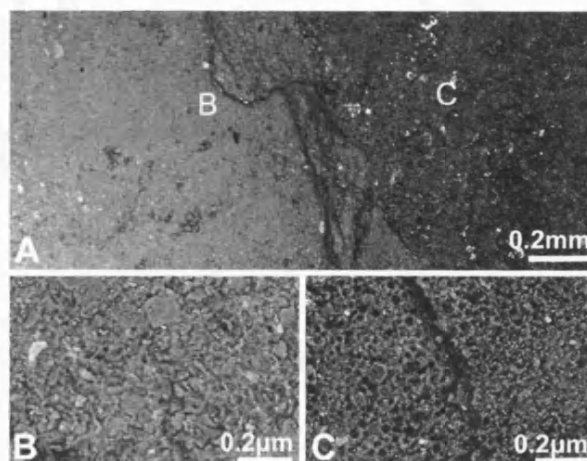


**Figure 3.3.** SEM back scattered electron image comparing the surface of specimen C1376 and the host sediment (location on specimen shown in Fig. 3.1A). **A.** Boundary between the specimen C1376 (B) and sediment (C), labels **B** and **C** also refer to the location of enlargements B. and C. **B.** Specimen under higher magnification. **C.** Sediment under higher magnification, showing the characteristic pitted texture.
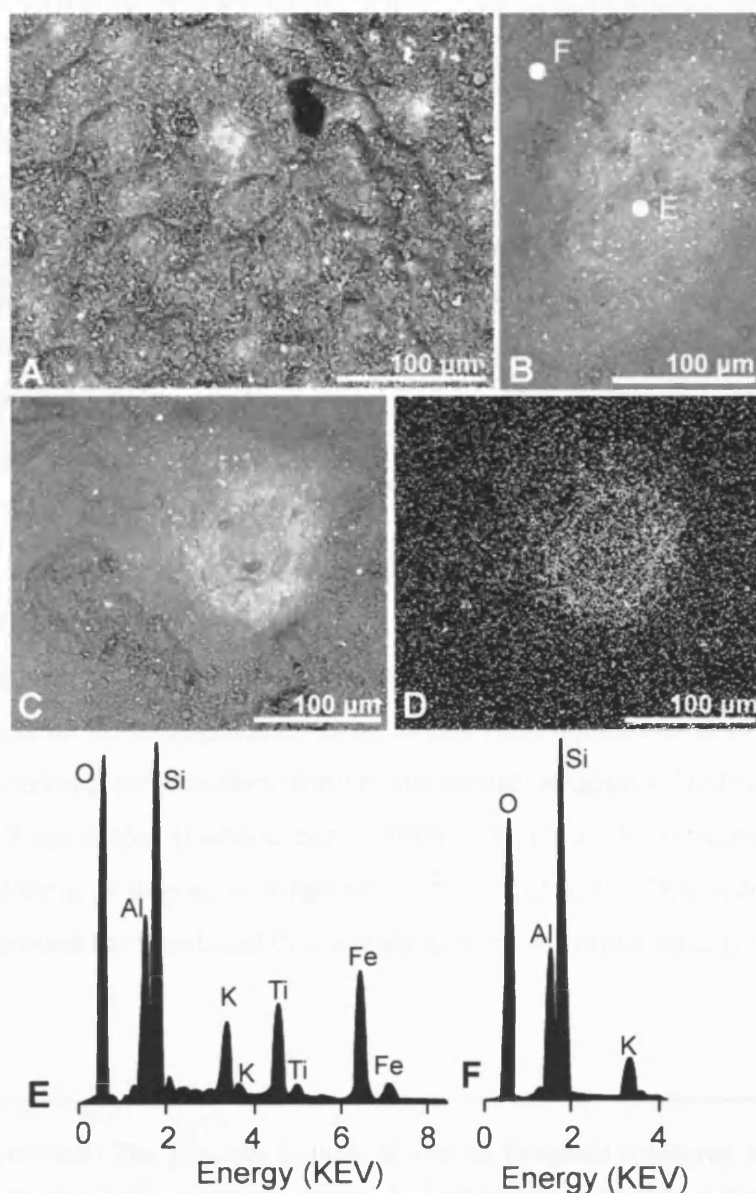
**Figure 3.4.** The texture found over the elevated central part of specimen C1376 (within the area labelled as 3d in Fig. 3.1A) consists of raised sinuous lines, with rounded depressions. **A.** Back scattered electron image of the raised sinuous lines. **B.** Enlargement to show the centre of one of the rounded depressions. The spots labelled E and F denote the positions of the EDX traces E. and F. **C.** and **D.** Back scattered electron image and elemental map for Fe for a second enlarged area of the central texture. **D.** There is an elevated iron concentration compared to surrounding area. Maps for the other elements did not show any elevated concentrations. **E.** EDX trace; peaks indicate a clay mineral signature and elevated Fe, there is also a peak for titanium although maps of the same area did not show an abundance of this element. **F.** EDX trace; peaks indicate the presence of clay minerals only, with no Fe.

DISCUSSION

It is hypothesised that specimen C1376 is a scyphozoan cnidarian. However, although scyphozoan medusae or 'jellyfish' are an important component of present day pelagic ecosystems, their low preservation potential leads to them being rare and often equivocal in the fossil record (Hagadorn *et al.* 2002). When they are found as fossils, internal features of jellyfish are often poorly preserved or lacking. Also, in many instances supposed fossils are in fact inorganically formed structures or trace fossils, or their fossil nature may be uncertain (Hagadorn *et al.* 2002). Therefore, to test the hypothesis it is important to compare the specimen with abiological structures that appear similar to jellyfish and with other putative jellyfish fossils.

Possible inorganic origins include nodules, pyrite and marcasite mineral growths, pseudomorphs after mineral growth and fluid escape structures. These structures can form circular features with relief, which may be confused with medusoid fossils (Cloud 1968, 1973; Hagadorn *et al.* 2002; Rasmussen *et al.* 2002). Rare nodules exist in the Soom Shale, and on adjacent bedding surfaces these form positive relief structures. Nodules typically range in size from 1–7 cm across (Gabbott pers. comm. 2007) and the surrounding laminae are deflected around them as they grow diagenetically (Fig. 3.5A, B). This sediment disturbance is not observed around the fossil, and thus a nodular mode of formation is refuted for C1376.

Figure 3.5. (overleaf) The principal features of circular inorganic structures, trace fossils and organisms of taxonomically enigmatic origin. A. Laminae over the top of a nodule from the Soom Shale have become distorted, the arrow points to the greatest distortion; a lamina is highlighted in red. B. Laminae next to the nodule, the arrow points to where the laminae start to become affected, laminae are highlighted in red. C. A diagrammatic representation of a pyrite rosette based on photographic images from Cloud (1973). The radiating structures, which are 4–6cm in diameter, are thought to have been formed by post-depositional mineral growth between bedding surfaces (Cloud 1973). D. and E. Features of the putative fossils *Eoporpita* and *Hiemalora* respectively, from De (2006), where the specimens are described as Ediacaran fossils. This interpretation has been questioned by Lipps (2006) who claims that the structures are a result of fluid escape in a microbial mat environment. F. A diagrammatic representation of a scratch circle based on photographic images from Jensen *et al.* (2002). Typical specimens generally have regularly spaced ridges and outer dimensions range from a few centimetres to more than 15 cm (Jensen *et al.* 2002). G. A reconstruction of the taxonomically enigmatic genus *Stellostomites* from Zhu *et al.* (2002).
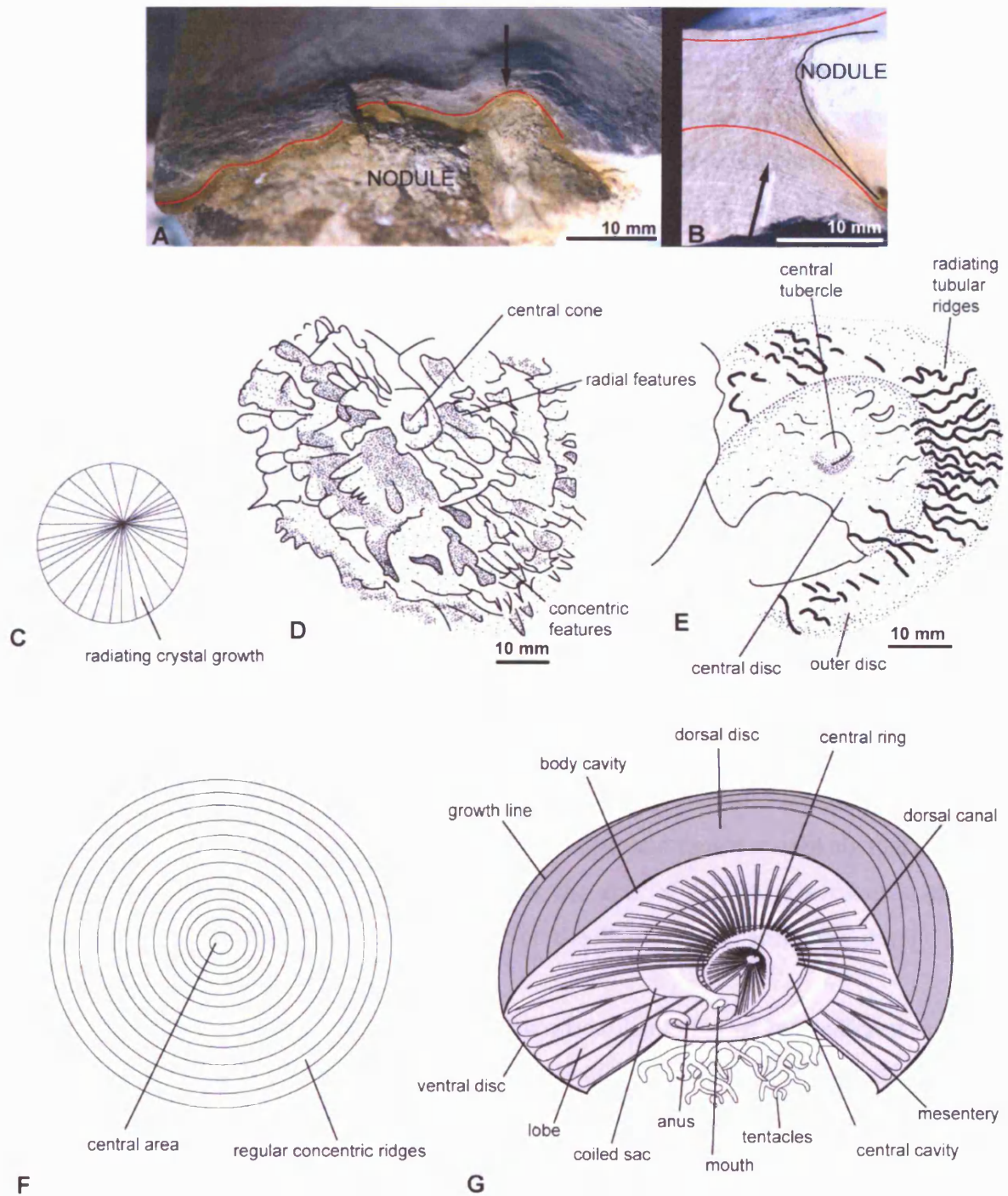
Diagenetic marcasite and pyrite growth can produce circular structures around one to several centimetres in size with radiating fine lines from the centre to the edge (Cloud 1973; Rasmussen *et al.* 2002) (Fig. 3.5C). These structures form by directed crystal growth constrained between surfaces such as bedding surfaces or along joints (Cloud 1968). Casts of cubes of pyrite near the centre of structures or thin films of pyrite over the specimen are evidence of an original pyrite or marcasite origin (Cloud 1973). C1376 has a similar clay mineral composition to the sediment so this mode of formation can be discounted; however, in the centre there are some circular patches that have elevated iron concentrations along with a clay mineral composition. This could be evidence of diagenetic pyrite growth, although this might itself be influenced by the presence of a fossil. In medusoid fossils from the Ordovician William Lake Lagerstätte, Canada, internal structures have become secondarily pyritised (G. Young, pers. comm. 2006). Also, many of the Soom Shale fossils, for example the arthropods, exhibit elevated concentrations of iron (Chapter 6). Therefore, it is more likely that the elevated iron in small patches in the centre of the specimen is related to the preservation of an organism as opposed to being evidence that the structure is an abiological mineral growth.

Original pyrite and marcasite growth can be replaced to form psuedomorphic structures (J. Hagadorn, pers. comm. 2007), which could have a clay mineral composition. Like original pyrite or marcasite growth structures, C1376 has radiating lines, but these extend from the edge of the central raised feature and not from the centre of the structure. Also, chemical analyses of the Soom Shale host sediment have shown that it was characterised by low iron concentrations (Gabbott 1998) and this would have limited diagenetic growth of the polymorphs pyrite and marcasite, and thus it is unlikely that pyrite or marcasite could have grown to form structures the size of C1376. Therefore a mineral pseudomorph mode of formation is refuted for the Soom Shale specimen despite some superficial similarities.

Gas escape structures can cause post-deposition disruption of the sediment and also collapse of overlying or underlying laminations, none of which are observed around C1376. It has been suggested that pseudofossils resembling medusoids can be the result of fluid escape in microbial mat environments, where the mats provide an unusual depositional environment due to their low horizontal strength and high vertical strength (Lipps 2006). As the presence of a microbial mat has not been discounted for the Soom Shale (Gabbott 1999), it is important to evaluate the evidence for the presence of circular and dome-like discoidal pseudofossils in microbial mat environments.

Lipps (2006) claimed that the putative medusoids *Hiemalora* (Fedonkin 1980, 1982) and *Eoporpita* (Wade 1972) are pseudofossils. Features of *Eoporpita* as described by Wade (1972) include radial symmetry, two series of tentacles, a single large central cone and an aboral surface with fine radial striae (Fig. 3.5D). *Hiemalora* also exhibits a central area surrounded by a few to many thick, tentacle-like impressions extending away from the central area (Narbonne 1994; Lipps 2006) (Fig. 3.5E). Specimens of both organisms have been found from the Zimny Coast, White Sea, the East European Platform; the Dniester Basin, Podolia, Ukraine; the Mackenzie Mountains, Northwestern Canada, the Vindhyan Basin of India (De 2006) and the Flinders Ranges, South Australia (Narbonne 1994; McCall 2006). Lipps (2006) interpreted the morphological features of these putative organisms as having formed by the escape of liquid or gas from layers below or within a stratified microbial mat. The structures formed as fluid reached an impenetrable layer, where it first made a convex structure, and then channelled out from that (Lipps 2006). The Soom Shale specimen has a round central area, but does not exhibit any of the characteristic thick tentacle-like structures produced through liquid or gas escape, and thus this mode of formation can be discounted. Moreover, there is no other evidence for fluid escape structures in the Soom Shale. Therefore abiotic modes of formation have been refuted for C1376.

Trace fossils previously described as cnidarians include scratch marks formed by tubular organisms (Jensen *et al.* 2002). One of these is the fossil *Kullingia*, initially described as a chondrophorine hydrozoan (Narbonne *et al.* 1991), which has concentric lines emanating from a central pore (Jensen *et al.* 2002) (Fig. 3.5F). Jensen *et al.* (2002) stated that the scratch marks possess several concentric ridges and a central pore and these features are not seen in C1376. Round marks left by burrowing organisms are not considered as a possible interpretation of C1376 because there are no burrows in the Soom Shale sediment owing to the inhospitable sediment pore waters.

Taxonomically enigmatic groups with a circular structure include the genus *Eldonia*, from the Chengjiang biota (Lower Cambrian, China) and the Burgess Shale (Middle Cambrian, Canada) (Conway Morris and Robison 1988; Chen *et al.* 1989; Chen and Erdtmann 1991) and allied forms that bear similarities to this genus such as *Stellostomites* and *Pararotadiscus* (Middle Cambrian, south China) (Zhu *et al.* 2002). These fossils have a central circular structure and lines that extend radially to the margin. However, they differ from C1376 because they all possess a prominent coiled sac and bifurcate tentacles surrounding a mouth (Zhu *et al.* 2002) (Fig. 3.5G) and none of these structures are seen in

C1376. Therefore biologically produced trace fossils and affinities to known organisms of enigmatic origins are discounted for C1376.
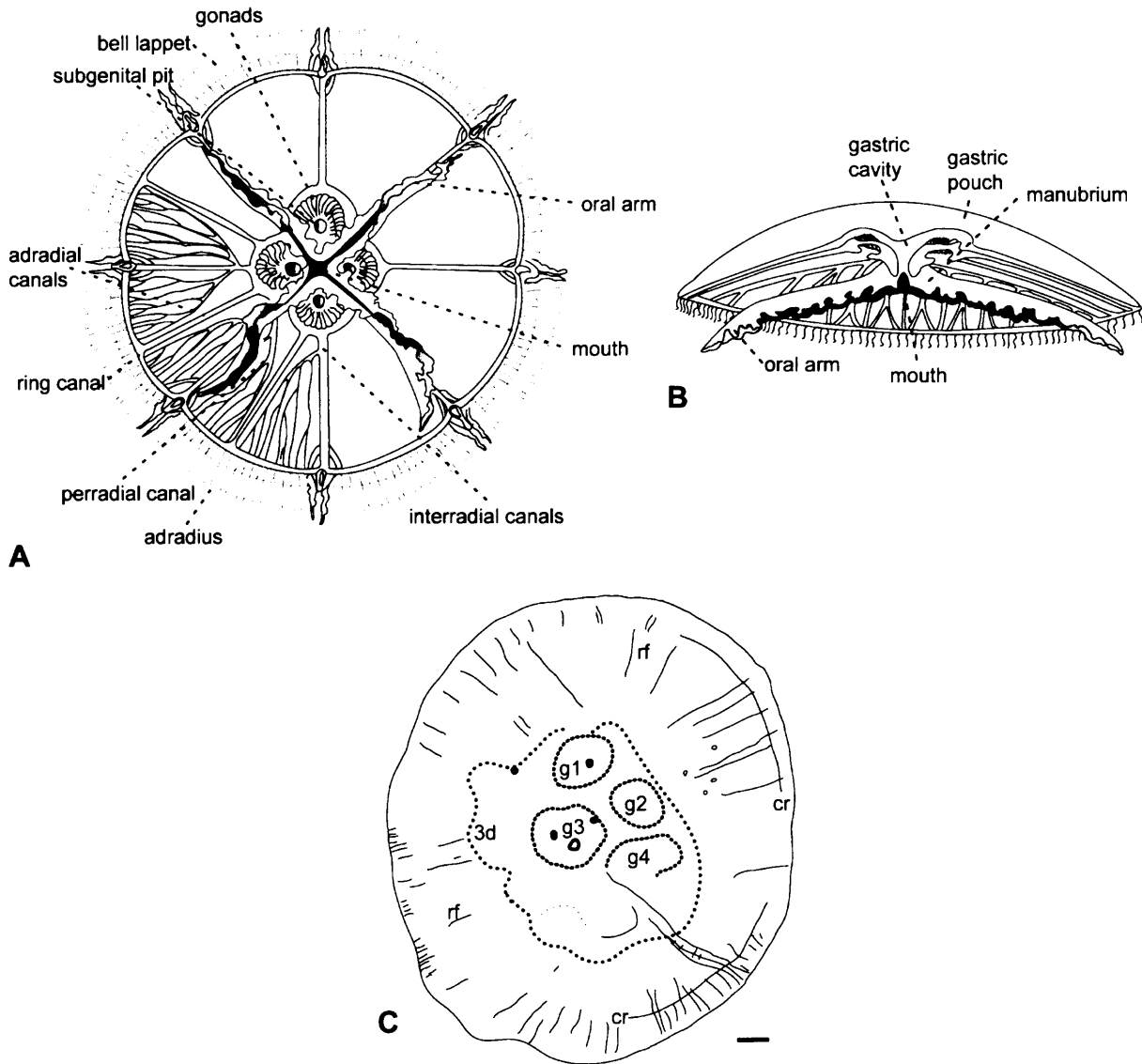


**Figure 3.6. A.** and **B.** The main features of the modern jellyfish *Aurelia* (from Meglitsch 1972) **A.** Oral view of *Aurelia* **B.** *Aurelia* in section, from the side. **C.** The main features of the medusoid specimen C1376. The labels **rf** refer to the fine radiating features all around the specimen, which may relate to the radial canals of the modern specimen; **3d** highlights the extent of the area of three dimensional preservation, possibly caused by the collapse of the mouth and gastric cavity; **g1–g4** refer to circular structures at the centre of the fossil that may represent gastric pouches or gonads; **cr** highlights the possible presence of a concentric ring structure that may be similar to the ring canal of the modern specimen. Scale bar = 1 mm.

Other disc shaped fossils include organisms belonging to the phylum Cnidaria in the medusoid stage. Anatomical details characteristic of living species of the phylum Cnidaria include a clear indication of a mouth or gastric cavity (Fig. 3.6A, B) (Palmer 1996). However, decay experiments on recent Cnidaria show that the oral structures of these soft bodied organisms are often not preserved (Norris 1989; Palmer 1996). The differentiation of the class Scyphozoa is largely dependent on characters which are typically not preserved in fossilised medusoids, such as the position and presence of coelenteron gonads, gastric filaments and pouches (Pickerill 1982).

Despite the evidence of decay experiments and the rarity of soft-tissue preservation jellyfish fossils are found in the fossil record as impressions and as body fossils, in subaerial and subaqueous environments (Pickerill 1982; Baird *et al.* 1986; Hagadorn *et al.* 2002; Viohl 1990; Etter 2002*a*; Gaillard *et al.* 2006; Young *et al.* 2006). After discounting abiological methods of formation as well as trace fossil and enigmatic organism origins for C1376, a Cnidarian affinity can be considered. The structures present on the specimen can be compared with scyphozoan features (Fig. 3.6). The raised circular part in the centre of the Soom Shale fossil can be interpreted as the site of collapse of the mouth or the gastric cavity, the four raised structures in the centre of the fossil can be interpreted as the gastric pouches and/or gonads. The fine radiating structures may be radial canals; the concentric ring could be the ring canal. The interpretation of the features in this manner is consistent with the hypothesis that C1376 represents a scyphozoan cnidarian.

*Subaerial preservation of jellyfish*

With the exception of chondrophorine hydrozoans, most cnidarian medusae are difficult to preserve because they have no durable hard parts (Stanley 1986). Jellyfish impressions are found, but they are still relatively rare fossils (Gaillard *et al.* 2006). Decay experiments have shown that jellyfish can be preserved as impressions in the sediment if they have been exposed subaerially. This is because the organisms invoke bell pumping as a mechanism of freeing themselves, and this can excavate an impression of the umbrella (Schäfer 1941, 1972; Bruton 1991; Rozhnov 1998; Hagadorn *et al.* 2002). There have been several recorded instances of the subaerial preservation of jellyfish as impressions in the fossil record, including specimens from the Late Cambrian of Southern New Brunswick (Pickerill 1982) and specimens from the Late Cambrian of central Wisconsin (Hagadorn *et al.* 2002).

The impressions described from New Brunswick number over 100 (Pickerill 1982). They were possibly washed onto a shoreline or offshore bar and stranded as swash accumulations at or above immediate high tide during a storm or unusual tide activity (Pickerill 1982). They are circular, subcircular or elliptical discs and the majority of the specimens are 60–80 mm in diameter, which is larger than C1376, at a maximum of 16.15 mm in diameter. Well-preserved New Brunswick specimens exhibit a central circular stomach (Pickerill 1982) (Fig. 3.7A), possibly homologous to the central circular structure of C1376, and radial canals in multiples of 12 or more, most commonly 16 (Pickerill 1982); these structures are not clear on C1376, but may relate to the faint lines extending from the central area. The centralised stomach region of the New Brunswick specimens usually preserves no fine detail and typically constitutes about 30–35% of the total diameter of individual specimens (Pickerill 1982); in C1376 the raised central area constitutes 40–50% of the total diameter of the fossil. The margins of the New Brunswick specimens are composed of concentric ridges (typically two) and there is the faint hint of a concentric ridge at the edge of the fossil in some areas of C1376 (Fig. 3.6C).

The medusoids from central Wisconsin were thought to have been stranded subaerially subumbrella down (Hagadorn *et al.* 2002). The fossils are preserved in positive relief, where the decomposition of the sediment-laden gastrovascular cavity was thought to have left sediment mounds. They also possess negative relief, where concave rings formed around the sediment mounds when the jellyfish repeatedly contracted their bell margins, touching the substrate and excavating a moat-like circular depression near their bell margin (Hagadorn *et al.* 2002) (Fig. 3.7B). The fossils lack diagnostic characters but were assigned to the cnidarians because of their radial symmetry (Hagadorn *et al.* 2002).

*Subaqueous preservation of jellyfish*

It has been suggested that dead jellyfish sinking to the sea floor retain so much buoyancy that they can make no identifiable impression on the bottom (Schäfer 1972; Bruton 1991). However, Hertweck (1966) conducted experiments that indicated that, at least under conditions of dead calm water, medusae impressions could be produced underwater. Medusoid-like organisms and jellyfish have been described from several Konservat Lagerstätten in aqueous environments either as impressions, or more rarely as body fossils. Examples of jellyfish have been identified from the following deposits: Cerin limestone, France (Gaillard *et al.* 2006), Mazon Creek Lagerstätte, USA (Baird *et al.* 1986), Solnhofen

limestone, Germany (Viohl 1990), Grès à Voltzia shales, France (Etter 2002*a*) and the William Lake Lagerstätte, Canada (Young *et al.* 2006). Several different mechanisms are invoked to explain their preservation.

Abundant jellyfish impressions have been described from the Upper Jurassic lithographic limestones of Cerin, France where rapid covering by a microbial mat is thought to have promoted preservation (Gaillard *et al.* 2006). The fossils were discovered in what was thought to be a lagoon, which, during the interval of jellyfish preservation, was deep and mainly flooded, with a clear marine influence (Gaillard *et al.* 2006). The specimens belong to two taxa of Scyphozoa and two taxa of Cubozoa. The scyphozoans have a morphological resemblance to the recent genus *Aurelia*, as they are discoidal, with an entire circular margin and four central organs in the form of a horseshoe or almost complete circle in some specimens (Fig. 3.7C). There is no described evidence of tentacles (Gaillard *et al.* 2006). The cubozoans exhibit tentacles (Fig. 3.7D), connected to the umbrella by a basal expansion termed the pedalia (Gaillard *et al.* 2006). The Soom Shale specimens do not possess any clear tentacles and thus differ from the cubozoans of Cerin. The general morphology of the scyphozoans named *Paraurelia* is similar to the Soom Shale specimen, although the *Paraurelia* specimens have more clearly-defined central organs.

Medusoid impressions have been discovered from the Middle Pennsylvanian Mazon Creek shale of Northeast Illinois, from a subaqueous palaeoenvironment (Foster 1979; Baird *et al.* 1985*a*, 1985*b*, 1986). They are interpreted to have been preserved by undergoing rapid burial, followed by the early diagenetic formation of siderite (Baird *et al.* 1986). The originally soft-bodied coelenterates can be distinguished from the surrounding matrix by their greater or lower relief (Foster 1979). The most common medusoid is the scyphozoan *Essexella asherae*, which is preserved with negative relief due to weight pressure (loading) of the undecayed lower surface of the jellyfish on soft mud prior to concretion formation (Baird *et al.* 1986). It differs from the Soom Shale specimen as it has a bell structure with a cylindrical sheet hanging below it (Foster 1979, Selden and Nudds 2004) (Fig. 3.7E). There are also several uncommon forms such as *Anthracomedusa*, a cubozoan, which differs from C1376 by having four bunches of numerous tentacles (Foster 1979, Selden and Nudds 2004) (Fig. 3.7F).

The Upper Jurassic Solnhofen limestone of southern Germany contains occasional jellyfish body fossils of different species, including *Rhizostomites admirandus* (Viohl 1990). The Lagerstätte is a stagnation deposit; obrution and bacterial sealing are thought to have contributed to the exceptional preservation (Viohl 1985, 1996; Barthel *et al.* 1990; Etter
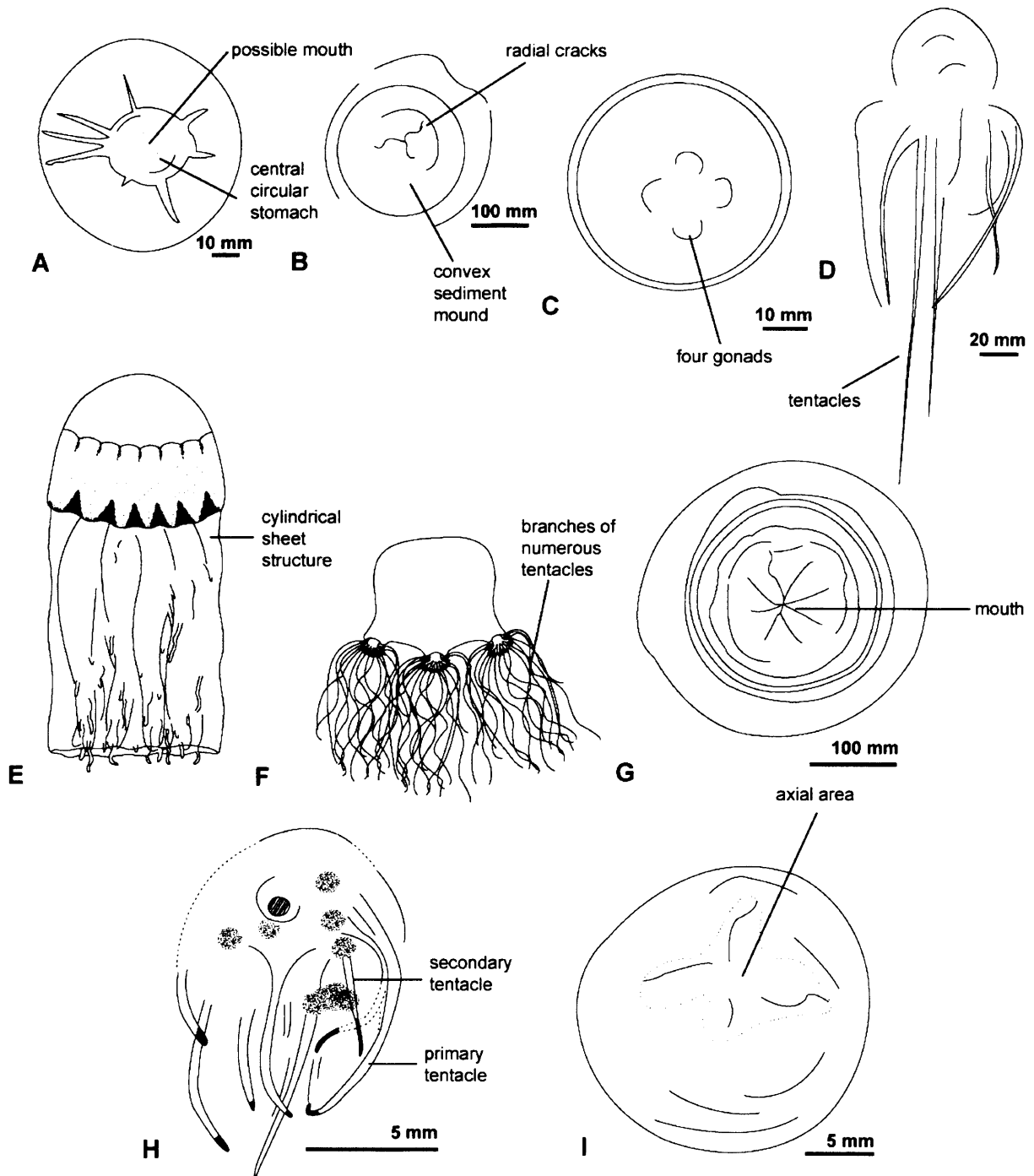
2002*b*). Shrinkage patterns in the jellyfish indicate dehydration, which is thought to have been caused by hypersaline waters, a result of deposition in a restricted basin (Seilacher *et al.* 1985; Barthel *et al.* 1990; Etter 2002*b*). The jellyfish have two zones of circular muscle separated by a ring canal (Barthel *et al.* 1990). Unlike C1376, there is a cross-shaped mouth in the middle of the animal (Fig. 3.7G). Four gonads surround the mouth of the Solnhofen specimens (Barthel *et al.* 1990), which may be homologous to the four structures on C1376. Unlike C1376 the Solnhofen specimens have tentacles (Barthel *et al.* 1990).

In the lower Triassic Grès à Voltzia of northeastern France, medusoid body fossils are preserved in shales, and provide evidence of mass mortality in restricted water areas (Etter 2002*a*). The fossils are found in a deltaic setting, which fluctuated cyclically from brackish to hypersaline waters (Gall 1983). Fossils from this site show minimal signs of decay, with soft parts preserved as organic material, or as a thin crust of iron oxides (Gall 1990). Preservation has been attributed to microbial mats, which are thought to have covered and sealed carcasses in a reducing environment and produced a mechanical and geochemical envelope that rapidly protected the soft-bodied organisms from decay (Gall 1990; Etter 2002*a*). Specimens of the medusa *Progonionemus* have visible gonads and stinging cells and are possibly related to the Limnomedusae (Grauvogel and Gall 1962; Gall 1990; Etter 2002*a*). The genus differs from the Soom Shale specimen by having very long tentacles 9–40 mm in length (Grauvogel and Gall 1962) (Fig. 3.7H), but some of the specimens do exhibit four gonads and possibly gastric pouches (Grauvogel and Gall 1962).

Well preserved cnidarian medusae body fossils are common in a single horizon of the Late Ordovician William Lake Lagerstätte in central Manitoba, Canada in what is thought to be very shallow restricted waters (Young *et al.* 2006). The environment of deposition has been interpreted as a low-latitude coastal setting, probably in a tidal flat to lagoon (Young *et al.* 2006). The medusoids are three-dimensional although some flattening has occurred (G. Young, pers. comm. 2006). Some of the structures are composed of carbonate, others exhibit pyritised internal structures, seen as darker axial areas and some are mixed carbonate and pyrite (G. Young, pers. comm. 2006, 2007). They are preserved in several different ways, but the best specimens were probably washed up on the tidal flat where they died and became stuck to the sediment. They then became covered by soft mud in a water solution before they had time to completely desiccate (G. Young, pers. comm. 2006). The fossils have a similar radial outline (Fig. 3.7I) and size to the Soom Shale medusoid, but do not have raised domes at their centre.

The Soom Shale medusoid was preserved because of factors relating to the environment of deposition which included a lack of bioturbation and quiet water conditions (Gabbott 1998; Gabbott et al. 2003), which would have prevented the decay of the organism. The current model for the taphonomy of the Soom Shale, which has been invoked for the preservation of soft tissues in other specimens such as conodonts (Gabbott et al. 1995) and eurypterids (Braddy et al. 1995, 1999; Gabbott 1998; Gabbott et al. 2001), suggests that labile soft tissues were replaced rapidly after death by authigenic clay minerals (Gabbott 1998; Gabbott et al. 2001). C1376 is the only medusoid specimen to be found from the Soom Shale, a site of soft tissue preservation. The presence of fossils in the Soom Shale is sporadic, and many different faunal elements, especially the entirely soft-bodied ones, are only represented by one specimen. This suggests that there may have been only localised episodic preservational environments suitable for soft tissue preservation, leading to the rarity of fossils in the deposit. This coupled with the extremely low preservation potential of this group, would account for the discovery to date of only a single medusoid specimen.

**Figure 3.7.** (overleaf) The principal features of some fossil Cnidarians. **A.** A diagrammatic representation of a jellyfish impression from Southern New Brunswick based on a photographic image from Pickerill (1982). Specimens preserve the outline of the stomach and an unspecialized mouth; external margins are defined by concentric ridges and furrows (Pickerill 1982). **B.** A diagrammatic representation of a jellyfish impression from Central Wisconsin based on a photographic image from Hagadorn et al. (2002). Specimens show a central convex mound of sediment, sometimes characterised by quadripartite or radial cracks, which is surrounded by a convex sediment ring (Hagadorn et al. 2002). **C.** and **D.** Diagrammatic representations of jellyfish impressions from Cerin, France based on photographic images from Gaillard et al. (2006), **C.** Paraurelia is characterised by four central symmetrical imprints, probably corresponding to gonads (Gaillard et al. 2006). **D.** The cubozoan Bipedalia exhibits long tentacles (Gaillard et al. 2006). **E.** and **F.** Diagrammatic reconstructions of jellyfish impressions from the Mazon Creek shale of Northeast Illinois (from Foster 1979). **E.** The scyphozoan Essexella has a cylindrical sheet hanging below a bell structure (Foster 1979; Selden and Nudds 2004). **F.** The cubozoan Anthracomedusa possesses four branches of numerous tentacles (Foster 1979; Selden and Nudds 2004). **G.** A diagrammatic representation of a jellyfish body fossil from the Solnhofen limestone of southern Germany based on a photographic image from Barthel et al. (1990). The specimen preserves a central cross-shaped mouth (Barthel et al. 1990). **H.** A diagrammatic representation of a jellyfish body fossil from the Grès à Voltzia of northeastern France based on photographic image from Grauvogel and Gall (1962). The organism possesses primary and secondary tentacles. **I.** A diagrammatic representation of a jellyfish body fossil from the William Lake Lagerstätte in central Manitoba, Canada based on a photograph supplied by Graham Young (2007). The jellyfish preserve a radial area, with a darker axial area (G. Young, pers comm. 2006, 2007).

A — possible mouth, central circular stomach, 10 mm

B — radial cracks, convex sediment mound, 100 mm

C — four gonads, 10 mm

D — tentacles, 20 mm

E — cylindrical sheet structure

F — branches of numerous tentacles

G — mouth, 100 mm

H — secondary tentacle, primary tentacle, 5 mm

I — axial area, 5 mm

PALAEOECOLOGY

The Soom Shale medusoid specimen exhibits similar morphological features to the extant genus *Aurelia*, which is a common cosmopolitan jellyfish (Fig. 3.6). *Aurelia* is an opportunistic eurythermal and euryhaline genus occurring in a wide range of marine environments in almost all seas (Lindquist 1959; Maaden 1959; Franc 1994; Gaillard *et al.* 2006). Modern jellyfish exist in waters of different temperatures, and therefore it is probable that the fossil group would have been able to tolerate the cool waters in which the Soom Shale was deposited. The new fossil can be considered as part of the Soom Shale zooplankton, adding to the caryocaridids, the only previously recognised zooplanktonic group (Whittle *et al.* 2007).

SUMMARY AND CONCLUSIONS

There have been several described occurrences of the mass stranding of medusoids, recorded by impressions in subaerial environments. Isolated medusoid impressions and body fossils are preserved in subaqueous environments due to depositional circumstances such as association with microbial mats, stagnation and catastrophic burial. The Soom Shale scyphozoan specimen represents a body fossil of a zooplanktonic organism preserved in a subaqueous environment. The medusoid was preserved because a lack of bioturbation and quiet water conditions prevented decay, enabling labile soft tissues to be replaced rapidly after death by authigenic clay minerals (*cf* Gabbott 1998; Gabbott *et al.* 2001).

<div style="text-align: right;">

# Chapter 4

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# Late Ordovician scolecodont apparatuses from the Soom Shale Lagerstätte, South Africa

**ABSTRACT** – More than 20 examples of partial scolecodont apparatuses have been recovered from the Soom Shale Lagerstätte, South Africa. The scolecodonts were found in association with chitinozoans, algae, conodont apparatuses and the enigmatic needle-like fossil *Siphonacis*. The family Xanioprionidae is identified and the species *Xanioprion*? n. sp. is distinguished, but the material is poorly preserved. The family Mochtyellidae is also identified, and *Synaptogenys rietvleiensis* n. gen., n. sp. is described. Some poorly preserved specimens may represent a third family. The specimens provide the first described scolecodont fauna from South Africa and the first apparatus based taxonomic study of specimens from Gondwana. It is possible that the polychaete worms had either a benthic or a planktonic mode of life. The association of scolecodonts with chitinozoans means that polychaete worms should be reconsidered as one of the contenders for the production of chitinozoans.

## INTRODUCTION

Scolecodonts are the durable jaw elements of polychaete annelid worms. As the soft-body anatomy of polychaete annelids has a very low preservation potential, scolecodonts provide the best fossil record for the Polychaeta and enable reconstructions of long lost communities and phylogeny (Hints & Eriksson, 2007). Scolecodonts are particularly numerous in Ordovician, Silurian, and Devonian deposits and are found all over the world. The oldest scolecodonts have been recorded from the topmost Cambrian of Newfoundland, although diversity and abundance remained very low until the Darriwilian (Williams *et al.*, 1999; Hints & Eriksson, 2007). In the late Mid Ordovician, species and genus level diversity increased. Extinction rates of scolecodonts were low in the Ordovician, increasing only slightly in the latest Late Ordovician (Hints & Eriksson, 2007).

Fused scolecodont jaw apparatuses (or natural assemblages) are rare in the fossil record, as they generally become disarticulated (Eriksson *et al.*, 2004). In the fossil record individual jaw elements approximately 0.2–2 mm in size are most commonly found (Hints, 2002). These individual jaws are acid resistant and can be recovered in great numbers by dissolving limestones and shales (Eriksson *et al.*, 2004). Finds of complete polychaete jaw apparatuses are valuable, particularly for reconstructions that include the identification of the type, number and arrangement of the elements (Bergman, 1989). Ordovician and Silurian polychaete jaw apparatuses have been most studied (Snajdr, 1951; Kozlowski, 1956; Martinsson, 1960; Kielen-Jaworowska, 1961; 1962; 1966; Szaniawski, 1970; Szaniawski & Wrona, 1973). The number of multi-element species known currently from the Ordovician rock record just exceeds 200 and the number of apparatus-based jawed polychaete genera exceeds 50, representing 15–20 families (Hints & Eriksson, 2007).

Late Ordovician scolecodonts are most common from North America (Stauffer, 1933; Eller, 1942; 1945; 1969; Hints, 1998) where they represent a warm water fauna (Eriksson & Bergman, 2003) and Baltoscandia (Hints, 1998) where they represent a colder-water fauna. Ordovician scolecodonts are scarce from higher palaeolatitudes such as Gondwana and the peripheral palaeoplates (Eriksson *et al.*, 2004), and no thorough apparatus based-taxonomic studies have been published from these regions (Hints & Eriksson, 2007). Jaw elements have been recorded from the Ordovician of Australia, Iran, India, North Africa, China and France (Hints & Eriksson, 2007). We describe the first scolecodonts known from South Africa and provide the first apparatus-based descriptions of specimens from Gondwana.

The Soom Shale Lagerstätte scolecodonts were found on bedding planes in proximity to chitinozoans, algae, the enigmatic needle-like organism *Siphonacis* and the giant elements of the conodont *Promissum pulchrum* Kovács-Endrödy, 1986. Fossils from the Soom Shale quarries include conodonts (Theron *et al.*, 1990; Aldridge & Theron, 1993; Gabbott *et al.*, 1995), myodocopid ostracods (Gabbott *et al.*, 2003), eurypterids (Braddy *et al.*, 1995) and naraoiids (Fortey & Theron, 1994). Also present are chitinozoans (Cramer *et al.*, 1974; Gabbott *et al.*, 1998), algae (Gabbott, 1998), brachiopods (Aldridge *et al.*, 1994), orthoconic cephalopods (Gabbott, 1999), trilobites (Moore & Marchant, 1981) and bivalved arthropods (Whittle *et al.*, 2007). Twenty-two specimens of scolecodont apparatus have been identified in differing states of preservation. This contribution describes and illustrates these scolecodont apparatuses, which are assigned to two families, the Mochtyellidae and Xanioprionidae.

## Scolecodont taxonomy

The majority of the Palaeozoic scolecodonts are interpreted as belonging to polychaetes of the extant order Eunicida (Kielan-Jaworowska, 1966; Szaniawski, 1996; Eriksson & Bergman, 2003), although the order Phyllodocida has also been identified in latest Palaeozoic strata (Nakrem et al., 2001; Eriksson & Bergman, 2003). There are five structural types of apparatus within the Eunicida, based on the arrangement of elements and their number and shape; these are labidognath, prionognath, placognath, ctenognath and xenognath (Ehlers, 1864–1868, Kielan-Jaworowska, 1966; Mierzejewski & Mierzejewska, 1975; Szaniawski, 1996; Eriksson et al., 2004) (Fig. 4.1). The earliest known scolecodont fossils have primitive, usually symmetrical jaw apparatus architecture of placognath and ctenognath type (Hints & Eriksson, 2007). In addition to these five distinctive types, some intermediate forms have been recognised (Hints, 1999; Eriksson, 2000). These different structural types of apparatus do not correspond strictly to taxonomic units but they are useful for inferring evolutionary patterns (Kielan-Jaworowska, 1966; Szaniawski, 1996; Eriksson, 2000). The two groups described from the Soom Shale are of placognath type.

The buccal armature of most eunicids is composed of one pair of ventral mandibles and a multi-element, dorsal maxillary apparatus (Szaniawski, 1996). The maxillary apparatus comprises a number of maxillae (abbreviated M), which are generally paired and numbered in roman numerals from posterior to anterior (Eriksson et al., 2004). Also, a basal plate may be present close to the MI r (first maxilla in right position), and a laeobasal plate close to MI l (first maxilla in left position). Minor supporting jaws such as an intercalary tooth (It) and lateral teeth (Lt) may be present (Eriksson, 2000) (Fig 4.2 A., Fig 4.3 A. and B.).

Some forms can have more than one ridge of denticles on the first pair of maxillae (MI), and are known as compound jaws. These ridges may be denticulated or smooth. Those with one ridge of denticles are known as simple jaws. Compound ridges on the MI r are known as the main ridge, basal ridge and second ridge (Fig 4.2 A). These ridges have been interpreted as being homologous to the MI jaw element, basal plate and MII jaw element, respectively of the more advanced apparatuses (Kielan-Jaworowska, 1966). On the MI l, there are the main ridge and laeobasal ridge, thought to be homologous to the MI l jaw element and laeobasal plate of more advanced groups (Kielan-Jaworowska, 1966) (Fig 4.2 A).

## Distribution and ecology

Some species of polychaete are eurytopic, tolerating different environments. For example, members of the extant family Onuphidae can be found in all the oceans of the world

and at all depths. Others are stenotopic, flourishing in specialised environments (Bergman, 1989; 1995; Hints, 2000; Eriksson, 2001; Eriksson & Bergman, 2003); for example, most paulinitid species show a preference for a particular habitat, with the highest diversity of faunas in relatively shallow, sheltered lagoonal environments (Bergman, 1989). Some groups have a limited geographic and depth distribution (Paxton, 1986; Eriksson, 2000) and are very sensitive to facies (Szaniawski, 1996); most fossil species are each restricted to only one palaeocontinent (Hints & Eriksson, 2007).
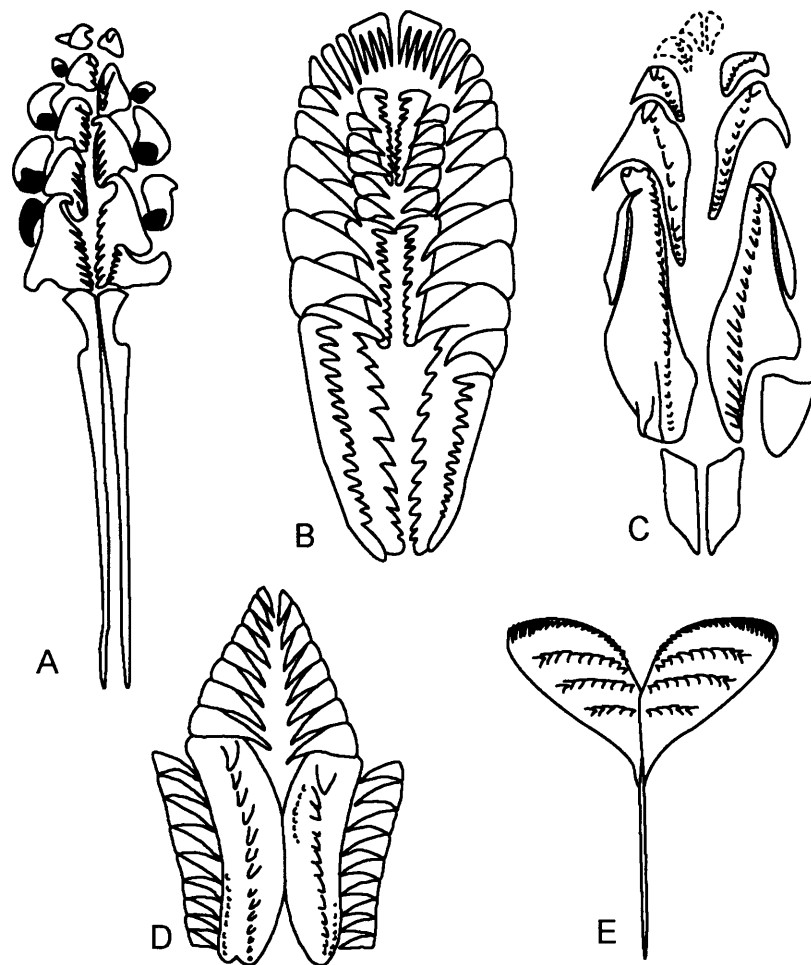


Fig 4.1. The five different types of eunicid scolecodont maxillary apparatus (from Kielan-Jaworowska, 1966; Mierzejewski and Mierzejewska, 1975; Szaniawski, 1996; Glasby et al., 2000; Eriksson et al., 2004). A. Prionognath type; Oenone fulgida (Savigny, in Lamarck 1818). B. Ctenognath type; Tetraprion pozaryskae Kielan-Jaworowska, 1966. C. Labidognath type; Ramphoprion elongatus Kielan-Jaworowska, 1962. D. Placognath type; Mochtyella polonica Kielan-Jaworowska, 1966. E. Xenognath type; Archaeoprion quadricristatus Mierzejewski & Mierzejewska, 1975.
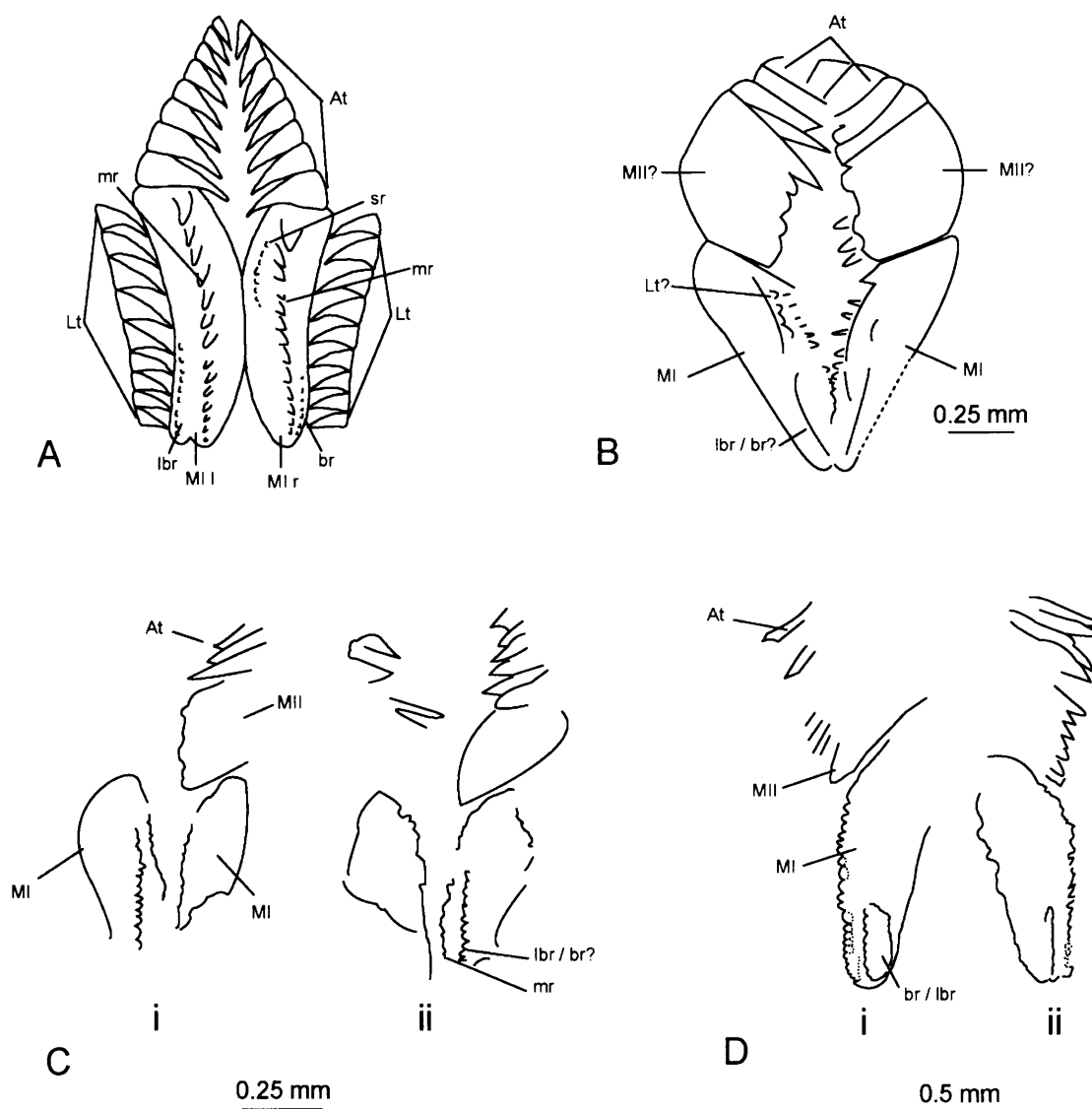
**Fig 4.2.** Mochtyellidae maxillary apparatuses showing the arrangement and numbering of the jaws **A.** *Mochtyella polonica* (from Kielan-Jaworowska, 1966) is illustrated as comparison to specimens from the Soom Shale. B– D. Camera Lucida drawings of the mochtyellid apparatuses *Synaptogenys rietvleiensis* n. gen., n. sp. from the Soom Shale. **B.** C853b; **C.** i.C2021a, ii. C2021b; **D.** i. C2030a, ii. C2030b. Abbreviations – *At* – Anterior teeth, *br* – basal ridge, *lbr* – laeobasal ridge, *Lt* – lateral teeth, *MI l* – first maxilla left, *MII l* – second maxilla left, *MI r* – first maxilla right, *MII r* – second maxilla right, *mr* – main ridge, *sr* – second ridge.

The majority of Recent Eunicida live in shallow water sediments, especially near shore, but some are pelagic (Szaniawski, 1996). Fossil jawed polychaetes were facies controlled and the abundance and taxonomic diversity of scolecodonts increase with decreasing depositional depth, as shallower water environments provided more suitable living conditions than deeper ones (Bergman, 1979; 1989; Eriksson, 1997; Hints, 2000; Eriksson & Bergman, 2003). Although water depth was presumably the primary influence on scolecodont

distribution, other controlling factors such as temperature, light, salinity, turbidity and access of nutrients, which are commonly correlated to water depth, may have been important (Eriksson & Bergman, 2003).
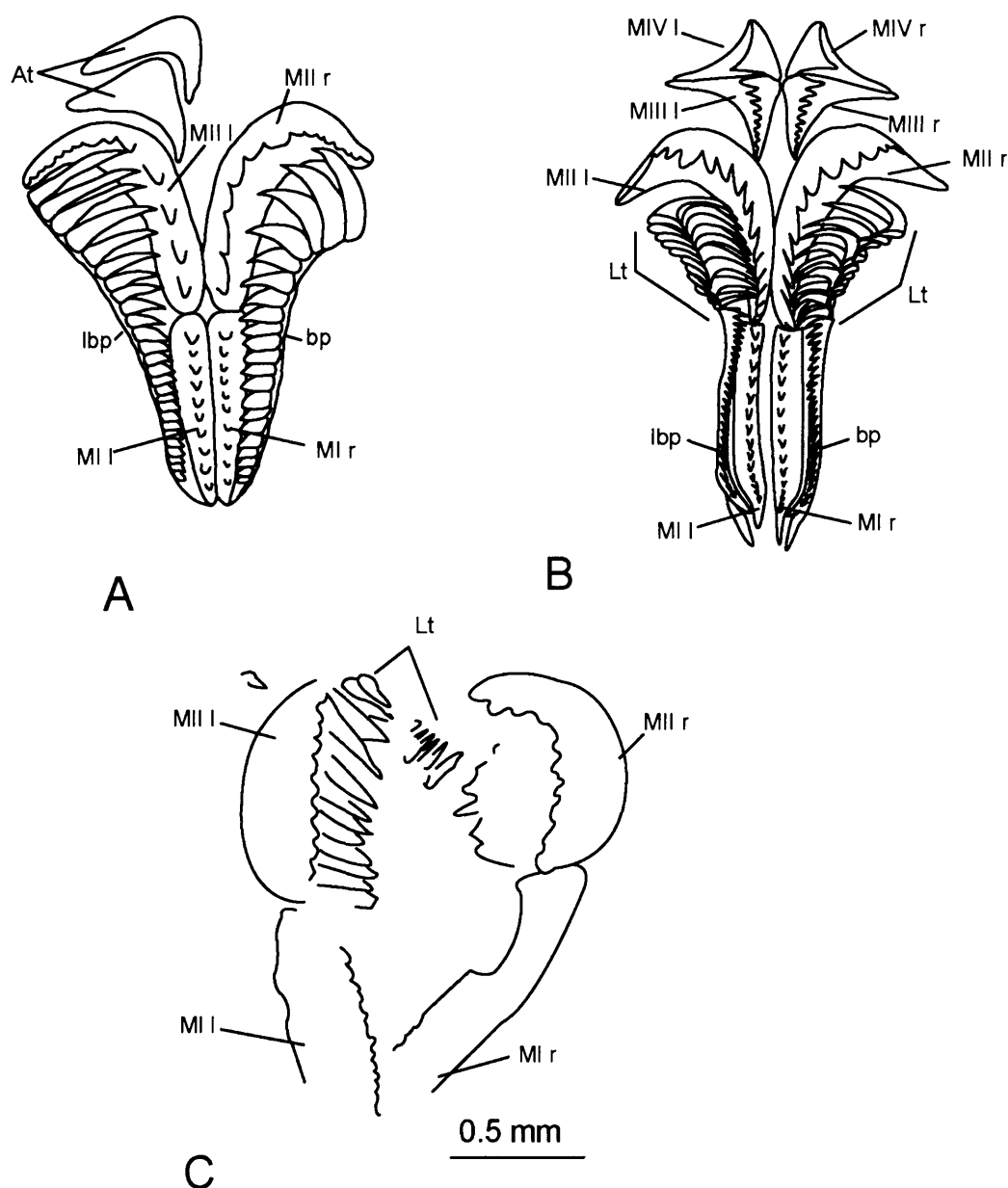


Fig 4.3. Xanioprionidae maxillary apparatuses showing the arrangement and numbering of the jaws. A. *Xanioprion borealis* (from: Kielan-Jaworowska, 1966). B. *Xanioprion walliseri* (from: Szaniawski & Wrona, 1973). C. *Xanioprion*? n. sp. from the Soom Shale. Abbreviations – *At* – Anterior teeth, *bp* – basal plate, *lbp* – laeobasal plate, *Lt* – lateral teeth, *MI l* – first maxilla left, *MII l* – second maxilla left, *MI r* – first maxilla right, *MII r* – second maxilla right, *MIII r* – third maxilla right, *MIII l* – third maxilla left, *MIV r* – fourth maxilla right, *MIV l* – fourth maxilla left, *mr* – main ridge, *sr* – second ridge.

## Geological Setting

The Late Ordovician Soom Shale Konservat-Lagerstätte is located in the Cedarberg Mountains, north of Cape Town. An exceptionally preserved soft-bodied fauna has been recovered from several localities (Gabbott et al., 1995; Gabbott, 1998; Aldridge et al., 2001).

Late Ordovician continental reconstructions have placed the tip of South Africa at between about 30° and 45° S (Beuf et al., 1971; Smith, 1997; Sutcliffe et al., 2000; Cocks & Torsvik, 2002; Fortey & Cocks, 2003; Young et al., 2004). The Soom Shale was deposited in the Hirnantian (Sutcliffe et al., 2000; Young et al., 2004), and is the lower member of the Cedarberg Formation, part of the Table Mountain Group. The Soom Shale mainly consists of mud and siltstone, totalling 10–15m in thickness. The overlying Disa Member, the upper part of the Cedarberg Formation, is composed of micaceous siltstone (Gray et al., 1986).

The Soom Shale was deposited in marine conditions, in a quiet water basin (Aldridge et al., 2001). The laminated fine-grained lithology shows very little evidence of current activity or bioturbation (Gabbott et al., 2003). It is thought that the water depth was about 100 m across the majority of the basin. It has been suggested that bottom waters in the basin may have been quite cool (Gabbott, 1998). The sediment pore waters were largely anoxic; geochemical analyses indicate that euxinic bottom waters may have prevailed at times (Gabbott, 1998).

Cool, anoxic waters were thought to have contributed to the exceptional preservation of some fossil material in the Soom Shale. Non-mineralized anatomy is preserved as organic films, or as authigenic clay mineral replacements (Gabbott, 1998; Gabbott et al., 2001). Original biominerals, for example aragonite, calcite and apatite, have been completely dissolved leaving moulds, which have been subsequently compacted (Gabbott, 1998; Gabbott et al., 2001). Some fossils, for example Caryocaris, show several different preservation styles on a single specimen, including organic material and a clay mineral coating that is either authigenic, diagenetic or metamorphic (Whittle et al., 2007).

## MATERIALS AND METHODS

The repository of the specimens (prefixed C) used in this study is the Council of Geosciences of South Africa, Belville. The specimens originated from Keurbos Quarry (18°58'E, 32°16'S) near to the town of Clanwilliam, South Africa. Of the 22 partial apparatuses discovered, most specimens only represent two attached jaw elements, whereas others are much more complete. The specimens are degraded and therefore much taxonomic information has been lost.

The fossils were studied using an optical microscope, drawn with the aid of a camera lucida, and photographed using a digital camera and Scanning Electron Microscope (Hitachi S-3600N). Analysis was carried out with scanning electron microscope energy dispersive X-rays (SEM EDX) using an Oxford Instruments detector. For SEM EDX analysis uncoated material was used in partial vacuum mode at 15Kv. Elemental mapping was used to show the relative abundance of chemical elements in different areas of the fossils and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) to be determined, from different areas on the specimens and from the sediment.

## PRESERVATION OF SPECIMENS

It is thought that polychaete jaws are formed through thickening and hardening of pharyngeal cuticle (Szaniawski, 1996). The jaws of polychaetes are composed mainly of scleroprotein, with only trace amounts of chitin (Voss-Foucart *et al.*, 1973; Szaniawski, 1996). The amino acid composition of the proteins differs between taxa, and the degree of sclerotization of the protein also varies greatly (Szaniawski, 1996). The preservation of scolecodonts ranges from deformed, flattened, and fragmented specimens, to exquisitely three-dimensionally preserved ones, with a glossy appearance, which show original morphology and micro-ornamentations (Eriksson *et al.*, 2004).

The Soom Shale specimens occur as flattened, degraded, and often fragmented specimens on bedding surfaces. Many of the higher-level diagnostic features, such as the size and shape of denticles, are not preserved. EDX analysis of scolecodont specimens produced peaks consistent with carbon, which can be seen clearly as the black areas on the fossils in hand specimen and under the SEM in backscatter mode (Fig 4.4A. and B.), and clay minerals, which appear white when seen in hand specimen and are identical in colour to the sediment under SEM backscatter (Fig 4.4A. and C.). Where carbon is found on the specimen in the part, clay minerals are often found at the same point on the counterpart and vice versa (Fig 4.5H. and I.; Fig 4.6D and E). Some specimens (for example C319b) have negative relief and the corresponding surface (C319a) has positive relief (Fig 4.5A and B.).

The scolecodonts exhibit organic preservation in the form of carbon and are also composed of clay minerals. This style of preservation is found on several other Soom Shale fossils, for example conodont eye capsules and chitinozoans, where it appears that the clays have coated the surface of the organic substrate (Gabbott *et al.*, 1998; Aldridge *et al.*, 2001). Occasionally the clay minerals have a slightly fibrous texture. This may relate to way in which it originally grew when it replicated the fossil, or may have been created by the

subsequent metamorphism of the fossils (Whittle *et al.*, 2007). The carbon is often cracked into a mosaic-like appearance (Fig. 4.4A.); this is likely to be related to the dehydration of the fossil during diagenesis and/or metamorphism.
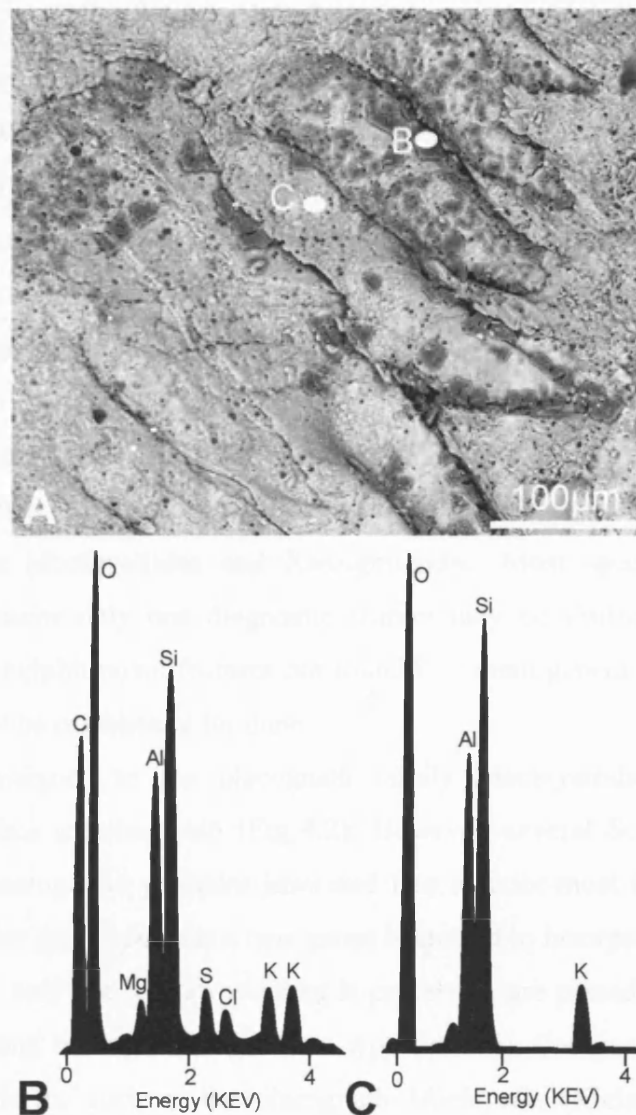


Fig. 4.4. **A**. SEM image of part of scolecodont C319a from where EDX traces shown in B and C were taken. The carbon shows up clearly under backscatter mode because it is compositionally distinct from the sediment. B. and C. EDX traces for areas of the scolecodont apparatus. **B**. Dark areas on the scolecodont specimens correspond to a carbon composition, a clay mineral composition is also present, which may be due to beam overlap or beam penetration through the carbon. **C**. Areas that appear white when seen with the naked eye correspond to a clay mineral composition.

The easiest method of processing samples for scolecodonts is to dissolve rock in acid. Scolecodonts are often present in samples processed for palynological or conodont investigations (Szaniawski, 1996). Slides prepared by Cramer *et al.*, (1974) primarily to identify chitinozoans from the Soom Shale yielded no scolecodont specimens when restudied. This is not surprising given their preservation mode, as parts of the specimens exhibit a clay mineral composition and the sediment is also composed of clay minerals, traditional extraction methods will not yield scolecodonts at this site. Also, carbon, when preserved on the specimens, has a mosaic texture. Upon acid treatment this carbon would break up into unidentifiable fragments. The number of scolecodonts from the Soom Shale may be vastly underestimated because the specimens are small (1–2 mm) and are often sediment coloured, so they may not be recognised during collecting.

## THE SOOM SHALE SCOLECODONT FAUNA

The Soom Shale scolecodont fauna appears to include representatives of two main groups, the families Mocthyellidae and Xanioprionidae. Most specimens are extremely degraded and sometimes only one diagnostic feature may be visible. Some of the more complete specimens exhibit novel features not found in current genera and thus a new genus and new species must be established for them.

Specimens assigned to the placognath family Mochtyellidae exhibit compound posterior jaws and free anterior teeth (Fig 4.2). However, several Soom Shale specimens, although they have compound posterior jaws and free anterior-most teeth, also have fused posterior-most anterior teeth, and thus a new genus is erected to incorporate them. A selection of specimens, where only the MI jaw element is preserved, are placed in the Mochtyellidae based on the compound nature of this jaw (see Appendix iii). Compound jaws are generally found in primitive forms such as the placognath *Mochtyella* (Kielan-Jaworowska, 1966; Szaniawski, 1996). However, compound MI jaws have been noted in the prionognath *Skalenoprion* and the labidognath *Langeites* where it is thought that the basal plate fused to form a compound jaw (Kielan-Jaworowska, 1966). These groups can be discounted because in more complete apparatuses, labidognath and prionognath scolecodonts have carriers, which are jaws below the MI jaw elements; these are not noted from Soom Shale scolecodonts. Also, placognath scolecodonts such as the mochtyellids, have rows of anterior teeth (Hints, 2002), clearly seen in many of the specimens (e.g. C853) (Fig 4.2; Fig 4.6). Finally, the Soom Shale specimens are identified as belonging to the family Mochtyellidae because the overall morphology of the MI jaw element is very similar to that of other members of the family.

The mochtyellid specimens from the Soom Shale all have MI jaws preserved; these may occur with MII jaws and anterior teeth, or the MII jaw elements and anterior teeth may be badly degraded or completely missing (see Appendix iii). There is no instance where the MII and anterior teeth are found preserved without the MI elements. Within the fauna, 14 specimens have been identified as possibly belonging to the family Mochtyellidae, making this the most abundant scolecodont group in the Soom Shale.

The members of the family Xanioprionidae were assigned based upon the long thin nature of the MI elements and the arcuate MII elements (Fig 4.3). In the Xanioprionidae the MII jaws have a strong outward curvature and are, generally, similar in outline (Edgar, 1984). One of the Soom Shale specimens (C1048) has arcuate MII elements, with the anterior of the elements pointing outwards. Two of the specimens exhibit arcuate MII elements with the anterior of the elements pointing inwards (C319 and C1976). This feature has not been documented before. These three specimens all have MI and MII jaw elements. C319 and possibly C1976 also have a string of lateral teeth (Fig 4.3; Fig 4.5). Specimen C1951 may represent the lateral teeth preserved alone; therefore, the number of specimens that belong to the family Xanioprionidae in the Soom Shale is possibly four (see Appendix iii).

Three specimens are unplaced taxonomically as they possess novel features that have thus far not been identified in any other investigated scolecodont groups and/or because they were not preserved well enough to permit identification (see Appendix iii). This may indicate that they belong to a new family; however, it would be unwise to erect such a high taxonomic grouping based on specimens with such poor preservation. Finally, one specimen (C1143) is left unidentified, as the material was not available for study.

## SYSTEMATIC DESCRIPTIONS

Class **Polychaeta** Grube, 1850

Order **Eunicida** Dales, 1963

Family **Xanioprionidae** Kielan-Jaworowska, 1966

? Genus *Xanioprion* Kielan-Jaworowska, 1962

**Type species.** *Xanioprion borealis* Kielan-Jaworowska, 1962 from a mid or late Ordovician age erratic boulder, Poland

**Diagnosis.** 'Nearly symmetrical jaw apparatuses consisting of three jaws, some lateral teeth and one or more anterior teeth on each side. MI straight, subrectangular. MII arcuate, larger than MI and arranged in front of them. Laeobasal and basal plates finely denticulated with denticles decreasing posteriorly in size. Pulp cavity of laeobasal and basal plates narrowly open. MIII subtriangular, finely denticulated. Lateral teeth arcuate, long, sharply pointed. Anterior teeth (or MIV) arranged in front of MIII, subtriangular in outline.' Emended diagnosis Szaniawski & Wrona (1973, p. 236), after Kielan-Jaworowska (1962).

*Xanioprion*? n. sp.

**Material.** C319 and C1976.

**Locality and horizon.** Keurbos Quarry, near Clanwilliam, South Africa. Soom Shale Member, Cedarberg Formation, Table Mountain Group.

**Age.** Late Ordovician (Hirnantian).

**Description.** Apparatus almost symmetrical. More complete specimen (C319) consists of right and left MI elements, right and left MII elements situated anteriorly of MI elements, and a string of teeth that are possibly lateral teeth. Maximum length of apparatus 1.6 mm, maximum width 1.3 mm. On C319, right MI is an elongate jaw, length 1 mm, width approximately 0.2 mm (tips of denticles missing). Incomplete left MI at least 0.76 mm in length, width 0.26 mm (tips of denticles missing). Main portion of jaw nearly straight, elongate, composed of a row of approximately 14 denticles, relative size of which cannot be determined due to degradation.

Right MII length at least 0.7 mm, width 0.23 mm (tips of denticles missing). Clearly arcuate jaw, anteriorly pointing towards centre of apparatus. Tips of denticles eroded away, but there are approximately 9–10 visible. Incomplete left MII length at least 0.76 mm, width approximately 0.36 mm (to tips of denticles). Jaw slightly arcuate; anteriorly the jaw points towards the centre of the apparatus, approximately 9–10 denticles visible (C319), anterior end of MII 1 missing (Fig 4.3; Fig 4.5).

Specimens have large centrally positioned teeth, which are possibly lateral teeth as they appear to be associated with the MII elements, 15 visible on the left hand side of C319. These long elongate lateral teeth very closely adjoin one another and vary in length, smaller

anteriorly becoming longer medially. Lateral tooth series appears to sit ventrally to MII elements, where they are seen emerging towards the centre of the jaw apparatus (Fig 4.3; Fig 4.5). It is considered that the apparatus in C319 is seen in dorsal view because the denticles are evident. In ventral view, only denticle pits are evident on the MI and MII jaw elements of *Xanioprion* (e.g. Szaniawski & Wrona, 1973; Plate II 3b; 2b).
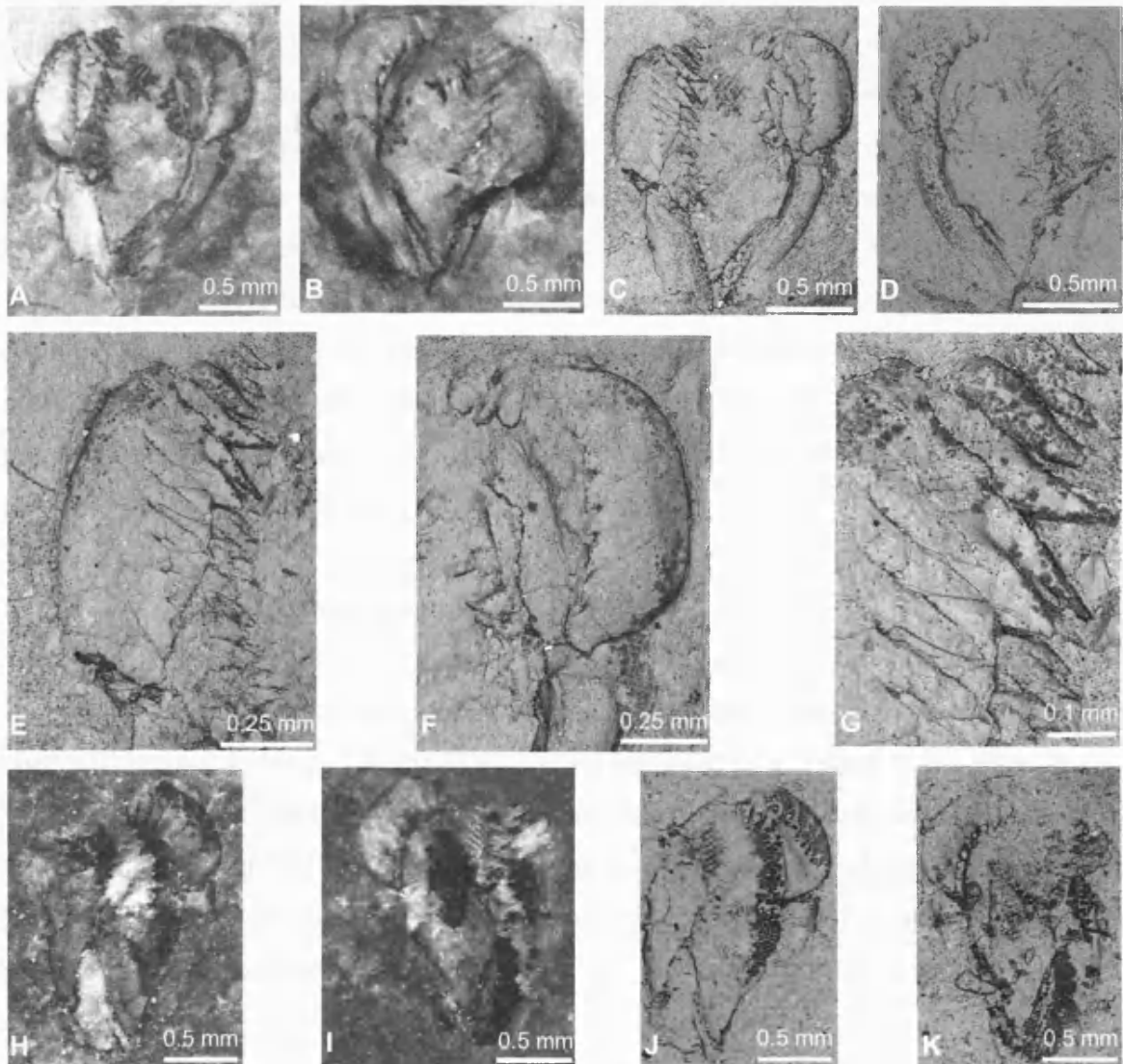


**Fig. 4.5.** The xanioprionid *Xanioprion*? n. sp. from the Soom Shale. **A.** C319a; **B.** C319b is mostly preserved in negative relief; **C. – G.** SEM back scattered electron images; **C.** C319a; **D.** C319b; **E.** C319a enlargement of MI l and possible lateral teeth; **F.** C319a enlargement of MI r showing the clear arcuate nature of this jaw; **G.** C319a enlargement of possible lateral teeth, which can be seen sitting ventrally to the MI l; **H.** and **I.** C1976a and b respectively arcuate MII jaw and parts of possible lateral teeth visible. Where the specimen has a composition of carbon (plus clay minerals) on the part (black areas) a composition of clay minerals only is seen on the counterpart (white areas); **J.** SEM back scattered electron image of C1976a; **K.** SEM back scattered electron image of C1976b, arcuate MII jaw clear.

**Remarks**. The specimens have been assigned to the family Xanioprionidae and tentatively to the genus *Xanioprion* because they exhibit a symmetrical jaw apparatus with longitudinally elongate MI jaw elements and MII jaw elements that are arcuate. When establishing the genus, Kielan-Jaworowska (1962) stated that the M3 jaw element (subsequently renamed MII, Kielan-Jaworowska, 1966) is anteriorly bent outwards. MII elements of *Xanioprion*? n. sp. differ from other members of the genus in this respect as they exhibit an inward curvature (Fig 4.3). The basal plate and laeobasal plate are not evident on the fossil specimens; normally these adhere to the outer margins of the MI elements (Szaniawski & Wrona, 1973). When the apparatus is seen in dorsal view the teeth that may possibly be homologous to the lateral teeth in other members of the genus appear to be located ventrally to, and along the length of the MII elements, as are lateral teeth in *Xanioprion walliseri* Szaniawski & Wrona 1973. However, these teeth differ in *Xanioprion*? n. sp. because they appear to be placed centrally in the apparatus as opposed to laterally. The Xanioprionidae are considered to possess primitive placognath type jaw apparatuses, as they exhibit characters considered as primitive, including a gaping myocoele, one denticulated ridge per maxilla, and a symmetrical jaw arrangement in the apparatus (Hints & Eriksson, 2007).

Family **Mochtyellidae** Kielan-Jaworowska, 1966

**Diagnosis.** 'Asymmetrical jaw apparatuses of placognath type, consisting of jaws with gaping openings of the pulp cavities in the posterior part and two rows of teeth in the anterior part. Series of lateral teeth forming two chains on both sides of the posterior part of the apparatus are, as a rule, present. Carriers lacking. Basal and laeobasal plates are elongated jaws, shorter (*long.*) than MI; MII if present is single right. Intercalary and laeointercalary teeth sometimes present.' Kielan-Jaworowska (1966, p.53).

Genus *Synaptogenys* n. gen.

**Type species**. *Synaptogenys rietvleiensis*, by monotypy.

**Derivation of name.** Gr. *synaptos* – joined together, *genys* – jaw, on account of the MII jaw elements.

**Diagnosis.** Jaw apparatus consisting of two compound jaws in the posterior part. Right and left MI provided with two ridges of denticles: laeobasal/basal ridge and main ridge, both denticulated. Chains of lateral teeth possibly covering MI dorsally. Large jaws, designated MII, present anterior of MI on both the left and right side of apparatus, with approximately five denticles. Anterior teeth free, consisting of approximately 4–5 pairs.

Species *Synaptogenys rietvleiensis* n. sp.

**Derivation of name.** After Rietvlei in the Cedarberg Mountains, South Africa.

**Diagnosis.** As for genus.

**Holotype.** C853 (figs 4.2B, 4.6A–C)

**Paratype.** C2030 (Figs 4.2D, 4.6 L–O)

**Other material.** C1948 and C2021.

**Locality and horizon.** Keurbos Quarry, near Clanwilliam, South Africa. Soom Shale Member, Cedarberg Formation, Table Mountain Group.

**Age.** Late Ordovician (Hirnantian)

**Description.** Symmetrical jaw apparatus, approximately 1.7 mm in total length and 1.1 mm total width (C853). More complete specimens consist of right and left MI jaws, right and left MII jaws and free anterior teeth. Lateral teeth may be visible on C853.

MI jaws sub rectangular; C853 MI r element length 0.9 mm, width 0.24 mm (tips of denticles missing); length MI l 1.03 mm, width 0.27 mm (tips of denticles missing). MI jaws consisting of main ridge and either basal (MI r), or laeobasal (MI l) compound ridge. Denticles of MI main ridge decrease in size posteriorly; on C2030b there are at least 19. Compound ridge appears towards posterior of MI jaw element, seen clearly in C2030b. Basal or laeobasal ridge denticulated in this specimen, consisting of approximately nine small denticles. Anterior-most margin of MI jaws (r and l) directed posterio-medially, posterior of MI elements (r and l) rounded.

Anterior of MI elements on right and left side of the apparatus there are relatively large, subquadrate elements designated here as MII (length and width approximately 0.52 mm, tips of denticles missing, measured on C853). On C853, these jaw elements each have approximately 6–7 denticles. Anterior of the MII jaws there are some free anterior teeth, approximately 3–4 in number on C853. On specimen C853 there are four triangular, possibly lateral, teeth covering the anterior part of MI l (Fig 4.2B; Fig 4.6B).

**Remarks.** The MI jaws bear a resemblance to the genus *Mochtyella* in the presence of compound ridges (seen clearly on C2030), and if seen only as isolated elements, would possibly have been placed within this genus. Posterior elements of *Synaptogenys rietvleiensis* are especially similar in morphology to *M. trapezoidea* Kielan-Jaworowska, 1966 as both exhibit compound ridges, laeobasal and main ridges on the MI l jaw, and basal and main ridges on the MI r. Also, the MI l and r of *M. trapezoidea* and *S. rietvleiensis* both have a straight anterior margin, directed postero-medially and a rounded posterior margin.

The genus *Mochtyella* has free anterior teeth (Fig 4.2A.) (Kielan-Jaworowska, 1966). *S. rietvleiensis* differs from *Mochtyella* as it has large anterior jaw elements with approximately five denticles, big enough to be designated MII. However, in *Mochtyella*, anterior teeth are not frequently recorded. In *M. angelini* Mierzejewski, 1978, five anterior teeth are known, decreasing in size anteriorly, with the last one provided with three tips. Kielan-Jaworowska (1966) described the anterior teeth of *M. trapezoidea* as being imperfectly known, but they have two tips. Therefore, members of the genus *Mochtyella* are known to possess anterior teeth with more than one tip, but in *S. rietvleiensis* the jaw elements are designated as MII because they are relatively large with many denticles, not just two or three tips. *S. rietvleiensis* differs from all other genera in the family Mochtyellidae because it has paired MII elements, rather than one single right hand MII element.

It is thought that the three ridges on the MI right side of the apparatus in compound genera such as *Mochtyella* are homologous to the MI r jaw element, the basal plate and the single MII jaw element of more advanced scolecodonts such as the genus *Pistoprion* (Kielan-Jaworowska, 1966). The main ridge and the laeobasal ridge on the left hand side of the apparatus are thought to be homologous to the MI l jaw element and laoebasal plate (Kielan-Jaworowska, 1966) and there is no left hand side MII element. Therefore, the overall structure of the apparatus is asymmetrical. In *S. rietvleiensis* the posterior-most anterior teeth appear fused, forming the MII jaws on both the right and left side of the apparatus. This is in conflict with the hypothesis that the MI r second ridge separated to form a single MII element on the

right hand side of the apparatus. The presence of the MII jaw elements on both sides of the apparatus in *S. rietvleiensis* means that the overall shape of the apparatus is symmetrical. Symmetrical jaw apparatuses, such as those seen in the family Xanioprionidae are considered primitive (Hints & Eriksson, 2007). If the symmetrical jaw apparatus of *S. rietvleiensis* is considered primitive, it indicates that the anterior teeth evolved to become free from an ancestor with fused teeth. Then, subsequently the compound ridges separated to form individual elements in more advanced groups. The MII jaws in the genus *Synaptogenys* are not homologous to the single MII jaw in more derived apparatuses.

The feature of large MII jaws in *S. rietvleiensis* may indicate that the diagnosis of the family Mochtyellidae needs to be amended, or that *S. rietvleiensis* should be placed within a new family. However, the overall shape of the MI jaws is very similar to other mochtyellids and thus *S. rietvleiensis* has been placed within this family. With so few specimens, which are so badly preserved, I am unwilling at present to amend the well established diagnosis of Kielan-Jaworowska (1966).

## PALAEOECOLOGICAL IMPLICATIONS

The recognition of scolecodonts in the Soom Shale increases the geographical range of the Mochtyellidae and the Xanioprionidae to include the marginal Gondwanan palaeocontinent region. Ordovician scolecodont species have previously been recorded on the margins of at least two palaeocontinents (Baltica and Laurentia); and scolecodonts described from North America (Stauffer, 1933; Eller, 1942; 1945; 1969) show great similarities to those from Estonia and the neighbouring areas (Hints, 2000). Thus it seems that oceanic basins did not constitute unpassable barriers for some polychaetes (Hints, 2000). Representatives of the Mochtyellidae and Xanioprionidae are more common in the cold-water Baltic region than in the warmer-water Laurentian region in the Mid-Late Ordovician (Hints, 1998; 2000; Eriksson & Bergman, 2003; Hints & Eriksson, 2007). As these two groups are the only ones unequivocally recorded from the Soom Shale deposit, which has evidence of cold to glacial conditions, it is possible that some members of these families were more tolerant to colder conditions. However, as polychaetes are known to be sensitive to many environmental factors, other reasons may account for their occurrence in the Soom Shale. Although polychaetes are widespread, some endemism is evident when comparing coeval assemblages from different parts of the world (Eriksson, 2000). The distinctive morphology of the Soom Shale specimens may also reflect a degree of endemism.

At the present day polychaetes have a wide variety of modes of life, including vagrant benthos, sessile, pelagic, and parasitic (Eriksson *et al.*, 2004). It is unlikely that the Soom Shale specimens were infaunal as sediment pore waters were almost certainly anoxic (Gabbott, 1998; Gabbott *et al.*, 2001), there is little evidence of bioturbation and burrows have not been identified. However, Courtinat & Howlett (1990) stated that bioturbation may become invisible after burial diagenesis, so a burrowing mode of life cannot be absolutely ruled out.

The anoxic and/or euxinic conditions would have discouraged benthic forms; however, some extant and fossil species of polychaete worms have been shown to tolerate lower oxygen concentrations, and it is possible that inhospitable conditions were not continuous. In modern environments polychaete worms are reported from below the oxygen minimum zone, and from areas with pollution (Courtinat & Howlett, 1990). Bodergat & Ikeya (1988) have demonstrated that the number of crustaceans diminishes in less oxygenated waters as a result of poor tolerance for variations in oxygen content, whereas polychaete worms are still present. Polychaete worms have also been reported from dysaerobic environments in the French black shales of the Toarcian, Kimmeridgian and Cenomanian–Turonian boundary, where the specimens include dorvelleids and mochtyellids (Courtinat & Howlett, 1990). Previous to this, the genus *Mochtyella* had only been reported from the Palaeozoic. Courtinat & Howlett (1990) postulated that the genus *Mochtyella* survived by adapting to extreme environments of low dissolved oxygen content or of great depths or of both. Therefore, it is possible that the Soom Shale mochtyellids were also adapted to a low oxygen environment, explaining their domination of the scolecodont fauna.

**Fig. 4.6.** (overleaf) The mochtyellid *Synaptogenys rietvleiensis* n. gen, n. sp. from the Soom Shale. **A.** C853a; **B.** C853b; **C.** SEM back scattered electron image of C853b; **D.** and **E.** C1948a and b respectively. Where the specimen has a composition of carbon (plus clay minerals) on the part (black areas) a composition of clay minerals only is seen on the counterpart (white areas); **F.** SEM back scattered electron image of C1948a; **G.** SEM back scattered electron image of C1948b; **H.** C2021a; **I.** C2021b; **J.** SEM back scattered electron image of C2021a; **K.** SEM back scattered electron image of C2021b; **L.** C2030a; **M.** C2030b; **N.** SEM back scattered electron image of C2030a; **O.** SEM back scattered electron image of C2030b.
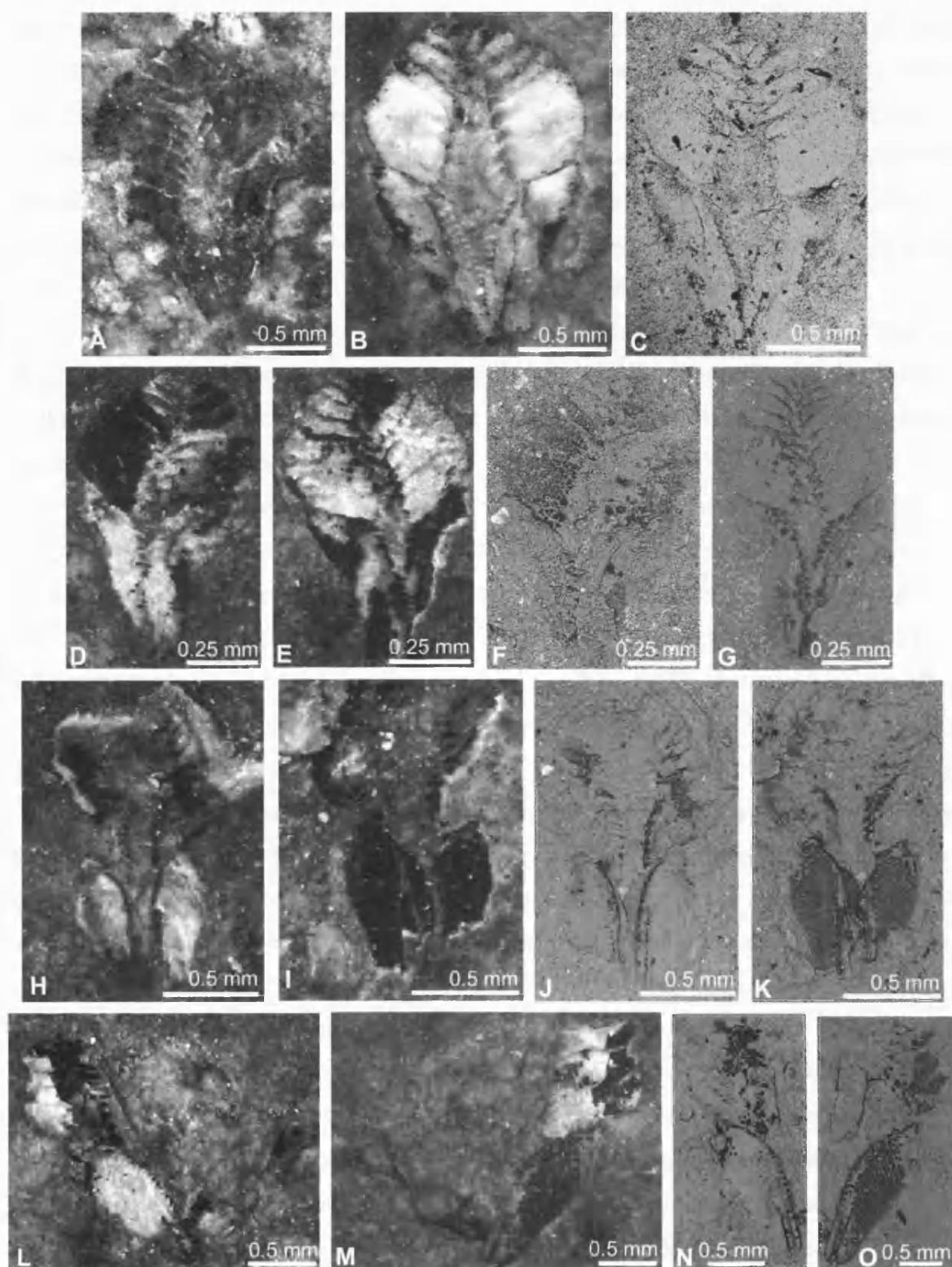
There may have been episodes in the deposition of the Soom Shale where bottom waters were more oxygenated. Gabbott (1998) stated that anoxic–euxinic conditions prevailed, but there were also brief periods of oxygenation (Aldridge *et al.*, 2001; 2006) when orthocones became colonised by epibionts while they lay on the sea floor (Gabbott, 1999). Also, the presence of organisms such as eurypterids, which were probably capable of swimming but lived mostly on the substrate (Braddy *et al.*, 1995), benthic or epibenthic specimens of *Lingula* and a lobopod (see Chapter 5), which probably had a benthic mode of life, suggests that there were times when bottom waters were oxygenated. Therefore, the scolecodont-bearing polychaete worms may have been benthic organisms.

The specimens could also have been planktonic, living in the water column. This is a likely mode of life, because the bottom waters were dominantly anoxic–euxinic (Gabbott, 1998). If they were planktonic they add to the low number of known zooplankton inhabiting the environment of the Soom Shale.

Recent polychaetes use a wide variety of food sources and show a great diversity of feeding habits (Fauchald & Jumars, 1979), although a carnivorous or scavenging nature for fossil polychaetes has been inferred from the morphology of the jaws (Eriksson *et al.*, 2004). The Soom Shale polychaete worms may have been scavengers, active predators or detritivores feeding off of dead organisms, or they may have fed on phytoplankton. As active predators or scavengers they would add to the already large number of organisms occupying this niche in the habitat (Aldridge *et al.*, 2001).

Chitinozoans are organic walled microfossils that are found abundantly in the Soom Shale. Their biological affinities remain enigmatic, although they are often regarded as the eggs of a metazoan (Laufeld, 1974). There is a restricted fauna preserved in the Soom Shale, reducing the number of candidates for chitinozoan production, and a relationship with the polychaetes is one of the possibilities (Gabbott *et al.*, 1998). Extant polychaetes produce large numbers of eggs, shed freely into the sea or laid in mucous masses. However, when Gabbott *et al.*, (1998) assessed the alternative hypotheses, polychaetes were known from the Soom Shale from only two complete jaw apparatuses and a single isolated element. Although polychaetes could not be ruled out as the producers of chitinozoans it was concluded that they appeared rather too uncommon to be considered as the likely producer (Gabbott *et al.*, 1998). Conodonts and orthocone cephalopods were considered more likely candidates based on the number of specimens (Gabbott *et al.*, 1998). However, in two more years of collecting, the number of scolecodonts, elements and apparatuses, has increased from three to 22, suggesting that they may be much more abundant than previously thought. Conodonts and orthoconic

cephalopods are still candidates for the production of the chitinozoans in the Soom Shale, but the increased number of scolecodonts discovered gives weight to the hypothesis of Laufeld (1974) that polychaete worms could have been the organisms responsible for the production of chitinozoans.

Chapter 5

AN ORDOVICIAN XENUSIID LOBOPODIAN FROM THE SOOM SHALE LAGERSTÄTTE, SOUTH AFRICA

**Abstract:** The first xenusiid lobopodian from the Ordovician is described from the Soom Shale Lagerstätte, South Africa. The organism shows features homologous to the twelve species of Palaeozoic marine lobopodians described from the Middle Cambrian Burgess Shale, the Lower Cambrian Chengjiang biota, the Lower Cambrian Sirius Passet Lagerstätte and the Lower Cambrian of the Baltic. The discovery is the first definite marine lobopodian to be described outside of the Cambrian. It provides a link between marine Cambrian lobopodians and the possible Carboniferous onychophoran *Helenodora*. The new fossil preserves an annulated trunk, lobopods with clear annulations, and possible curved claws. It represents a rare record of a benthic organism from the Soom Shale, and demonstrates intermittent water oxygenation.

XENUSIID lobopodians are exclusively marine organisms and have been described previously from Cambrian exceptionally-preserved biotas. These records include seven species from the Early Cambrian Chengjiang Lagerstätte, China (Hou *et al.* 2004*a*; J. Liu *et al.* 2006): *Luolishania longicruris* Hou and Chen, 1989; *Paucipodia inermis* Chen, Zhou and Ramsköld, 1995; *Cardiodictyon catenulum* Hou, Ramsköld and Bergström, 1991; *Hallucigenia fortis* Hou and Bergström, 1995; *Microdictyon sinicum* Chen, Hou and Lu, 1989; *Onychodictyon ferox*, Hou, Ramsköld and Bergström, 1991 and *Jianshanopodia decora* Liu, Shu, Han, Zhang and Zhang, 2006. The following species have been described from the Middle Cambrian Burgess Shale of Canada: *Aysheaia pedunculata*, Walcott, 1911; *A.? prolata* Robison, 1985 and *Hallucigenia sparsa* (Walcott, 1911). The lobopodian *Hadranax augustus* Budd and Peel, 1998 has been described from the Lower Cambrian (upper Atdabanian) Sirius Passet Lagerstätte in Peary Land, North Greenland. Finally, *Xenusion auerswaldae* Pompeckj, 1927 has been described from Early Cambrian rocks from the Baltic

region. These Cambrian lobopodians show a great variety of body shape, size and ornamentation, but all possess a segmented onychophoran-like body, paired soft-skinned annulated lobopods, and in most cases body sclerites (Bergström and Hou 2001).

Other fossil lobopodians have been described from the Carboniferous (Thompson and Jones 1980), Cretaceous (Grimaldi *et al.* 2002) and Tertiary (Poinar 2000); none have been documented from the period between the end of the Cambrian and the Carboniferous. The fossil lobopodian *Helenodora inopinata* Thompson and Jones, 1980 from the Carboniferous Mazon Creek of Northern Illinois was described as a possible onychophoran, because the specimen possesses an annulated body and the annuli are thought to bear possible papillae; limbs and possible jaws are also preserved (Thompson and Jones 1980). The habitat of *Helenodora* remains uncertain because the biota includes a mixture of terrestrial, freshwater and marine organisms (Thompson and Jones 1980). The onychophoran *Cretoperipatus burmiticus* Engel and Grimaldi, 2002 (in Grimaldi *et al.* 2002) from the Cretaceous amber of Myanmar (Burma) has been identified from a terrestrial environment, and interpreted as a true onychophoran as it has antennae, a ventral mouth with entognathous jaws, oral papillae and paired lobopods each with a pair of terminal claws (Grimaldi *et al.* 2002). Other terrestrial onychophorans have been reported from the Tertiary Dominican amber, the age range for which has been suggested as 15–45 million years (Lambert *et al.* 1985; Poinar and Poinar 1999), and the Baltic amber, which is considered to be Eocene in age (around 40 million years) (Larsson 1978; Poinar 1992). They were assigned to two new families and named *Tertiapatus dominicanus* Poinar, 2000 and *Succinipatopsis balticus* Poinar, 2000. The families are both characterised by the presence of simple legs lacking foot portions, with claws (Poinar 2000), which Poinar (1996) stated are similar to those of the Cambrian *Aysheaia* and the Pennsylvanian *Helenodora* lobopodians.

Here I describe a new occurrence of a xenusiid lobopodian and discuss the morphological interpretation, taphonomy and significance of this Late Ordovician marine specimen.

GEOLOGICAL SETTING AND FAUNA

The argillaceous Soom Shale Member is a 10–15m thick unit and is the lower member of the Cedarberg Formation, which occurs towards the top of the Table Mountain Group in South Africa. The Soom Shale occurs immediately above glacial tills, and dropstones are present at the base of the member; water temperatures are thought to have been relatively cool (Gabbott

1998). In this respect the Soom Shale is thought to represent an unusual restricted marine fauna (Aldridge *et al.* 1994).

The Soom Shale represents an interval that may be equivalent to the *persculptus* graptolite zone of the Hirnantian (Late Ordovician) (Sutcliffe *et al.* 2000; Young *et al.* 2004). Palaeogeographical reconstructions indicate that the Soom Shale was deposited at approximately 30–45° S (Beuf *et al.* 1971; Smith 1997; Sutcliffe *et al.* 2000; Cocks and Torsvik 2002; Fortey and Cocks 2003; Young *et al.* 2004). Subaerial tillites of the Pakhuis Formation occur below the Soom Shale, and shallow marine siltstones of the Disa Member overlie it. The depositional basin was in an intracratonic setting; water depths of approximately 100 m have been suggested (Gabbott 1999). Dominantly quiet water conditions are indicated by a lack of flow-induced sedimentary structures and the taphonomy of the fossils. The Soom Shale sediment was largely anoxic; geochemical analyses indicate that euxinic bottom waters prevailed at times (Gabbott 1998). In some areas the shale has been transformed into a sheared slate by metamorphism, and this has destroyed some of the primary internal features (Aldridge *et al.* 1994).

The Soom Shale community consists of invertebrates, early vertebrates and algae. In particular there are a number of arthropod taxa (Moore and Marchant 1981; Fortey and Theron 1994; Braddy *et al.* 1995; 1999; Gabbott *et al.* 2003), conodonts (Theron *et al.* 1990; Aldridge and Theron 1993; Gabbott *et al.* 1995), agnathans (Aldridge *et al.* 2001), brachiopods (Aldridge *et al.* 1994), orthoconic cephalopods (Gabbott 1999) and enigmatica (Aldridge *et al.* 2001). Many of the fossils exhibit soft part preservation, which can include muscle tissue (Gabbott *et al.* 1995). It is thought that authigenic replication of the fossils through replacement by clays with associated alunite group minerals has led to this preservation, sometimes with a high degree of fidelity (Gabbott 1998; Gabbott *et al.* 2001).

## MATERIALS AND METHODS

The repository of the specimen (prefixed C) is the Council of Geosciences of South Africa, Belville. The specimen was discovered from Keurbos Quarry near Clanwilliam (18°58'E, 32°16'S) in a light grey siltstone. The lobopod is a very rare fossil discovery from the Soom Shale as it is the only specimen ever to be found of this group in thirteen years of collecting. The specimen, designated C1974, occurs in multiple pieces that comprise part (C1974 a, d), and counterpart (C1974 c, b, e). The specimen is incomplete, the anterior and possibly the

posterior portions are missing. The fossil was studied using an optical microscope, drawn with the aid of a camera lucida and photographed, with and without ammonium chloride coating, using a digital camera (Cannon EOS 5D). Elemental analysis was carried out using a Hitachi S-3600N Scanning Electron Microscope Energy Dispersive X-ray facility (SEM EDX). For SEM EDX analysis uncoated material was used in partial vacuum mode at 15Kv. Elemental mapping was used to show the relative abundance of elements in different areas of the fossil and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) of the fossil to be determined.

## DESCRIPTION

Phylum LOBOPODIA Snodgrass, 1938

Class XENUSIA Dzik and Krumbiegel, 1989

Order ARCHONYCHOPHORA Hou and Bergström, 1995

*Description.* The specimen is incomplete, with a length of at least 70.7 mm and a width of at least 31 mm. The central body portion appears sub-cylindrical and shows clear transverse annulations in some places (Figs 5.1; 5.2), visible at a density of approximately 7–8 mm$^{-1}$ (Fig. 5.3 F). The body is elongated and tapers towards the posterior, appendages decrease in size and the central trunk extends beyond what is probably the final posterior appendage. At the anterior end, appendages become more crowded; this end of the fossil is incomplete (Figs 5.1; 5.2).

There are no cephalic or caudal structures that clearly suggest the orientation of the fossil. However, there is variation in the position and size of the lobopods. This has been noted in other taxa in relation to the orientation of the organism. *Paucipodia* has a body that tapers at both ends, extending beyond the final lobopods; appendages are longest in the middle and become shorter towards the anterior and posterior (Hou *et al.* 2004*a*). However, in *Cardiodictyon* and *Luolishania*, crowding of appendages has been noted at the anterior end of the body, and this has been suggested as giving an impression of initial cephalisation (Bergström and Hou 2001). In C1974, the appendages get smaller towards one end of the body, and the body extends slightly beyond the smallest appendage (Figs 5.1; 5.2). This decrease in lobopod spacing towards one end of the fossil, and the apparent increase in

appendage complexity indicate that it is most likely the anterior of the fossil, although evidence of cephalic features cannot confirm this.

On the left hand side of the body (part) the appendages are elongate, unjointed, preserved in positive relief and taper towards their termination. They have been numbered from posterior (where they can be clearly recognised individually) to anterior (where the individual extent of each appendage is not clear) (Fig. 5.2). There are 11 appendages preserved, the anterior-most appendages from a8–a11 are more crowded and appear complex owing to the presence of branches and/or ornamentation (Figs 5.1; 5.2; 5.2A, C). Appendage a11 has a large branch (Figs 5.1; 5.2; 5.3A), which is further divided into three or four tips distally. This degree of complexity is not clear on any of the other appendages, and thus a11 may be the front appendage; it is possibly a modified anterior-most appendage. Posterior of a8–a11 there are seven appendages labelled a7–a1, which are simple lobes with clear margins (Figs 5.1, 5.2); these appendages decrease in size towards the posterior of the organism. On some (for example a7, a6, a5 and a4) there are traces of transverse annulations (Figs 5.2; 5.3E). On a5 and a6 (C1974b), there is an indication of a feature with positive relief along the axis of some of the lobes (Figs 5.1; 5.2), which may be homologous to the fine canal seen in the appendages of other lobopods (Chen *et al.* 1995; Bergström and Hou 2001; J. Liu *et al.* 2006).

On the right of the body the appendages are preserved in two dimensions (Fig. 5.2); in some, coloured mineral films indicate their position (Fig. 5.1). Some of the appendages roughly correspond to the position of the lobes on the left side of the body although they are slightly offset (Fig. 5.2). However, they cannot be matched up exactly because they are not preserved all along the entire length of the body, and they are very faint in some places. It is likely that the body has become slightly twisted, and thus the appendages no longer lie exactly opposite each other. The impressions of some of the transverse annulations from the lobes can be seen with the density of approximately 2–3 mm$^{-1}$ (Fig. 5.3B).

On appendages a3, a4, possibly a5, a8 and a9 (those from the left hand side of the body, where preservation is clearest) claws are evident, which are curved with their convex edge facing anteriorly and are much darker than the surrounding matrix (Fig. 5.2). There are possibly two claws per appendage on a3 and a4; they are curved and one may be slightly bigger than the other (Fig. 5.3D). The more complex appendages (a8 and a9) possibly carry more claws.

There is a gut trace down the centre of body, which is evident as a raised structure along most of the length of the organism (Figs 5.1; 5.2). The gut is mostly covered by

overlying tissue, but can be seen in a few places, where underlying areas have been exposed. In these areas it can be seen as darker than the surrounding tissue and preservation occurs as organic carbon in two patches (Fig. 5.2).
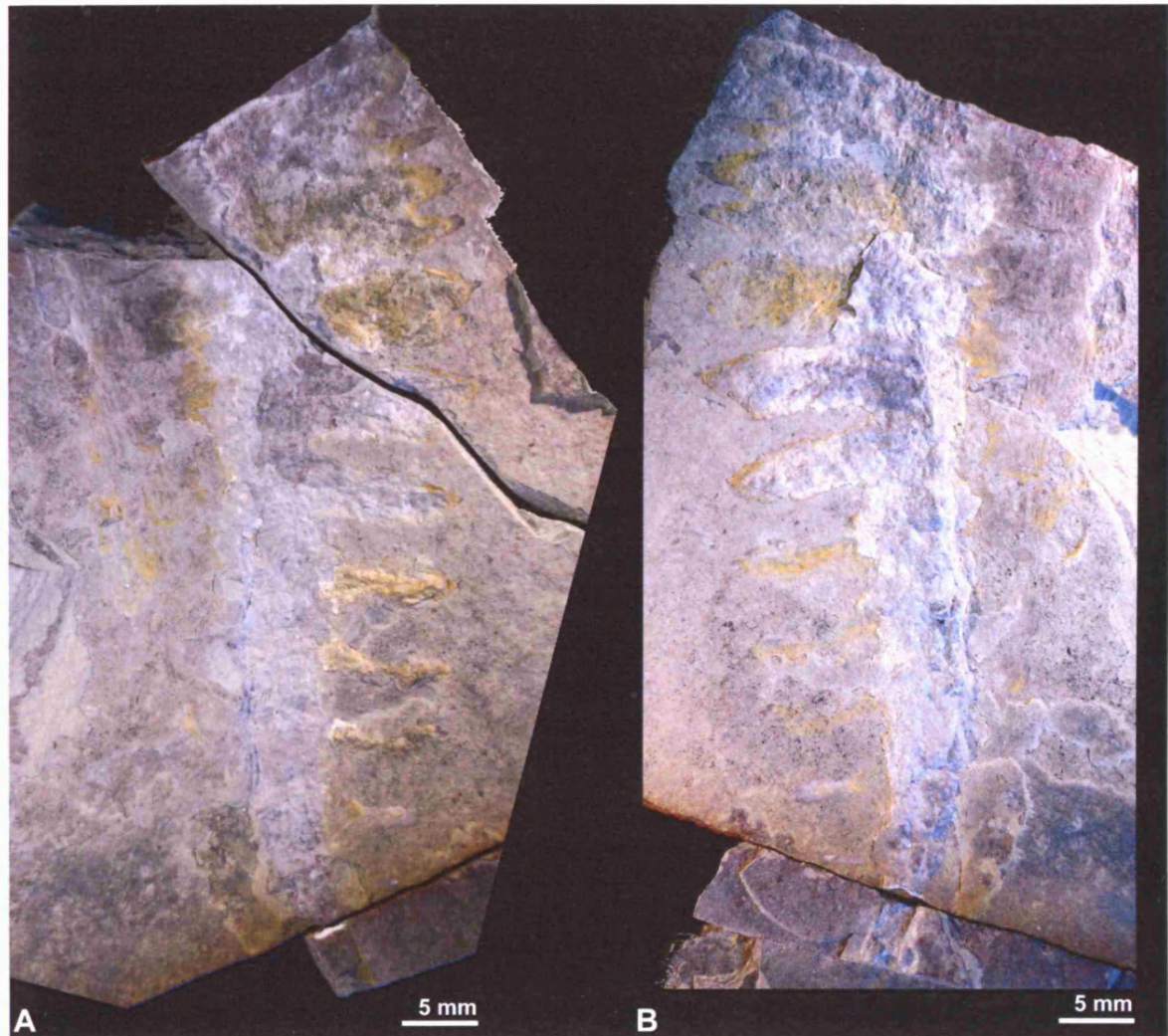


**Figure 5.1.** Lobopod specimen C1974 from the Soom Shale. Two sets of appendages are visible on the specimen, on either side of the main trunk (see Fig. 5.2 for composite explanatory drawing). **A.** Counterpart, the main trunk of the organism is mostly preserved in negative relief. **B.** Part, the trunk is mostly preserved in positive relief.
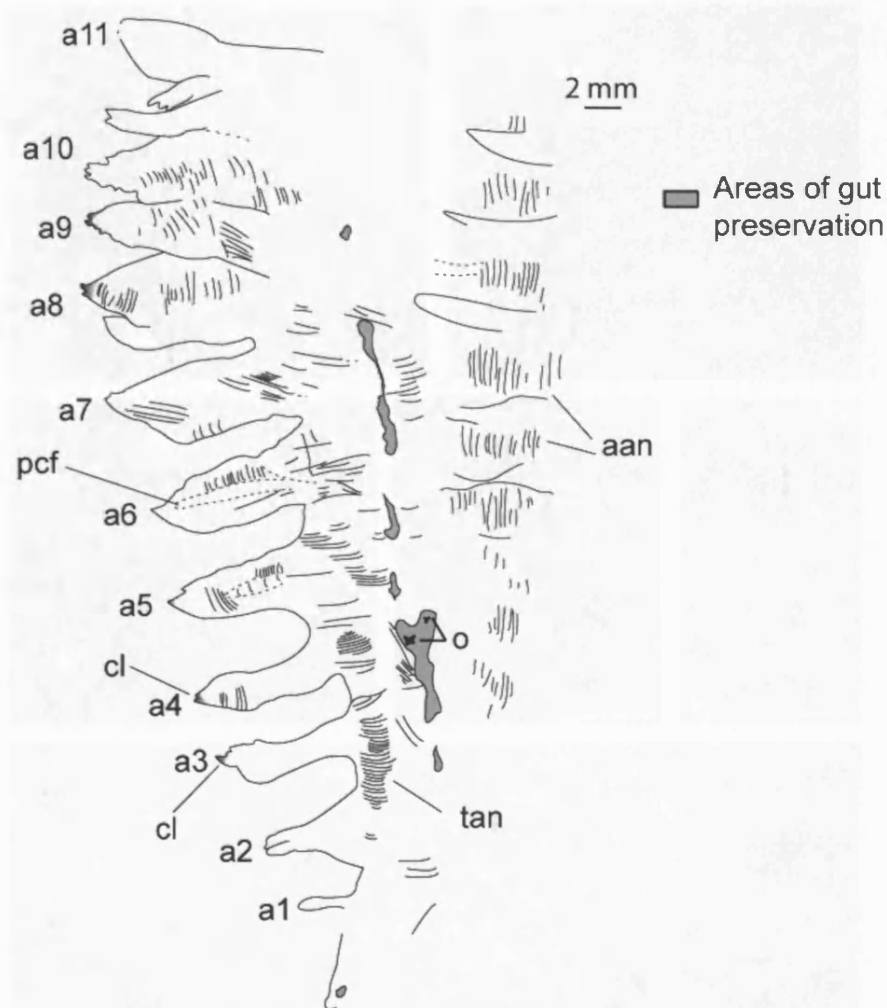
**Figure 5.2.** Composite camera lucida drawing of C1974 part and counterpart (C1974a, b, c, d and e). **a1–a11** refer to the appendages on the left side of the body that are mostly preserved in positive relief, with a11 being the anterior-most appendage and a1 the posterior-most appendage. Dark areas on the distal tips of these appendages are claws (labelled **cl**). The appendages on the right side of the body are faintly preserved; however, some of the annulations on this side are seen as clear black lines (labelled **ann**). Annulations can also be seen on some of the appendages on the left side of the body and on the main trunk of the body (labelled **tan**). Features with positive relief can be seen along the centre of a6 and possibly a5, labelled **pcf** on a6. The areas where the gut trace can be seen are shaded in grey; the letter **o** refers to the area of organic preservation that appears in the region of the gut.
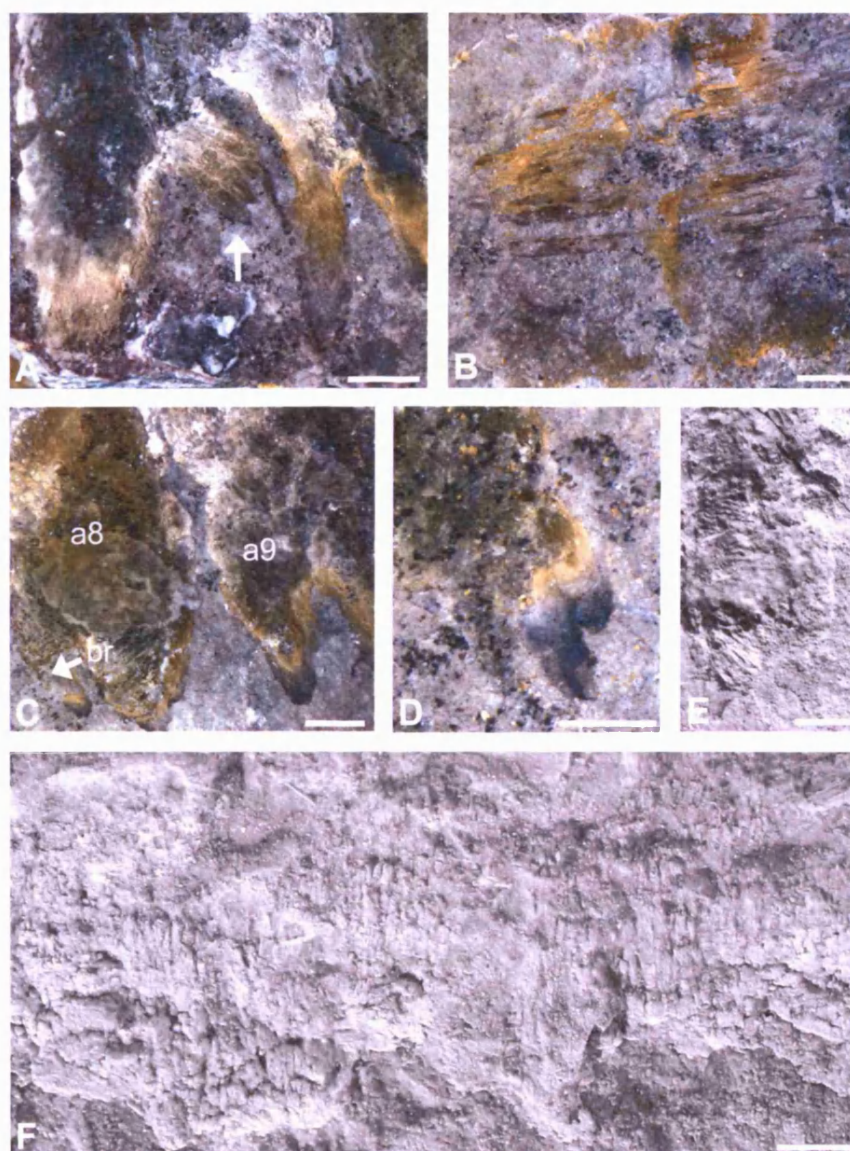
**Figure 5.3.** Features of lobopod specimen C1974, from part (C1974 a, d) and counterpart (C1974 b, c, e). **A.** The anterior-most preserved appendage a11, with apparent proximal branching structure (arrowed) (from part); scale bar = 2 mm. **B.** Annulations on two-dimensionally preserved appendages, opposite a6 and a5 (see Fig. 5.2) (from counterpart). Annulations on this side of the body occur at a density of approximately 2–3 mm$^{-1}$; scale bar = 1 mm. **C.** Complex anterior appendages a8 and a9 (see Fig. 5.2) (from counterpart), **br** = branching structure; scale bar = 2 mm. **D.** Curved claw on end of appendage a3 (see Fig. 5.2) (from counterpart); scale bar = 1 mm. **E.** Annulations on appendage a7 (from part), specimen whitened with ammonium chloride; scale bar = 2 mm. **F.** Annulations on the body of the specimen between appendages a6 and a5 (see Fig. 5.2) (from part), specimen whitened with ammonium chloride. Annulations on the body occur at a density of 7–8 mm$^{-1}$; scale bar = 1 mm.

*Remarks.* The appendages of C1974 resemble the parapodia of annelids, or the lobopods of lobopodia. The fossil is not considered to be a member of the Annelida because it lacks terminal bundles of setae typically found on annelid parapodia (Robison 1987), and it has terminal claws not seen in annelids.

The Soom Shale specimen is incomplete, but the complexity of the appendages indicates that only a small portion of the anterior-most end is missing. The specimen is similar in size to other xenusiid lobopodians, for example *Paucipodia* (Hou *et al.* 2004*a*), *Hadranax*, which is also incomplete at the anterior and posterior ends (Budd and Peel 1998) and is similar in width to *Jianshanopodia*, although this Chengjiang fossil is much longer (J. Liu *et al.* 2006).

Modern onychophorans have a pair of claws on each lobopod and most fossil lobopodians have clawed lobopods, but the number and arrangement of claws varies (Hou and Bergström 1995). For *Xenusion* (Hou and Bergström 1995), *Hadranax* (Budd and Peel 1998), or *Jianshanopodia* (J. Liu *et al.* 2006) there is no conclusive evidence for claws. Multiple claws occur on *Aysheaia*, which has up to seven at the tip of each lobopod (Bergström and Hou 2001). In *Luolishania* and *Cardiodictyon* each lobopod terminates in 4–5 claws (Hou and Bergström 1995; Bergström and Hou 2001). The Soom Shale specimen has a pair of curved claws, one being larger than the other. This arrangement is similar to *Onychodictyon* (Ramsköld 1992; Bergström and Hou 2001), *Microdictyon* (Hou and Bergström 1995), *Hallucigenia* (Ramsköld 1992; Hou and Bergström 1995) and *Paucipodia* (Hou *et al.* 2004*a*) where each leg is terminated by one or a pair of claws, although in *Onychodictyon* there is evidence of smaller accessory claws adjacent to the major pair in at least one leg (Ramsköld 1992).

The appendages of the Soom Shale specimen are stout such as those in *Jianshanipodia* and *Hadranax* (Budd and Peel 1998; J. Liu *et al.* 2006). Modified anterior appendages are seen in many Cambrian specimens including *Aysheaia* (Ramsköld and Hou 1991), *Luolishania* (Hou and Chen 1989), and possibly *Onychodictyon* (Ramsköld 1992) where frontal appendages appear to be more slender. *Hadranax* has a frontal branched appendage (Budd and Peel 1998). Complex appendages are noted all long the body in the rare lobopod *Jianshanopodia* (J. Liu *et al.* 2006), which also has large frontal appendages. Evidence for modified anterior appendages is lacking in *Microdictyon*, *Cardiodictyon* and *Xenusion* (Ramsköld 1992). The Soom Shale specimen appears to only have complex modified appendages in the anterior of its body; the more posterior appendages are simple. The exact structure of the appendages is unclear, but some branching does occur on at least one

appendage, which may be similar to the branched frontal appendage of *Hadranax* (Budd and Peel 1998).

The overall specimen size, cylindrical body with annulations and the stoutness of the appendages, with more complex lobopods occurring anteriorly indicates that the Soom Shale specimen is most similar to *Jianshanipodia*, *Hadranax* and *Aysheaia*, but differs from these genera by not possessing tubercles. However, this may be taphonomic, because unusually the Soom Shale internal soft tissues are preserved more frequently than external cuticular features. In possessing claws it differs from *Jianshanipodia*, *Xenusion* and *Hadranax*. There is no evidence that anterior appendages are directed to the side as opposed to downwards as in *Aysheaia* (Bergström and Hou 2001).

Although features including annulations and fleshy unjointed lobes place the specimen within the xenusiid lobopodians, a group which currently consists of Cambrian organisms alone, the specimen does not possess any features that definitively place it within any of the currently described genera. Also, the specimen does not possess any novel features that make it distinct and, therefore, it cannot be placed in a new genus or species; its familial relationships cannot be resolved on the basis of observable features. Because of these limitations, the specimen is not named below order level, but additional specimens may resolve its affinities.

PRESERVATION

The centre of the trunk and appendages on the left are preserved in positive relief; some of these appendages also have flat film-like preservation towards their termination. Wherever positive relief occurs, the opposing side, part or counterpart has negative relief. The appendages on the right side of the body are preserved two-dimensionally as mineral films on both the part and the counterpart (Figs 5.1; 5.2). The area of positive relief of the main body has elevated levels of Si, Al and K and is thus composed of clay minerals, probably illite ($(KAl_3Si_3O_{10}(OH)_2)$ (Fig. 5.4). In most areas the appendages have an elevated abundance of sulphur relative to the sediment (Fig. 5.5), but are additionally composed of Si, Al and K, which are also found in the sediment. The occurrence of sulphur could be consistent with the presence of alunite ($KAl_3(SO_4)_2(OH)_6$), previously identified in fossils from the Soom Shale by Gabbott (1998), in addition to a clay mineral signature. On the left hand side of the body the appendages are preserved with relief on both part and counterpart, whereas appendages on

the right hand side are preserved as thin mineral films on both part and counterpart; decay induced collapse appears to have occurred before mineralization in the latter case.
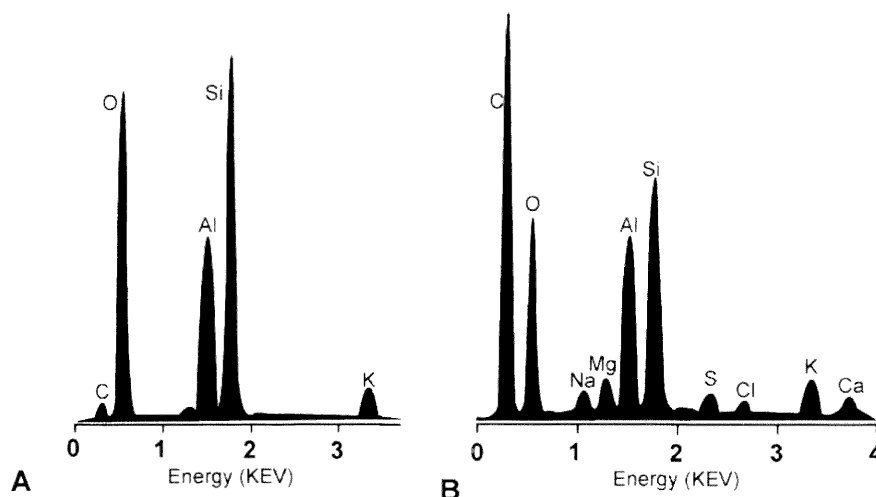


**Figure 5.4.** SEM EDX traces from C1974 a. **A.** Clay mineral signature of the main body of C1974, peaks in Si, K and Al are probably consistent with the presence of illite. **B.** Carbon plus clay mineral signature for organic preservation in gut region of C1974 a (labelled **o** on Fig. 5.2).

An elevated concentration of Fe appears around areas of positive relief, on the appendages of the left side of the body and along the margins of the body; there is no correlation between Fe and S distribution (Fig. 5.5B–D; H –J). However, Fe abundance is correlated with S on the two-dimensional appendages on the right side of the body (Fig. 5.5E–G). This pattern may be explained by pyritization of the nonmineralized tissues, followed by oxidation of the sulphides in localized areas; a similar mode of preservation was described by Gabbott et al. (2004) in the Chengjiang biota. Fe enrichment is most prevalent surrounding areas of positive relief, and/or on the margins of structures, suggesting that it may have preserved the more recalcitrant original cuticular tissues, which would have surrounded the more labile soft tissues. This explains why the pyrite film of the two-dimensional appendages on the right side of the body preserves the clearest annulations on the specimen. This selective preservation of more recalcitrant tissue has been noted in other Lagerstätten where pyritization occurs. Pyritization is known to preserve arthropod cuticle in the Hunsrück Slate (Briggs et al. 1996) and Beecher's Trilobite Bed (Briggs et al. 1991a) but there is no known record of pyrite replacing labile tissues such as muscle (Canfield and Raiswell 1991). In C1974 it appears that alunite and clay minerals, which occur over the majority of the positive relief on the specimen, preserve the soft tissues of the organism.

The gut trace appears as a raised area along the axis of the organism; generally it has the same clay mineral composition as the main body. However, in some places where the overlying sediment has been removed a darker colouration is evident and this correlates with enriched sulphur (Fig. 5.6). In a couple of areas (Figs 5.2; 5.4B), there is a small amount of organic carbon preservation in the region of the gut. Again, this elevated sulphur may be related to alunite preservation and/or to pyritization. Alternatively, the preservation of the gut trace could be related to the sulphurization of organic carbon, in a similar manner to that suggested by McNamara *et al.* (2006). This can occur very early in diagenesis, potentially before microbial degradation of extremely labile tissues (McNamara *et al.* 2006).

In the Soom Shale soft-tissue is preserved rapidly after death by authigenic clay mineralization (Gabbott *et al.* 2001) whereas original biominerals, for example aragonite, calcite and apatite have been completely dissolved leaving moulds, which are subsequently compacted (Gabbott 1998; Gabbott *et al.* 2001). Many of the systematic characters of fossil lobopods are cuticular and, because specimen C1974 preserves mostly labile, non-cuticular anatomy, comparison with other species is difficult. External ornamentation such as tubercles, nodes and sclerites are absent, either because they are not preserved or because they were not present on the organism. Annulations are present on a few areas on the body, an indication that some surficial characteristics have the potential to be preserved. The presence of a gut and the preserved soft-tissues of the organism indicate that the specimen is a body fossil and not a moult.

**Figure 5.5.** (overleaf) SEM EDX analysis C1974a. The maps show that iron occurs in greatest abundance in different areas to where sulphur occurs in greatest abundance (B. – D.; H. – J.), except on the mineral films which preserve the appendages on the right side of the body (E. – G.). **A.** The locations of SEM analyses B.–J. are shown on the camera lucida drawing of the specimen; the area of SEM analysis for Fig. 5.6 is also shown. For the SEM EDX element maps C., D., F., G. and I. light areas indicate a relative high abundance of each respective element. **B.** Back scattered electron image of distal tip of appendage a7, the label **pr** refers to the area of positive relief. **C.** Sulphur **D.** Iron **E.** Back scattered electron image area of appendage on right side of body opposite a7 and a6, **aan** highlights the appendage annulations, **map** highlights the margin of the appendage. **F.** Sulphur **G.** Iron **H.** Back scattered electron image of distal area of appendage a6, pr highlights the area of positive relief. **I.** Sulphur **J.** Iron.
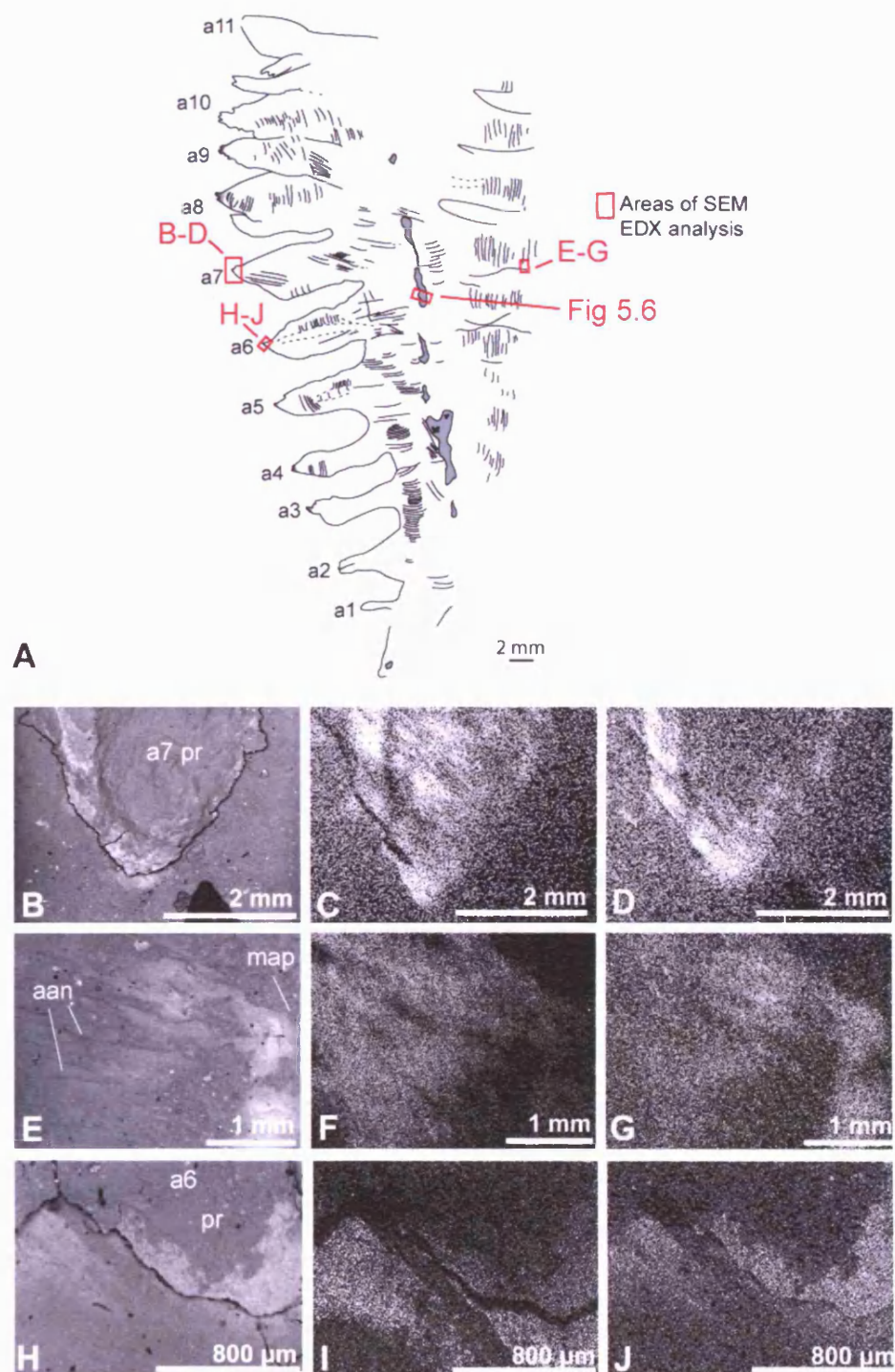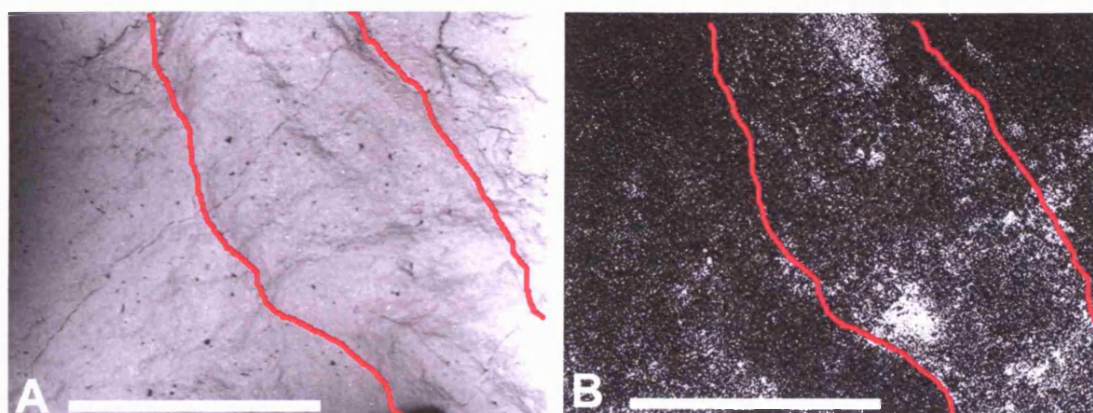
**Figure 5.6.** SEM EDX analysis of gut trace of C1974a (location of this SEM analysis is shown in Fig. 5.5A). The gut can be seen as a raised axis down the centre of the specimen, which is darker than the surrounding sediment in some places and is shown enclosed in the red lines, as the area of positive relief does not show clearly in the back scatter image. **A**. Back scattered electron image and **B**. SEM EDX element map where light areas indicate a relative high abundance of sulphur; scale bars = 2 mm. Elevated levels of sulphur are seen in patches, coincident with other elemental abundances indicative of a clay mineral composition.

## DISCUSSION

The morphology of Cambrian lobopodians, along with their occurrence with other taxa has led to their interpretation as benthic (Bergström and Hou 2001) or epibenthic organisms (Chen *et al*. 1995), and carrion feeders (Hou and Bergström 1995; Bergström and Hou 2001; Hou *et al*. 2004*a*, *b*). *Aysheaia* specimens have commonly been found associated with sponges (Whittington 1978) and several specimens of *Hallucigenia* have been found on organisms of unknown affinity (Conway Morris 1977). *Paucipodia* and *Microdictyon* have been found compressed on *Eldonia* specimens (Bergström and Hou 2001) and eldoniids have been interpreted as living on the sea-bottom (Dzik *et al*. 1997). However, Chen and Zhou (1997) suggested that *Eldonia* may have been pelagic, and the specimens of lobopodians found in association with *Eldonia* were thus pseudopelagic.

   Whilst the Soom Shale specimen has not been found in association with any other taxa, its morphology is consistent with it being benthic. Gabbott (1998) indicated that there was intermittent water oxygenation during the deposition of the Soom Shale, which means conditions could be hospitable for rare benthic taxa. It is possible that the organism fed

directly on algal material seen to cover most bedding planes or it may have fed on carrion. This would increase the already large number of taxa from the Soom Shale that have been identified as active scavengers/predators.

The vast majority of fossil lobopods occur in the Cambrian marine environments of the Chengjiang biota and Burgess Shale. This discovery provides evidence that the lobopodians were also present in marine environments during the Late Ordovician. The Carboniferous fossil onychophoran *Helenodora* could be from a terrestrial, a freshwater or a marine environment (Thompson and Jones 1980). Unequivocal terrestrial lobopodians were identified from Cretaceous amber from Myanmar (Grimaldi *et al.* 2002) and Tertiary Dominican amber (Poinar 1996, 2000). Hou and Bergström (1995) stated that lobopodians could not have become terrestrial organisms much earlier than the Late Silurian due to a lack of potential prey available on land for a successful invasion. This new discovery confirms that lobopodians lived in marine environments beyond the Cambrian at least until the Late Ordovician.

All of the previously described body fossils of xenusiid lobopodians and onychophorans come from warm subtropical and tropical environments. The deposition of the Early Cambrian Chengjiang sediments took place in relatively shallow, tropical, shelf seas (Babcock *et al.* 2001); the middle Cambrian Burgess Shale marine lobopodians are thought to have lived close to the palaeo-equator (Conway Morris 1979), and the Carboniferous Mazon Creek lobopodian *Helenodora* existed at a site that was within 10° of the palaeo-equator (Ziegler *et al.* 1979; Rowley *et al.* 1985; Schellenberg 2002) and had a warm, wet climate (Schopf 1979; Phillips and Dimeichele 1981; Phillips *et al.* 1985; Schellenberg 2002). The terrestrial onychophoran specimens from the Dominican amber were preserved in Northern Europe, during the tropical climate of the Eocene (Poinar and Poinar 1999, Poinar 2000). Present day onychophorans occur sporadically and discontinuously in tropical to subtropical regions and in wet temperate regions of the southern hemisphere (Meglitsch 1972; Reinhard and Rowell 2005). The fossil record of isolated sclerites, which have been identified as phosphatized lobopodian plates, is diverse and widespread during the early Cambrian (Zhang and Aldridge 2007). Occurrences have been documented from Asia, northwest Europe, north and central Europe, north and central America (Bengtson *et al.* 1986), Australia (Bengtson *et al.* 1986; Bengtson 1990), England (Hinz 1987; Hinz-Schallreuter 1997), Mexico (McMenamin and McMenamin 1990) and from localities in China (Tong 1989; Ramsköld 1992; Li and Ding 1996; Li and Zhu 2001; Zhang and Aldridge 2007). This widespread diversity of lobopodian plates indicates a wider distribution of Cambrian lobopodians outside

of subtropical regions. The evidence presented here demonstrates that lobopodians could inhabit cooler, non-tropical waters and lends support to the evidence from lobopodian plates that lobopodians had a much wider distribution than their current body fossil record indicates.

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**Chapter 6**

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# NEW ARTHROPODS FROM THE SOOM SHALE LAGERSTÄTTE, LATE ORDOVICIAN, SOUTH AFRICA

**Abstract:** Arthropods are the most diverse phylum in the Soom Shale Lagerstätte, and are currently represented by numerous specimens. To this substantial arthropod community three new groups are added, increasing this diversity. Large bivalved carapaces occur that may be compared with several fossil groups, but have no internal preservation that proves a definitive relationship. A long segmented arthropod fossil exhibits different types of appendages, which may have been used for swimming and feeding. The exact affinities of this organism cannot be determined due to the poor quality of the fossil material. An elongate arthropod fossil with unusual features is also described, but the specimen is poorly preserved. The organism had large, robust and jointed uniramous first appendages, however there is currently not enough evidence to confirm a relationship within the arthropods; the morphology of the specimen suggests that it was a nektonic predator.

ARTHROPODS from the Soom Shale Konservat Lagerstätte exhibit a great degree of diversity, and most of the taxa described to date represent new species. The arthropods currently known include trilobites (Cocks and Fortey 1986), naraoiids (Fortey and Theron 1994), eurypterids (Braddy *et al.* 1995, 1999), ostracods (Gabbott *et al.* 2003) and caryocaridids (Whittle *et al.* 2007), as well as partial arthropods and specimens as yet unidentified. Many of the taxa, for example the myodocopid ostracods and the caryocaridids, are of evolutionary and palaeoecological importance (Gabbott *et al.* 2003; Chapter 2; Whittle *et al.* 2007), and some of the specimens, for example the eurypterids, exhibit remarkable soft-tissue preservation (Braddy *et al.* 1995, 1999). In this contribution three new arthropods are described; their preservation and palaeoecology are discussed.

## ARTHROPODS FROM THE SOOM SHALE: A REVIEW

The Soom Shale arthropod fauna includes the trilobite *Mucronaspis olini* Temple, 1952, the material of which comprises two imperfect dorsal exoskeletons, a large cephalon and fragments of exoskeleton (Cocks and Fortey 1986). The specimens were discovered from near the base of the Soom Shale at Buffels Dome (19°50'E, 33°30'S) (Moore and Marchant 1981) (Fig. 1.1).

Thirty-six specimens of the naraoiid species *Soomaspis splendida* Fortey and Theron, 1994 have been identified; the genus and species are endemic to the Soom Shale Lagerstätte. Specimens have been collected from Soom Shale sites at Keurbos (18°58'E, 32°15'S) (Fortey and Theron 1994), Kromrivier (19°17'E, 32°32'S) and Sandfontein (19°14'E, 32°40'S) (Fig. 1.1). Cladistic analyses provided evidence that *Soomaspis* and naraoiids are a sister group to the rest of the clade of trilobite-like arthropods (Fortey and Theron 1994).

The ostracod genus and species *Myodoprimigenia fistuca* Gabbott, Siveter, Aldridge and Theron, 2003 known only from the Soom Shale, is the earliest and only Ordovician occurrence of the superorder Myodocopa (Gabbott *et al.* 2003). Specimens have been collected at Keurbos (Gabbott *et al.* 2003) and Kromrivier (Fig. 1.1). The morphology of the ostracods supported evidence that the fossils were a sister group to the Upper Silurian 'cyprinid' myodocopes and allied forms (Gabbott *et al.* 2003).

Twenty specimens of eurypterid have been discovered from the Soom Shale to date, from Keurbos (Braddy *et al.* 1995), Kromrivier (Braddy *et al.*1999) and Sandfontein (Fig. 1.1). Some have been assigned to *Onychopterella augusti* Braddy, Aldridge and Theron, 1995 a species unique to the Soom Shale ecosystem. The exceptional preservation of lamellate book gills on some specimens provided a synapomorphy that supported a sister group relationship between eurypterids and scorpions (Braddy *et al.* 1995, 1999).

Two fossils of the phyllocarid species *Caryocaris cedarbergensis* Whittle, Gabbott and Aldridge, 2007, known only from the Soom Shale, were collected from Keurbos and Sandfontein (Whittle *et al.* 2007) (Fig. 1.1). The species was interpreted to represent the last appearance of an Ordovician caryocaridid genus, occurring after a long gap in their fossil record (Whittle *et al.* 2007). The specimens represented the first identified caryocaridids from the South African margin of palaeocontinental Gondwana, and the first evidence of the presence of *Caryocaris* in an icehouse environment, in a possible inner-shelf setting (Whittle *et al.* 2007).

*Palaeoecology of arthropods*

The naraoiids and trilobites were nektobenthic predators and/or scavengers (Aldridge *et al.* 2001). The eurypterids were nektobenthic organisms, being bottom dwelling but with the ability to swim (Braddy *et al.* 1995). Braddy *et al.* (1995) suggested that eurypterids may have been the top predator in the Soom Shale ecosystem, probably feeding on other arthropods, worms and possibly conodonts. Evidence from bromalites from the Soom Shale has indicated the presence of a durophagous predator in the Soom Shale community, and eurypterids are a possible contender for the production of these bromalites (Aldridge *et al.* 2006). Ostracods were found in association with orthoconic cephalopods, suggesting that they fed on cephalopod carrion as nektobenthic scavengers, extending the evidence of this lifestyle in ostracods back by 200 million years (Gabbott *et al.* 2003). It was hypothesised that the caryocaridids from the Soom Shale represented an epipelagic cold-adapted stenothermic group and were zooplanktonic organisms, of which there are very few representatives in the Soom Shale community (Whittle *et al.* 2007).

*Preservation of arthropods*

There is no evidence to suggest that any significant lateral transport of Soom Shale specimens took place before they reached the sea floor, as conodont assemblages remain fully articulated, fossils remain randomly aligned, epibenthic brachiopods remain attached to orthocones and soft tissues, which would have decayed during prolonged floating, are preserved in several organisms (Gabbott 1998). Also, ostracod specimens have co-joined valves, which would have been disarticulated had transport occurred (Gabbott *et al.* 2003).

Preservation of the arthropods in the Soom Shale is variable, but many of them, for example the naraoiids and trilobites, are preserved as internal and external moulds with no trace of the original exoskeleton (Moore and Marchant 1981, Cocks and Fortey 1986, Gabbott 1998). Ostracods in the Soom Shale have been preserved through early diagenetic mineralization by clay minerals, and shell microstructure can be discerned in some specimens (Gabbott *et al.* 2003). Exfoliation of mineral layers occurs on some specimens, exposing folded cuticle below (Gabbott *et al.* 2003). Most of the eurypterids in the Soom Shale are also preserved as internal and external moulds, but a few have exoskeletal material present that has been replaced by clays and alunite group minerals (Gabbott 1998; Gabbott *et al.* 2001). Rarely, in some specimens, traces of internal soft tissues are preserved, including

muscular tissue associated with the appendages and telson, respiratory structures (areas of the branchial chambers) and an apparently spiral valve in the anterior part of the alimentary canal (Braddy *et al.* 1995). The carapaces of the two caryocaridid specimens are preserved with no internal tissue or furcal rami. There are distinct layers of the clay mineral illite and alunite in both carapaces and one specimen also shows a carbon layer. It is suggested that this might represent layers of the carapace, but the illite, which is fibrous, may represent a mineral overgrowth (Whittle *et al.* 2007).

The arthropods from the Soom Shale show a variety of taphonomic pathways. These include situations where the original biominerals have been completely dissolved leaving moulds, which were subsequently compacted (Gabbott 1998; Gabbott *et al.* 2001). In other cases, authigenic replication of the fossil material, including soft tissues, has occurred through replacement by clay minerals (Gabbott 1998; Gabbott *et al.* 2001), although this mode of preservation has been questioned (Butterfield *et al.* 2007). There is also alunite replacement of fossil material and some organisms are preserved as organic films with associated clay mineralization (Gabbott 1998; Gabbott *et al.* 2001). Generally, for the arthropods, as well as for other organisms from the Soom Shale, the highest fidelity preservation occurs where clays have templated internal soft tissues (Gabbott *et al.* 2001). Whilst this provides spectacular details of easily decayed tissues, this mode of preservation does not preserve the external, more recalcitrant morphology of the organisms. It is these unpreserved external features that usually provide the most important evidence of the precise affinities of fossil arthropods.

GEOLOGICAL SETTING

The Soom Shale Member is part of the Table Mountain Group, and outcrops in the Cedarberg Mountains, South Africa. It directly overlies tillites of the glaciogenic Pakhuis Formation and has thus been interpreted as a post glacial transgressive unit, possibly deposited during the *persculptus* graptolite zone of the Hirnantian (Late Ordovician) (Sutcliffe *et al.* 2000; Young *et al.* 2004). The depositional setting is thought to have been in a quiet water basin close to a retreating ice front (Theron and Thamm 1990); dropstones at the base of the unit indicate cold water conditions. The Soom Shale is bounded by subaerial tillites below and shallow marine siltstones above and the depositional basin was in an intracratonic setting, therefore the depth of the water was unlikely to have been great (Gabbott 1999) and a depth of at least 100m has been suggested based on a lack of sedimentary structures (Gabbott 1999); this would represent an inner shelf setting.

A lack of flow-induced sedimentary structures and the taphonomy of the fossils indicate that water conditions were predominantly quiet. Geochemical analyses of trace elements such as molybdenum and degree of pyritization showed that the Soom Shale sediment was anoxic, and that euxinic bottom waters prevailed at times, although oxygenated bottom waters also occurred intermittently (Gabbott 1998; Gabbott *et al.* 2001). Metamorphism has transformed the shale and siltstone into a sheared slate in some areas, destroying primary internal features (Aldridge *et al.* 1994).

As well as exceptionally preserved arthropods, the Soom Shale is also known for invertebrates such as brachiopods (Aldridge *et al.* 1994) and orthoconic cephalopods (Gabbott 1999) and early vertebrates such as conodonts (Theron *et al.* 1990; Aldridge and Theron 1993; Gabbott *et al.* 1995) and agnathans (Aldridge *et al.* 2001). Algae and enigmatica (Aldridge *et al.* 2001) have also been discovered.

## MATERIALS AND METHODS

The repository of the specimens (prefixed C) used in this study is the Council of Geosciences of South Africa, Belville. Large bivalved carapaces (specimen numbers C1321 and C914, which is incomplete) were collected from Sandfontein (19°14'E, 32°40'S). There are several other fossils in the Soom Shale collections that may have an affinity with the large bivalved carapaces (see Appendix v), but these are not included in this discussion because they are very poorly preserved and also in some cases because their morphology differs slightly from C1321 and C914. Another new arthropod group is represented by C1707, collected from Keurbos Quarry (18°58'E, 32°16'S) near to the town of Clanwilliam, South Africa. The fossil is incomplete at both the anterior and posterior ends. C1927, part and counterpart, also discovered at Keurbos Quarry, represents the third type of new arthropod and this fossil is incomplete at the posterior end.

The fossils were studied using an optical microscope, drawn with the aid of a camera lucida, and photographed using a digital camera and Scanning Electron Microscope. Analysis was carried out using scanning electron microscope energy dispersive X-rays (SEM EDX) with a Hitachi S-3600N. For SEM EDX analysis uncoated material was used in partial vacuum mode at 15Kv. Elemental mapping was used to show the relative abundance of elements in different areas of the fossils and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) of the fossil to be determined, from different areas on the specimens and from the sediment.

RESULTS

*Bivalved Carapaces*

*Description.* Carapaces with a maximum preserved length of 37 mm measured on C1321 (32.5 mm on C914, incomplete) and a height of 18.5 mm (19.5 mm C914). The carapaces are sub ovate in lateral view, the straight edge of the carapace is interpreted as the dorsal margin, the ventral margin is curved with a clear doublure that has a uniform width of 0.4 mm. The carapace has some relief (2–3 mm) on the part (C1321a), and this is greatest in the centre and towards the posterior of the carapace. The carapace becomes less inflated towards the anterior margin.

On both carapaces, the posterior and central parts are preserved in positive relief, and towards the anterior the fossils are preserved in two-dimensions. The two-dimensional areas of the carapace are smooth whilst the positive relief areas are uneven and irregular, which is possibly a taphonomic feature. On C1321b, there is a well-defined curved line (shown as 'l' on Fig. 6.1B) towards the anterior margin of the fossil. This line is convex towards the anterior, and can be seen to extend from the dorsal margin for two-thirds of the carapace height. This line appears to mark a change from the positive relief preservation to the two-dimensional preservation. Beyond this line the fossil continues, and appears to taper to a point, but it becomes less clear (Fig. 6.1). On C914 the anterior margin is similar in shape to the well-defined line on C1321; it is very probable that the carapace extended beyond this, in a similar manner to C1321. The posterior margin of C1321 is clearer and more rounded; on C914 it is not preserved. On C1321 there is a gap in the posterior margin of the carapace, and there is a similar gap in the anterior margin of C914 (Fig. 6.1). As these gaps occur in different areas on the two carapaces, they are likely to be taphonomic features rather than reflecting morphology.

*Remarks.* Bivalved carapaces occur in many arthropod groups and can exhibit similar external morphology (Siveter *et al.* 1995); because C914 and C1321 lack crucial diagnostic internal features including appendages and have no evidence of eyes or telsons they are difficult to assign. The possible relationships of the Soom Shale specimens to other bivalved arthropods are considered below, but a definitive relationship cannot be confirmed. The only other carapaces described from the Soom Shale belong to the caryocaridids (Whittle *et al.* 2007;

Chapter 2). The new carapaces clearly differ from the *Caryocaris* specimens as they are much larger, and do not possess a pronounced horn-like rostrum.

Leperditicopid arthropods are large bivalved organisms known as fossils from the Ordovician to the uppermost Devonian. These arthropods were a recurrent constituent of communities associated mainly with shallow marginal habitats that were subjected to environmental stress, for example tidal flats, reef-flats, lagoons, embayments, or estuarine complexes (Vannier *et al.* 2001). Taxonomic relationships of the group remain inconclusive due to a lack of soft-part preservation (Vannier *et al.* 2001). Adult leperditicopid specimens range from five to about 50 mm in length (Vannier *et al.* 2001), which encompasses the size of the Soom Shale carapaces. Some leperditicopid arthropods have valves that are equal sized, with a range of carapace designs from highly lobate and ornamented to smooth. Others have an asymmetric carapace with no pronounced structure except a tiny eye tubercle (Vannier *et al.* 2001), a feature not seen on the Soom Shale carapaces.

An Ordovician ostracod-like carapaced arthropod was described from the Tremadoc of Central England by Siveter *et al.* (1995). This specimen has an apparent gap in the anterior margin of the valves and an adjacent overhang, which Siveter *et al.* (1995) stated may be homologous to the rostral incisure and the dorsally projective rostrum of many myodocopid ostracods (Siveter *et al.* 1995). The carapaces from the Soom Shale do not appear to show these features. There are gaps in the margin of the specimens, but these are regarded as taphonomic features. There is also no evidence of a rostrum on either of the Soom Shale carapaces. The Tremadoc arthropod carapace is also of a much smaller size; the maximum length and height of the specimens is ca. 2250–1650 µm and ca. 1950–1100 µm (Siveter *et al.* 2001). Therefore, an affinity with the carapaced arthropod of Siveter *et al.* (1995) has been discounted.

Thylacocephalans were relatively large bivalved arthropods, which ranged in size from approximately 15 mm to 250 mm. They had a segmented body that was almost entirely enclosed within a laterally compressed carapace (Vannier *et al.* 2006). The carapaces tend to be ovoid, typically with an anterior rostrum-notch complex; a posterior rostrum may almost be present. Thylacocephala or bivalved arthropods that could be interpreted as such have been identified from the Lower Silurian to Upper Cretaceous (Mikulic *et al.* 1985; Schram *et al.* 1999, Vannier *et al.* 2006), and Vannier *et al.* (2006) proposed that some Cambrian arthropods also have thylacocephalan affinities; however the group currently has no record in the Ordovician (Vannier *et al.* 2006). The reason for this is unknown but Vannier *et al.* (2006) suggested that the absence of fossil sites in shallow water settings with suitable

conditions for their preservation might well be a factor. The Soom Shale has been interpreted as a shallow water setting, and the specimens are within the thylacocephalan size range; however, the Soom Shale specimens do not possess rostra and do not appear to have an anterior notch.

There are several carapaced arthropods reported from the Burgess Shale of Canada and the Chengjiang biota, China. Some have an abdomen and tail that extend beyond the carapace, whereas others have a carapace that covers all or nearly all of the body (Briggs *et al.* 1994; Hou *et al.* 2004*b*). The Soom Shale carapaces are similar in external morphology to some of these Cambrian carapaces, for example *Canadaspis*, which is found from the Burgess Shale and Chengjiang biota (Briggs *et al.* 1994; Hou *et al.* 2004*b*). However, without any preserved internal features, telsons or appendages relationships with other groups cannot be adequately assessed.
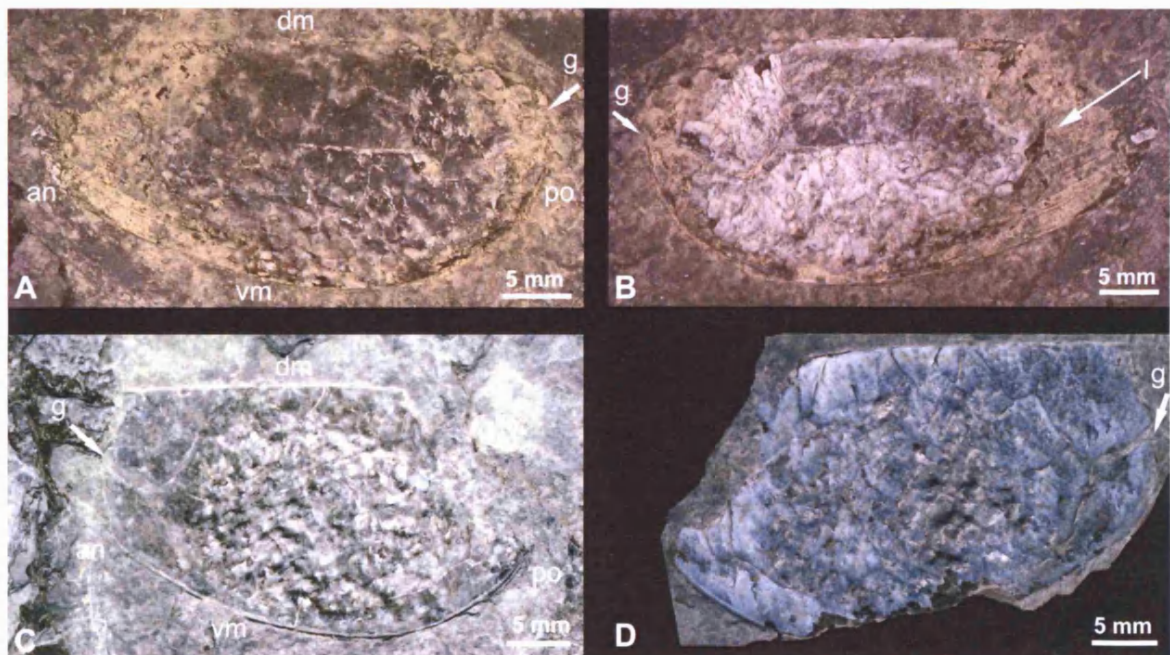


**Figure 6.1.** Large bivalved carapaces from Soom Shale Lagerstätte. **A.** and **B.** C1321a and C1321b respectively. The specimen has a gap (labelled g) in the posterior margin, and a clear line (labelled l) towards the anterior of the fossil. **C.** and. **D.** C914a and C914b respectively. C914 is incomplete posteriorly and possibly anteriorly, there is a gap (labelled g) towards the anterior of the fossil. **dm** = dorsal margin; **vm** = ventral margin; **an** = anterior; **po** = posterior.

*Preservation.* Both of the carapaces occur in grey-black siltstone and neither have any associated soft-tissues or appendages. C1321 is complete, but C914 is incomplete posteriorly

and possibly also anteriorly (Fig. 6.1). The preservation of both of the specimens is extremely complex. On the parts of both specimens patches of organic carbon and possibly alunite are preserved (Fig. 6.2). A layer of clay minerals (enriched in the elements Si, Al and K), generally with a fibrous habit, appears above and below the carbon (Figs 6.2; 6.3A, B, D). On the counterparts the specimens are covered by a thick mat of extremely fibrous clay minerals. The underlying carbon is revealed in some areas, and there is some possible alunite preservation as well (Figs 6.3C, E; 6.4).

Due to the transgressive nature of the split of the fossil, the part and counterpart of the specimens show different aspects of an overall three-dimensional structure. In places over the carapace weathering has destroyed the organic and alunite mineral films. That the fibrous clay minerals occur above and below the carbon on the part, and in a thick layer above the carbon layer in the counterpart suggests that the clay minerals grew around the organism in a similar manner to that described in the *Caryocaris* specimens (Chapter 2, Whittle *et al.* 2007).

The similarity of preservation styles between *Caryocaris* carapaces, C1321 and C914 may relate to the mechanism by which different parts of an arthropod carapace are replicated by minerals in the Soom Shale. It may also relate to how the more rigid carapaces are subject to an overgrowth of minerals during diagenesis or metamorphism. It has been seen that the slightly more resistant fossils from the Soom Shale, for example *Caryocaris* (Chapter 2, Whittle *et al.* 2007) and scolecodonts (Chapter 4), are subject to areas of preservation of organic material (carbon with an associated clay mineral signature) and areas of fibrous clay mineral preservation. Many of the softer body fossils in the Soom Shale are now preserved in non-fibrous clay minerals.

Elemental mapping shows that C1321 has a coating of pyrite over the entire carapace and in the surrounding sediment (Figs 6.2; 6.5). This mode of preservation was not seen in the caryocaridids, nor is it present in any other Soom Shale specimens to such a degree. Cubes can be seen at higher magnification (Fig. 6.5B) and they appear to overlie and coat the organic and clay mineral layers, indicating that the pyrite did not replicate a particular part of the carapace (Fig. 6.2). The oxidation of this pyrite may be responsible for the yellow halo seen around C1321, which is uncommon in Soom Shale specimens.
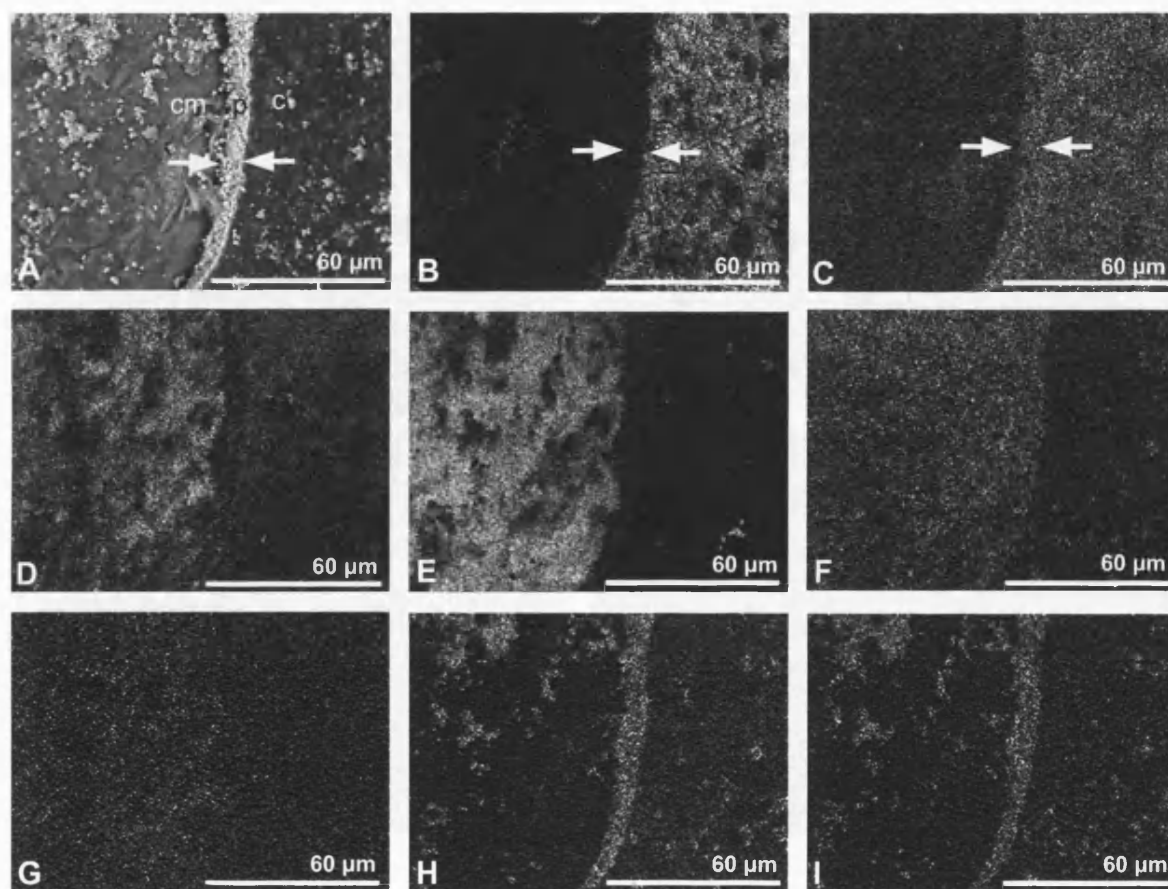
**Figure 6.2.** SEM analysis of carapace of C1321a. **A.** SEM back scattered electron image of area on the carapace. The carapace has layers with different compositions: a carbon rich top layer (labelled **c**); a layer enriched in phosphorus (possibly related to alunite preservation) below the carbon (labelled **p**), shown between the white arrows on A–C; a lower layer that is fibrous and has a clay mineral composition (labelled **cm**). B. – I. SEM EDX element maps where light areas indicate a relative abundance of each element. **B.** Carbon. **C.** Phosphorus. **D.** Aluminium. **E.** Silica. **F.** Potassium. **G.** Magnesium. **H.** Sulphur. **I.** Iron. The elevated region of phosphorus (map C) extends slightly beyond that for carbon (map B), where the carapace steps down to the level below. Phosphorus also appears in the carbon layer, possibly due to beam penetration. Elevated abundances of sulphur and iron are coincident, indicating that pyrite overlies all layers of the carapace.
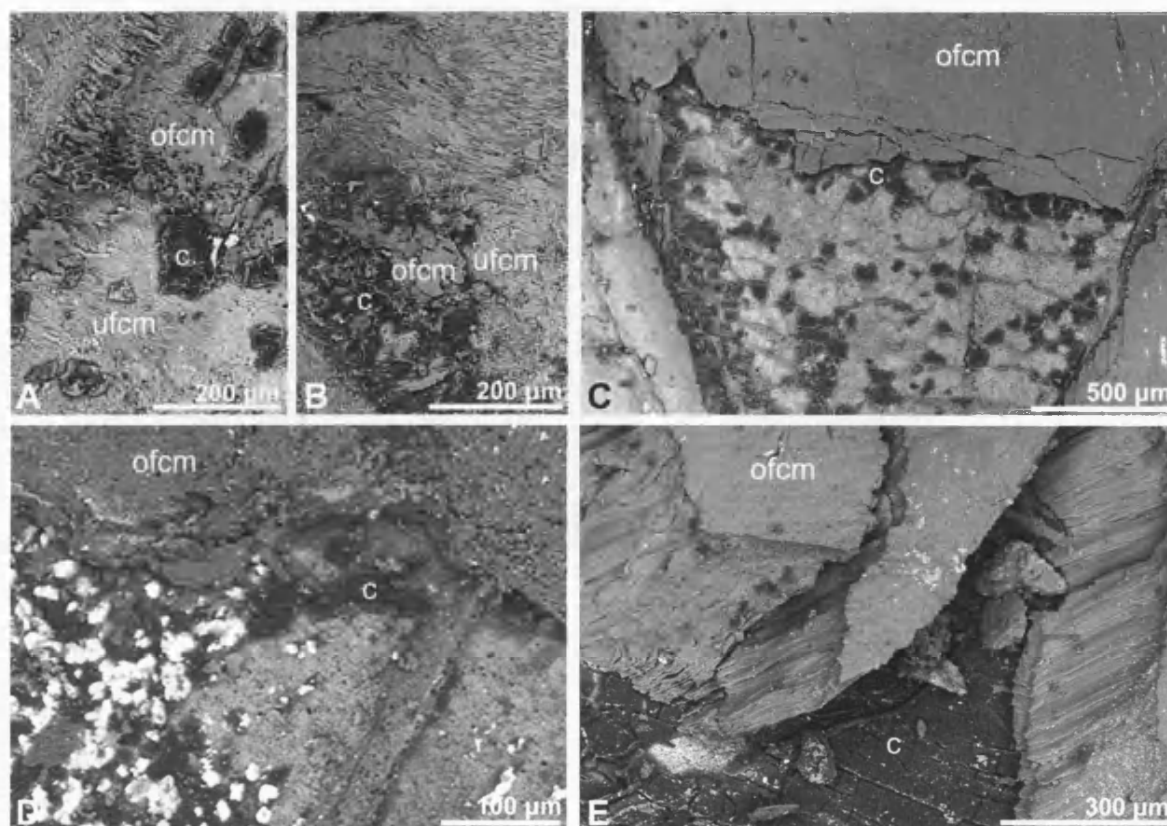
**Figure 6.3.** SEM back scattered electron images of large carapaces from the Soom Shale. **ufcm** = underlying fibrous clay minerals; **ofcm** = overlying fibrous clay minerals; **c** = carbon. From the evidence preserved from different areas in both C914 and C1321, it appears that fibrous clay minerals overlie the organic preservation in both of the carapaces. **A.** and **B.** C914a small patches of cracked carbon are overlain and underlain by fibrous clay minerals. **C.** C914b patches of cracked carbon are overlain by fibrous clay minerals **D.** C1321a fibrous clay minerals overlie carbon **E.** C1321b a thick mat of fibrous clay minerals overlies carbon.
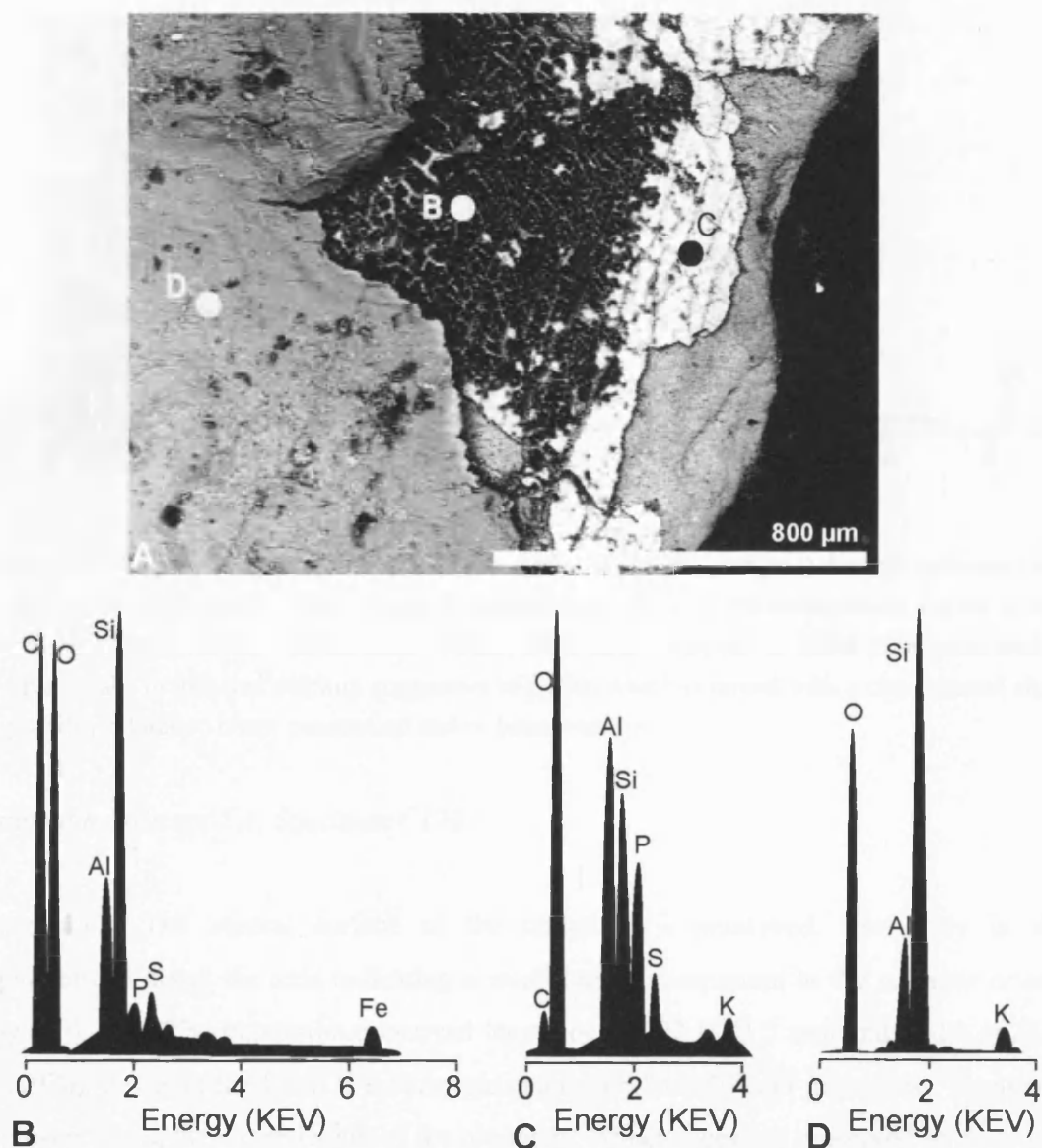
**Figure 6.4. A.** SEM back scattered electron image of carapace (C914b) showing location of SEM EDX traces B–D. **B.** SEM EDX spectrum for the dark layer of the carapace shows elevated carbon along with a clay mineral composition. **C.** SEM EDX spectrum for the light layer of the carapace shows elevated phosphorous, possibly related to alunite preservation (*cf.* Whittle *et al.* 2007) along with a clay mineral composition and carbon. This mixed composition is seen on the part and counterpart of both carapace specimens; it generally occurs below the carbon layer on the counterpart, although it is unclear how it relates to other compositions on the part. **D.** SEM EDX spectrum for the overlying fibrous layer shows that it has a clay mineral composition. The carapace C914 has a carbon-enriched layer overlying a phosphorus rich layer, both of which are sandwiched between layers of clay minerals.
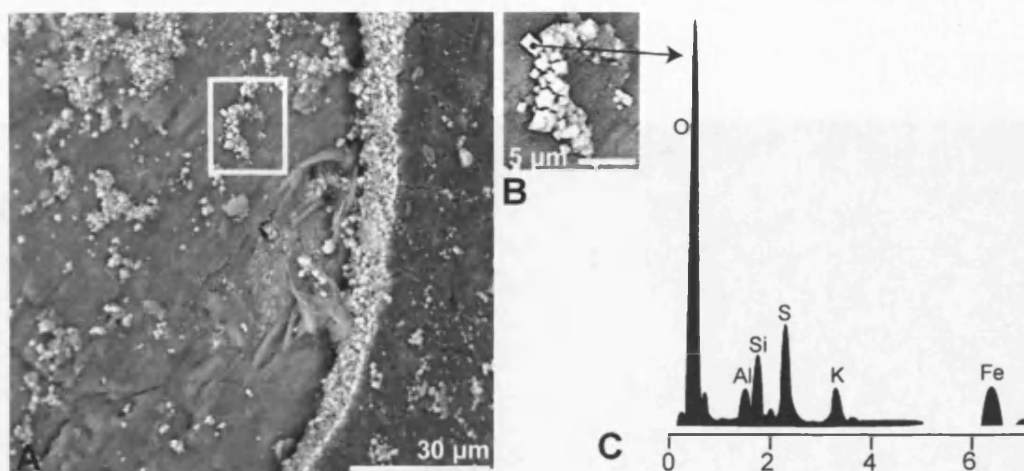
**Figure 6.5.** Pyrite on C1321a. **A.** SEM back scattered electron image. All of the carapace layers are covered with pyrite. The rectangle indicates the location of the enlargement shown in B. **B.** Enlarged pyrite cubes, with location of SEM EDX point analysis. **C.** SEM EDX point analysis gives peaks in iron and sulphur, suggestive of pyrite, which is mixed with a clay mineral signal, possibly related to beam penetration and/or beam overlap.

*Enigmatic Arthropod A: Specimen C1707*

*Description.* The ventral surface of the organism is preserved. The body is slightly asymmetrical about the axis indicating a small lateral component to the collapse orientation (Figs 6.6; 6.7). The maximum preserved length of C1707 is 81.3 mm and width is 25.1 mm (C1707a), however the fossil is incomplete anteriorly, laterally and posteriorly. Segmentation is present along the entire length of the organism. Appendages are preserved on both sides of the fossil, they are directed inwards towards the centre of the organism on both sides of the body; there is one appendage per segment. Appendage types appear to differ along the body indicating regional specialisation.

Towards the anterior of the fossil, there are at least 6 elongate appendages preserved (Figs 6.6; 6.7). These anterior appendages are articulated, with associated structures, including a long thin projection anteriorly, and lobes posteriorly (Figs 6.8A; 6.9A; 6.10A, E). These elongate appendages are interpreted as multiarticulate and biramous, but are only seen on the side of the body that is complete. These appendages are interpreted as being towards the anterior of the fossil and are possibly thoracic appendages. They are not interpreted as the anterior-most appendages as the fossil continues beyond them for at least several millimetres

(Fig. 6.6). Anterior of the thoracic appendages there is no evidence of any cephalic features or antennae, as the fossil is incomplete (Figs 6.6; 6.7).
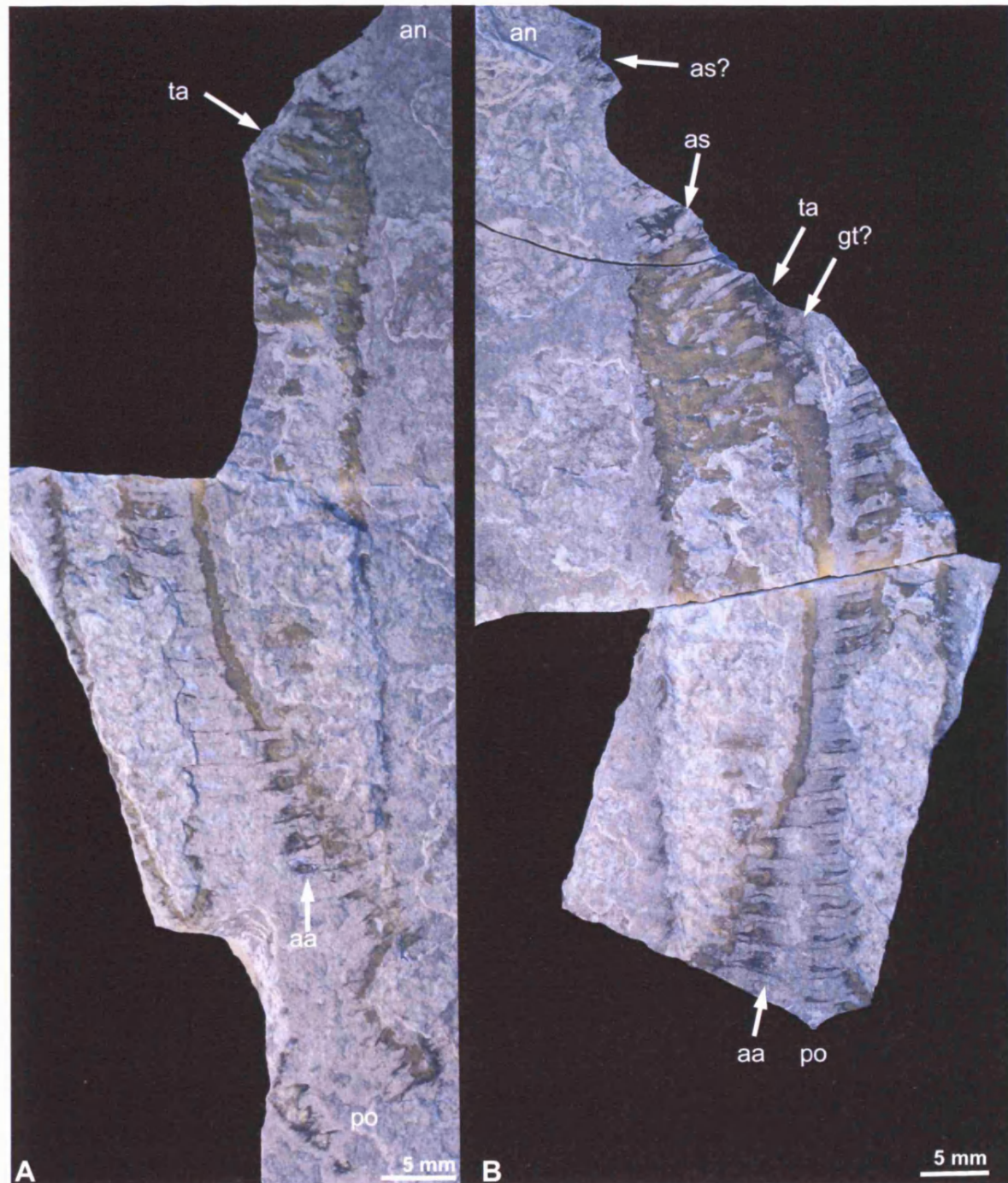


**Figure 6.6.** C1707, with main features labelled, Fig. 6.7 shows more detailed features. The ventral surface of the organism is preserved. The fossil is incomplete anteriorly and posteriorly. **A**. Counterpart **B**. Part. **ta** = thoracic appendages, **aa** = abdominal appendages, **as** = anterior structures, **gt?** = possible gut trace, **an** = anterior, **po** = posterior.
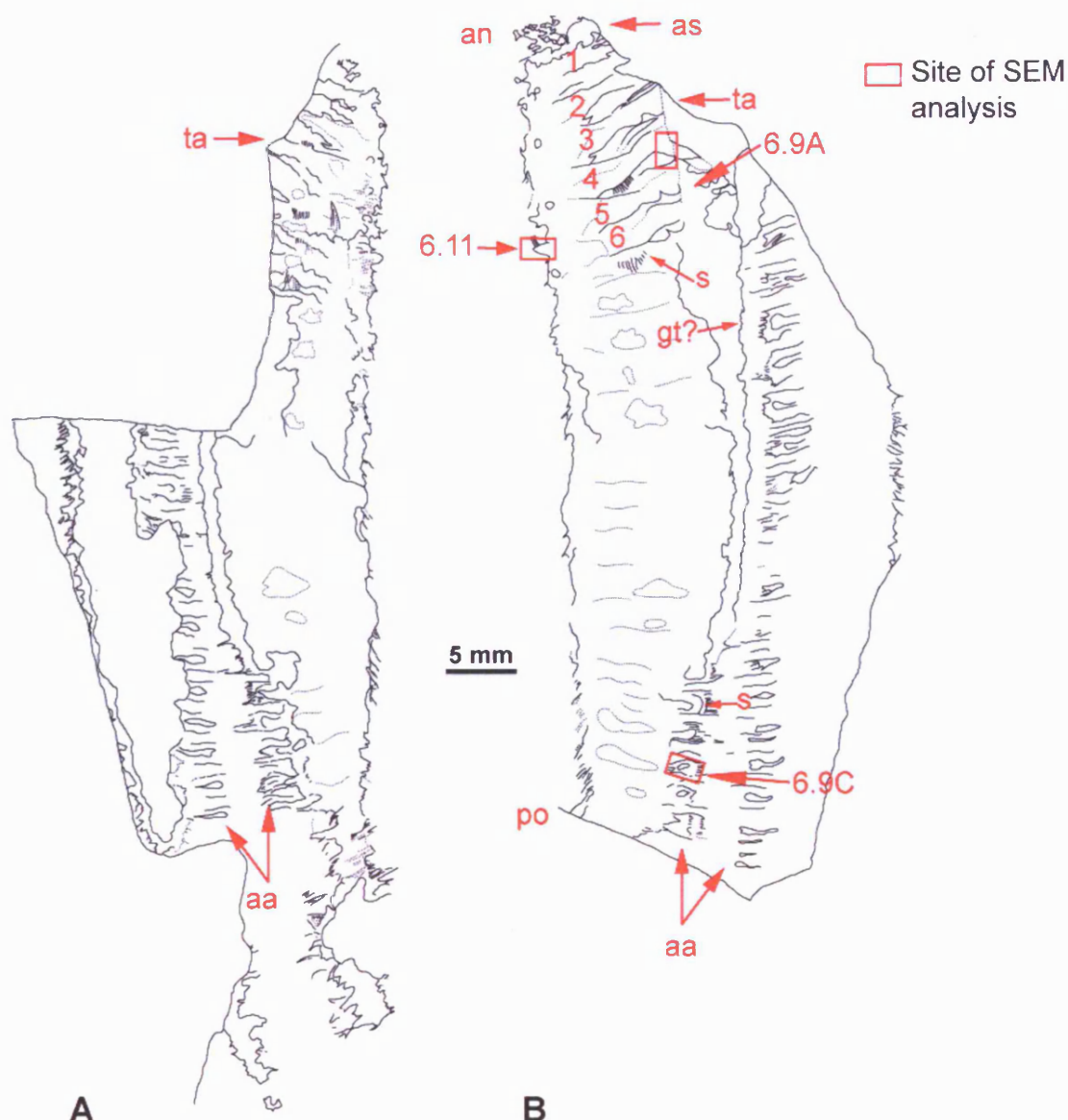
**Figure 6.7.** Camera lucida drawings of C1707, with sites of SEM analysis for Figs 6.9 and 6.11 highlighted. **A.** Counterpart **B.** Part. **ta** = thoracic appendages, which are numbered 1 – 6; **aa** = abdominal appendages; **as** = anterior structure; **s** = setae; **gt?** = possible location of gut trace; **po** = posterior-most area of fossil; **an** = anterior-most area of fossil. The anterior and posterior ends of the fossil are missing.

The elongate appendages do not continue down the length of the organism; instead smaller appendages are seen on both sides of the body, and continue towards the posterior termination of the fossil. These are possibly appendages of the abdomen. Approximately 11 are visible on the left side in C1707a, with 19 on C1707b, and 6 on the right side in C1707a and b (Figs 6.6; 6.7; 6.8B, C; 6.9C). Many of these appendages are obscured and some are not

preserved. These appendages appear paddle-shaped and are setiferous at their termination (Fig. 6.8C). The preservation of these appendages is not very clear, but there appear to be long, thin pointed structures extending next to the main paddle, which might be a second ramus (Figs 6.8B, C). Towards the posterior of the fossil these structures are slightly longer than the paddle-like ramus. The dark band running medially down most of the fossil may be the gut trace (Figs 6.6; 6.7).
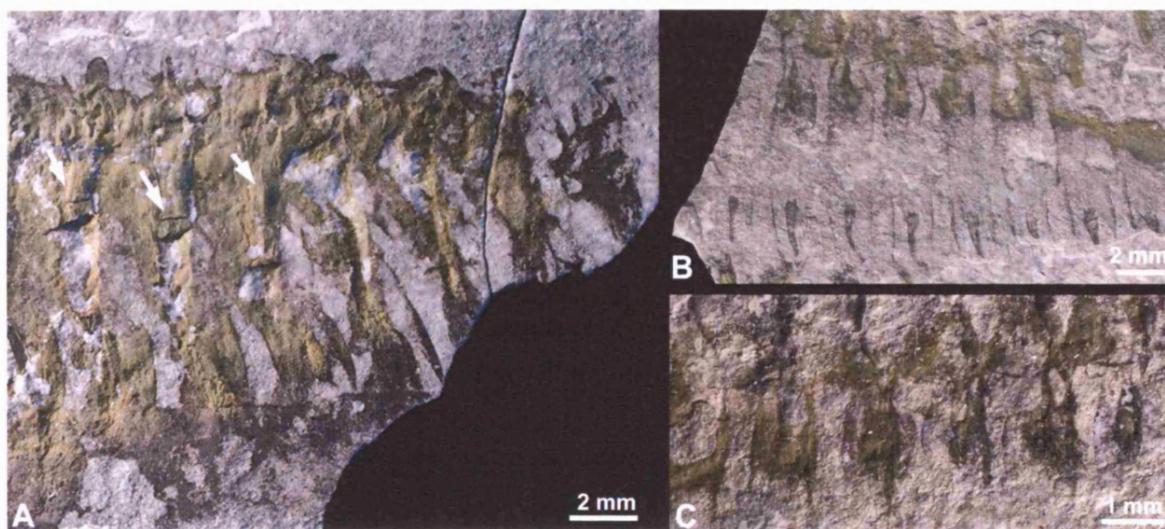


**Figure 6.8.** Appendages from C1707. **A**. Possible thoracic appendages appear to be complex, with branching structures (see Fig. 6.10A). Proximally, some of these appendages have been preserved in positive relief (arrowed). **B**. and **C**. Possible abdominal appendages appear to be paddle-like and setiferous.

*Remarks*. Due to the incompleteness and orientation of the organism the different morphologies of the appendages are not particularly clear. This, and the lack of an anterior and posterior end of the fossil, makes it hard to deduce the affinities of this organism. Fossil marine arthropods include crustaceans, chelicerates and trilobites and there are also many primitive arthropod forms (Chen *et al.* 1995*b*). Trilobites have been discounted because, except for uniramous antennae, biramous appendages in members of this group are virtually identical all the way down the body (Raymond 1920; Størmer 1939; Whittington 1975), unlike the differing appendage types that are exhibited by C1707.

Chelicerates have a pair of preoral appendages, which are developed as jointed chelicerae or pincers (Størmer 1955). There is no evidence of these on the specimen, although it does appear to be incomplete at the anterior. Chelicerates also possess a body divided into a prosoma (cephalothorax) and opisthosoma (abdomen) of six and 12 or fewer segments,

respectively (Dunlop and Selden 1998; Selden and Dunlop 1998). C1707 appears to have a head region, a thorax with a different sort of appendage, and an abdominal region containing at least 19 segments with appendages, and for these reasons the chelicerates are discounted.
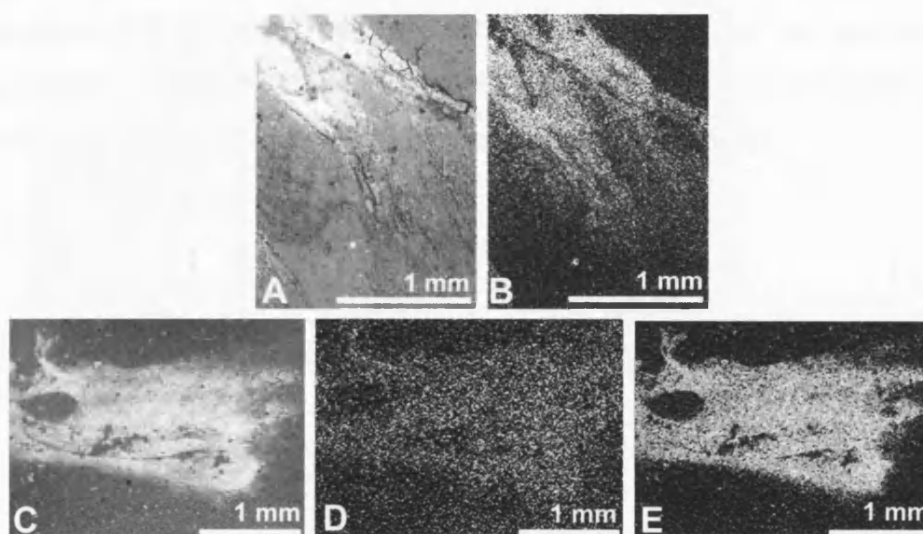


**Figure 6.9.** SEM EDX analyses of thoracic and abdominal limbs of C1707, for location of sites of analysis see Fig. 6.7. **A.** SEM back scattered electron image of distal portion of large thoracic appendage. **B.**, **D.** and **E.** element maps where light areas indicate a relative high abundance of each element. **B.** Element map for iron. **C.** SEM back scattered electron image of a small abdominal appendage. **D.** Element map for sulphur. **E.** Element map for iron. Both appendage types have an elevated level of iron; the small appendages also have elevated levels of sulphur.

Crustaceans are morphologically diverse (Robison and Kaesler 1987). A sound knowledge of appendage structure is needed to confirm an affinity within the crustaceans (Schram 1982). The lack of diagnostic head appendages and the poor preservation of other appendages in C1707 mean that the organism cannot be placed definitively within this group. The paired appendages of crustaceans are typically biramous, but some appendages, for example antennules, may be uniramous (Moore and McCormick 1969). Crustacean tagmata can include head, thorax and abdomen (Robison and Kaesler 1987). C1707 appears to have some biramous appendages; and the appendages are differentiated in different body regions, which possibly represent a head, thorax and abdomen. An affinity with trilobites and chelicerates has been discounted; the appendages and general morphology of C1707 can be compared to crustaceans but a definitive relationship to any group cannot be confirmed based on the available material (Fig. 6.9). To prove that C1707 had an affinity with the crustaceans,

additional specimens with preserved head appendages would be needed to resolve relationships.

The elongate thoracic appendages may have been adapted for a specific function such as feeding. Many anatomical features are functionally controlled (Walossek and Müller 1998) and appendages that are broad, flattened and bear fringes of setae are used in swimming (Brusca and Brusca 2002) therefore, as the abdominal appendages appear paddle-like and are fringed with setae the organism was probably predominantly nektonic.
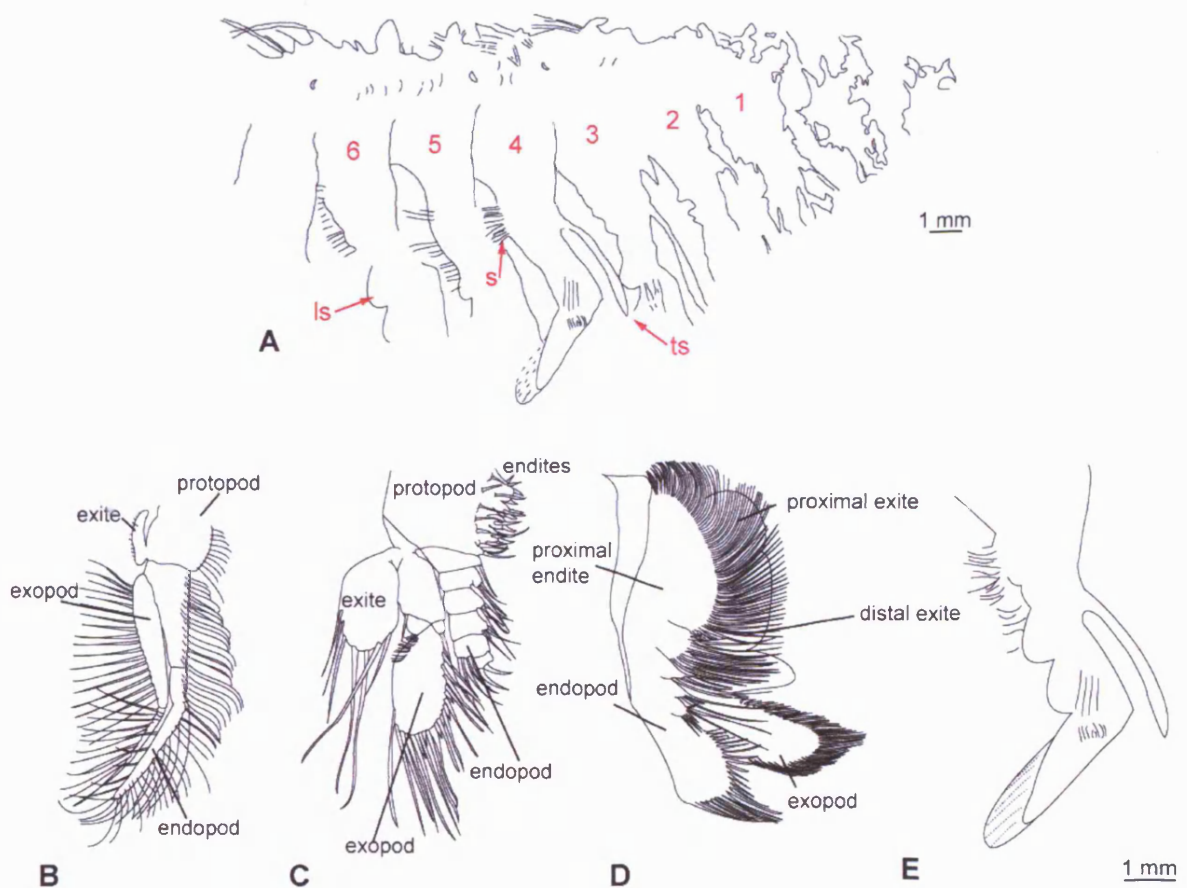


Figure 6.10. A comparison of appendages of C1707 with crustacean appendages. A. Camera lucida of C1707b (see Fig. 6.8). Labels 1–6 indicate the possible positions of the thoracic appendages; ls = lobate structure; ts = thin structure; s = setae. B. Fifth thoracic leg of *Paranebalia longipes* (after Calman 1909) C. Fifth thoracic leg of *Hutchinsoniella macracantha* (after Sanders 1955) D. Median view of trunk limb of *Chirocephalus diaphanous* in its natural position with backwardly directed exites and endites (after Cannon 1928) B. – D. Taken from Manton (1969). E. Possible features of thoracic limb from C1707. Features from the appendages shown in A primarily on appendage 4, but with some details added using evidence from other appendages.
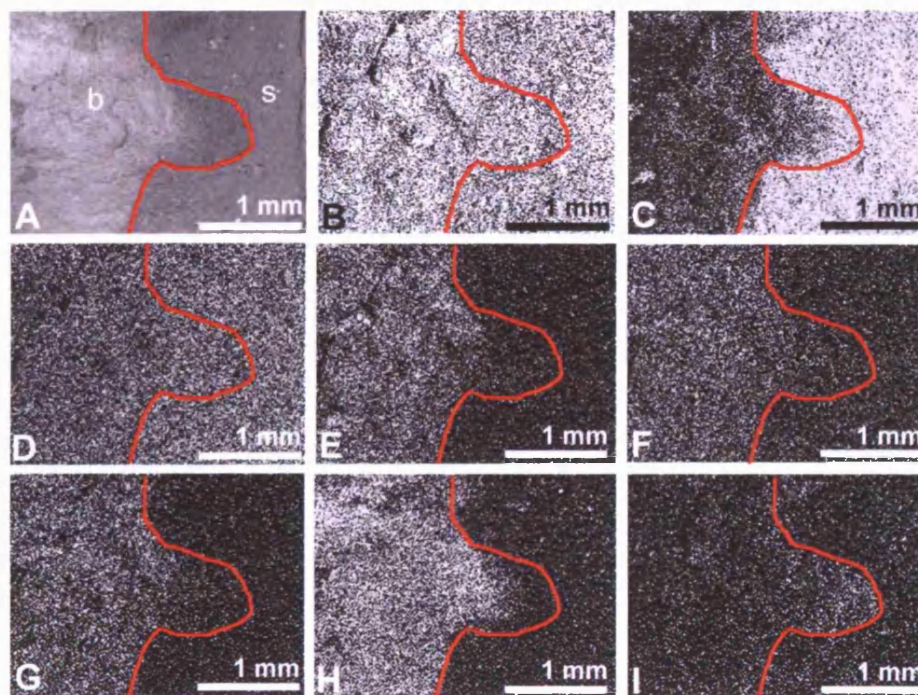
**Figure 6.11.** SEM EDX analysis of the body of C1707 (labelled **b**) in comparison to the sediment (labelled **s**), with the boundary between the two highlighted in red. Location of site of analysis given in Fig. 6.7. **A**. SEM back scattered electron image of the edge of the body of C1707, and the sediment. **B.–I.** element maps where light areas indicate a relative high abundance of each element. **B.** Aluminium **C.** Silica **D.** Potassium **E.** Phosphorus **F.** Calcium **G.** Sulphur **H.** Iron **I.** Carbon. The body of the fossil is preserved by an alunite/clay mineral mixture, with the presence of oxidised pyrite and some organic carbon preservation laterally (I).

*Preservation*. C1707 is preserved within a grey siltstone and consists of part (C1707a) and counterpart (C1707b). The part is incomplete as the anterior of the fossil is missing. The counterpart is also incomplete and is in multiple pieces (Figs 6.6; 6.7). The fossil is preserved mostly in two dimensions, although the anterior appendages have some relief proximally (Fig. 6.8). The body of the specimen shows enrichment in P, S, K, Al and Ca relative to the matrix (Fig. 6.11) and Si is also present on the body of the fossil. These elements can be accounted for by the presence of minerals in the alunite solid solution series, e.g. crandallite $(CaAl_3(PO_4)_2(OH)_5.H_2O)$ or alunite $(KAl_3(SO_4)_2(OH)_6)$ identified from the Soom Shale by Gabbott (1998), as well as clay minerals. Some of the structures present laterally along the body are preserved as organic carbon (Fig. 6.11I). Elevated Fe levels are also seen on the body of the specimen (Fig. 6.11H), and this may relate to pyrite, which has subsequently

become oxidised; however, iron occurs as a common impurity in alunite, and this may be the reason for its presence (Fig. 6.11). The appendages have elevated Fe and S (Fig. 6.9) and none of the elements comprising alunite are elevated. The appendages are thus preserved by pyrite, which has subsequently oxidised in places.

*Enigmatic Arthropod B: Specimen C1927*

*Description.* Multisegmented bilaterally symmetrical organism; with clear indentations in the body margin that highlight clear segmentation. The organism is large and elongate, with a maximum width of 35 mm (excluding appendages) and a maximum preserved length of 148 mm. C1927 tapers slightly at the anterior, it does not show any evidence of tapering towards the posterior, but is incomplete at this end. It is hypothesised that the tapering anterior represents the cephalic region (Figs 6.12; 6.13); posterior of this the fossil reaches maximum width and the segmentation can be seen clearly. This is interpreted as the start of the thorax, which consists of at least 19 segments (C1927 b + c); a maximum of 12 segments can be discerned on C1927a.

The anterior-most cephalic appendages project laterally (Figs 6.12; 6.13A, B; 6.14C). These appendages are uniramous, large and robust, consisting of approximately four or five podomeres, some of which appear to have spinose projections (Figs 6.13C, D; 6.14C). The structure of the distal part of the appendage is not clear. There are two or possibly three more appendages in the cephalic region; the preservation of these appendages is unclear (Figs 6.12; 6.13A, B). The second appendage appears larger and more robust than the third appendage, and the fourth appendage is very faint. The position of muscle attachment areas on the body of the fossil and faint marks next to the body suggests that these appendages were possibly biramous (this can be best observed for the appendage structures labelled a3 on Fig. 6.13A).

Reniform eye structures occur laterally on each side of body; they appear to be sitting on top of the first appendage (Figs 6.12; 6.13; 6.14A, B, C), and have a maximum length and width of 2.5 mm. The structures are not within the cephalic region; therefore it is possible that the eyes were pedunculate, although there is no visible evidence of a stalk.

Appendages of the thorax are preserved faintly along the body as mineralized marks in the sediment (Figs 6.12; 6.13 A, B; 6.14D). They are not clearly attached to the body anywhere and their precise morphology cannot be discerned. However, it can be seen that they comprised at least a long, thin and elongate part. There is possibly one appendage per section. The thorax has two rows (one either side) of three-dimensionality, with faint

striations, which may be the sites of preservation of exopods or may be related to soft tissues associated with appendage attachment (Figs 6.12; 6.13A, B). There are also clear oval structures, which may be parts of appendages or areas of appendage attachment (Figs 6.12; 6.13A, B; 6.15A).
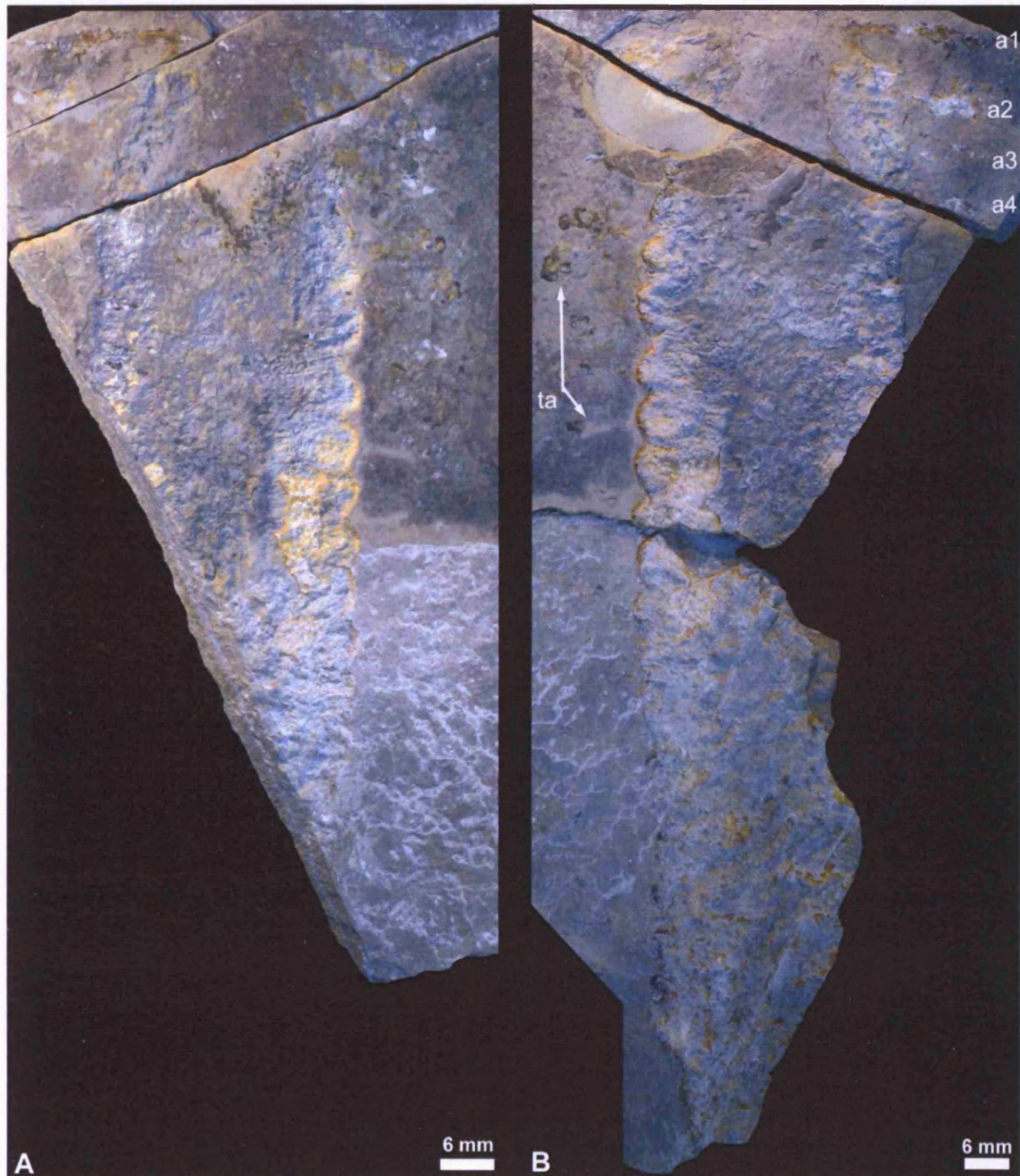


**Figure 6.12.** Part and counterpart of C1927. **A.** C1927 a, d. **B.** C1927 e, b, c. The organism has a high length to width ratio. See Fig. 6.13 for explanatory drawing.
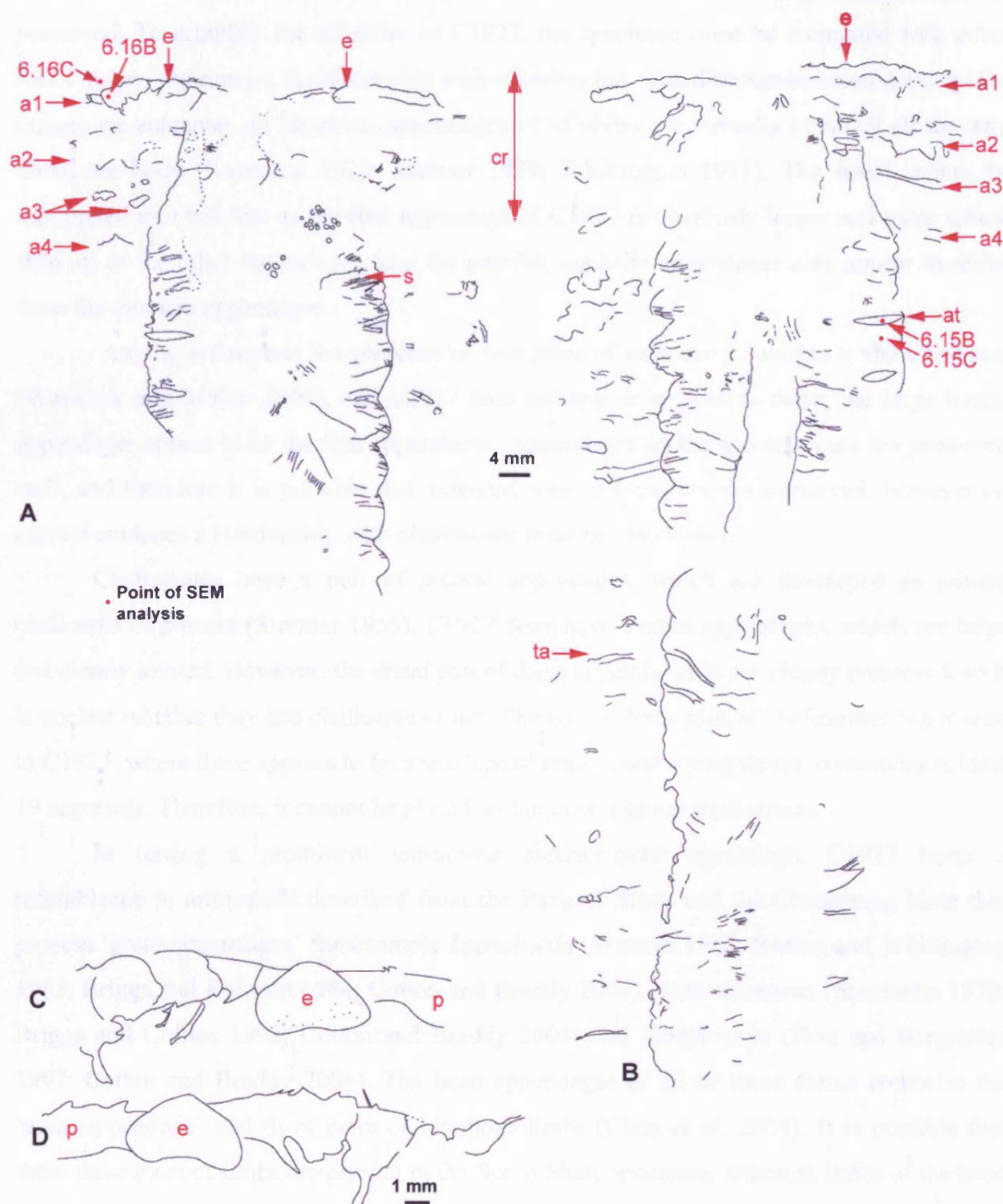
**Figure 6.13.** C1927, with sites of SEM point analysis for Figs 6.15 and 6.16 highlighted. **A.** C1927a, d. and **B.** C1927e, b, c. part and counterpart of C1927. **a1** = appendage 1; **a2** = appendage 2; **a3** = appendage 3; **a4** = appendage 4; **at** = possible area of appendage attachment; **cr** = cephalic region; **e** = eye; **s** = highlights the striations down the edge of the body; **ta** = thoracic appendage. **C** and **D.** Part and counterpart of the best preserved first appendage preserved on C1927d. **p** = proximal; **e** = eye.

*Remarks*. The fossil does not yield a great deal of anatomical information, and is poorly preserved. To establish the affinities of C1927, the specimen must be compared with other fossil marine arthropods. A relationship with trilobites has been discounted because except for uniramous antennae, all biramous appendages of trilobites are virtually identical all the way down the body (Raymond 1920; Størmer 1939; Whittington 1975). The fossil cannot be interpreted as a trilobite as the first appendage of C1927 is obviously larger and more robust than all of the other appendages, and the possible cephalic appendages also appear to differ from the thoracic appendages.

Among arthropods the presence of two pairs of antennae is unique to the Crustacea (Walossek and Müller 1998), and C1927 does not appear to possess these; the large lateral appendages appear to be the first appendages. Appendages on the specimen are not preserved well, and therefore it is possible that antennae were present but not preserved, however on current evidence a relationship with crustaceans must be discounted.

Chelicerates have a pair of preoral appendages, which are developed as jointed chelicerae or pincers (Størmer 1955). C1927 does have frontal appendages, which are large and clearly jointed. However, the distal part of these appendages is not clearly preserved, so it is unclear whether they had chelicerae or not. The typical body plan of chelicerates is not seen in C1927, where there appears to be a small head region, and a long thorax containing at least 19 segments. Therefore, it cannot be placed within crown group chelicerates.

In having a prominent uniramous anterior-most appendage, C1927 bears a resemblance to arthropods described from the Burgess Shale and the Chengjiang biota that possess 'great-appendages' for example *Leanchoilia* (Walcott 1912; Bruton and Whittington 1983; Briggs and Robison 1984; Cotton and Braddy 2004), *Alalcomenaeus* (Simonetta 1970; Briggs and Collins 1999; Cotton and Braddy 2004) and *Fortiforceps* (Hou and Bergström 1997; Cotton and Braddy 2004). The head appendages of all of these forms comprise the 'great-appendage' and three pairs of biramous limbs (Chen *et al.* 2004). It is possible that these three pairs of limbs are present in the Soom Shale specimen, although limbs of the head region are unclear, they do appear to be biramous. However, C1927 differs from the 'great-appendage' arthropods, as its first appendages appear to be laterally projecting as opposed to being anteriorly directed.

The morphology of 'great-appendages' led to the hypothesis that the grasping chelicerae of crown-group Chelicerata originated from this limb-shaped raptorial appendage (Waloszek *et al.* 2005; Chen *et al.* 2004; Maas *et al.* 2004). The 'great-appendage' arthropod

group is discussed as belonging in the same clade as the chelicerates in the cladistic analysis of Cotton and Braddy (2004).

The large jointed frontal appendage of C1927 may hint at a relationship with the chelicerates, but the elongate body, a primitive characteristic, indicates that the fossil does not belong within the crown group. Therefore, like the 'great-appendage' arthropods, it is possible that C1927 may be a stem group chelicerate, although there is currently not enough evidence from the specimen to determine its affinities. This new enigmatic specimen from the Soom Shale may indicate that arthropods with a primitive morphology were present in the Late Ordovician. A robust frontal appendage suggests a grasping function, and the arthropod was probably an active predator. Little evidence of mode of life can be gleaned from the thoracic appendages, except that they do not appear to be stout or robust and were probably not functional as walking appendages. A very high length to width ratio of the body has been cited as suggesting a nektonic form (Fortey 1974; Briggs et al. 1991b; Briggs and Bartels 2001) and this mode of life is proposed for the Soom Shale specimen. This would have allowed the organism to swim higher in the water column, thus evading the conditions at the sea-bottom, which were anoxic at times (Gabbott 1998).

Figure 6.14. (overleaf) Features of C1927. A. Cephalic region C1927e of part. The eye is very faintly preserved (arrow). There is very little preserved in the centre of the cephalic region, positive relief structures run down either side of the body. The first appendages are the most clearly preserved, although others can be discerned. B. Cephalic region C1927d of counterpart. Two eye structures are most strongly evident on the counterpart (highlighted by the arrows). The first appendage is most clearly seen on the left hand side, an enlargement of this appendage is shown in C. C. Enlarged first appendage (on C1927d) with clear eye structure (highlighted by arrows). D. Thorax of specimen (C1927b), whitened with ammonium chloride to highlight relief. Clear indentations can be seen in the body margin. Some faint marks can be seen, which are probably the appendages of the thorax (highlighted by the arrows).
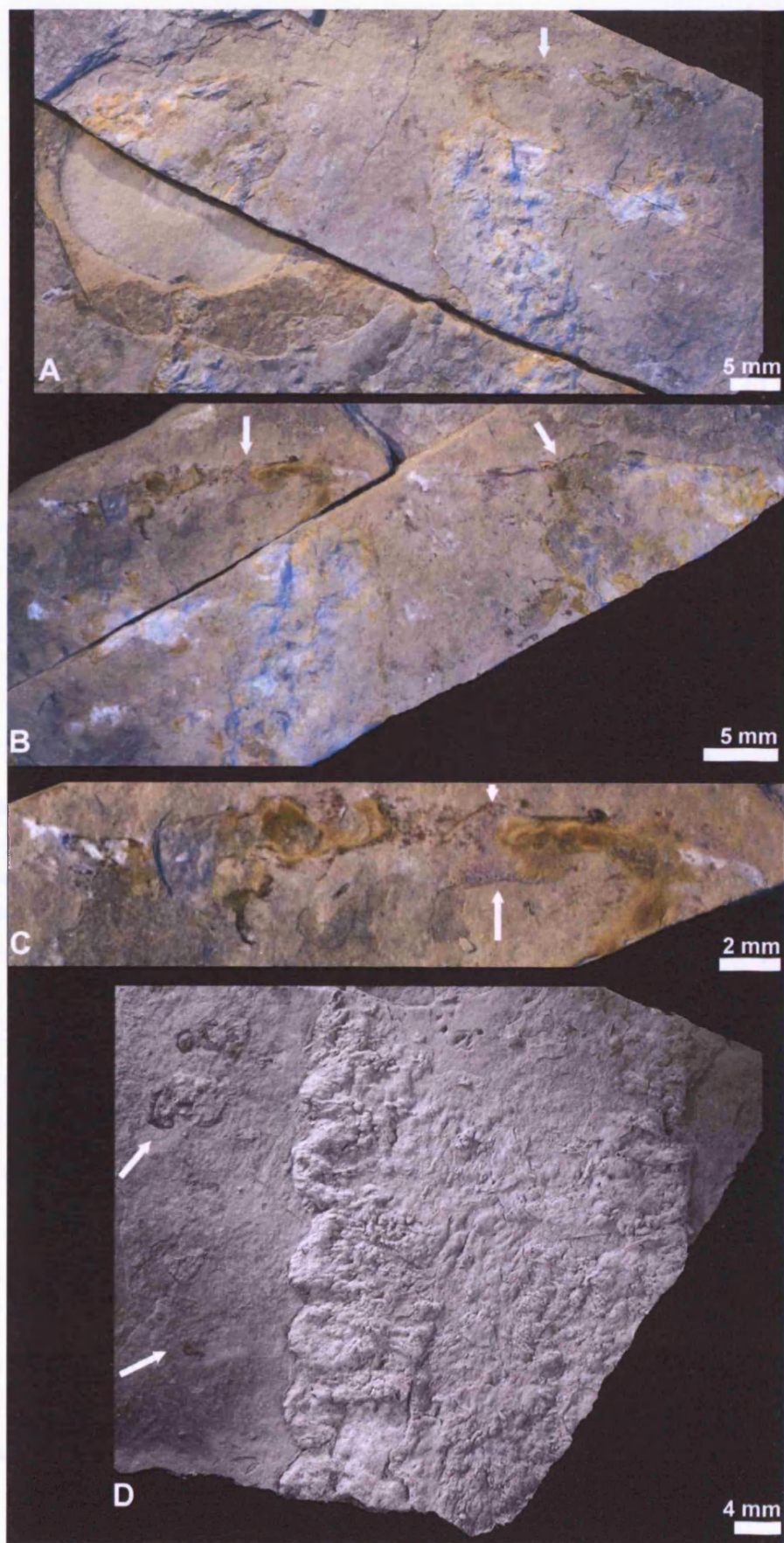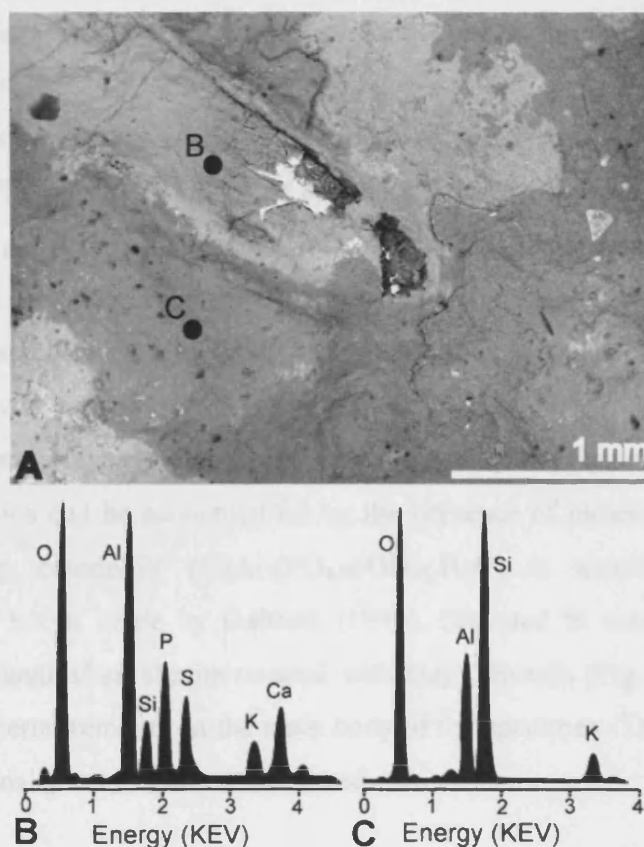
**Figure 6.15.** Preservation of C1927 **A**. SEM back scattered electron image of area of body with location of SEM EDX analyses B and C, these points are also located on Fig. 6.13. **B**. SEM EDX analysis of point on a structure possibly related to appendage/appendage attachment. The structure has a mixed alunite and clay mineral composition **C**. SEM EDX analysis of point on the body of C1927. The main body of the specimen generally has a clay mineral composition.

*Preservation.* C1927 is preserved within a grey siltstone and consists of part (C1927 e, b and c) and counterpart (C1927 a and d). The part is incomplete and in multiple pieces. A portion of the cephalic region is missing on the left hand side of the part; the right hand side of the thorax is missing, as is the posterior of the organism. The counterpart is also in multiple pieces and incomplete, as a portion of the thorax and the posterior of the organism are missing (Figs 6.12; 6.13).

C1927 is preserved dorso-ventrally; the main body exhibits positive relief in some areas, (Fig. 6.14D) and there is most relief at the edges of the main body. Axially the fossil is two-dimensional, and positive relief is seen towards the preserved margins (Fig. 6.14 A, B). The frontal appendages are the best preserved and other cephalic appendages can be discerned (Figs 6.12; 6.13; 6.14A–C). Other possible appendages are preserved very faintly in two

dimensions and mainly appear as patches of mineral films in the sediment next to the body (Figs 6.13B; 6.14 D).

The main body has elevated concentrations of Si, Al and K, consistent with a clay mineral signature (Fig. 6.15A, C). The first appendages have a clay mineral signature but are also enriched in Fe, suggesting the presence of pyrite, which has become oxidised (Fig. 6.16). These iron-rich first appendages are the clearest structures preserved on the fossil, suggesting that they were more robust than the body of the specimen. The appendages of C1927 may have been more heavily cuticularised than the rest of the body.

There are clear structures that have elevated levels of the elements P, S, K, Al and Ca (Fig. 6.15A, B), which can be accounted for by the presence of minerals in the alunite solid solution series, e.g. crandallite $(CaAl_3(PO_4)_2(OH)_5.H_2O)$ or alunite $(KAl_3(SO_4)_2(OH)_6)$ identified from the Soom Shale by Gabbott (1998). Elevated Si can also be seen, which indicates a mixed signal of an alunite mineral with clay minerals (Fig. 6.15A, B). It appears that no cuticular material remains on the main body of the specimen. This is possibly because the cuticle was originally very lightly mineralized.
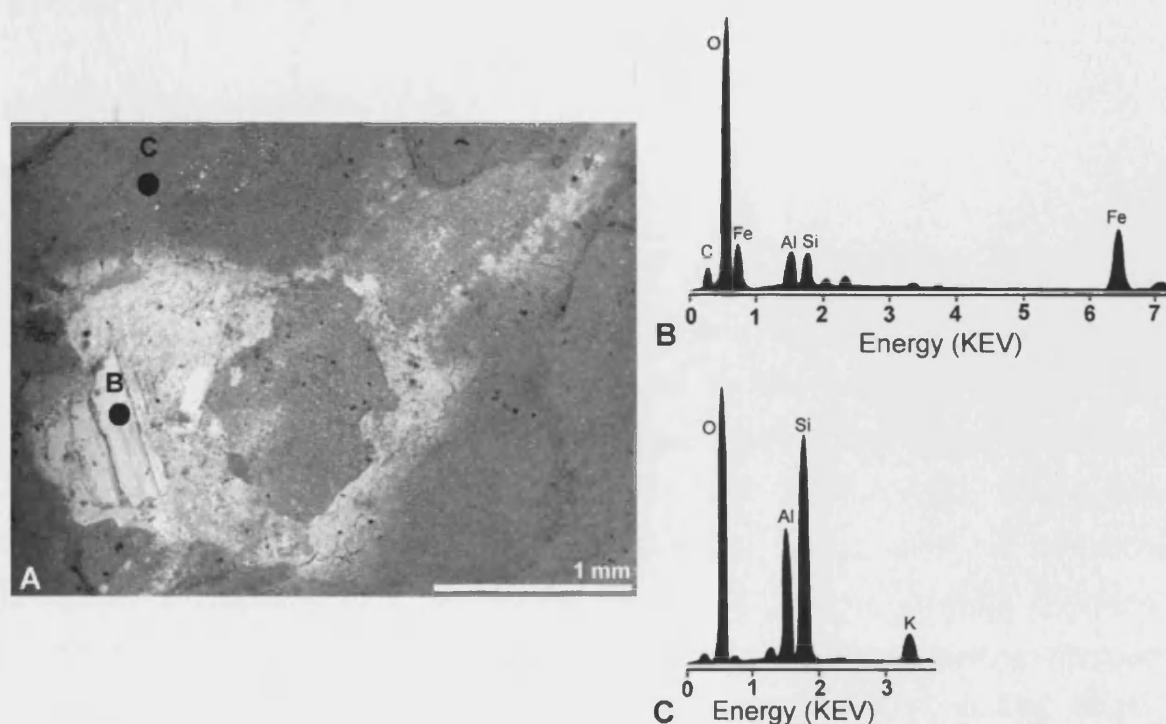


**Figure 6.16. A**. SEM back scattered electron image of the distal tip of the first appendage, location of SEM EDX analyses B and C, these points are also located on Fig. 6.13. **B**. SEM EDX trace of appendage showing a clay mineral signature and elevated iron concentration. **C**. SEM EDX trace of sediment, which shows a clay mineral signature.

CONCLUSIONS

Arthropod diversity in the Soom Shale has been increased to include three new taxa, an unidentified bivalved carapace and two new enigmatic specimens. The new taxa add two predominantly nektonic organisms to the Soom Shale ecosystem, one of which was an active predator. The new arthropods from the Soom Shale show taphonomic modes seen in other Soom Shale arthropods such as clay mineral and alunite preservation. Fibrous clay minerals overcoat the bivalved carapaces in a similar manner to the clay minerals seen in *Caryocaris* specimens described from the Soom Shale by Whittle *et al.* (2007). Two specimens exhibit pyrite preservation, particularly on appendages and pyrite also coats one of the carapaces.

Chapter 7

# THE BIOTA OF THE SOOM SHALE: PALEOECOLOGICAL AND TAPHONOMIC SYNTHESES, CONCLUSIONS AND FUTURE WORK

THE overall aim of this research project has been to enhance our understanding of the diversity of the Soom Shale ecosystem. The following synthesis of the diversity and palaeoecology of the Soom Shale provides the most up to date outline of the ecosystem based upon results from this thesis and from previous publications. The components of the fauna are outlined, their modes of life and interactions discussed and the Soom Shale ecosystem is compared to other fossil deposits; a synthesis of the taphonomy of the organisms is also given. Finally, the major conclusions from this study are given as well as some suggestions for future work.

## THE SOOM SHALE BIOTA

*Arthropods*

Five genera of arthropod have now been identified from the Soom Shale, as well as a selection of unidentified arthropod parts; arthropods are the most diverse phylum in the fauna. The named species are the trilobite *Mucronaspis olini* Temple, 1952 (Moore and Marchant 1981); the naraoiid *Soomaspis splendida* Fortey and Theron, 1994; the ostracod *Myodoprimigenia fistuca* Gabbott, Siveter, Aldridge and Theron, 2003; the eurypterid *Onychopterella augusti* Braddy, Aldridge and Theron, 1995 and the arthropod *Caryocaris cedarbergensis* Whittle, Gabbott, Aldridge and Theron, 2007. In addition unnamed arthropods include large carapaces, and two different taxa of unknown affinities (Chapter 6). Finally, there are many unidentified arthropod parts, including possible appendages (for example C1750 and C1541) (see Appendix vi).

*Molluscs*

Orthocones have been recovered from the Soom Shale but have not been identified to any taxonomic level (Gabbott 1999). Other molluscs include three incomplete specimens of trilobed bellerophontid monoplacophoran belonging to the family Sinuitidae. These have been tentatively identified as *Bucanella* sp. (Cocks and Fortey 1986). Five specimens of nuculanacean bivalves have been attributed to *Concavodonta* (Cocks and Fortey 1986).

*Lophophorates*

Discinoid brachiopods including orbiculoids (Cocks and Fortey 1986) and *Trematis* have been identified (Gabbott 1999). Rare rhynchonellids have been identified (Gabbott 1999; Aldridge *et al.* 2006) and seven specimens of the inarticulate brachiopod *Lingula* have also been found (Aldridge *et al.* 1994; Gabbott *et al.* 2001).

*Chordates*

Two species of conodont have been found, these are *Promissum pulchrum* Kovács-Endrödy, 1986 (Theron *et al.* 1990) and a second genus that appears to be related to *Icriodella* (R. J. Aldridge *pers comm.* 2007), which has recently been identified. An undescribed naked agnathan has also been identified, represented by at least twenty specimens (Aldridge and Purnell 2005).

*Annelids*

Annelids are represented in the Soom Shale fauna by 22 scolecodont specimens, which are the jaw apparatuses of polychaete worms. The species *Xanioprion*? n. sp. and *Synaptogenys rietvleiensis* n. gen. n. sp. have been identified (Chapter 4).

*Coelenterates*

There is one putative medusoid specimen, which possibly belongs to the class Scyphozoa (Chapter 3), and one other round structure has been noted from the quarries but does not contain any internal structure (Appendix ii).

*Phytoplankton*

Phytoplanktonic fossils have also been recognised, represented by leiospheres, sphaeromorphs and spherical bodies with smooth-walled or rarely granular or microechinate surfaces (Gray *et al.* 1986). Acritarchs have also been identified (Gray *et al.* 1986; Aldridge *et al.* 2001).

*Algae*

Almost all of the lamination surfaces of the Soom Shale are covered with ribbon-like metaphyte algae (Gabbott 1998). There are several different morphologies represented by the algae, but they have not been identified to any taxonomic level.

*Spores and Chitinozoans*

Small spores have been found (Cocks and Fortey 1986; Gray *et al.* 1986). Chitinozoans are found in abundance on some Soom Shale bedding surfaces, including *Ancyrochitina merga* Jenkins, 1970, *Conochitina oelandica* Eisenack, 1955, *Ancyrochitina* spp., *Cyathochitina dispar* Benoit and Taugourdeau, 1961, *Desmochitina minor* Eisenack, 1931, *Desmochitina* spp. and *Hoegisphaera* spp. (Cramer *et al.* 1974; Gabbott *et al.* 1998).

*Trace fossils*

Five categories of bromalite have been identified from the deposit based on shape, content and internal structure (Aldridge *et al.* 2006).

*Enigmatic organisms*

There are several fossils that remain enigmatic including the needle-like specimens of *Siphonacis*, which occur on many surfaces. Also, some larger fossils (such as C509 and C448) remain to be identified, as well as many incomplete specimens (for example C1190) (see Appendix vi).

PALAEOECOLOGY OF THE SOOM SHALE

Algae probably constituted the greatest biomass of the biota (Gabbott 1998) and this would have formed the base of the food chain. The bacterial decomposition of organic matter following algal blooms may have contributed to episodes of anoxia. It is unknown whether the algae were benthic and thus helped stabilize the sediment, or planktonic, although Gabbott (1998) and Gabbott *et al.* (2001) stated that the evidence for dominantly inhospitable bottom water conditions more strongly suggests a planktonic mode of life.

Anaerobic biofacies may include well preserved remains of nektonic or epiplanktonic invertebrates and vertebrates but are also characterised by a lack of *in situ* macrobenthic body fossils (Bottjer and Savrda 1990). Generally penetrative and surface bioturbation structures are absent in the Soom Shale (Gabbott 1998), these characteristics have been attributed to the anoxic nature of the sediment, and are thought to have limited the presence of infaunal and epifuanal benthic organisms (Gabbott 1998). However, *Lingula* specimens have been identified, and were interpreted as pseudoplanktonic or possibly infaunal when conditions were favourable (Gabbott *et al.* 2001). The discovery of further benthic organisms such as the lobopodian means that an infaunal interpretation for the mode of life of *Lingula* specimens is now more likely, and this is in accordance with the mode of life established for modern *Lingula* specimens (Clarkson 1996). Infaunal deposit feeding nuculanacean bivalves have also been identified from Buffels Dome (Cocks and Fortey 1986). Epifaunal benthic organisms are a rare component of the Soom Shale fauna, but their range has now been increased by the recognition of a lobopodian fossil (Chapter 5). It is possible that the scolecodont-bearing polychaete worms were benthic organisms (Chapter 4).

A large component of the fauna has been interpreted as nektonic/nektobenthic, including most of the arthropods (Braddy *et al.* 1995, 1999; Aldridge *et al.* 2001; Gabbott *et al.* 2003). There is evidence of episodes of bottom water oxygenation in the deposition of the Soom Shale (Gabbott 1998), although a timescale for these oxygenated periods has not yet been established. It is likely that during episodes of bottom water oxygenation benthic and nektobenthic organisms occupied the sea floor, increasing the bottom-dwelling component of the community. However, all of the arthropods were probably also capable of swimming, when conditions were inimical to sea floor inhabitation.

Large numbers of conodont apparatuses and elements (over 600) and relatively large numbers of orthocones (approximately 100) have been discovered. If many of the

nektobenthic/nektonic arthropods are considered as nektonic, then this niche was occupied by a large majority of the Soom Shale fauna.

*Caryocaris* constitutes part of the zooplankton, due to its pelagic lifestyle (Chapter 2), as does the scyphozoan medusoid (Chapter 3). It is possible that some of the polychaetes (scolecodonts) may have also had a pelagic mode of life and thus may have also formed part of the zooplankton (Chapter 4). Thus, this niche, previously not recognised to be occupied in the Soom Shale ecosystem, is now known to contain several organisms.

Where feeding strategies have been identified for Soom Shale organisms, generally a scavenging or predatory mode of life has been proposed, with brachiopods and bivalves occupying a filter feeding niche (Aldridge *et al.* 2001). Within the newly described organisms, the fossil polychaetes (Chapter 4) and the lobopod (Chapter 5) are interpreted to have had a predatory/scavenging mode of life. For the stem-group chelicerate a predatory mode of life is suggested. Therefore, evidence from the organisms studied here corroborates the conclusion that fossils that have been found from the Soom Shale represent what were predominately predatory and scavenging organisms.

*Community interactions*

Only a few organisms have been found in association with one another. Myodocopes ostracods were found in association with orthoconic cephalopods, suggesting that they fed on cephalopod carrion as nektobenthic scavengers and were thus epibenthic (Gabbott *et al.* 2003). Some discinoid brachiopods and rhynchonellids occur as epibionts associated with orthocones (Gabbott 1999; Aldridge *et al.* 2006).

No identifiable gut contents have been found in any of the fossils; however several types of bromalite have been discovered (Aldridge *et al.* 2006). Although the bromalites could not be assigned to the organisms which formed them, the presence of crushed discinoid valves and broken conodont elements demonstrate the presence of an effective durophagous predator and tiering within the predatory trophic level in the Soom Shale community (Aldridge *et al.* 2006).

*Comparison to other localities*

In having a high diversity of arthropod taxa, the Soom Shale is similar to other Palaeozoic Lagerstätten such as the Chengjiang biota and the Burgess Shale. In the Middle Cambrian

Burgess Shale arthropods account for the largest fraction of the fauna (37%) (Conway Morris 1979). Approximately 65% of all macroscopic fossils from the Early Cambrian Chengjiang biota and more than 50% of the described species are arthropods (Babcock et al. 2001). The Soom Shale differs from Cambrian Lagerstätten such as the Burgess Shale and the Chengjiang biota because conodonts are an abundant component of the Soom Shale fauna, with over 600 apparatuses and partial apparatuses collected, and the fauna also includes organisms such as scolecodonts and orthocones. This is a result of the Late Ordovician setting, as these organisms evolved and diversified after the deposition of the Burgess Shale and the Chengjiang biota.

In possessing few infaunal organisms, the Soom Shale fauna differs from the Chengjiang biota, in which this niche is occupied by a variety of forms (Hou et al. 2004b). The epifaunal component of the Soom Shale fauna is also small when compared to the Chengjiang biota and Burgess Shale. Among other benthic organisms, xenusiid lobopodians are diverse in the Chengjiang biota and Burgess Shale, but there is only one lobopodian from the Soom Shale Lagerstätte, and this specimen is the only lobopodian from the Ordovician. This suggests that the group was present throughout the Ordovician, perhaps with a much lower diversity and abundance than the Cambrian. It is likely that the group was present in other localities during the Ordovician, but has not been found preserved. This highlights the importance of the Soom Shale as a site of soft-tissue preservation during the Ordovician, a period from which Konservat Lagerstätten are rare.

Typical Mid Ordovician communities included benthic organisms such as sponges, corals, bryozoans, articulate brachiopods, bivalves, echinoderms and crinoids (Ausich and Bottjer 2001). Epifaunal brachiopods, infaunal brachiopods (Lingula) (Aldridge et al. 1994; Gabbott et al. 2001) and infaunal bivalves are recorded from the Soom Shale, although bivalves are rare, having only been found in one location (Buffels Dome) (Cocks and Fortey 1986). Benthic organisms absent from the Soom Shale Lagerstätte include sponges, gastropods and echinoderms. However, the Soom Shale community did include benthic lobopodians. Pelagic organisms present in the Soom Shale fauna that are found in other Ordovician communities include acritarchs, cephalopods, arthropods, chitinozoans and fish. However, graptolites, which were common in the Ordovician, have not yet been discovered from the Soom Shale Lagerstätte.

The Soom Shale was deposited in the Late Ordovician and other Late Ordovician Lagerstätten, such as the Manitoban sites and the Late Ordovician Moroccan deposit preserve a variety of invertebrate and vertebrate fossils, and soft-bodied problematica (Young et al.,

2006; Samuelsson *et al.* 2001) similar to the Soom Shale fauna. However, the Soom Shale is slightly younger than the other Late Ordovician Lagerstätten and is unusual because it was deposited in the Hirnantian, a time when many benthic and planktonic taxa became reduced in number (Brenchley 2001) and when a cosmopolitan *Hirnantia* brachiopod fauna dominated benthic associations (Brenchley 2001). The Hirnantian setting of the Soom Shale Lagerstätte may explain the absence of some organisms. The absence of sponges, echinoderms and possibly gastropods could also be a result of the episodic anoxic-euxinic bottom waters.

## TAPHONOMY OF THE SOOM SHALE

The carapaces of *Caryocaris cedarbergensis* (Chapter 2) and the unidentified large carapaces (Chapter 6) both have layered structures with each layer defined by a distinct mineralogical composition; they also have distinct growths of fibrous clay minerals. These clay minerals are probably illite, which was identified from the Soom Shale by Gabbott (1998). The poorly preserved scolecodonts (Chapter 4) are composed of cracked and degraded organic carbon with clay minerals, which in some cases also possesses a fibrous texture. Therefore, the more resistant fossils from the Soom Shale are preserved as organic material (carbon with an associated clay mineral signature) and these rigid fossils can be subject to an overgrowth of fibrous clay minerals, which could have occurred during diagenesis or metamorphism (Chapter 2; Whittle *et al.* 2007).

Many of the softer body fossils such as the medusoid are now preserved as unfibrous clay minerals, and the lobopod (Chapter 5) has a clay mineral and mixed alunite composition over the majority of the positive relief on the specimen, interpreted as the soft tissues of the organism. The putative crustacean C1707 (Chapter 6) also has an alunite and clay mineral composition for the body of the specimen. Therefore, this backs up evidence that labile tissues in the Soom Shale now have a clay mineral or alunite composition (Gabbott 1998; Gabbott *et al.* 2001).

The location of iron on the lobopod specimen (Chapter 5) led to the suggestion that it is the result of pyritization of cuticular tissues (Chapter 5). The appendages of the putative crustacean (C1707) and stem-group chelicerate (C1927) specimens (Chapter 6) all have elevated iron and sometimes sulphur, which is also linked to the oxidation of pyrite (Chapter 6). The iron-rich first appendages of C1927 are the clearest structures preserved on the fossil, suggesting that they were more robust than the body of the specimen (Chapter 6). The appendages of C1927 may have been more heavily cuticularised than the rest of the body.

Therefore, it appears that preservation by pyrite is partly responsible for the survival of cuticular material; this is a newly identified mode of preservation within the Soom Shale.

The pyrite preservation in the Soom Shale is mostly confined to areas of the carcasses but in one rare occurrence on C1321 (Chapter 6) pyrite cubes coat the entire fossil as well as the surrounding sediment. This suggests a variation in the environment of deposition of the Soom Shale from the normally iron depleted porewaters (Gabbott *et al.* 2001), or that in this case iron oxidation, due to weathering, was followed by leaching creating the halo of iron staining.

In the current taphonomic model for Soom Shale fossils (Gabbott 1998; Gabbott *et al.* 2001) it is indicated that the most labile tissues are replaced by clay minerals such as illite, more recalcitrant tissues are preserved as carbon and it is currently unknown whether alunite replaces tissues with a particular histology or decay profile. However, this model has been questioned by Butterfield *et al.* (2007) who stated that there is no evidence for the preservation of soft tissues by authigenic clays, and that the unit has been subject to late-stage aluminosilification. This assertion was made without Butterfield *et al.* (2007) undertaking any form of taphonomic study of Soom Shale specimens, and no suggestion is made for an alternative hypothesis of preservation for the Soom Shale specimens.

From the taphonomic studies in this thesis it can be seen that the preservation of fossils in the Soom Shale is due to an array of complex taphonomic pathways. Late-stage aluminosilification (*cf* Butterfield *et al.* 2007) may have occurred causing organic rich rigid fossils to be overgrown by fibrous clay minerals. However, soft-bodied specimens such as the lobopodian and the medusoid now have a clay mineral composition (sometimes along with an alunite composition), and these clay minerals do not have a fibrous morphology. Therefore, the model suggested by Gabbott *et al.* (2001), where the most labile tissues in the Soom Shale have been replaced by clay minerals such as illite, cannot be refuted based on evidence from this study.

## CONCLUSIONS

Documentation of previously undescribed organisms from the Soom Shale has led to the identification of three new species, the arthropod *Caryocaris cedarbergensis* n. sp., the scolecodont species *Xanioprion*? n. sp., and the scolecodont species *Synaptogenys rietvleiensis* n. gen., n. sp. Two new soft-bodied organisms, a scyphozoan medusoid and

xenusiid lobopodian, have also been identified as have three new types of arthropod: large bivalved carapaces, a putative crustacean and a stem-group chelicerate.

The identification of the new organisms has led to an addition to the Soom Shale ecosystem of two new zooplanktonic organisms (*Caryocaris* and a scyphozoan medusoid), a new benthic organism (lobopodian) and two nektonic organisms (putative crustacean and stem-group chelicerate).

Fibrous clay mineral coatings have been identified on several specimens, which could be a result of late-stage formation, thus complicating the authigenic clay mineral preservation model of Gabbott (1998) and Gabbott *et al.* (2001). A new aspect of preservation has been identified for the Soom Shale, where cuticular material is sometimes preserved as pyrite.

## FUTURE WORK

Most of the results for this study have been based on single specimens, and this is due to fossils being rare in the Soom Shale deposit. The specimens studied were discovered over thirteen years of fieldwork, yet many of them are the only representative of their group. Further fieldwork always has the possibility of adding new specimens to those already collected, and could provide further evidence to augment the findings of this research. A new fossil site has recently been identified in the Cedarberg Mountains (Theron *pers comm.* 2007), and therefore there is the potential to carry out more fieldwork.

There are a variety of fossils/part fossils left unidentified from the Soom Shale (see Appendix vi). Further study and an increased number of specimens through extra collection may lead to their identification. Documentation of fossil forms that remain enigmatic suggests that there is still a much greater diversity of organisms in the Soom Shale left to be discovered. Also, evidence from bromalite specimens (Aldridge *et al.* 2006) suggest the presence of a durophagous predator in the Soom Shale, the collection of more specimens may help to identify the organism responsible for the production of these bromalites.

As the fossils of the Soom Shale appear to represent a life assemblage, an accurate palaeoecological analysis could be attempted. This would involve an extensive period of fieldwork where bulk collection of fossils through the entire 10-15 m sequence could be undertaken. The data collected could then be used to produce an accurate trophic analysis, diversity study and reconstruction of the Soom Shale community.

Preservation of Soom Shale specimens appears to be the result of complex taphonomic pathways. Therefore, further extensive taphonomic study is needed to try and confirm and/or

constrain these mechanisms. In particular, fibrous material in the conodont specimen and conodont eyes should be re-analysed and compared to the soft-tissue preservation of other conodont specimens in the fossil record. The morphology of the Soom Shale fibrous muscle tissue should also be compared to fibrous clay mineral growth, such as that seen in the *Caryocaris* specimens (Chapter 2).

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# APPENDIX I: *CARYOCARIS*

Photographs show detailed features of specimens.
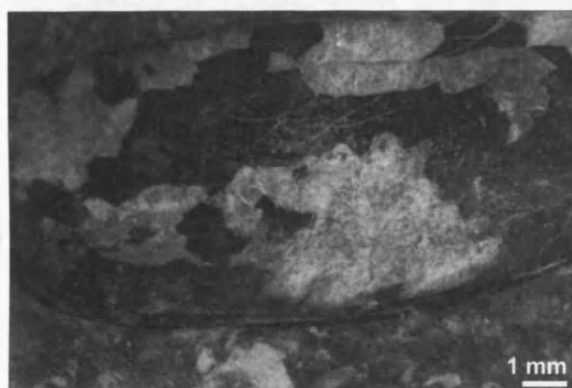


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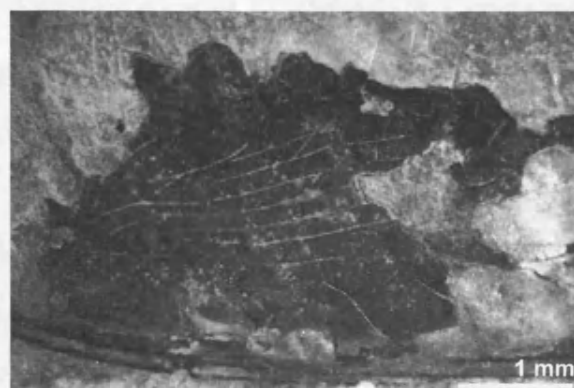


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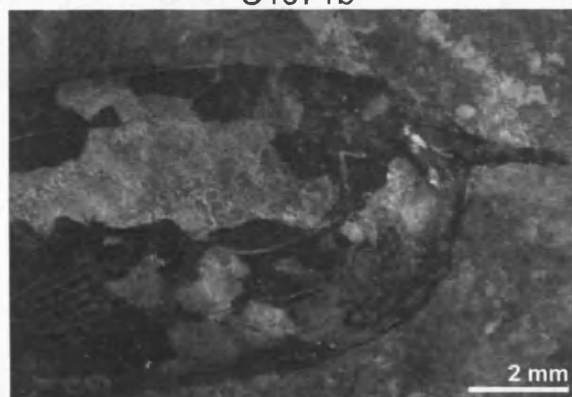


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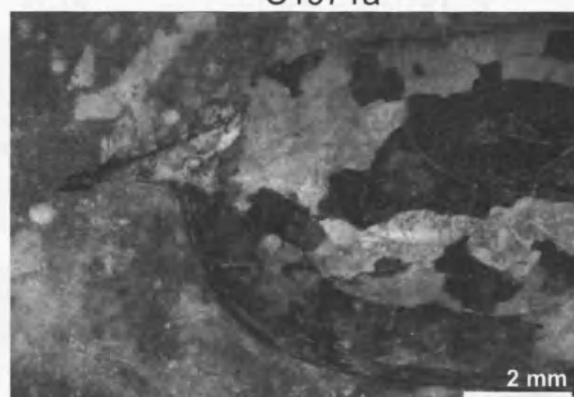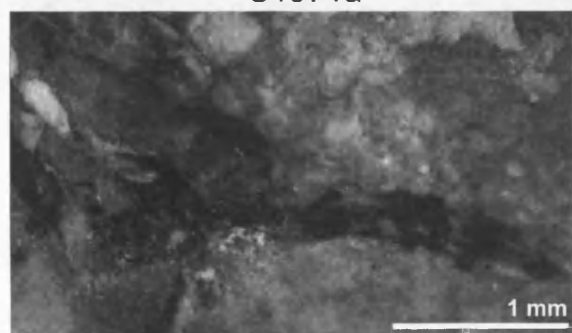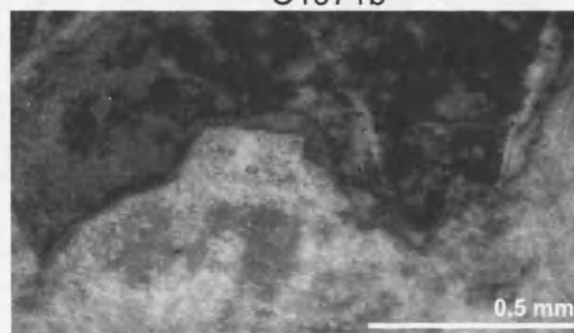


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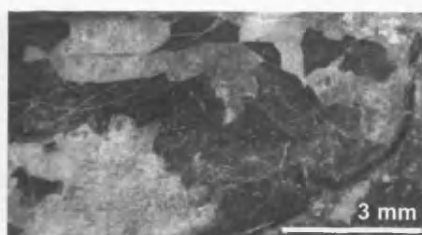
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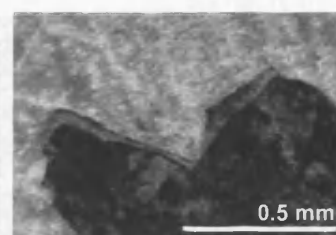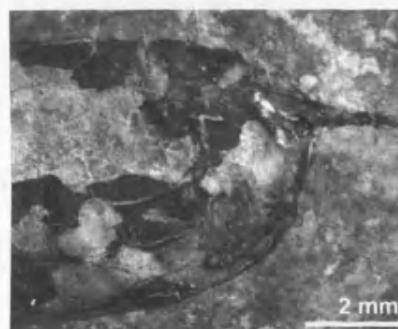
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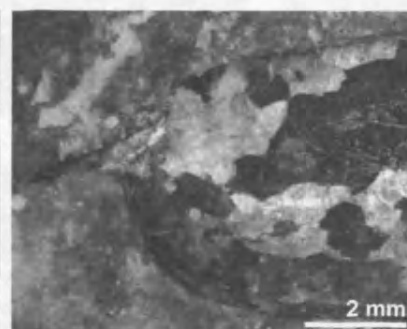
C1971b
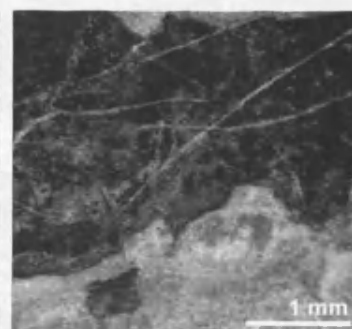
C1971a
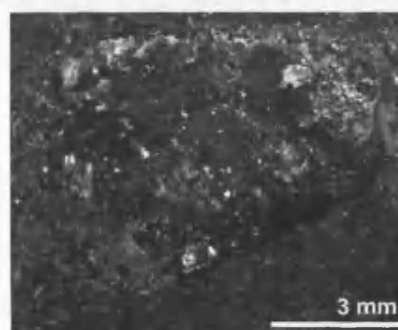
C1587b
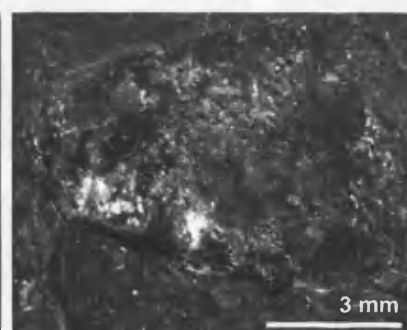
C1587a
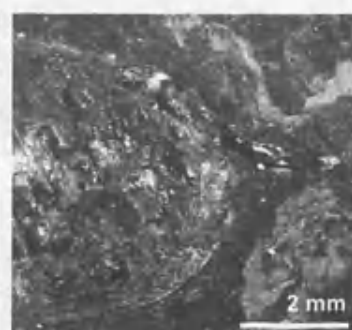
C1587a
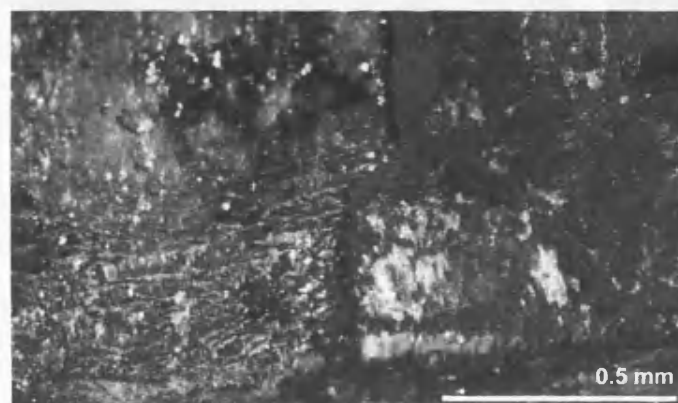
C1587a
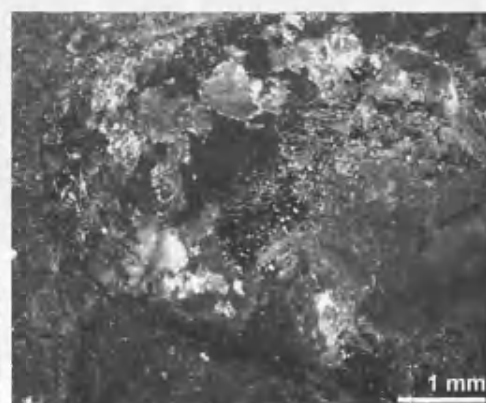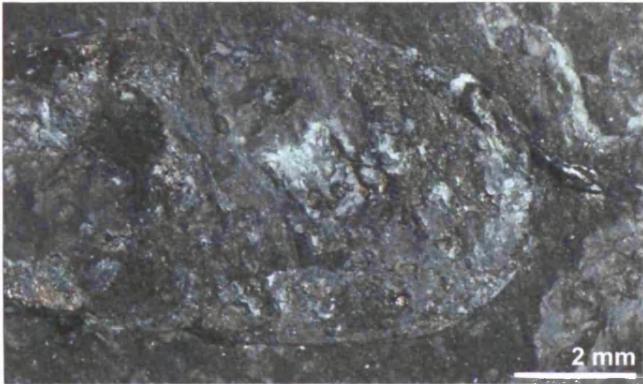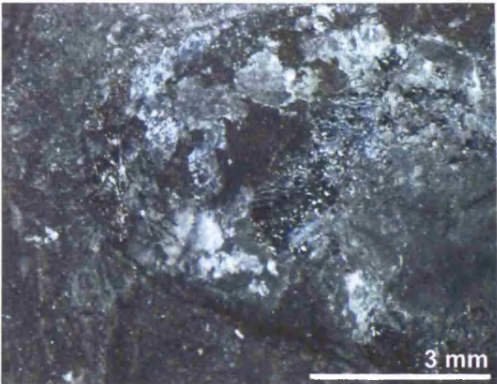
C1587a
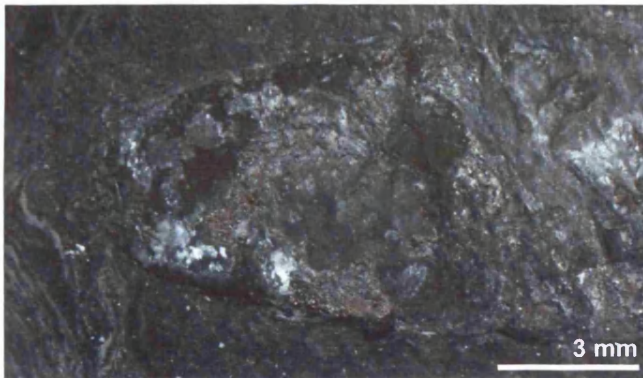
C1587a
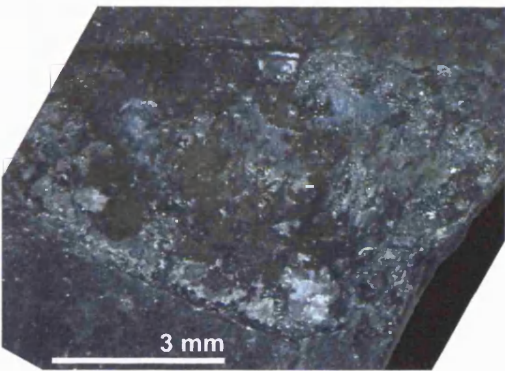


C1587a



C1587a



C1587b
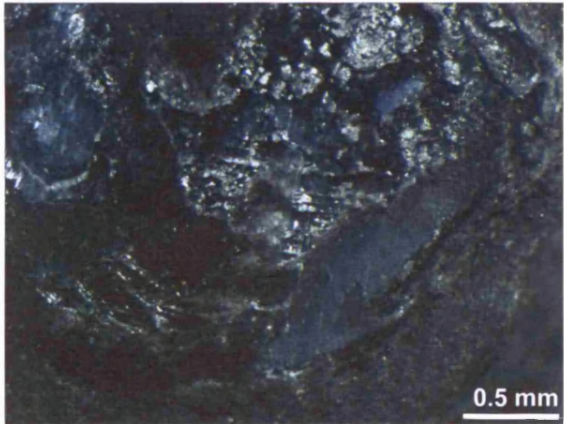


C1587b
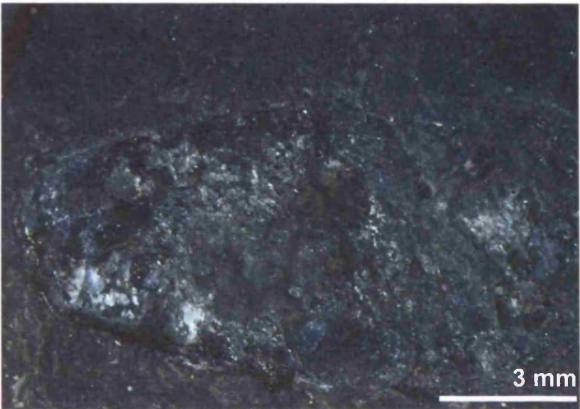


C1587a

SEM backscatter images show detailed preservation of specimens and morphological features.
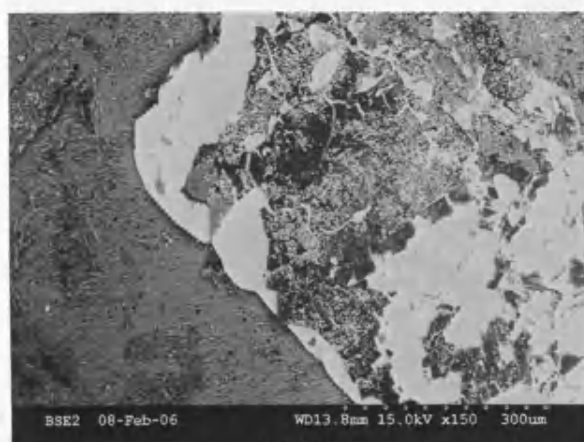


C1587



C1587



C1587
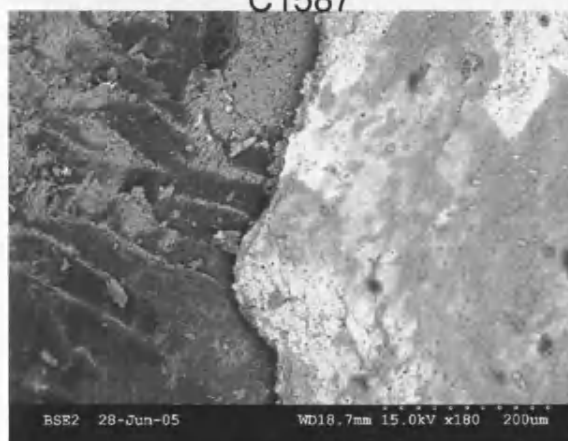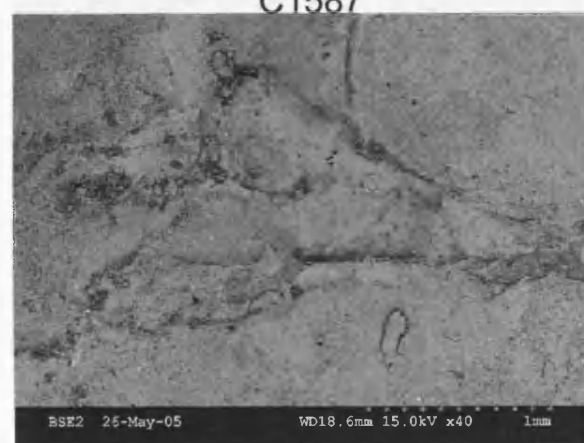


C1587



C1971b



C1971a
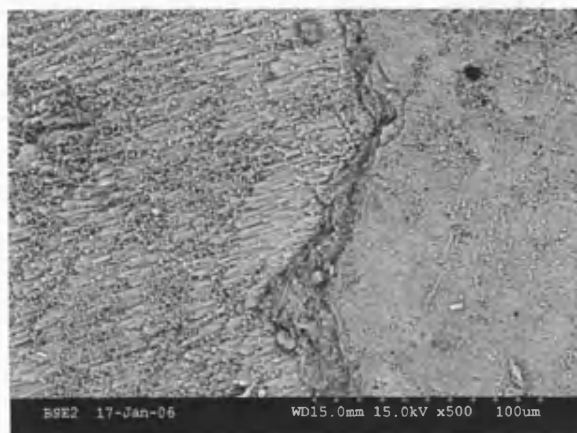
C1971
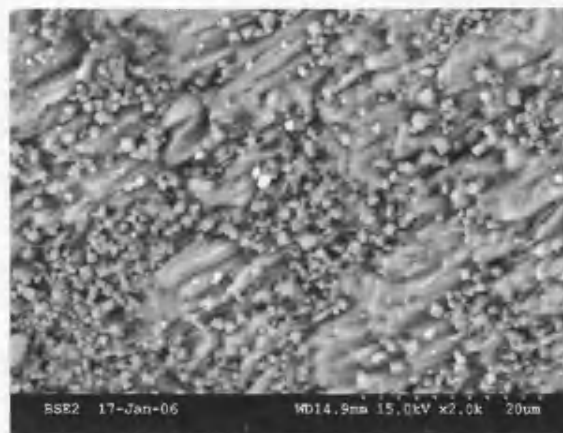
C1971
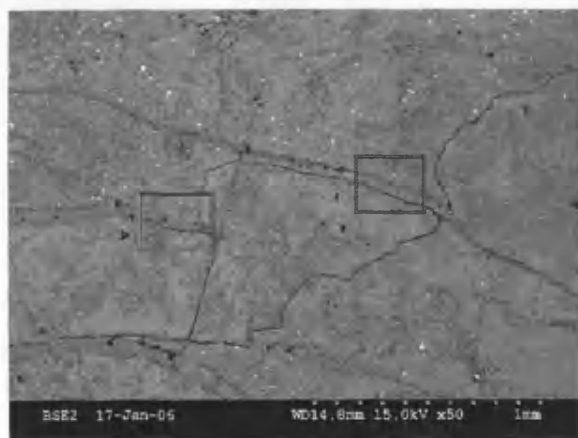
C1971
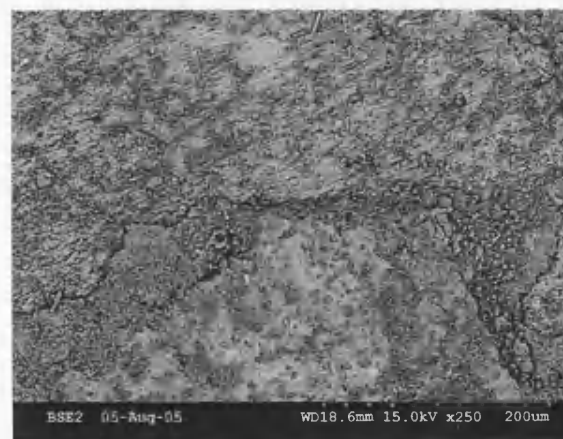
C1971

C1971

C1971

C1971b
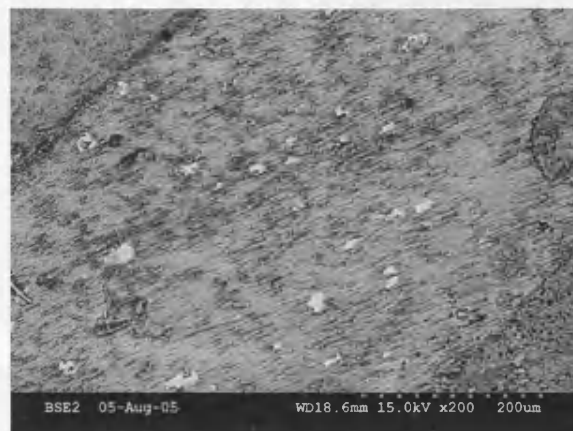


C1971



C1971
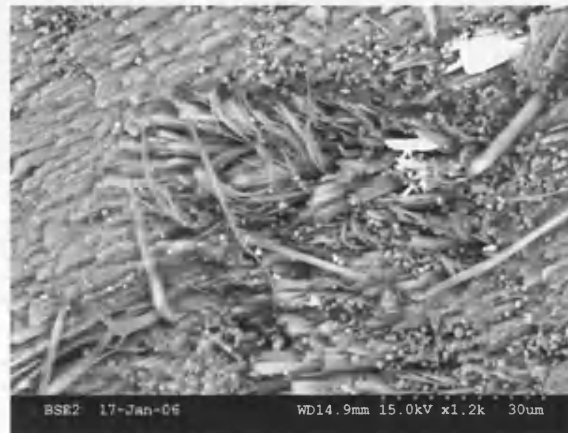


C1971
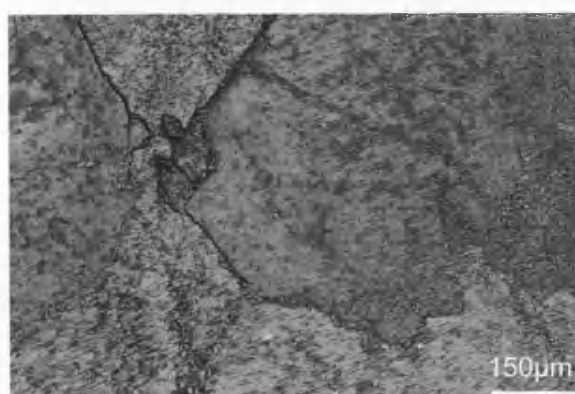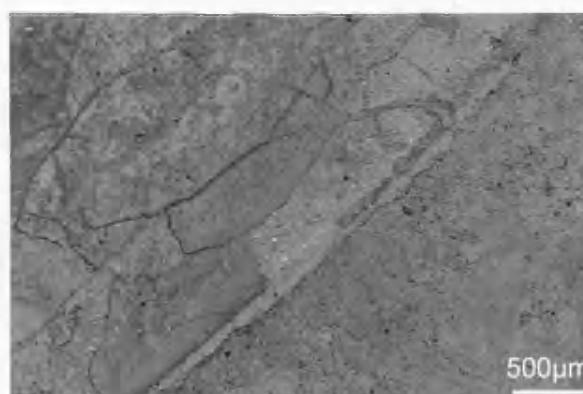


C1971
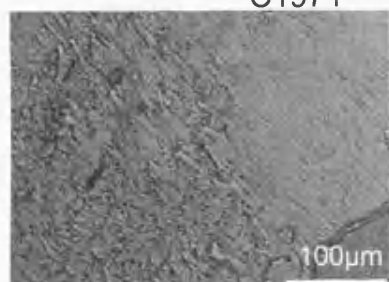


C1971
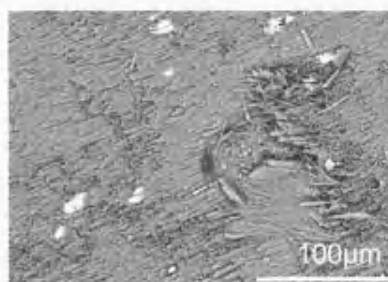
C1971
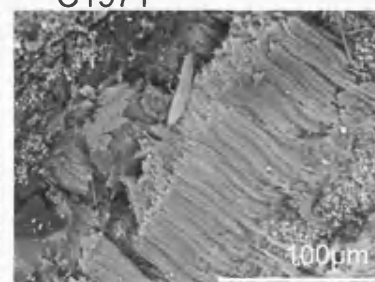
C1971

C1971

C1971

C1587b
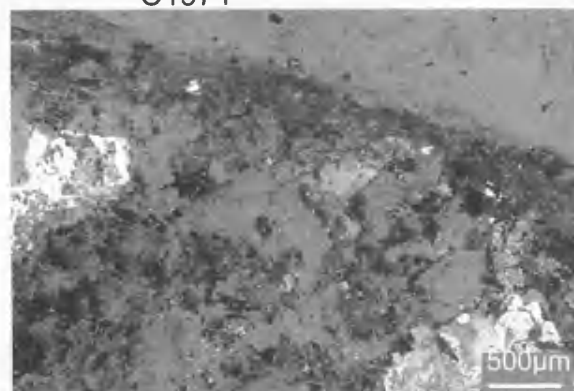
C1587

C1587

C1587
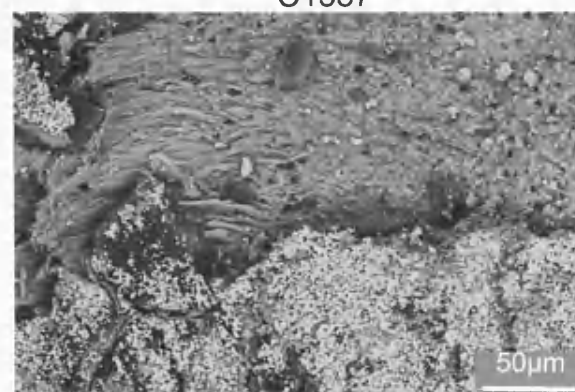
C1587

Original camera lucida drawings of specimens.

C1971b

1 mm

C1971a

1 mm

C1587a

1 mm

C1587b

1 mm
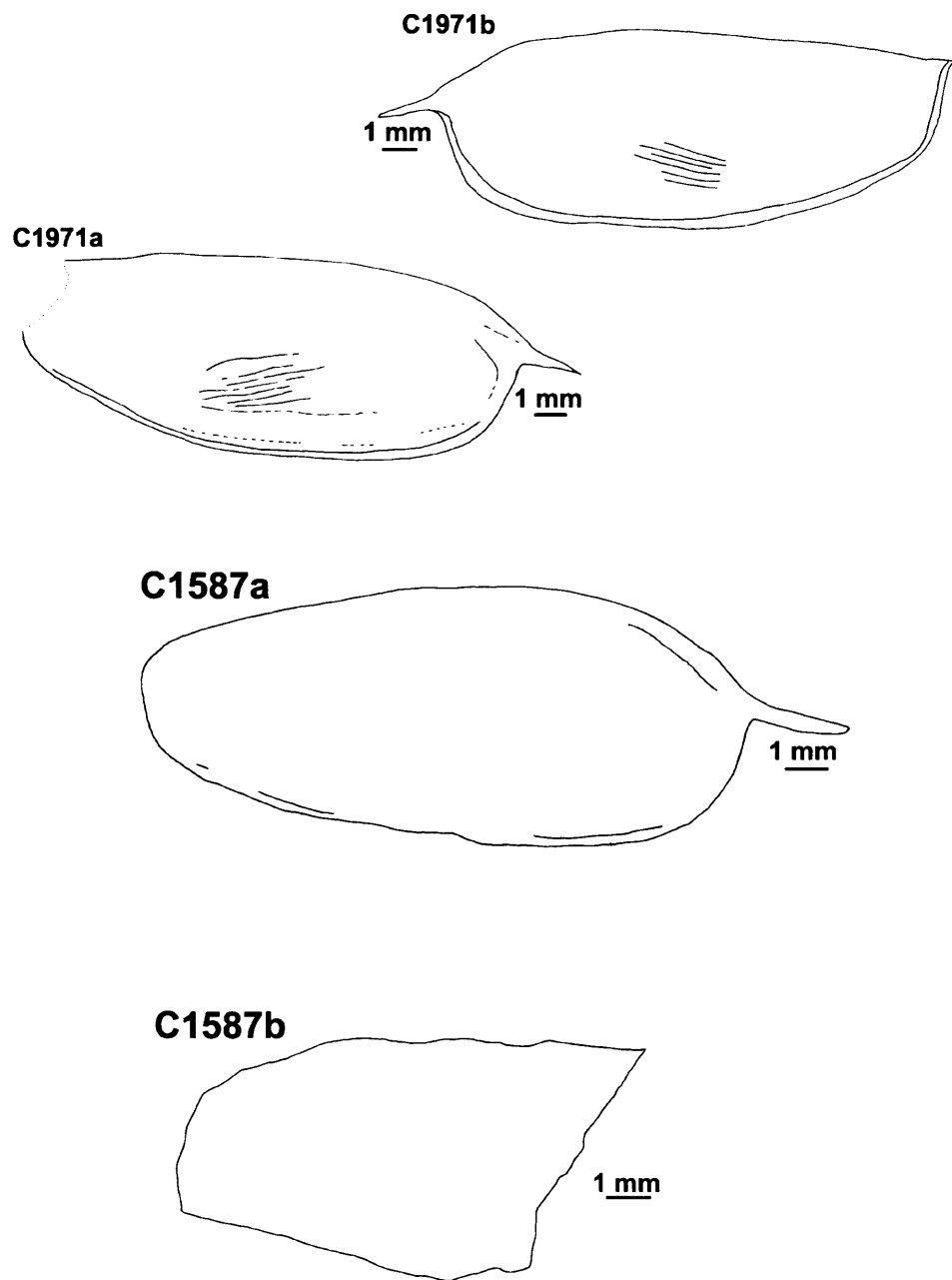
Original detailed camera lucida drawings highlighting the areas of differing preservation styles.



**C1971a**

1 mm

**C1971b**

□ brown
□ white

1 mm

**C1587b**



**C1587a**

178
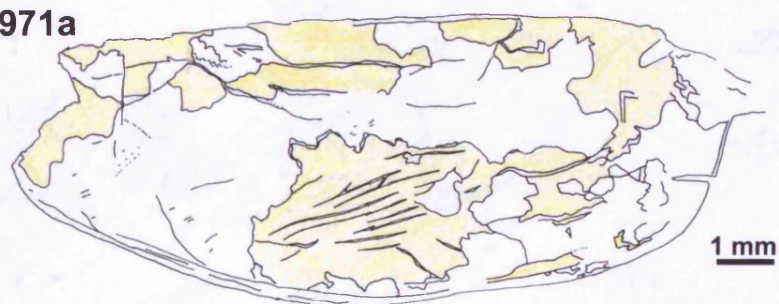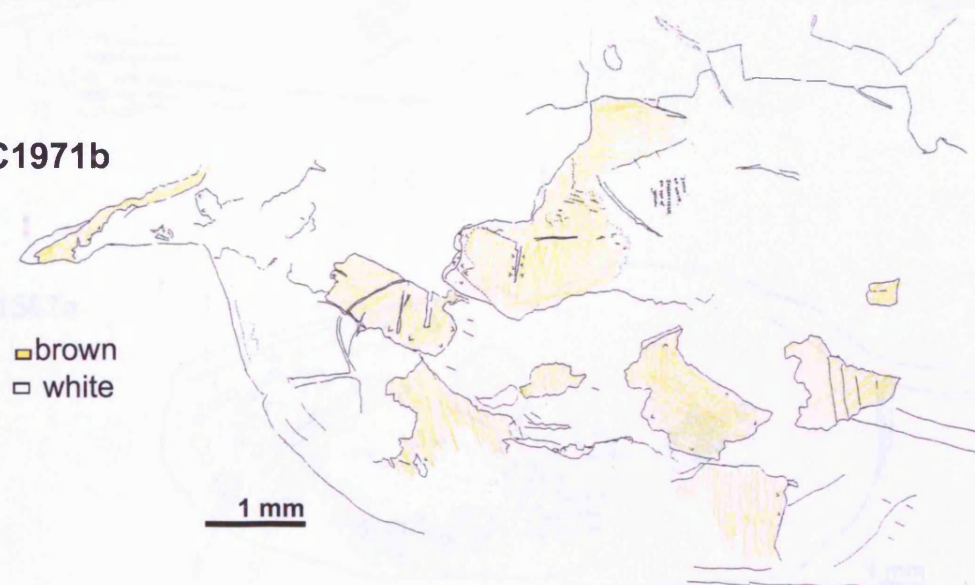
# APPENDIX II: PSEUDOFOSSIL

An additional radial structure from the Soom Shale that is probably not biological in origin.
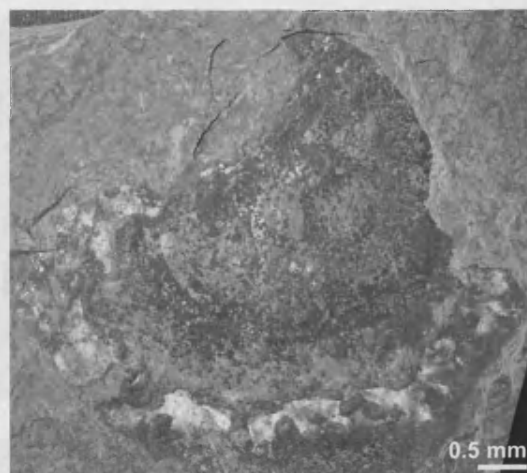


**C973**  Radial structure
Faint, especially at centre
Shiny white areas, mostly around margin

## APPENDIX III: SCOLECODONTS

Photographs of the complete Soom Shale scolecodont fauna.



C319a

C319b
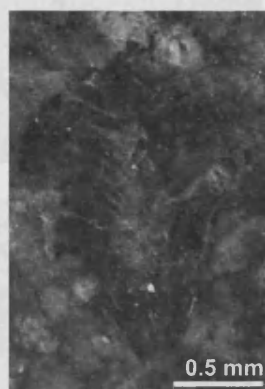
C853a
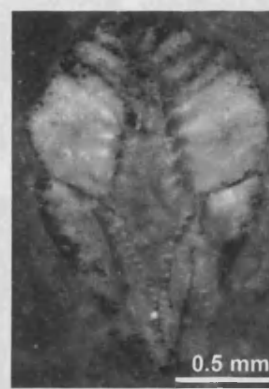
C853b

C1016ia

C1016ib

C1016iia

C1016iib

C1048a

C1048b

C1706a

C1706b

C1855a

C1855b

C1750

C1951a

C1951b

C1978a

c1978b

C1948a

C1948b

C1976a

C1976b

C2018

C1980a

C1980b

C1988a

C1988b

C2009i

C2009ii

C2033a

C2033b

C2021a

C2021b
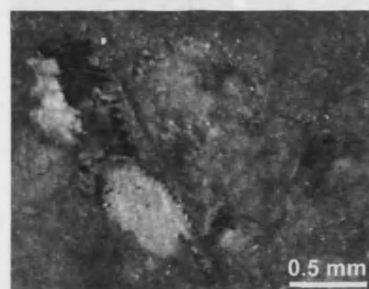
C2030a
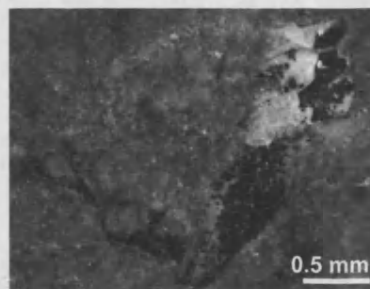
C2030b

C2014b

SEM backscatter images of the Soom Shale scolecodont fauna.



C319a    C319b    C853    C1016ia    C1016ib

C1016iia    C1016iib    C1048a    C1048b

C1706a    C1706b    C1750    C1855b    C1855a

C1948a    C1948b    C1951a    C1951b    C2018

C1976a     C1976b     C1978a     C1978b     C2009i

C2021a     C2021b     C1988a     C1988b     C2009ii

C2030a     C2030b     C2033a     C2033b     C2014a

C1980a     C1980b     C2014b
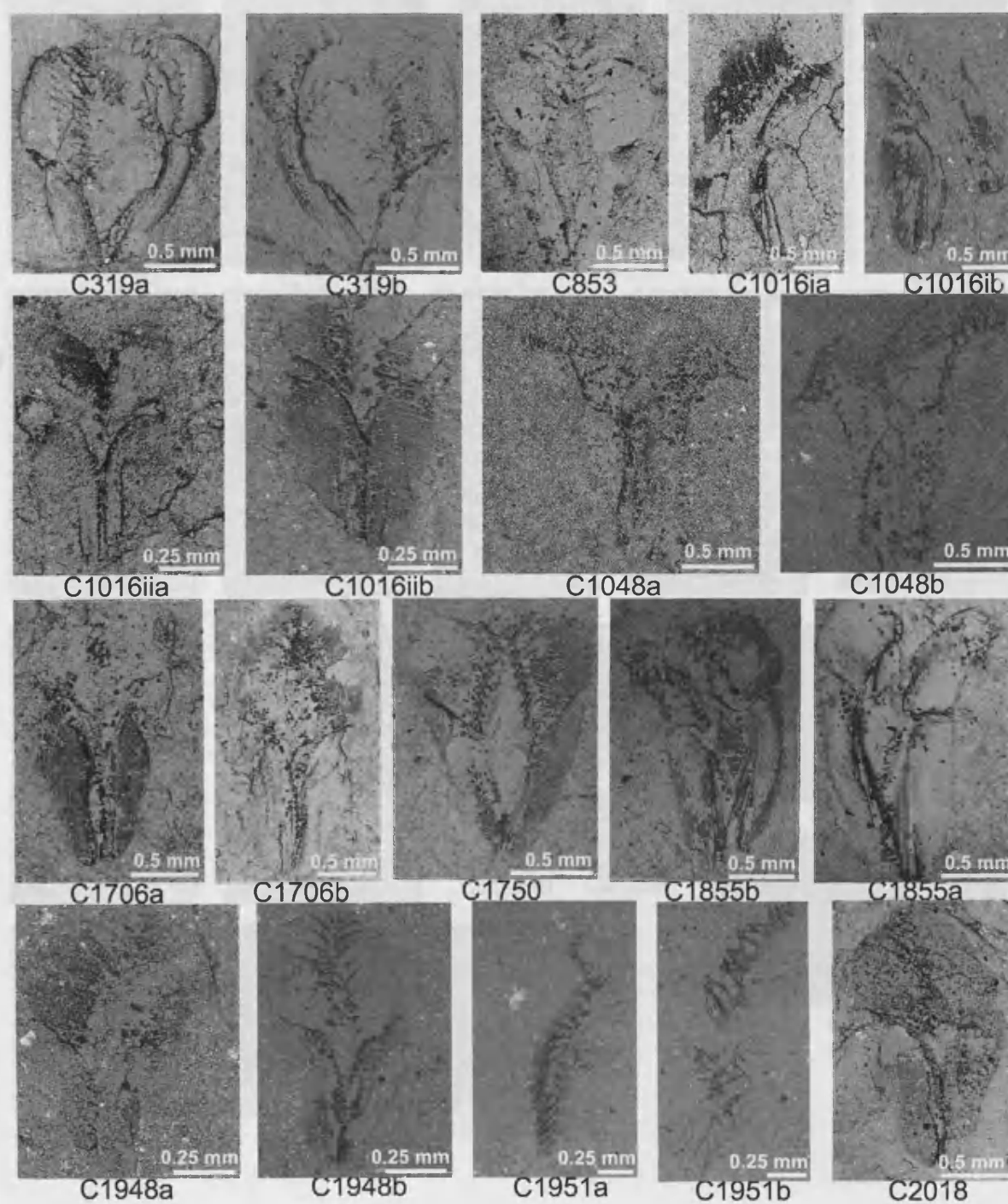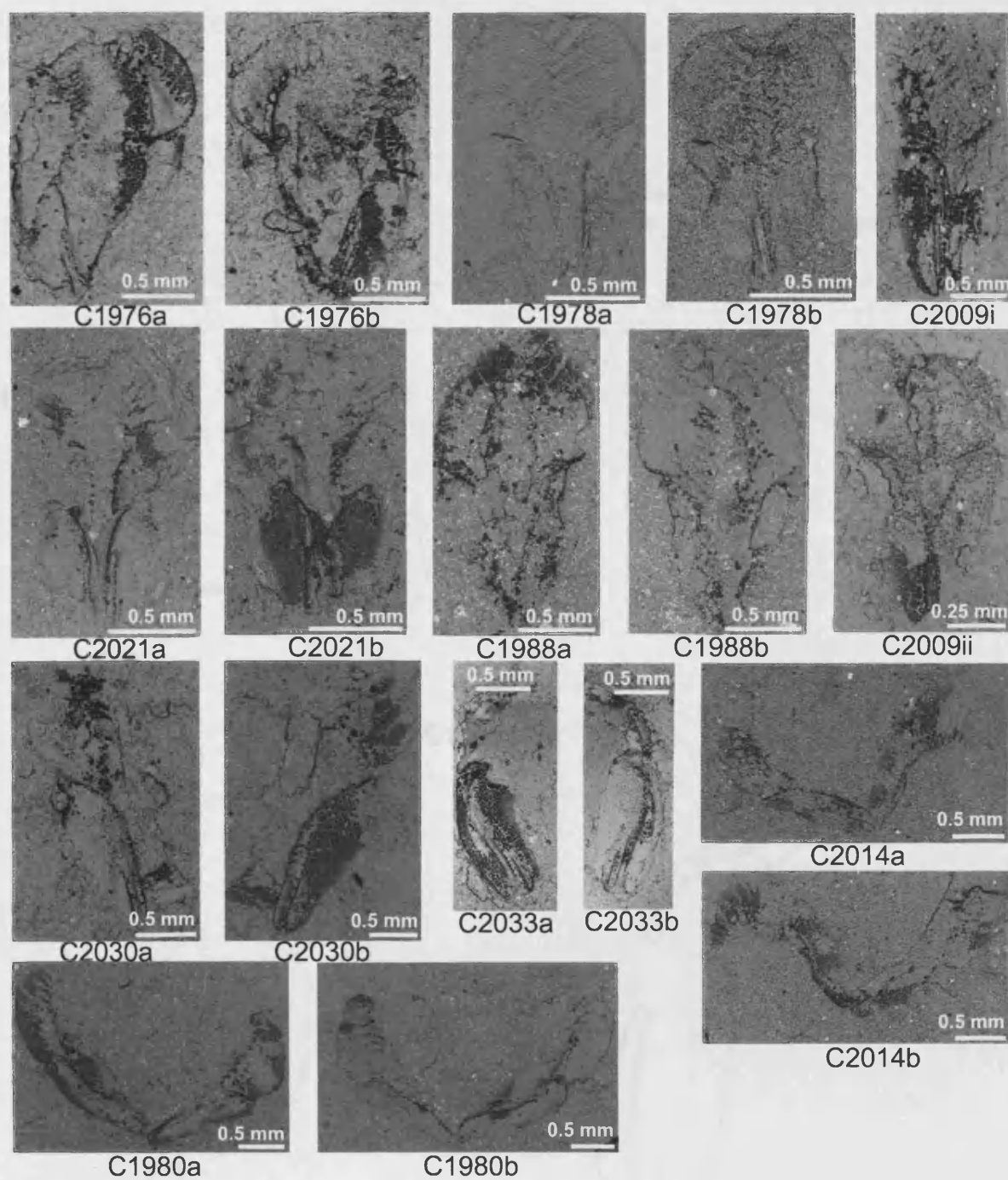
Camera lucida drawings of the Soom Shale scolecodonts that were not included in Chapter 4, with notes on possible affinities.

**C1750**
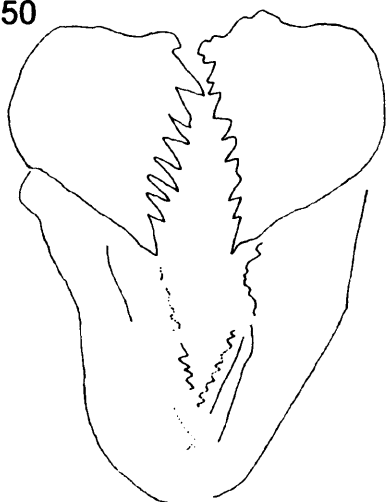
MII's clear denticles
*Synaptogenys* with anterior free teeth missing?

1 mm

**C1885b**
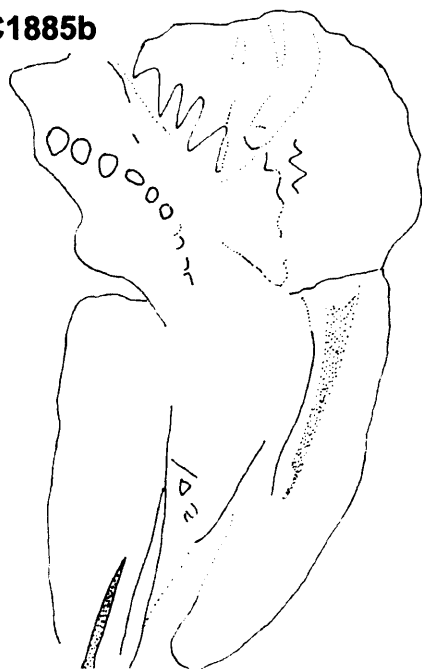
**C1885a**
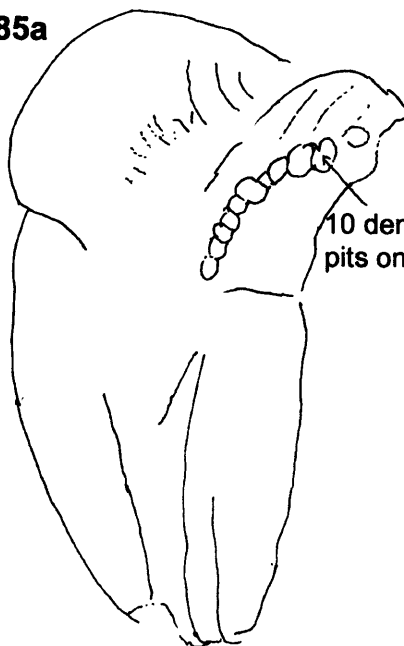
10 denticles on this side,
pits on counterpart

1 mm

1 mm

Unusual jaw configuration
r and I MII have different morphology
Affinities unknown

C1980b

C1980a

1 mm

Mostly silver

1 mm

Mostly black

Free anterior teeth?
MI long thin
No compound ridges
Affinities Unknown

C1016ia

1 mm

C1016ib

1 mm

Compound MI
Mochtyellid?

**C1016iia**  **C1016iib**



1 mm   1 mm
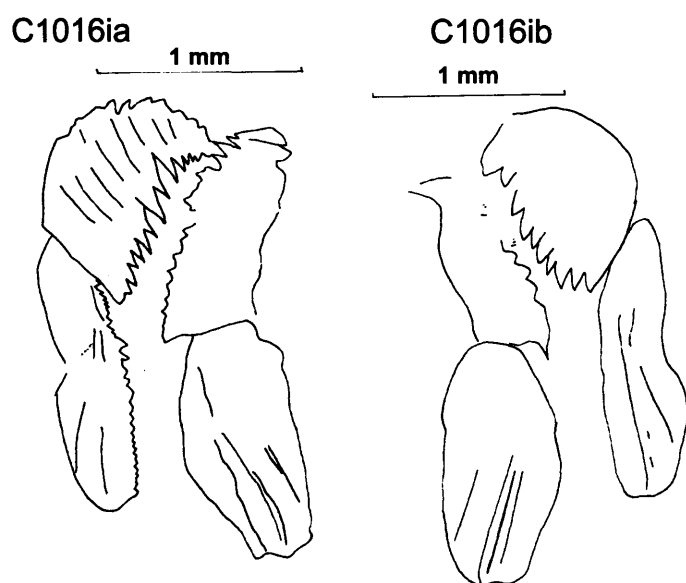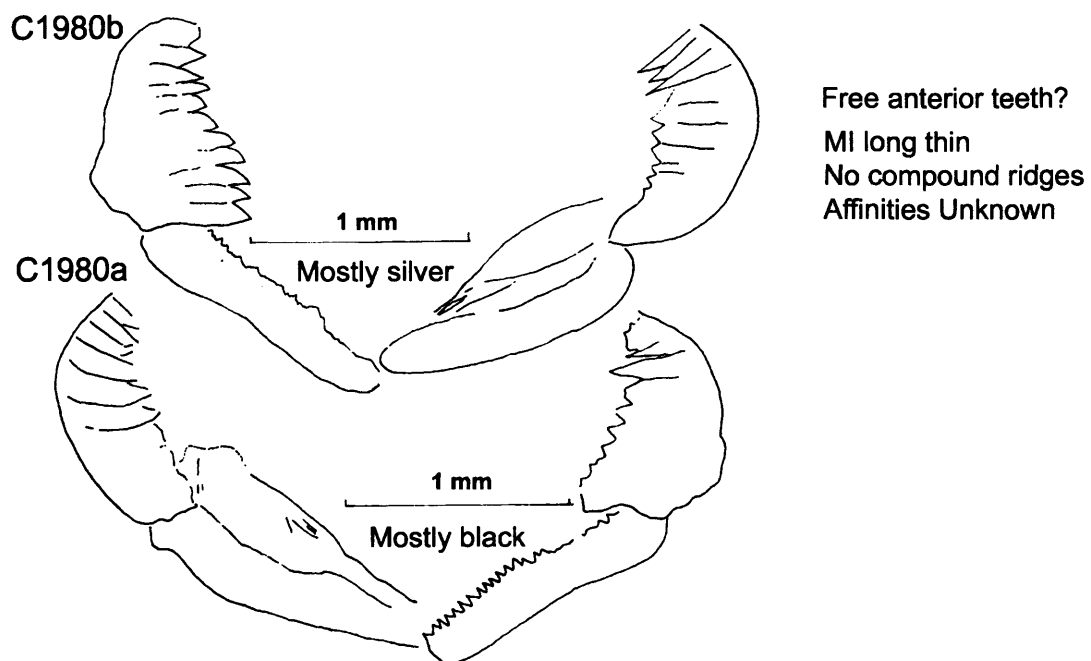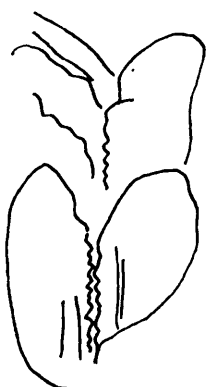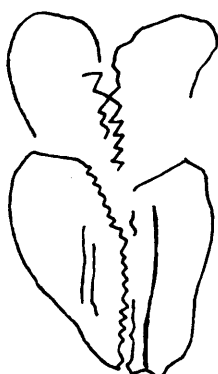
Compound MI?
Mochtyellid?
Possible anterior teeth
*Synaptogenys* ?

**C1951b**  **C1951a**



1 mm   1 mm

String of lateral teeth?
Xanioprion?

**C1048b**  **C1048a**



1 mm   1 mm

MI's long thin
Arcuate MII elements,
anterior of elements
point outwards
Xanioprionid

**C1976b**

**C1976a**

Curved MII's
Xanioprionid?
MII's curve inwards
*Xanioprion*? n. sp.

1 mm

1 mm

**C1706a**

**C1706b**

MI jaws possibly compound
Mochtyellid

1 mm

1 mm
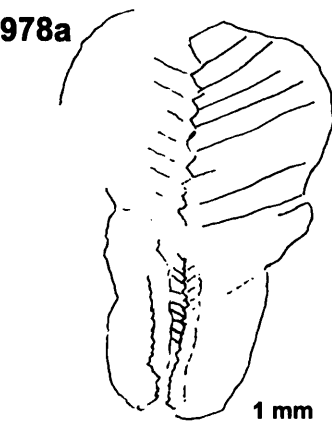
**C1978a**

**C1978b**

Compound MI's
Mochtyellid

1 mm

1 mm

**C1988b**

**C1988a**

Affinities unknown

1 mm

1 mm
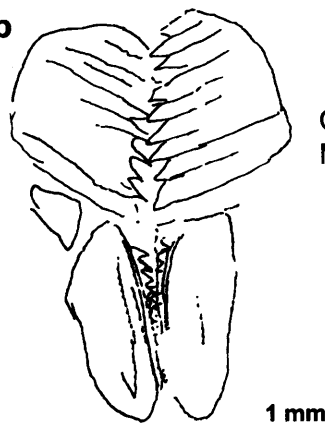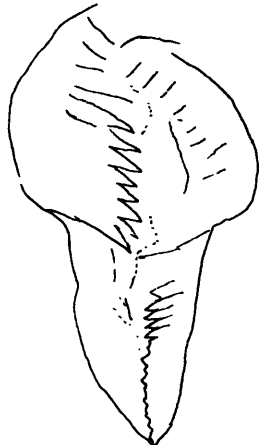
**C2018** Possible compound MI's
Mochtyellid?

1 mm

**C2009**

Possible compound MI's
Mochtyellid?

**C2033a**

**C2033b**

Possible compound
MI element

1 mm

1 mm

1 mm
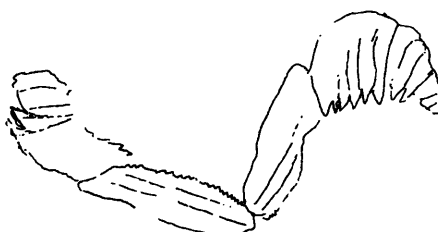
**C2014a**
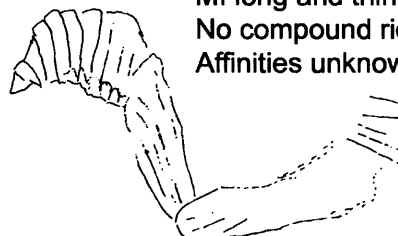
**C2014b** Possible free anterior teeth
MI long and thin
No compound ridges
Affinities unknown

1 mm

1 mm

SEM backscatter images of detailed features of some of the Soom Shale scolecodonts.
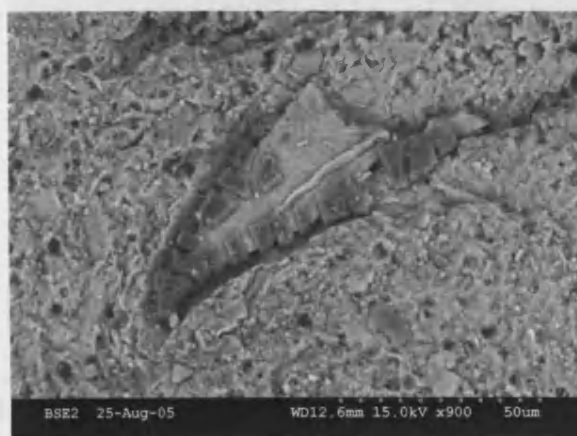


**C319b**
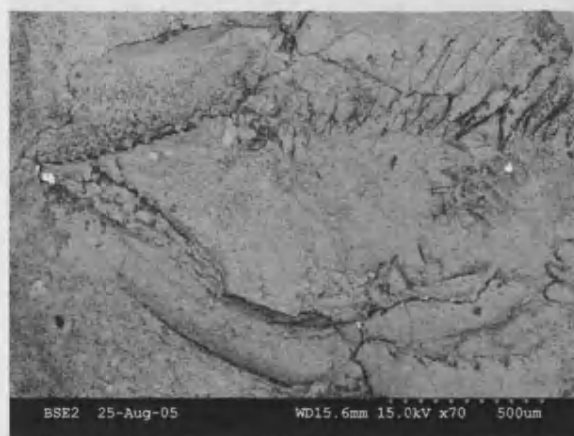


**C319a**
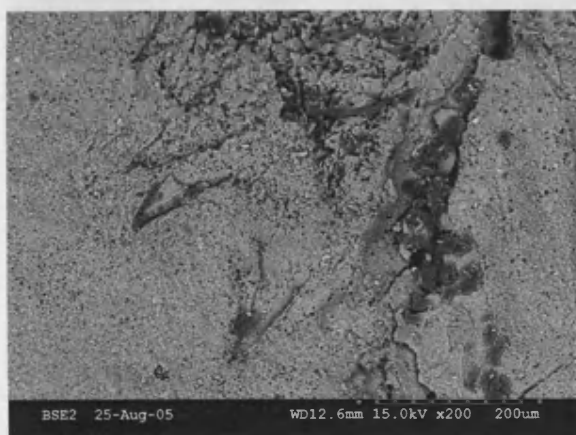


**C319b**
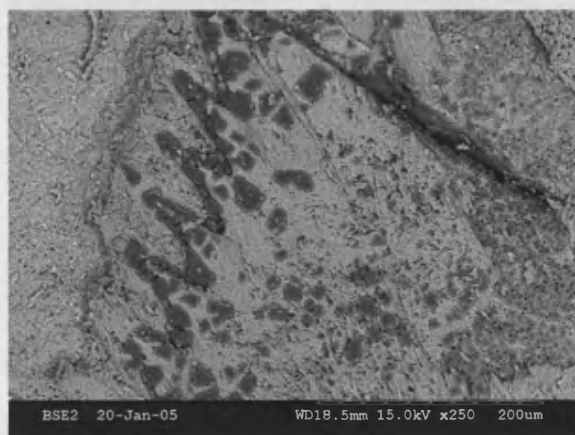


**C1750**
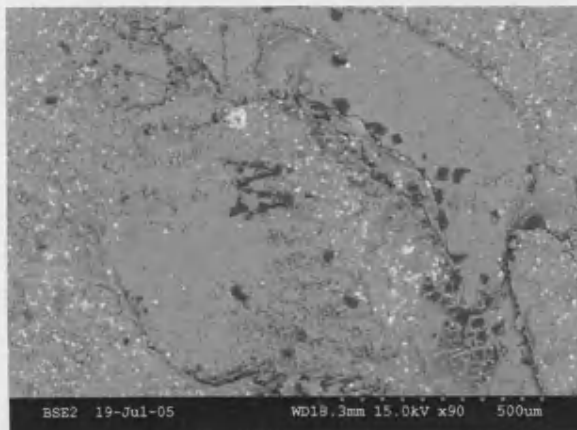
**C1988b**
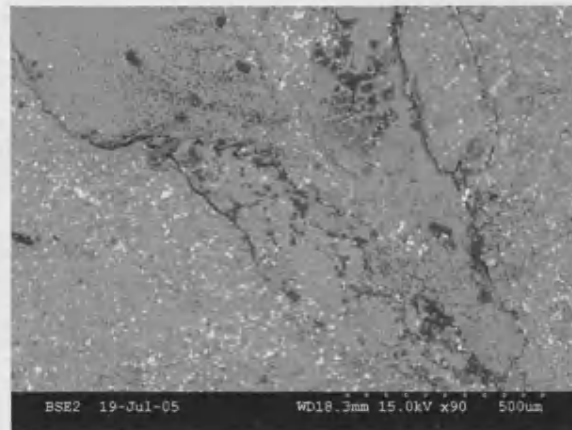
**C1988b**
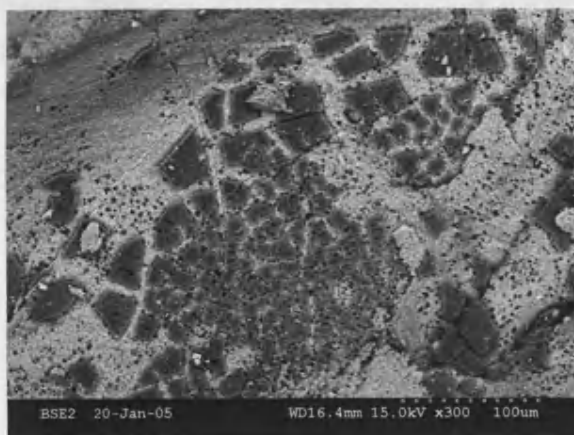
**C1885b**

**C1885b**
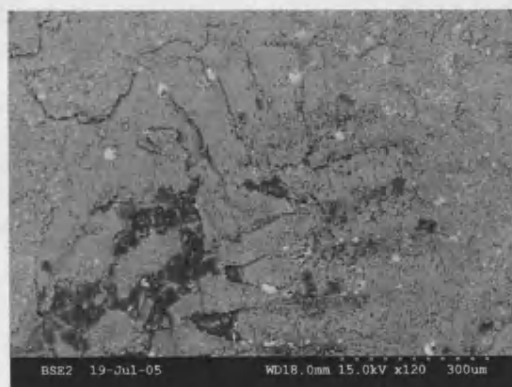
**C2009i**

# APPENDIX IV: LOBOPODIAN

Original camera lucida drawings of Lobopodian fossil, part and counterpart, which were used to create the composite drawing in Chapter 5.

**C1974a**

**C1974b,c,e**



1 mm
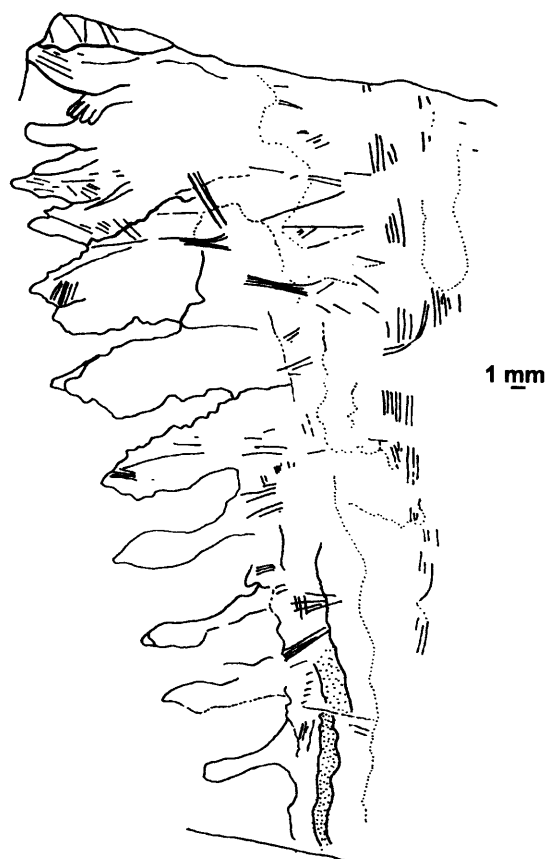
SEM backscatter images of detailed features of lobopodian specimen.
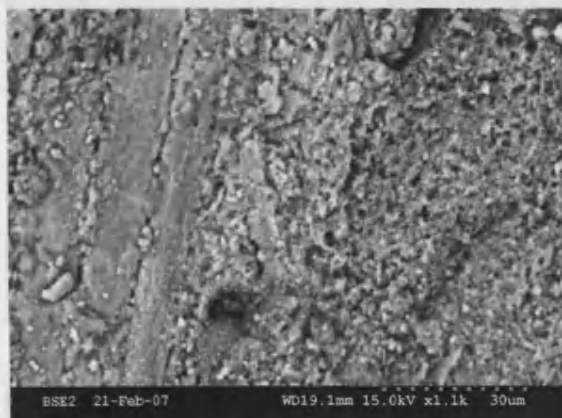

Right side appendages, annulations
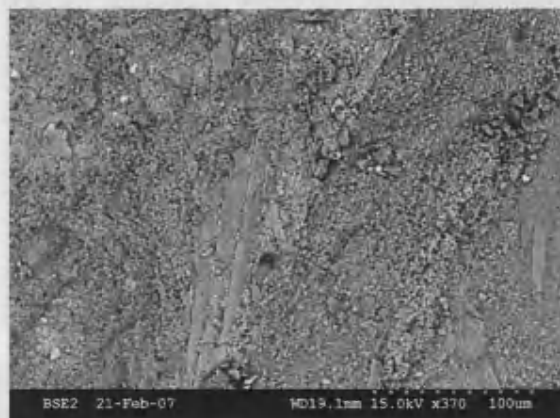

Right side appendages, annulations
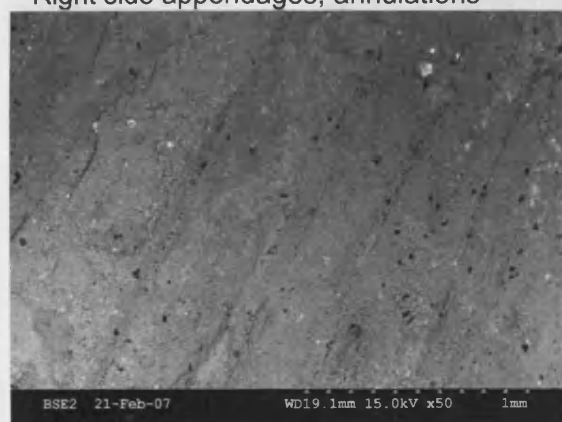

Right side appendages, annulations


Right side appendage, annulation
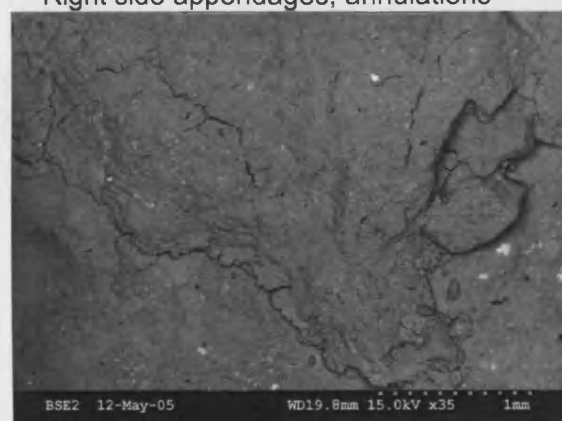

Edge of body


Left side appendage
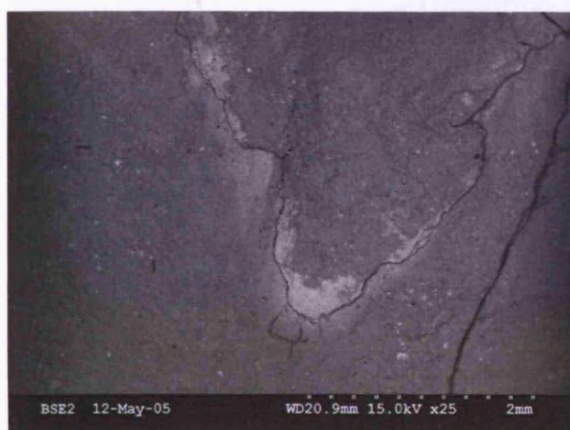
Appendage left side of body
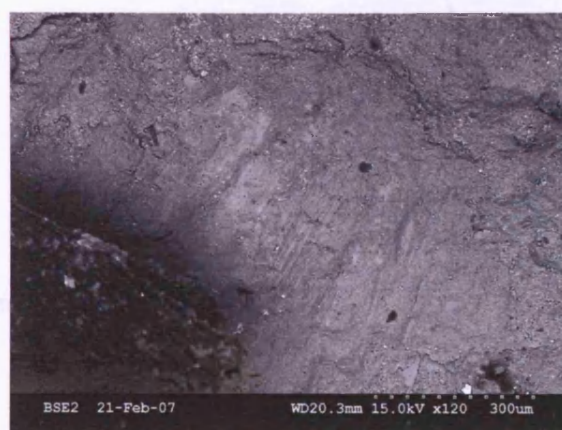


Central structures anterior region



Central structures anterior region enlarged

Detail of central region of C1974a, the elevated gut trace and annulations can be seen.



**C1974a**

# APPENDIX V: NEW ARTHROPODS

## CARAPACES

SEM backscatter images to show detailed features of the specimens.
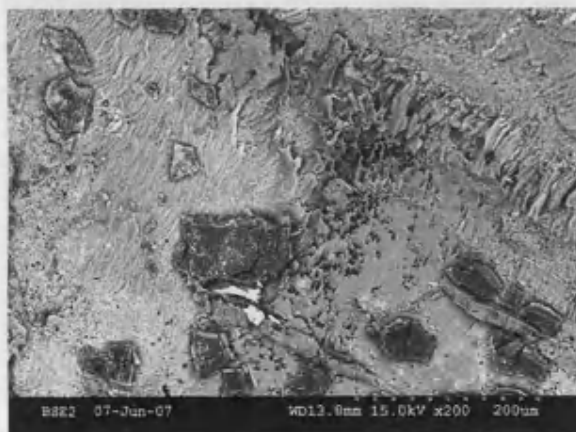

**C914a**
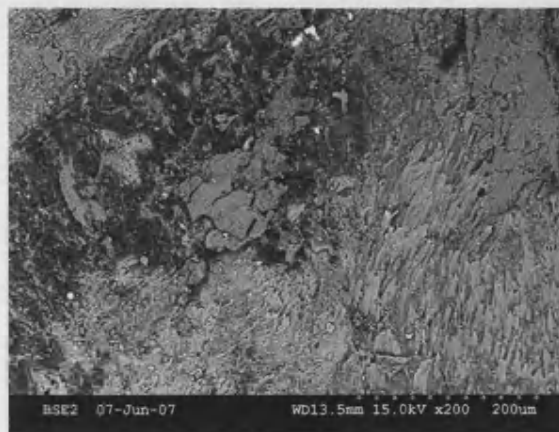

**C914a**
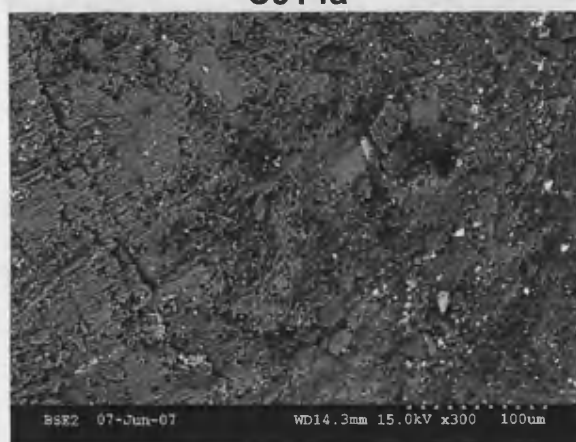

**C914a**


**C914a**


**C914a**
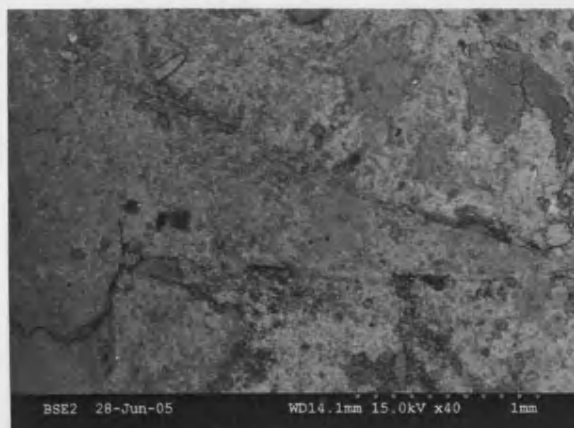
**C1321a - gap in margin**
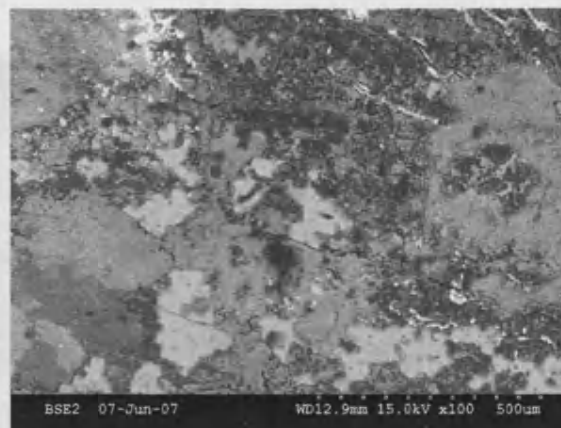


**C1321a**



**C1321b**
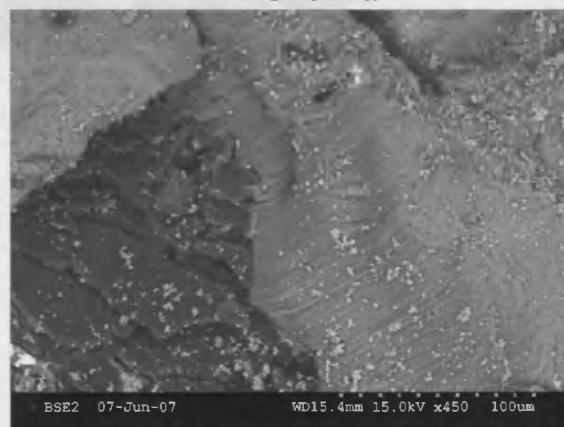


**C1321b**
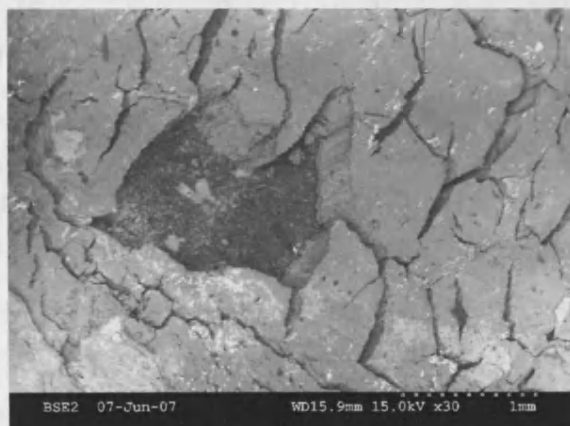


**C1321b**
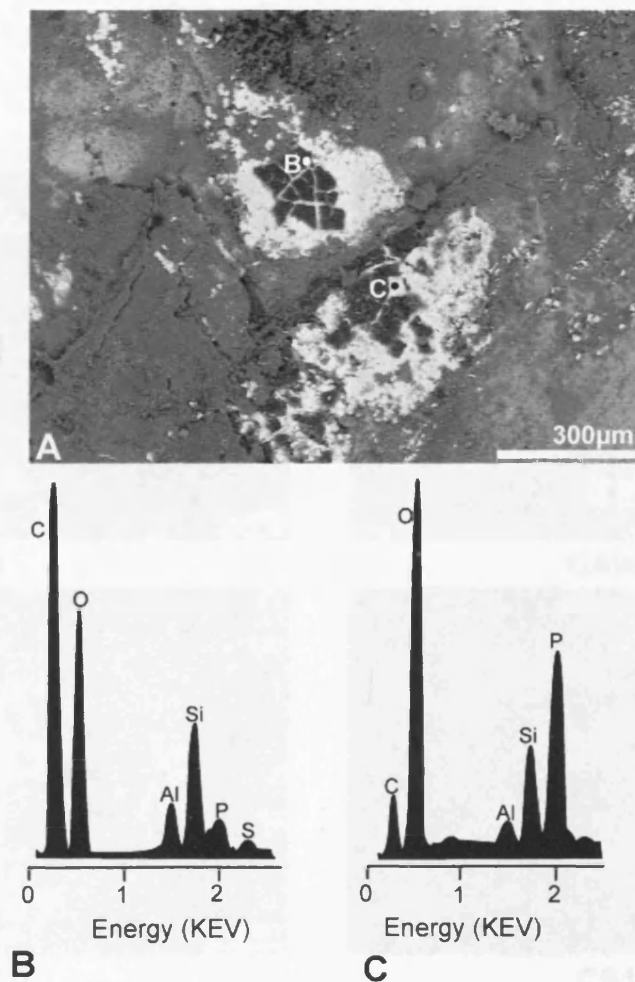
The different layers of preservation of carapace of C1321. **A**. A layer enriched in carbon (B) overlies a layer enriched in phosphorus (C). B and C denote the location of SEM EDX analysis B. and. C. **B**. Shows elevated carbon as well as a clay mineral signature; the small peak in phosphorus may be due to beam penetration. **C**. Shows elevated phosphorus plus clay mineral signature; the small peak in carbon may be due to beam penetration.

## OTHER POSSIBLE CARAPACES

The specimens are poorly preserved and/or show different morphologies and could thus not be grouped with the carapaces described in Chapter 6.


C890a
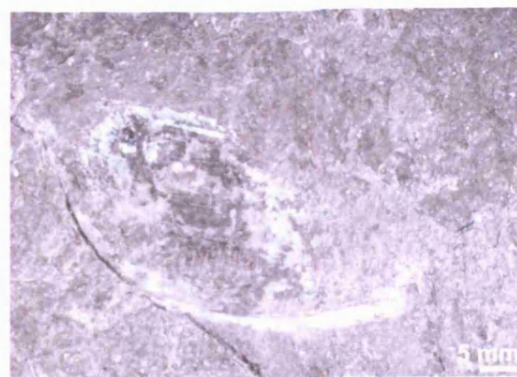

C890b


C916b


C916a
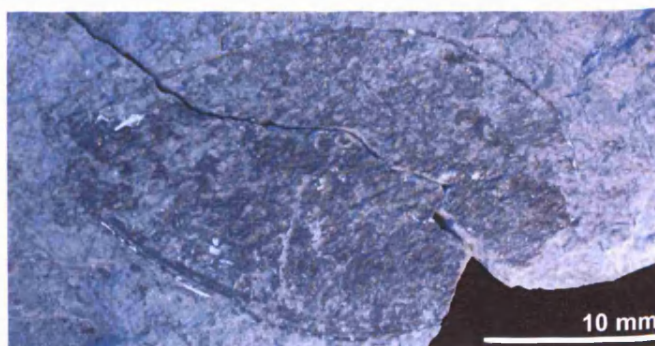

C1090a

C1707

Original camera lucida drawings to show details of morphology and/or preservation.

## C1707b Thoracic appendages

1 mm



indented
raised
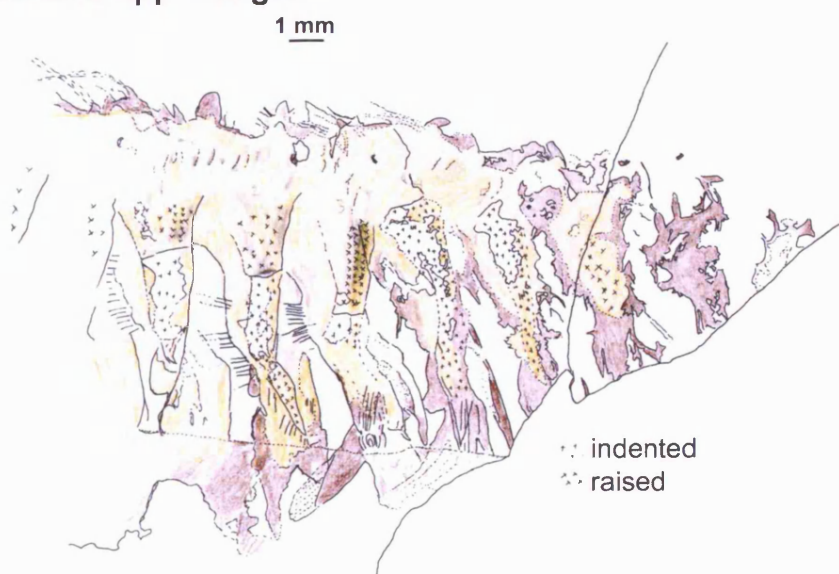
## C1707b abdominal appendages - enlarged

1 mm
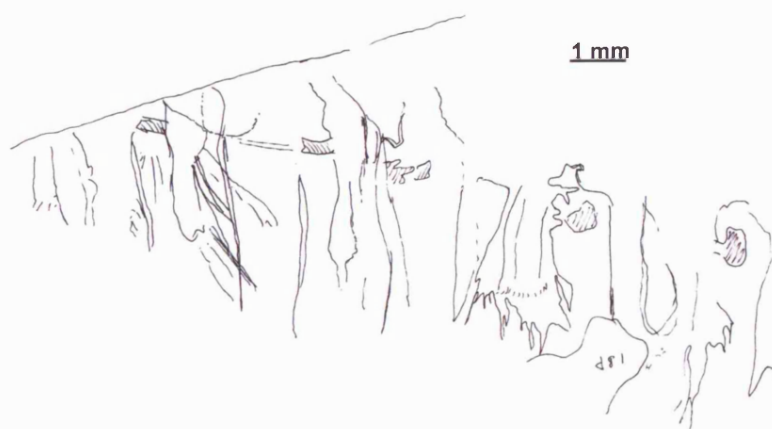
## C1707b Thoracic appendages enlarged



1 mm

## C1707a anterior 1 mm

SEM backscatter images to show details of the features of C1707.
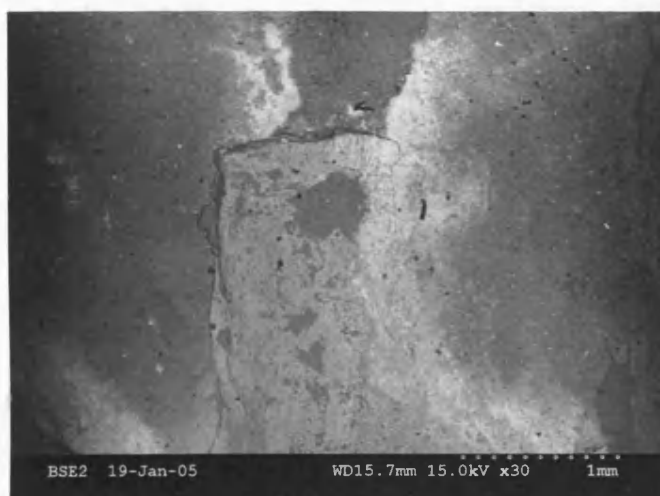

Proximal part of thoracic appendage
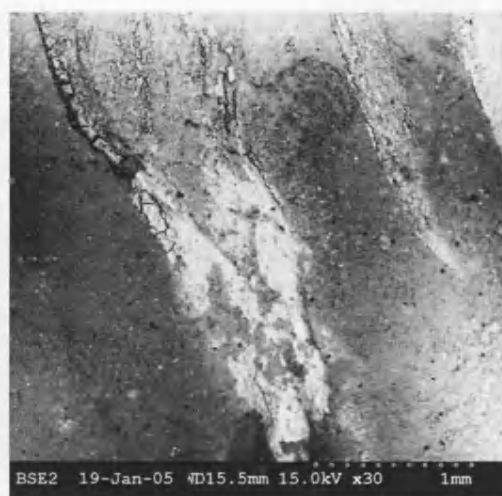

Distal part of thoracic appendage
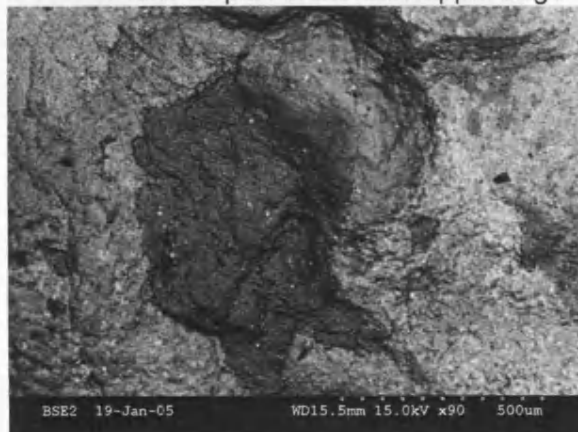

Structure above thoracic appendages on body
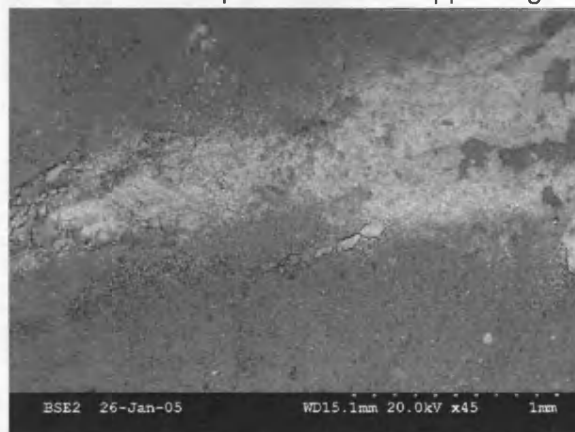

Thoracic appendage right proximal, to left distal


Proximal area of thoracic appendage

C1927

Additional photographs of C1927 to show morphological features.



**Posterior counterpart**



**Part, lighting highlights segmentation**



**Counterpart, anterior**



**Counterpart, central area**
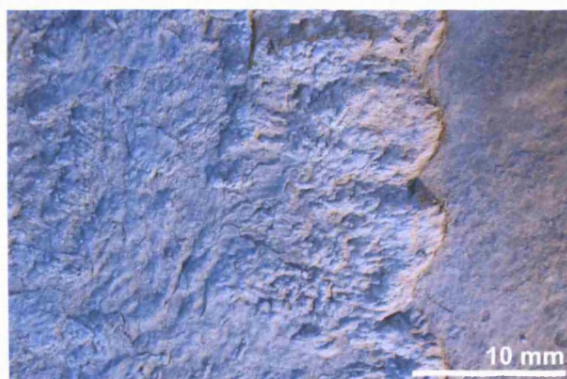
**C1927b centre of body**
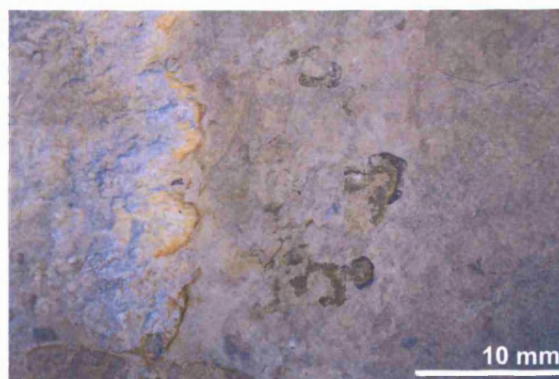


**C1927b thoracic appendages?**

SEM backscatter images of C1927 to show details of morphological features.
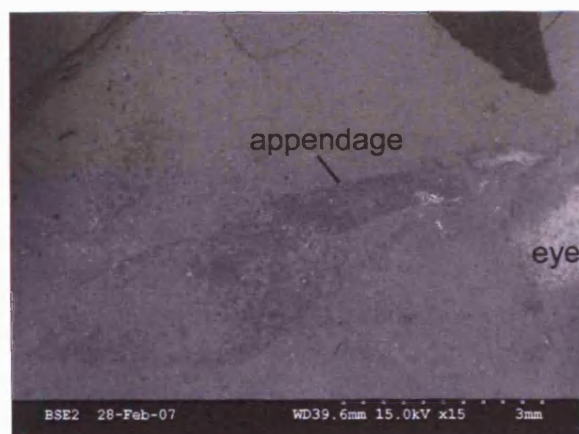


**First appendage**
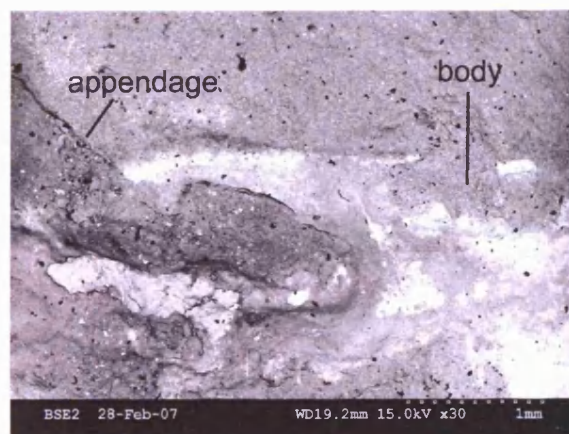


**First appendage, proximal**
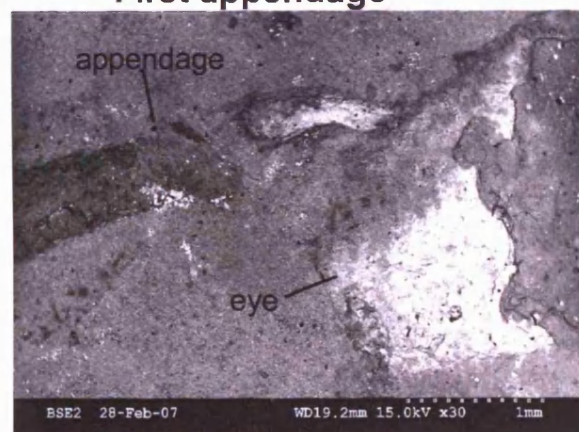


**First appendage**



**Structure on body**
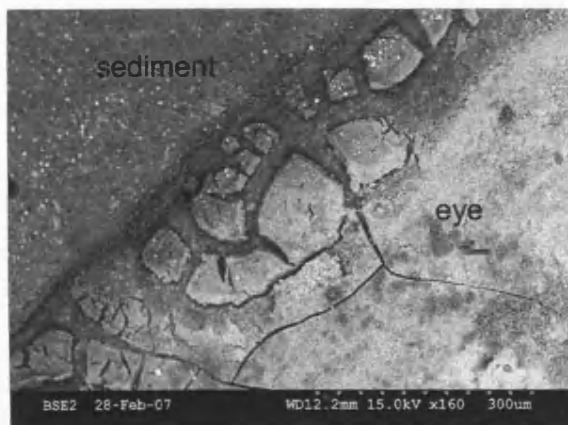
**Edge of eye and sediment**
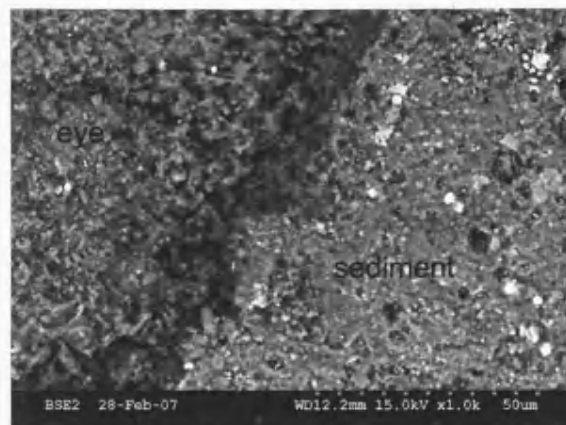

**Edge of eye and sediment**
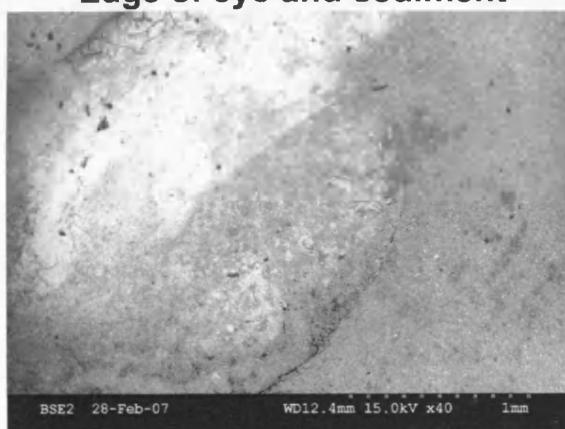

**Eye**
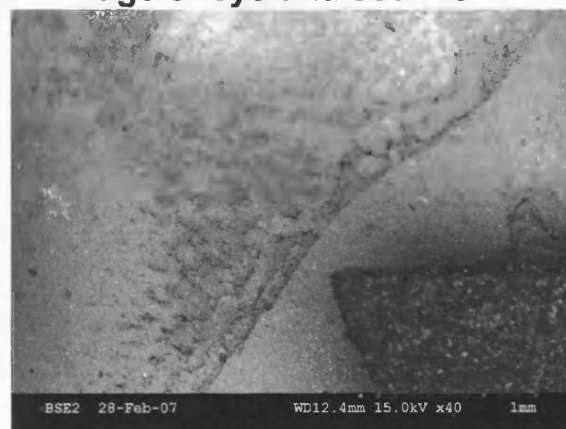

**Bottom of eye**

# APPENDIX VI: ENIGMATICS

Camera lucida drawings and main features of organisms from the Soom Shale Lagerstätte that are not yet been identified.

**C863a**

⌐⌐⌐ = white shiny areas
length approx 3.9 cm

1 mm

Faintly preserved, no clear structures
Possibly segmented
Patchy brown mosaiic
and shiny white preservation

**C671**

1 mm
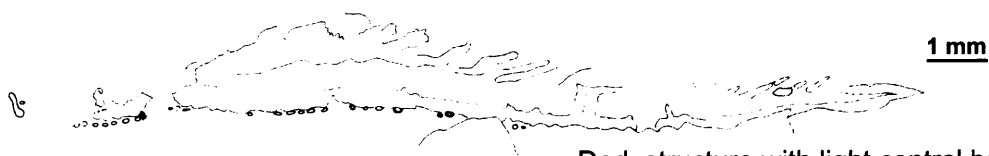
Dark structure with light central band
Small black circles below
Lobes above

**C1190a**
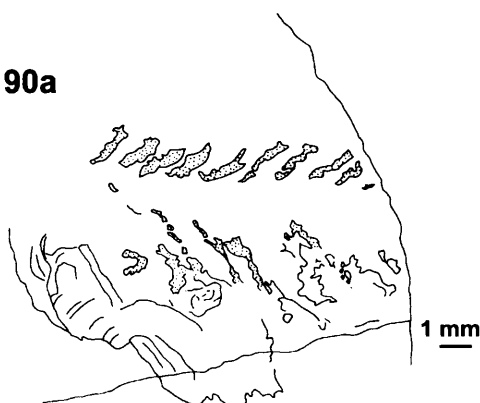
2 Series spines/segments
Top row 10
Lower row, more irregular
Lower left hand side,
lobe-like structures, algal?

1 mm

**C585a**

1 mm

Radiating dark structure

**C696**

Segmented?
Darker than sediment
Left of segmented area
- flecks of organic material
Disarticulated remains of
arthropod?

1 mm

**C509**

Length 45 mm
Width 12 mm
9 - 11 lobes (lower part of fossil)
3 attenuated arcs and
25 angled spines, some
extend into arcs (top part of fossil)

1 mm

**C1406**

Rock matrix covered in algae
Possibly algal in origin
Specimen dark grey,
some shiny white patches

1 mm

**C1372a**
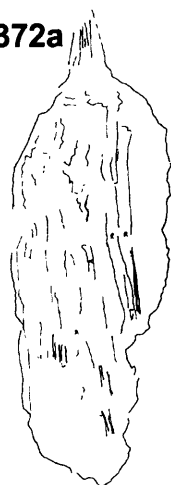
Very pronounced ridges
1 mm height in some areas
Sclerite?

**C1548b**

1 mm

Two structures?
One lying over other
Linear striations
Darker than sediment
Pair of sclerites?

1 mm

## C448a



Black outline
6cm long
2cm wide
Some internal structure
Blobs on surface (head? area)
Possibly 11 segments
Elongate body
Tapers posteriorly
No appendages
**1 mm −**

## C1541  1 mm



Two structures
Both black
Spikes orientated in one direction
Left one length 5 mm, width 1 mm
Right one length 5 mm width ~ 0.5 mm

## C1907
1mm

35 mm long
Width varies -
posterior 0.57 mm
tapers 0.43 mm anterior
Elongate
Internal structure
Central line some areas
Horizontal lines extend
from central line, create
chambers.
Segmentation differs
along length, so not
arthropod antennae.

Photographs of organisms that have not been identified



C1372
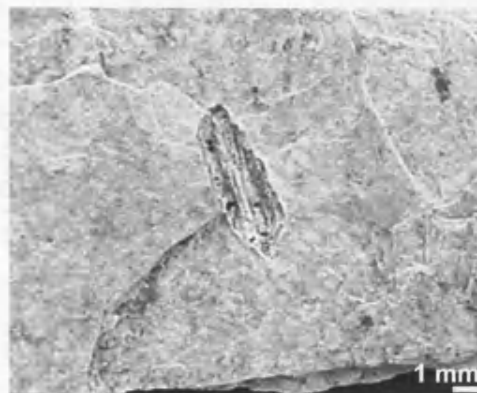
C1372

C1190
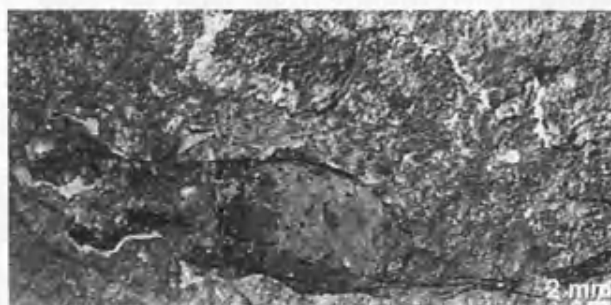
C1406

C585

C585

C1540b
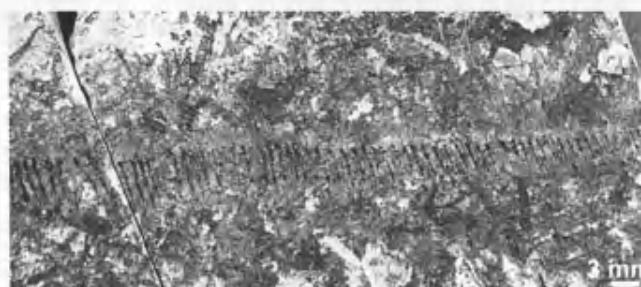
C1540a
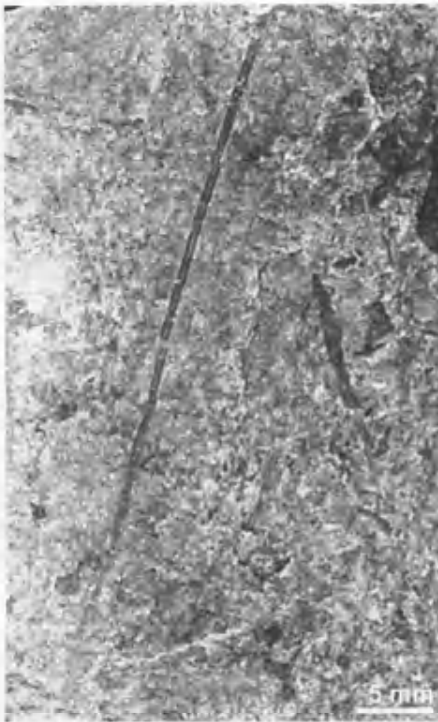
C1907
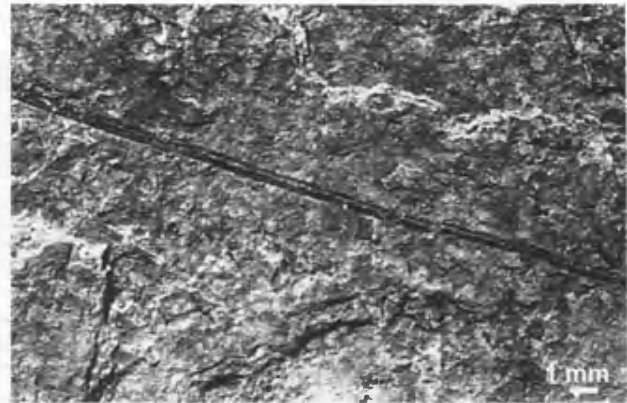


C1907



C1181



C1584



C1584
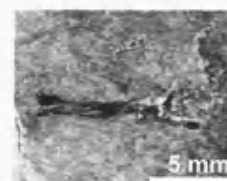


C931



C931



C696

C509b
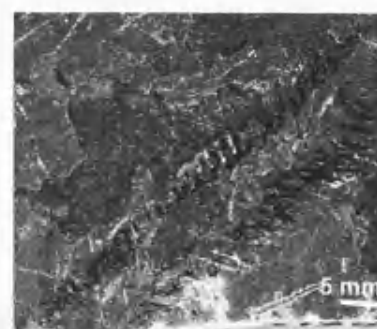
C509a

C509b
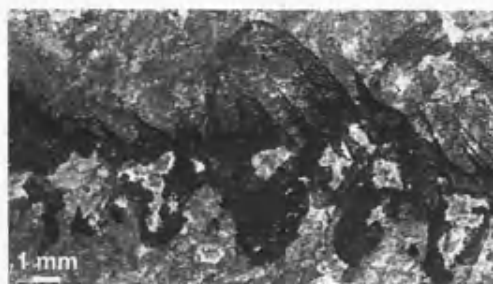
C509b

C984

C448

C1064

C1358

C863a

C1411

*SIPHONACIS*

Camera lucida drawings of *Siphonacis* specimens, with notes.

**C1777a**

spinose projections along top

1 mm

***Siphonacis*** From unumbered block

*Siphonacis*, folded over

1 mm

**C938**

*Siphonacis* - long elongate structures
ranging from 5 - 15 mm in length and approximately
0.5 mm in width. Many have central ridges running
down the centre. A few have small spinose
projections along their length.

1 mm
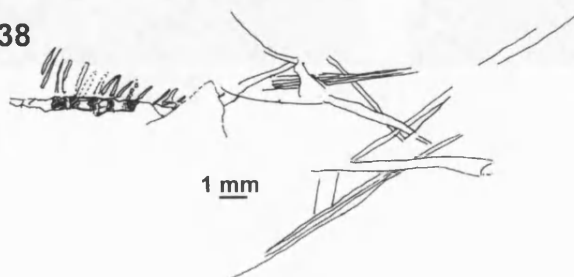
**C938**

Very spinose example on this block,
with darker bands of prservation
(left hand side)

1 mm

**C938**
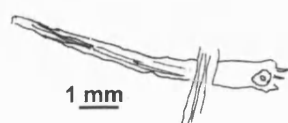
Some bigger specimens occur in isolation
Multiple smaller specimens can occur
together, overlapping each other

1 mm

Photographs of *Siphonacis* specimens
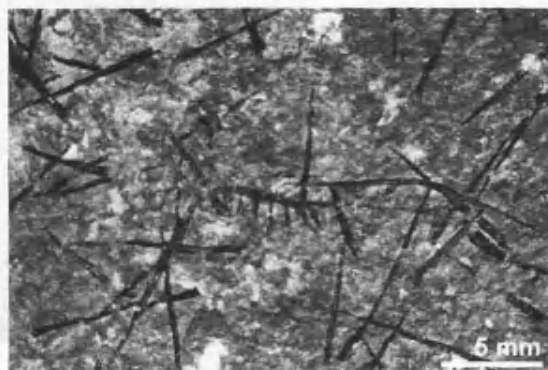


C936b
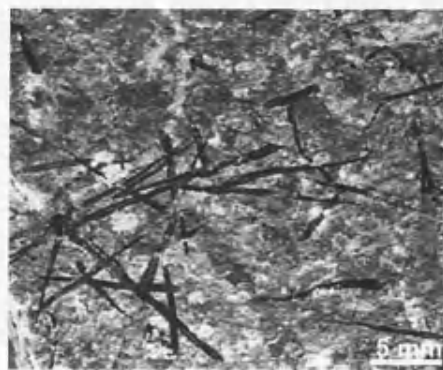
C1543
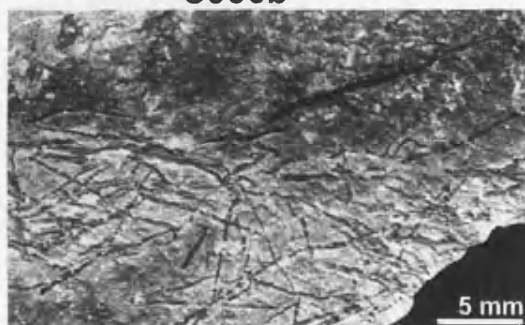
C1464
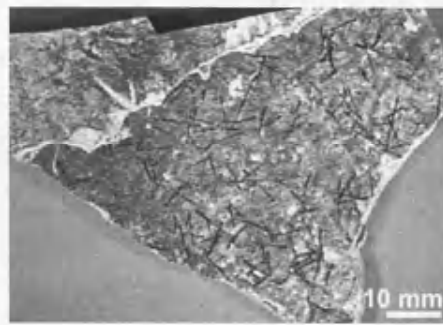
C936a
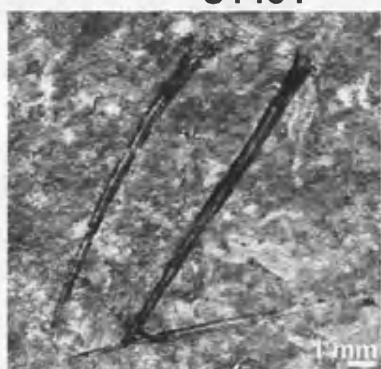
C725
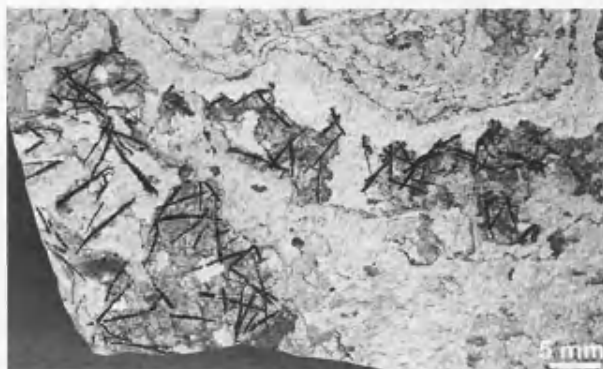
C956a

SEM backscatter images of *Siphonacis* specimens.
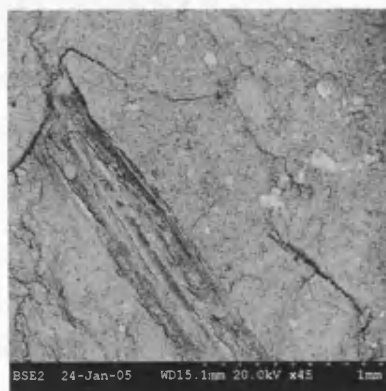


C935



C935
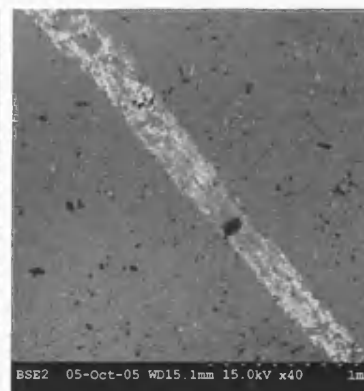


C600



C935
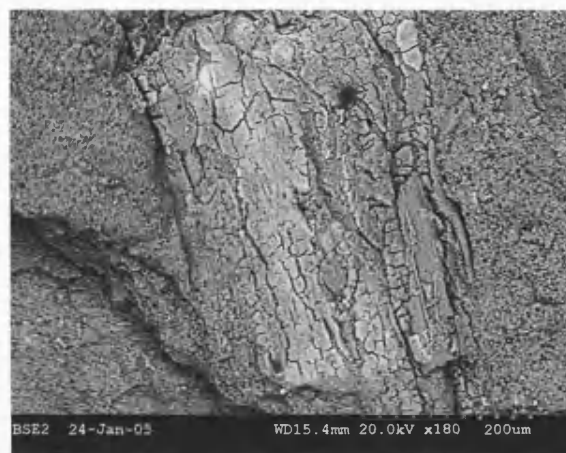


C935
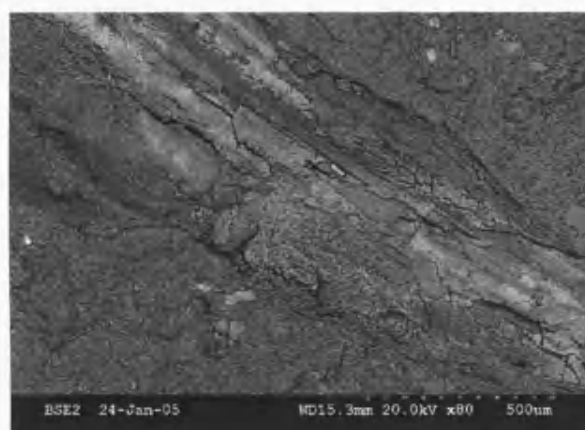


C935



C1004

# APPENDIX VII: PUBLICATIONS AND POSTERS

# Taphonomy and palaeoecology of a Late Ordovician caryocaridid from the Soom Shale Lagerstätte, South Africa

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## Abstract

A new species of caryocaridid is reported from the Late Ordovician of South Africa. The fossils show a complex, multi-layered structure that may represent exceptional preservation of the original arthropod exo-, endo- and epicuticle. Alternatively, the layered structure may comprise the carapace, with a mineralized cast of the internal void and a layer of fibrous illite external to the carapace. The genesis of the fibrous illite is important as it demonstrates that not all fibrous textures associated with fossils in the Soom Shale, and perhaps other Lagerstätten, can be interpreted as mineralized muscle tissue.

*Caryocaris cedarbergensis* n.sp. extends the geographical, ecological and temporal range of the family and provides the first evidence of a zooplanktonic constituent to the Soom Shale biota. The genus most likely represents a cool-adapted mesopelagic group during the Early–Middle Ordovician, which inhabited an epipelagic cold-water shelf environment during the Late Ordovician.
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*Keywords:* Caryocarididae; Soom Shale; Lagerstätte; Taphonomy; Palaeoecology; Ordovician

## 1. Introduction

The Soom Shale Konservat Lagerstätte (site of exceptional fossil preservation) contains several taxa displaying exceptional preservation of soft parts, most notably conodonts (Aldridge and Theron, 1993; Gabbott et al., 1995), eurypterids (Braddy et al., 1995, 1999) and enigmatic fossils. Compared with the Cambrian System, the Ordovician has few known Konservat Lagerstätten and of these the Soom Shale records the greatest number of taxa and the highest fidelity preservation of decay-prone tissues, principally as clay mineral replacements. Other occurrences of exceptional preservation in the

Ordovician are the Late Ordovician Beecher's Trilobite Bed of New York State, USA, known for trilobites with appendages and other soft tissues preserved in pyrite (Briggs et al., 1991); the basal Caradoc mudstones of the Llanfawr Quarries, Llandrindod, Powys, Wales, which preserve an abundance of graptoloids, chitinozoans and sponges in pyrite (Botting, 2004); the Middle Ordovician Winneshiek Lagerstätte from the St. Peter Sandstone in Northeast Iowa which includes conodont apparatuses and a variety of other fossils (including caryocaridids) preserved with associated soft-tissue impressions (Liu et al., 2005, 2006); an arthropod described from the Tremadoc of England with preserved appendages (Siveter et al., 1995); and two Late Ordovician shoreline biotas from Manitoba, Canada, one of which, along with other taxa, has well preserved cnidarian medusae (jellyfish) (Young et al., 2006).

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*E-mail address:* rjw35@le.ac.uk (R.J. Whittle).

The caryocaridids have been placed within the Class Malacostraca Latreille, 1806, and the Subclass Phyllocarida Packard, 1879; though there is currently no soft-tissue preservation of the head appendages to confirm their crustacean affinities. They were originally placed in the Family Ceratiocarididae Salter, 1860, by Salter (1863), but were established in their own family, the Caryocarididae by Racheboeuf et al. (2000). The caryocaridids attained their highest diversity and numerical abundance during the Arenig and Llanvirn (Early–Middle Ordovician) (Vannier et al., 2003). Previously, the family was known to range from the Tremadoc to the Early Caradoc (Braddy et al., 2004), when it was thought that they became extinct. They form a recurrent component of graptolite-bearing black, outer-shelf shales (Vannier et al., 2003; Braddy et al., 2004).

Here we report the occurrence of caryocaridids from the Soom Shale Lagerstätte; these specimens occur approximately 10 myr after the hitherto youngest caryocaridids from the early Caradoc of South America (Bulman, 1931; Vannier et al., 2003). The fossils are very rare, as only two specimens have been discovered in fifteen years of collecting. We also comment on the mode of preservation and palaeoecological significance of this new discovery.

### 1.1. Stratigraphy and sedimentology

The Cedarberg Formation, of which the Soom Shale is the lower member and the Disa Siltstone the upper member, constitutes the only significant fine-grained unit within the Lower Palaeozoic arenaceous Table Mountain Group (Rust, 1981), outcrops of which are found in the Western Cape, South Africa (Fig. 1). The Cedarberg Formation contains the only datable fossils within the entire sequence; these have indicated a late Ashgill (Rawtheyan or Hirnantian) age (Cocks et al., 1970; Cocks and Fortey, 1986; Theron et al., 1990). Sutcliffe et al. (2000) and Young et al. (2004) interpreted the Soom Shale as a postglacial transgressive deposit resulting from the demise of the Late Ordovician glaciers, as it directly overlies tillites of the glaciogenic Pakhuis Formation, thus representing an interval equivalent to the *persculptus* graptolite zone of the Hirnantian.

The Soom Shale comprises laminated mud and silt-stone and is 10–15 m in thickness. Soom Shale siltstones and mudstones are black when fresh, for example at Sandfontein, but weather to a pale grey colour in surface exposures at Keurbos (Gabbott, 1998). The black colour of palynomorphs and chitinozoans indicates that the sediment has undergone burial anchimetamorphism to temperatures of at least 200 °C (Cramer

et al., 1974; Gabbott et al., 2003). The laminae comprise alternations of silt and mud with darker layers, which may be degraded organic matter. The sediment is composed mostly of clay minerals, especially illites and mixed-layer clays, and detrital quartz. It also contains syngenetic/diagenetic pyrite and diagenetic chlorite and clay minerals (Gabbott, 1998).

### 1.2. Palaeogeography and palaeoenvironment

Previously, the basin in which Soom Shale was deposited was thought to be located at approximately 60° S (Gabbott et al., 1995; Gabbott, 1998; Aldridge et al., 2001); however, several continental reconstructions for the Late Ordovician have placed the tip of South Africa at between about 30° and 45° S (Fig. 2) (Beuf et al., 1971; Smith, 1997; Sutcliffe et al., 2000; Cocks and Torsvik, 2002; Fortey and Cocks, 2003; Young et al., 2004). The Soom Shale is a postglacial transgressive unit (Sutcliffe et al., 2000; Young et al., 2004), with dropstones recorded from the base of the member. This indicates a cold-water setting.

The depositional setting is thought to have been in a quiet water basin close to a retreating ice front (Theron and Thamm, 1990); water depth is unknown but was unlikely to have been great as the basin was in an intracratonic setting and the Soom Shale is bounded by subaerial tillites below and shallow marine siltstones above (Gabbott, 1999). On the basis of the lack of sedimentary structures, Gabbott (1999) suggested a water depth of at least 100 m, although she cautioned that it could be much shallower if microbial mats bound the sediment or if the sea surface was ice covered. This would represent an inner shelf setting. However, the water depth in the Soom Shale is imprecisely defined and not supported by a detailed sedimentological analysis. The laminated fine-grained nature of the Soom Shale might represent the outwashing of material during climatic amelioration and ice-sheet retreat (Theron and Thamm, 1990). Dominantly quiet water conditions in the Soom Shale lithology are indicated by a lack of flow-induced sedimentary structures and the taphonomy of the fossils. The Soom Shale sediment was largely anoxic; geochemical analyses indicate that euxinic bottom waters prevailed at times (Gabbott, 1998). In some areas metamorphism has transformed the shale and siltstone into a sheared slate, destroying primary internal features (Aldridge et al., 1994).

### 1.3. Palaeontology

To date, taxa found from the Soom Shale include conodonts (Theron et al., 1990; Aldridge and Theron, 1993; Gabbott et al., 1995), myodocopid ostracodes (Gabbott

et al., 2003), eurypterids (Braddy et al., 1995) and naraoiids (Fortey and Theron, 1994). Also present are chitinozoans (Cramer et al., 1974; Gabbott et al., 1998), marine phytoplankton (Gray et al., 1986), brachiopods (Aldridge et al., 1994), orthoconic cephalopods (Gabbott, 1999) and trilobites (Moore and Marchant, 1981), which are organisms indicative of a marine setting. The soft tissues of many taxa are preserved through replacement by illite, sometimes with alunite group minerals, frequently to a high degree of fidelity (Gabbott, 1998; Gabbott et al., 2001). Most notable is the preservation of conodont myomeres and eye muscles (Gabbott et al., 1995), and muscle tissue and gill tracts in eurypterid specimens (Braddy et al., 1995, 1999).

## 2. Materials and methods

The repository of the two specimens used in this study is the Council of Geosciences of South Africa, Bellville. Specimen C1971 is from Keurbos Quarry (18°58′E, 32°16′S) near Clanwilliam, and specimen C1587 is from Sandfontein (19°14′E, 32°40′S), 52 km from Clanwilliam, South Africa (Fig. 1). The fossils were studied using an optical microscope, drawn with the aid of a camera lucida, and photographed using a digital camera (Nikon E995). Photography and elemental analysis was carried out using a Hitachi S-3600N Scanning Electron Microscope with an Oxford Instrument Energy Dispersive X-ray facility (SEM EDX). For SEM EDX analysis
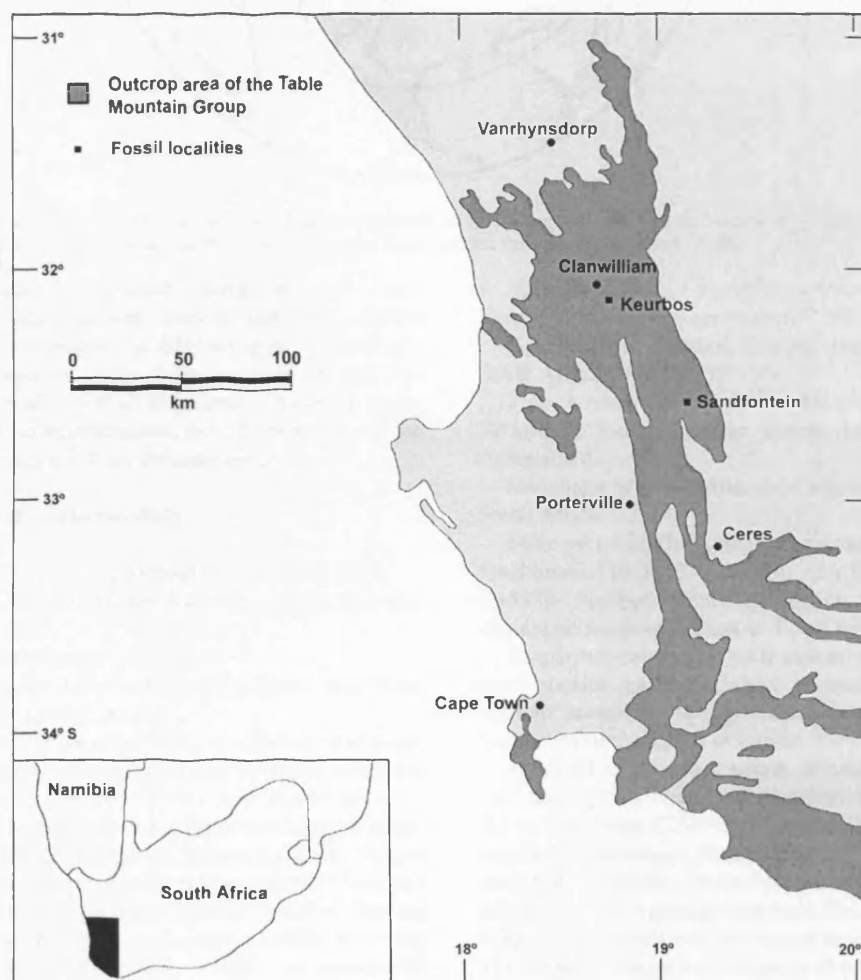


Fig. 1. The location of the Soom Shale sites at Keurbos and Sandfontein, from which the caryocaridid fossils were collected (from Gabbott et al., 2003).

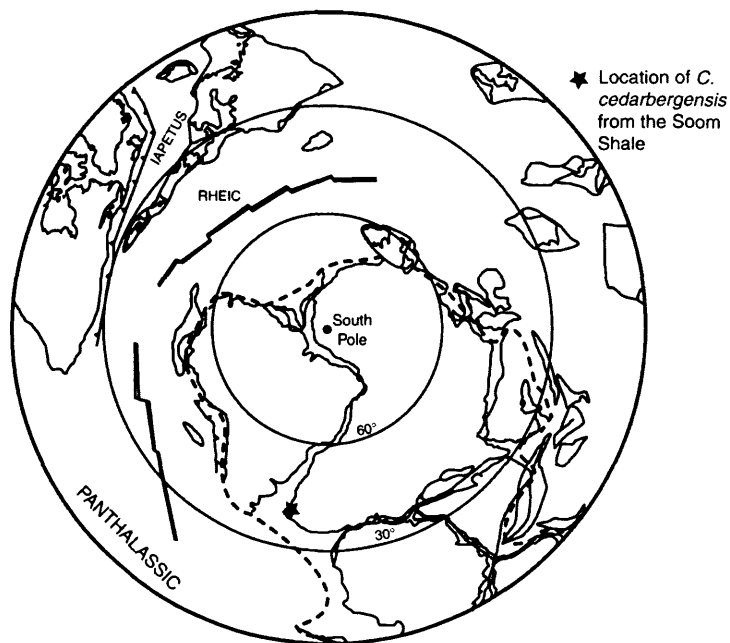The page has a running header with page number 386 and journal citation.

Fig. 2. A global reconstruction for the end of the Ordovician/beginning of the Silurian (440 Ma), with the location of *C. cedarbergensis* from the Soom Shale Lagerstätte (reconstruction from Fortey and Cocks, 2003 modified from Cocks and Torsvik, 2002).

uncoated material was placed in partial vacuum at 15 Kv. Elemental mapping was used to show the relative abundance of elements in different areas of the fossils and the sediment. EDX point analyses allowed the composition of very small areas (approximately 3–4 μm) of the fossil to be determined, from different parts of the two specimens and from the sediment.

## 3. Systematic palaeontology

Phylum Arthropoda Siebold and Stannius, 1845.

Family Caryocarididae Racheboeuf, Vannier and Ortega 2000.

Genus *Caryocaris* Salter, 1863

*Type species*: *Caryocaris wrightii* Salter, 1863 from the Skiddaw Group (Arenig).

*Diagnosis*: 'Elongated carapace with both dorsal and ventral convex margins (when seen in lateral view). No rostral plate. Pointed anterior end expressed as a prominent horn-like rostrum. Short anterodorsal spine. Posterior margin straight to oblique typically fringed with a row of minute secondary spinules. Indented posteroventral margin (one to several spinules). Narrow ridge and/or shallow furrow running parallel to ventral margin. Very thin, flimsy, weakly or uncalcified carapace.' (after Racheboeuf et al., 2000, pp. 322–323).

Species *Caryocaris cedarbergensis* n. sp.

*Holotype*: C1971, 1 complete carapace C1971b from Keurbos, with broken counterpart C1971a.

*Type locality*: Keurbos Quarry, near Clanwilliam, South Africa (18°58′E, 32°16′S).

*Type horizon*: Soom Shale Member, Cedarberg Formation, Table Mountain Group, Late Ordovician (Hirnantian).

*Derivation of name*: After the Cedarberg Mountains, South Africa.

*Other material*: One complete carapace C1587a from Sandfontein (19°14′E, 32°40′S), with half counterpart C1587b. Neither of the specimens has preserved abdominal segments, telson or furcal rami.

*Diagnosis*: *Caryocaris* with almost vertical anterior and posterior margins, a short, pronounced horn-like rostrum anteriorly, and a smooth posterior margin, without spines, spinules or combs.

*Description*: Carapace length of holotype 17.6 mm (16 mm C1587), elongate. Maximum height of valve 6.1 mm (5.5 mm C1587), greatest height of valve just anterior to mid-length. Height of posterior of valve less than that of anterior. Dorsal margin of carapace moderately convex. A pronounced horn-like rostrum, 2 mm long on both specimens, is directed anteriorly. Anterior margin below the rostrum angled at almost 90° to dorsal and ventral margins. Ventral margin moderately convex, similar to dorsal margin. Along the ventral border is a
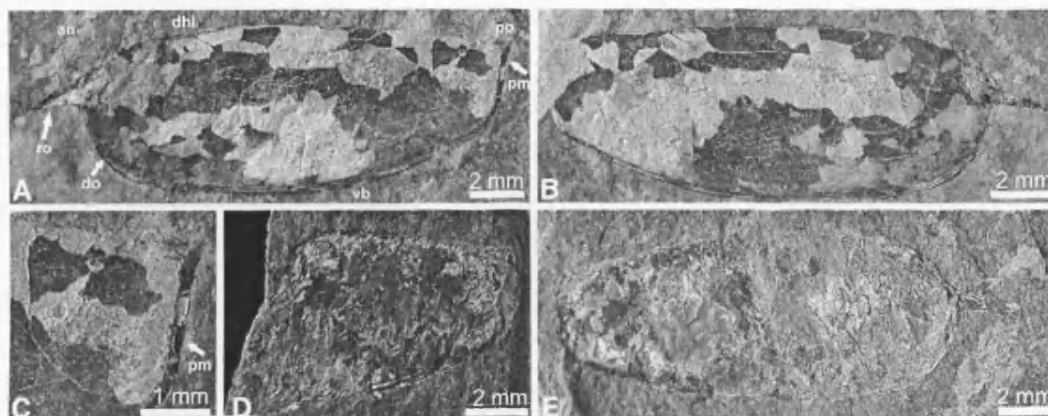
Fig. 3. The two specimens of *Caryocaris cedarbergensis* n. sp. A. and B. part and counterpart, respectively, of C1971, C. enlargement of smooth posterior margin of C1971. D. and E. counterpart and part of C1587. Principal morphological features of the composite moulds are shown on A and C. an = anterior, po = posterior, dhl = dorsal hinge line, pm = posterior margin, ro = rostrum, do = doublure, vb = ventral border. Scale bars = 2 mm, except in C = 1 mm.

clear and pronounced doublure, which has a uniform width of 0.5 mm. Posterior margin of carapace strongly angled at almost 90° to dorsal and ventral margins, with no spinules, fringe dorsal spines or ventral spines. Posterodorsal margin terminates at a point (Fig. 3).

*Remarks*: The overall shape of the carapace and the presence of the long process identified as the anterodorsal horn-like rostrum place this specimen within the genus *Caryocaris*. Previously described caryocaridids range in length from approximately 8.6–25.5 mm (Fig. 4); at 17.6 mm, *C. cedarbergensis* falls within this range. *Caryocaris cedarbergensis* differs from the type species *Caryocaris wrightii* Salter, 1863, *C. raymondi* Ruedemann, 1934 and *C. acuta* Bulman, 1931 by having a prominent rostrum. It also differs from *C. wrightii* and *C. raymondi* by possessing a smooth posterior margin without spines, spinules, bristles, teeth or a fine comb (Fig. 4). Although *C. acuta* does have a smooth posterior margin, it exhibits dorsal and ventral margins that are nearly parallel, unlike the curved margins of the new species.

The remaining described species of the genus *Caryocaris* all have prominent rostra, also described as anterodorsal spines or carapace horns (Fig. 4). *C. scanicus* Moberg and Segerberg, 1906 and *C. zhejiangensis* Shen, 1986 have rostra that are longer in relation to the size of the carapace than that of *C. cedarbergensis*. *C. scanicus* also has a posterior dorsal margin that ends in an elongate point (Moberg and Segerberg, 1906) and *C. zhejiangensis* has a spinose posterior margin (Fig. 4). *C. stewarti* Jell, 1980, *C. monodon* Gurley, 1896, *C. delicatus* Racheboeuf et al., 2000, and *C. subula* Chlupáč, 1970, all differ from *C. cedarbergensis* by exhibiting spines,

spinules, fringes and/or combs on the posterior margin. *C. subula* and *C. delicatus* also both possess oblique posterior margins (Fig. 4). *C. curvilata* Gurley, 1896 exhibits a similar carapace morphology to *C. cedarbergensis*, but differs by having a carapace horn slightly closer to the dorsal margin, and by having a spinose posterior margin (Fig. 4).

## 4. Taphonomy

Both of the specimens of *Caryocaris cedarbergensis* show a layered structure, each layer defined by a distinct mineralogical composition (Fig. 5). Six preserved layers on C1587 are interpreted as representing two valves each composed of three layers. Four preserved layers on C1971 may represent two valves each composed of two layers. In specimen C1587 each valve exhibits illite as the outside layer, carbon as the middle layer and alunite as the inner layer (Fig. 5A); and in C1971 each valve exhibits illite as the outside layer and alunite as the inner layer (Fig. 5B).

Enrichment in the elements Si, Al and K (Figs. 6C–E, K; 7B–D, L; 8C–E, J) is consistent with the presence of the clay mineral illite $(KAl_3Si_3O_{10}(OH)_2)$ identified from the Soom Shale by Gabbott (1998). This illite has a fibrous habit distinct from the detrital illite in the host sediment. Enrichment in P, S, K, Al and Ca relative to other areas of the carapace and the matrix (Figs. 6F, G, I; 7E–H, J; 8F–I) is accounted for by the presence of minerals in the alunite solid solution series, e.g. crandallite $(CaAl_3(PO_4)_2(OH)_5 \cdot H_2O)$ or alunite $(KAl_3(SO_4)_2(OH)_6)$ also identified from the Soom Shale by Gabbott (1998). The carapace of C1587 also has a very
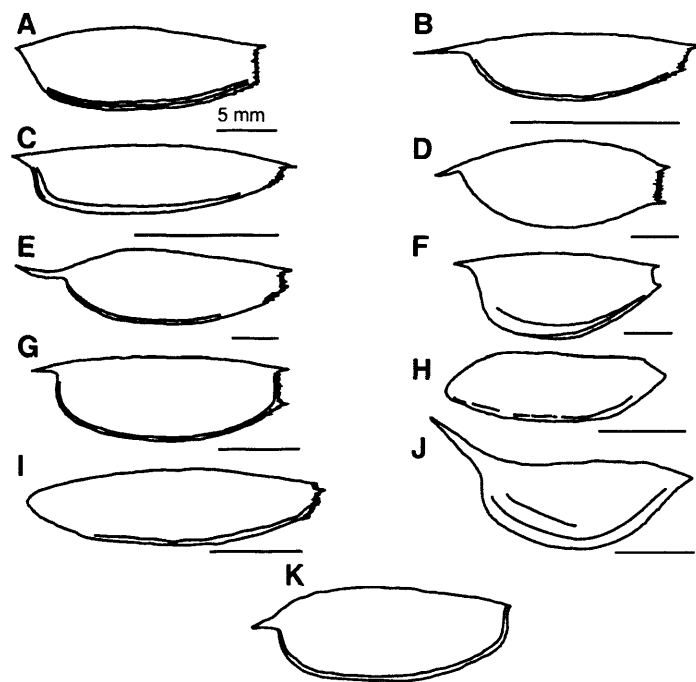
Fig. 4. Carapace outlines of members of the genus *Caryocaris*. A. and B: *C. wrightii* Salter, 1863 and *C. subula* Chlupáč. 1970 from the Llanvirn of Bohemia (after Chlupáč, 1970). C: *C. delicatus* Racheboeuf et al., 2000 from the Llanvirn of Argentina (from Racheboeuf et al., 2000). D: *C. stewarti* Jell, 1980 from the middle Tremadoc of Australia (after Jell, 1980). E: *C. zhejiangensis* Shen, 1986 from the Lower Ordovician of SE China (from Shen, 1986). F: *C.* cf. *monodon* (Gurley, 1896) from the Middle Ordovician of Norway (from Størmer, 1937). G: *C. curvilata* Gurley, 1896 from the Arenig/Llanvirn of Alaska (from Churkin, 1966). H: *C. acuta* Bulman, 1931 from the Caradoc of Peru (from Bulman, 1931). I: *C. raymondi* Ruedemann, 1934 from the Middle Ordovician (Caradoc) of North America (from Ruedemann. 1934). J: *C. scanicus* Moberg and Segerberg, 1906 from the Tremadoc of Scania (from Moberg and Segerberg, 1906). K: *Caryocaris cedarbergensis* n. sp. from the Ashgill of South Africa (this paper). Scale bars=5 mm.

distinct dark layer, between the illite and alunite layers, enriched in carbon relative to the rest of the carapace and the matrix (Figs. 6H, J; 7I, K), but also showing a clay mineral/alunite mineral signature (Figs. 6J; 7K). This carbon-rich layer is sheet-like and in some areas it shows brittle cracking features (Fig. 6B layer J, Fig. 7A layer K).

Vannier et al. (2003) suggested that the carapaces of the caryocaridids consist of three mineralized layers that may represent the typical cuticular structure of crustaceans (the epi-, exo- and endocuticle). The innermost endocuticle is the most labile layer (least decay resistant) because the fibrous chitin–protein matrix, from which it is made, has a much coarser structure (Raabe et al., 2005). In life, the exocuticle (middle layer) is protein rich and rigid (Vannier et al., 2003) due to the very fine woven structure of the fibrous chitin–protein matrix, which gives it a greater hardness and stiffness (Raabe et al., 2005). In the Crustacea the exocuticle is stiffened further by calcium carbonate (Addadi et al., 2003). The thin external waxy layer of the cuticle, the epicuticle, is intermediate in hardness between the exocuticle and endocuticle (Raabe et al., 2005).

The current taphonomic model for Soom Shale fossils (Gabbott, 1998; Gabbott et al., 2001) indicates that the most labile tissues are replaced by clay minerals such as illite, and more recalcitrant tissues are preserved as carbon. It is currently unknown whether alunite replaces tissues with a particular histology or decay profile. The illite layer occurs on the exterior of the valves and so cannot represent the labile inner endocuticle. The illite layer most probably represents the outer epicuticle, intermediate in hardness, the carbon the recalcitrant exocuticle and the alunite the labile inner endocuticle. Another alternative is that the illite could be an overgrowth on the outside of the fossil, rather than replacing or replicating a layer. In this scenario carbon represents the fossil carapace, and alunite has infilled the internal void. However, this is difficult to test in the case of C1971, where there is no preserved carbon layer. It is therefore necessary to consider the origin of the illite layer.
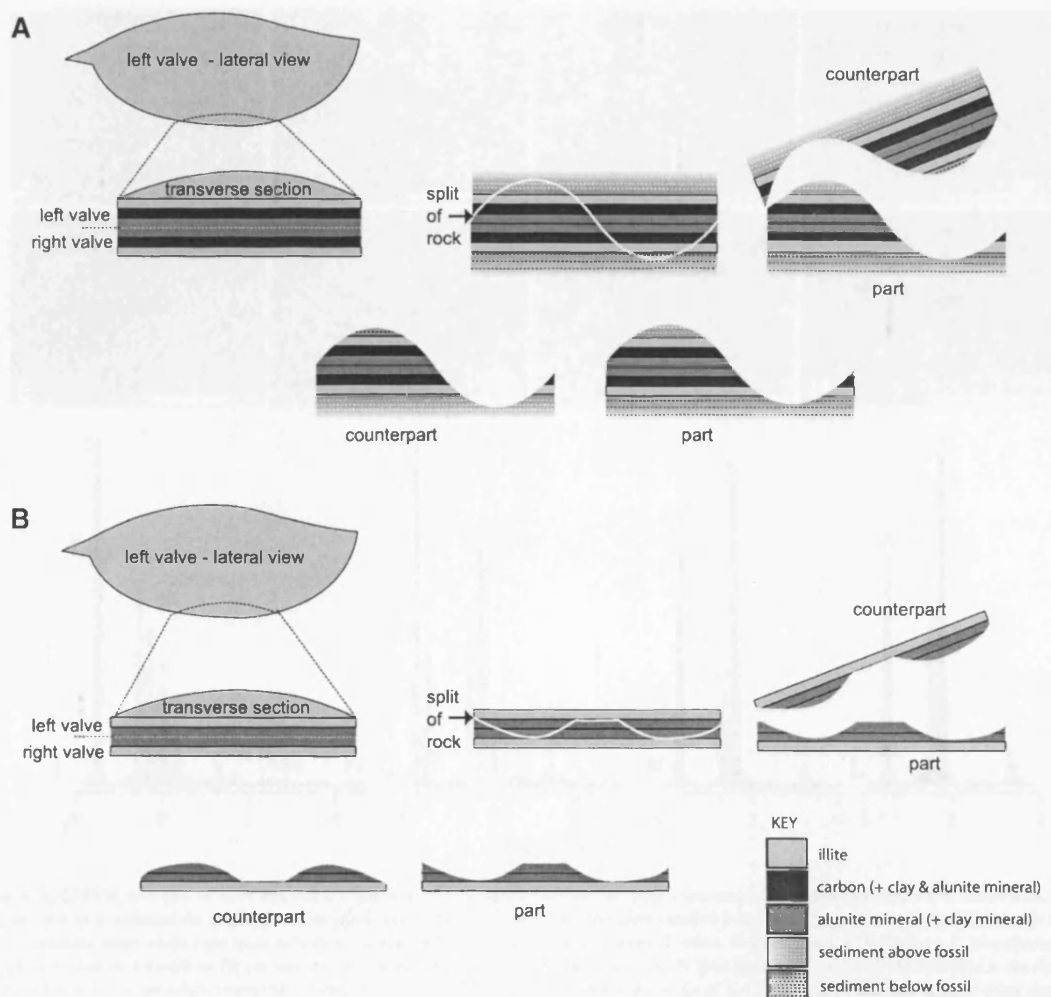
Fig. 5. Schematic diagram to show the composition and structure of the *Caryocaris* fossils from the Soom Shale. A. Diagrammatic representation explaining the way in which specimen C1587 has split revealing different parts of the layered structure in the part and counterpart of the fossil. Due to the transgressive nature of the split through the fossil, in places on both the part and counterpart all six layers may be seen, whereas at others only the underlying or overlying sediment is seen. B. Diagrammatic representation explaining the way in which specimen C1971 has split revealing the layered structure in the part and counterpart of the fossil. The split is more planar, and on both part and counterpart the illite layer lies underneath the alunite layer. Therefore, the alunite layer must have originally lain on the inside and the illite layer on the outside of the fossil.

The illite layer shows a fibrous habit on both specimens and on each the shiny white fibrous illite has the same orientation over the majority of the fossil (Fig. 9A), although in places it occurs in tufts (Fig. 9B). Some fibres have been measured at approximately 2 μm in diameter and 50 μm in length ($n$=20). They do not appear to show any ultrastructure such as banding. There are several possibilities to account for the fibrous habit of the illite; we consider these scenarios below.

1. Illite or a dioctahedral precursor (see discussion in Gabbott et al., 2001) could have replicated fibrous muscle tissue. This has been described from eurypterids (Braddy et al., 1995), and a conodont (Gabbott et al., 1995) from the Soom Shale. However, it is unlikely for the *Caryocaris* specimens because the fibres are not confined to any particular morphological features or areas of the carapace where muscle blocks would be expected. Additionally, there is no
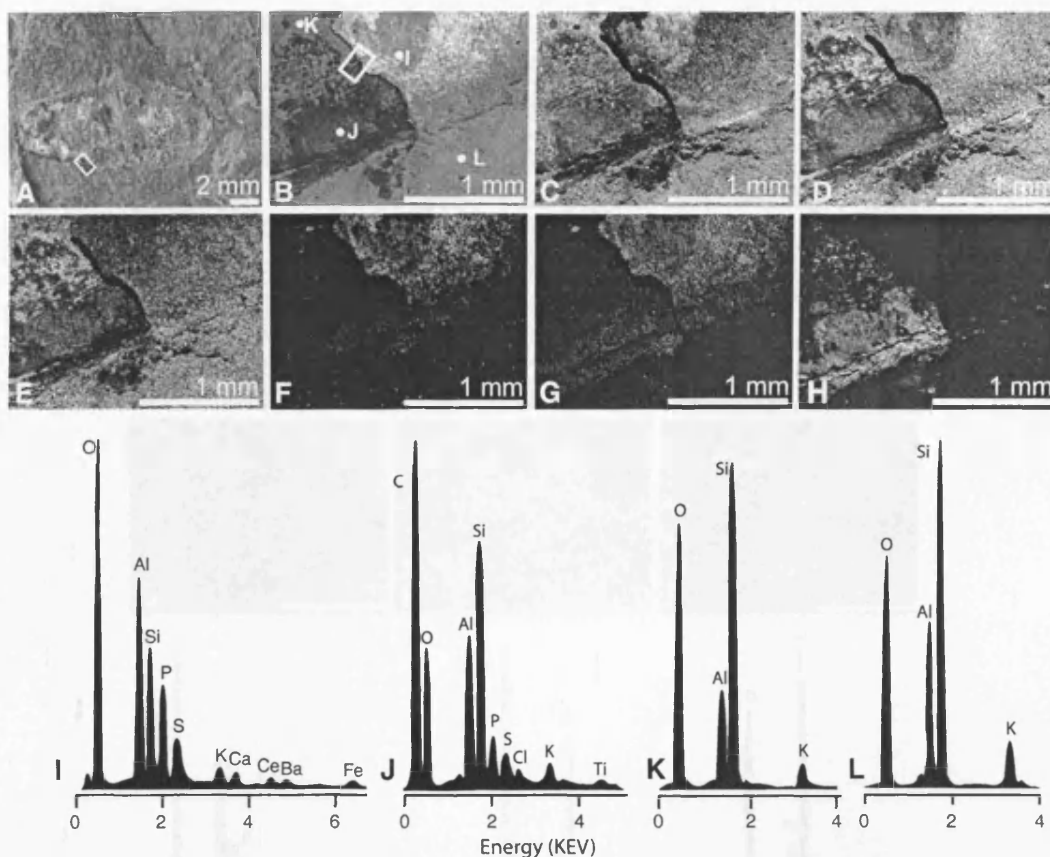
Fig. 6. A. C1587a, with area of SEM analysis (shown in B–H) indicated by the box. B. Back scattered electron image of boxed area shown in A. The square box on B indicates the location for analytical results shown in Fig. 7, and the spots labelled I–L denote the positions of the EDX traces I–L. C.–H. element maps where light areas indicate a relative high abundance of each element. C. silica. D. aluminium. E. potassium. F. phosphorus. G. sulphur. H. carbon. An analysis for calcium showed no areas of enhanced concentration. I. EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite, $CaAl_3(PO_4)_2(OH)_5 \cdot H_2O$; elemental peaks of S, Ce, Ba and Fe are indicative of other alunite-group minerals. J. Peaks indicate the presence of carbon and clay mineral/alunite mineral mixture. K. Peaks in Al, Si and K indicate the presence of illite. L. EDX trace indicates an illite signature for the host sediment.

evidence remaining of any internal structures such as appendages to which the muscle fibres would be attached, the fibres do not show the fibril bundles or banding that characterize muscle tissue in the conodont specimen (Gabbott et al., 1995), and the preserved fibres occur on the exterior of the valve.

2. The fibrous illite may have grown in pore spaces surrounding the fossil during diagenesis of the sediment, such as in examples of 'authigenic' mineral growth in sandstone reservoirs (Bjørlykke, 1998). 'Authigenic' illite in these cases refer to diagenetic reactions that usually occur at over 100 °C (Wilkinson and Haszeldine, 2002). Therefore, to avoid confusion we propose that the growth of 'authigenic' clay

minerals in voids, such as those that occur in reservoir rocks should be termed diagenetic growth. Only growth of clay minerals on the seafloor, or immediately after burial, when ambient seawater temperatures prevail, should be termed authigenic growth. There is a strong substrate control upon fibrous diagenetic illite formation, which occurs almost exclusively upon substrates that have a similar molecular surface configuration to illite so that the interfacial energy between the growing nucleus and the substrate is minimized (Wilkinson and Haszeldine, 2002). Nucleation control and rapid growth are the causes of the fibrous morphology of the crystals (Mullin, 1961; Wilkinson and Haszeldine, 2002). The
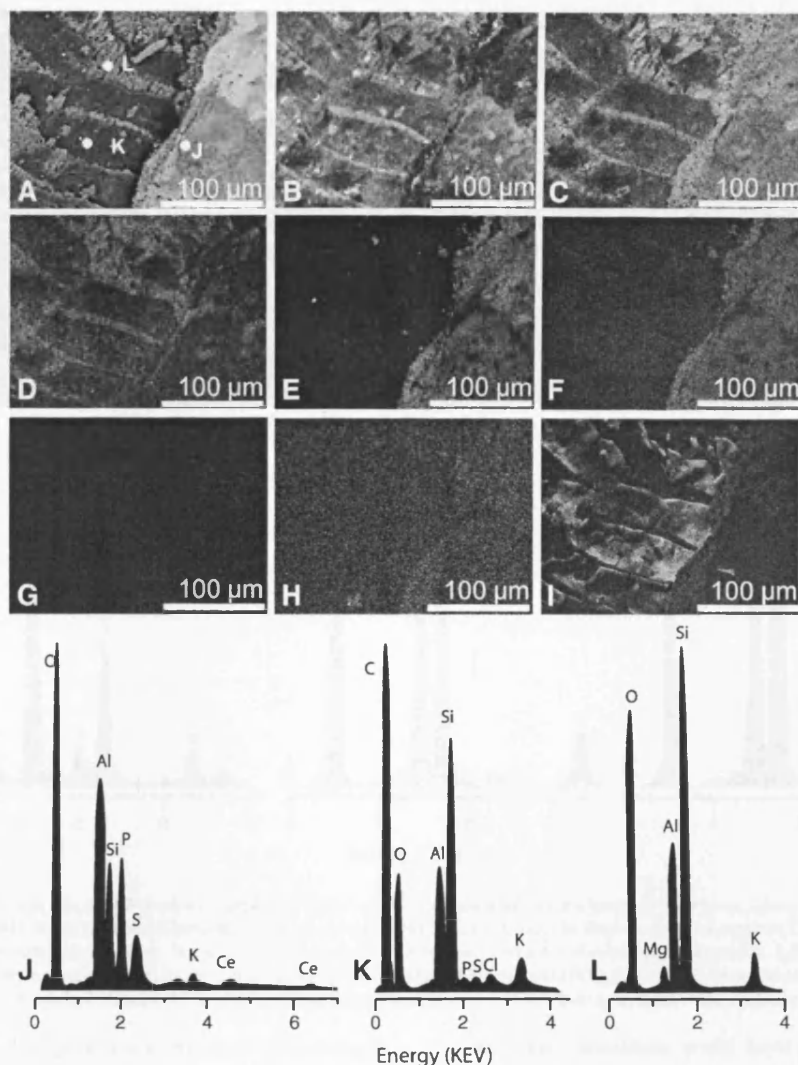
Fig. 7. C1587a, enlargement of area indicated by box on Fig. 6B. A. Back scattered electron image showing patch of cracked carbon (K) with fibrous illite in between (L). The layer with an alunite composition (J) overlies this. Spots labelled J–L denote the positions of the EDX traces J–L. B.–I. element maps where light areas indicate a relative high abundance of each element. B. silica. C. aluminium. D. potassium. E. phosphorus. F. sulphur. G. calcium. H. iron. I. carbon. J. EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite $CaAl_3(PO_4)_2(OH)_5 \cdot H_2O$; elemental peaks of S and Ce are indicative of other alunite-group minerals. K. Peaks indicate the presence of carbon and clay mineral/alunite mineral mixture. L. Peaks in Al, Si and K indicate the presence of illite.

Soom Shale sediment contains detrital illite (Gabbott et al., 2001), which may have provided some of the necessary chemical conditions for the nucleation of fibrous diagenetic illite. Fibrous or lath habits may have become further aligned upon compaction of the rock. Diagenetic illite with a fibrous habit precipitating on, or replacing a layer of, the *Caryocaris* carapaces cannot be discounted.

3. The fibrous illite may have grown authigenically on the sea floor or immediately after burial so that illite (or a dioctahedral precursor) either replaced a layer or layers of the carapace, or formed on a template of the organic material on the surface of the fossil. The fibrous morphology could be a result of the rapid growth necessary for authigenic illite to do this before the organic material decayed completely.
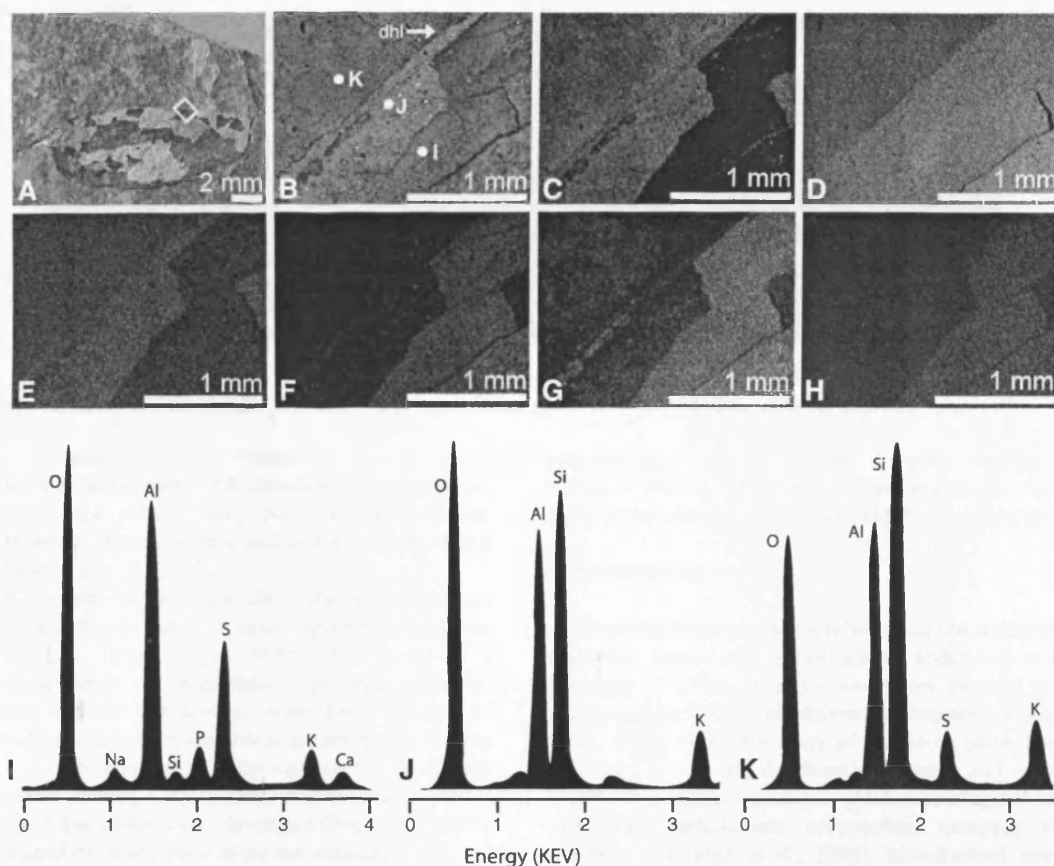
Fig. 8. A. C1971b, with area of SEM analysis indicated by white box. B. Back scattered electron image of boxed area, letters denote the position of EDX traces I–K, dhl = dorsal hinge line of carapace. C.–H. element maps and I.–K. EDX traces for the three layers of carapace. C. silica. D. aluminium. E. potassium. F. phosphorus. G. sulphur. H. calcium. An analysis for carbon showed no areas of enhanced concentration. I. EDX trace indicating a mixture of mineral(s) in the alunite solid solution series, probably dominantly crandallite $CaAl_3(PO_4)_2(OH)_5 \cdot H_2O$; elemental peak of S is indicative of other alunite-group minerals. J. Peaks in Al, Si and K indicate the presence of illite. K. EDX trace indicates an illite signature for the host sediment.

Authigenic illite growth is uncommon below around 100 °C (Wilkinson and Haszeldine, 2002) but there are reports of precipitation at temperatures as low as 40–50 °C (Harper et al., 1995; Ziegler and Long-staffe, 2000), and there is considerable debate as to whether illite can form at temperatures of less than 40 °C (Środoń and Eberl, 1984; Środoń, 1999; Wilson, 1999; Gilg et al., 2003). Gabbott et al. (2001) recognized that kinetic factors at low temperatures could prohibit direct illite growth, and suggested the initial precipitation of a dioctahedral phase, which was later illitized. Gabbott et al. (2001) also suggested that partial decay of organisms produced high $K^+:H^+$ activity ratios surrounding the Soom Shale fossils. This coupled with bacterial mediation, recently demonstrated by Tuck et al. (2006) to induce

rapid clay formation, could have overcome kinetic factors and lowered the temperature necessary for authigenic illite formation.

4. The fibrous illite on the *Caryocaris* carapaces may have been a result of metamorphism. The Soom Shale sediment probably underwent burial anchime-tamorphism temperatures of at least 200 °C (Cramer et al., 1974; Gabbott et al., 2003), the upper end of the scale for diagenetic illite formation at around 100–200 °C (Bjørlykke, 1998; Wilkinson and Haszeldine, 2002) and the lower end of the metamor-phically formed illite zone at around 200–350 °C (Sherlock et al., 2003). Therefore, non-fibrous illite that formed authigenically on the fossils could have been rendered fibrous during metamorphism, or fibrous illite could have formed directly during
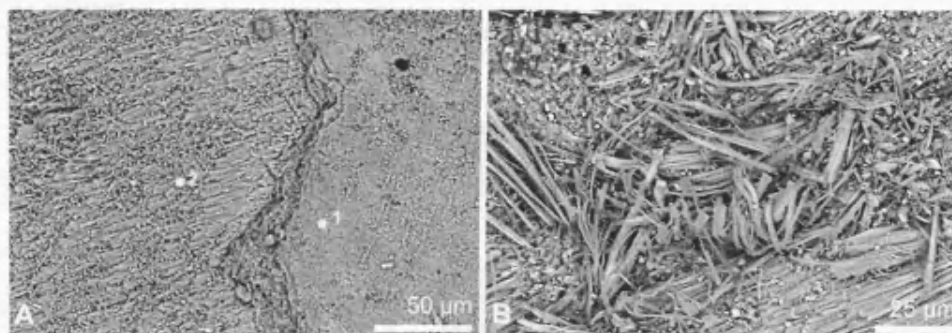
Fig. 9. Fibrous illite on specimen C1971. A. The layer on the right hand side (labelled 1) is composed of minerals in the alunite solid solution series; the layer on the left hand side (labelled 2) is composed of aligned fibrous illite. B. Shows fibrous illite, which can sometimes occur in tufts.

burial metamorphism. Fibrous phyllosilicates can form in association with fossils in strain shadows, where the fossils have acted as rigid bodies. However, these surround and do not cover the fossil (Sherlock et al., 2003).

It has been indicated that clay minerals can form on organic fossils through metamorphism independent of strain (Page et al., 2006). This occurs as a consequence of temperature dependent phyllosilicate-organic interactions, with the expulsion of volatiles in maturation and/or graphitisation leading to the precipitation of white mica on the most labile matter present. Clay minerals can become aligned if strain has subsequently developed (Page et al., 2006). Therefore, white mica is always associated with the most organic carbon-rich matter present (Page et al., 2006). This would explain the fibrous illite and carbon layers in C1587 but not in C1971 where there is no evidence of carbon, although there is a large proportion of fibrous illite. A higher degree of weathering could have led to the removal of carbon in this case, leaving just fibrous metamorphic phyllosilicate. However, there are carbon films known from other fossils from this locality, such as carbonized conodont eye capsules and many features of an undescribed naked agnathan, suggesting that carbon can survive the weathering.

Whilst replacement of muscle fibres by illite can be refuted, the growth of fibrous illite as an authigenic, diagenetic or metamorphic mineral cannot, as the temperatures at which illite forms are all possible in the history of the Soom Shale. In any event, it is unlikely that the fibrous habit of the illite reflects original tissue histology in these specimens. This serves as a cautionary note to palaeontologists trying to interpret soft tissues in the fossil record, particularly from Lagerstätten, and

suggests that there is a need to re-assess other occurrences of fibrous illite in Soom Shale specimens, especially in the conodont myomeres and the conodont eyes.

## 5. Palaeoecology

Caryocaridids have the morphological characteristics (carapace design and ultrastructure, abdominal morphology) of midwater active swimmers that are also recognized in Recent planktonic crustaceans (Vannier et al., 2003). Other members of the Soom Shale biota described to date are dominantly nektonic and nektobenthic organisms, such as conodonts, naked agnathans, orthoconic cephalopods, eurypterids, naraoiids and trilobites (Aldridge et al., 2001). Myodocopid ostracodes have been interpreted as nektobenthic based on their morphology and association with cephalopod carcasses (Gabbott et al., 2003). Phytoplankton has also been recognized (Gabbott et al., 2003). These new specimens of *Caryocaris* provide the first record of a zooplanktonic life habit in the Soom Shale.

All occurrences of *Caryocaris*, other than those in the Soom Shale, are associated with graptolites, indicating that caryocaridids were a cosmopolitan constituent of the Ordovician plankton. To date, no graptolites have been found from the Soom Shale Lagerstätte; although the presence of stenohaline organisms such as conodonts and cephalopods indicates that open marine conditions prevailed for much of the time (Theron et al., 1990). The absence of graptolites may reflect nonpreservation, although this is unlikely given the recalcitrance of graptolite periderm (Crowther, 1981). The nadir of graptolite diversity was in the Late Ordovician *extraordinarius* and *persculptus* zones, when the total world graptolite fauna consisted of only a few genera (Brenchley, 1997), and there was a low abundance of graptolites in high latitude environments (Lüning et al.,
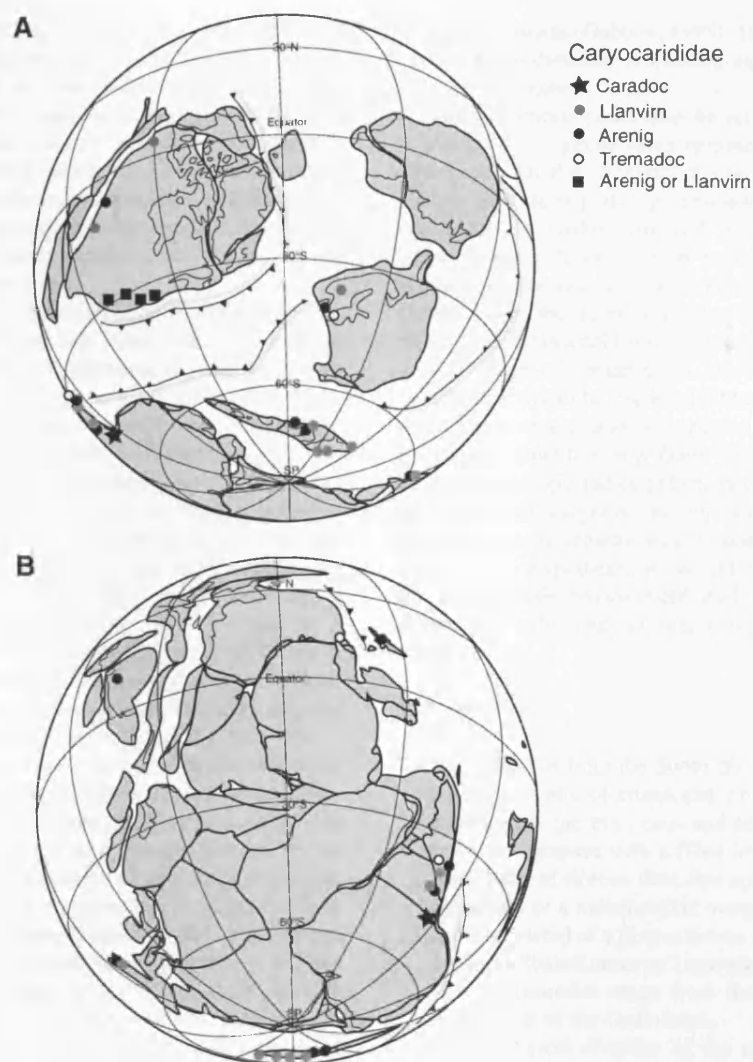
Fig. 10. Caryocaridid occurrence plotted on global maps for the Early Ordovician (Arenig; ca. 480 Ma), centred on the North Iapetus Ocean (A) and on the Gondwanan supercontinent (B) (Modified from Vannier et al., 2003. Continental distribution as given by Cocks, 2001; modified from C. R. Scotese PaleoGIS for Arcview package).

2000; Zalasiewicz, 2001). It is possible that graptolites were not present because there were none remaining at the time that were adapted to the palaeoenvironmental conditions of the Soom Shale. The presence of *Caryocaris* without graptolites in the Soom Shale might be an indication that *Caryocaris* could tolerate a wider range of palaeoenvironments than the graptolites.

Caryocaridids were cosmopolitan, and have been found previously from the major palaeoplates of Gondwana, Laurentia, Avalonia, Perunica, Baltica and South China

within a broad transequatorial latitudinal distribution (75° S–20° N) from the Tremadoc to Early Caradoc (Vannier et al., 2003) (Fig. 10). Specimens from the margins of Gondwana have been recorded from Australia (from the Tremadoc and Arenig) and South America, including the oldest (from the Tremadoc) and what were hitherto thought to be the youngest occurrences (from the early Caradoc) (Vannier et al., 2003). The Soom Shale specimens constitute the first record of Caryocarididae from the South African margin of Gondwana (Fig. 2) as well as the

youngest occurrence yet recorded. The Soom Shale was deposited in the Hirnantian (446–444 Ma), and thus the new species extends the range of this family by at least ten million years. The two specimens also provide the only evidence of *Caryocaris* during an icehouse environment, in a possible inner shelf setting, in a Lagerstätte thought to contain an unusual cold-water community (Aldridge et al., 2001). The lack of recorded caryocaridids in the Silurian suggests that they disappeared towards the end of the Ordovician extinction event.

Vannier et al. (2003) stated that the exact bathymetrical range of caryocaridids within the water column cannot be inferred from fossil evidence. Here we present the hypothesis that the genus *Caryocaris* most likely represents a cool-adapted, stenothermic, mesopelagic group during the Early–Middle Ordovician, and inhabited an epipelagic cold-water shelf environment during the Late Ordovician. The evidence for the Early–Middle Ordovician caryocaridids being mesopelagic stenothermic organisms is the wide distribution of the caryocaridids at that time. Present day cool-adapted stenothermic groups are known to have very wide distributions, from shallow depths in the cold waters of the Arctic and Antarctic, to deep waters across the globe including equatorial regions, where the waters are cold due to thermal stratification (Lalli and Parsons, 1995).

There is geological and recent evidence that some lineages, which dominantly occur in open ocean mesopelagic habitats, include more primitive or more derived species than those found in epipelagic settings on the continental shelf. These modes of derivation are known as polar submergence or emergence and examples of both are found in different isopod species at the present day (Brandt, 1992). Stratigraphic parsimony and the cold-water shelf setting of the Soom Shale fit with emergence in cold water being responsible for the occurrence of *Caryocaris* in the Soom Shale. The restricted presence of *C. cedarbergensis* in the Soom Shale indicates that the genus inhabited a cold-water inner shelf setting in the Hirnantian, and thus a change to an epipelagic habitat had occurred.

This hypothesis could be disputed if transport of the carapaces had occurred. The two specimens consist only of carapaces with no tail-pieces, suggesting that transport has disrupted the skeleton. However, there is no evidence to suggest that any significant lateral transport of other Soom Shale specimens took place before they reached the sea floor, as fossils such as conodont assemblages remain fully articulated, fossils remain randomly aligned, epibenthic brachiopods remain attached to orthocones and soft tissues, which would have decayed during prolonged floating, are preserved in several organisms (Gabbott, 1998). Therefore, assuming similar hydrodynamic properties, significant transport may be discounted.

The hypothesis could also be refuted if there were evidence for the genus being epipelagic throughout the Ordovician. In this scenario, the broad distribution of *Caryocaris* during the greenhouse climate of the Early–Middle Ordovician and the presence of the genus in the Late Ordovician in an icehouse climate would indicate that it was a eurythermic organism. However, in the Hirnantian the genus is currently only known from a cold-water setting; if it could tolerate a wide range of temperatures other Late Ordovician occurrences would be expected. Other Late Ordovician occurrences would also be expected if the genus followed cold-water bodies globally throughout its history, in the mesopelagic and epipelagic realm. Any discovery of Hirnantian caryocaridids in warm water and/or open ocean environments would necessitate reconsideration of our hypothesis, as would any evidence that the Soom Shale environment itself was warm-water rather than cold-water or that it represents a deeper water setting.

## 6. Conclusions

1) Caryocaridids from the Soom Shale either show the typical structure of crustacean cuticle, consisting of three layers, the epi-, exo- and endocuticle, or preserve the carapace with a filled internal void and an outer layer of fibrous illite that could be authigenic, diagenetic or a metamorphic overgrowth.
2) Not all material of a fibrous nature within fossils from the Soom Shale Konservat Lagerstätte is muscle tissue.
3) The caryocaridids range from the Tremadoc to the termination of the Ordovician.
4) The ecological diversity of the unusual cold-water community of the Soom Shale has been extended to include a new zooplanktonic organism, the first known from this Lagerstätte.
5) It is hypothesized that *Caryocaris* is a cool-adapted stenothermic genus that inhabited the mesopelagic realm during the Early–Middle Ordovician greenhouse phase, and that *C. cedarbergensis* is an epipelagic representative present in cold near-surface water during an icehouse phase.

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# SPECIAL NOTE

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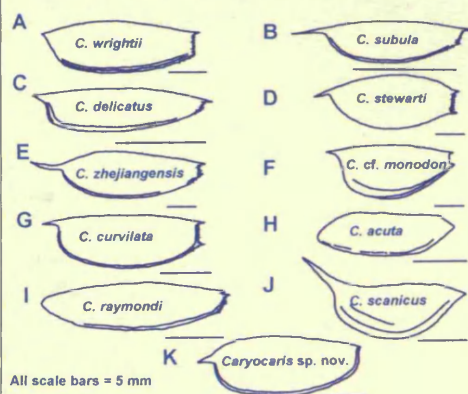in damage.

# New Zooplankton from the Soom Shale Lagerstätte South Africa

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**NATURAL ENVIRONMENT RESEARCH COUNCIL**

**University of Leicester**

## Introduction

A new species of caryocaridid has been identified from the Upper Ordovician of South Africa, extending the geographical, ecological and temporal range of the family. This is the second described occurrence of a member of the Crustacea from the Soom Shale Lagerstätte (the first being ostracodes), and the first described occurrence of the Class Malacostraca. The discovery of two specimens of *Caryocaris* sp. nov. provides new evidence of a zooplanktonic constituent to the Soom Shale biota and exhibits an exceptional level of preservation for which this conservation deposit has become known.

### Main representatives of *Caryocaris*



A  *C. wrightii*
B  *C. subula*
C  *C. delicatus*
D  *C. stewarti*
E  *C. zhejiangensis*
F  *C. cf. monodon*
G  *C. curvilata*
H  *C. acuta*
I  *C. raymondi*
J  *C. scanicus*
K  *Caryocaris* sp. nov.

All scale bars = 5 mm

A) Salter 1863 (type species), Arenig–Llanvim; Britain, Ireland, Germany and ?South Australia
B) Chlupáč 1970, Llanvim; Bohemia and Czech Republic
C) Racheboeuf *et al*. 2000, Llanvim; South America
D) Jell 1980, middle Tremadoc; Australia
E) Shen 1986, Arenig; China
F) (Gurley 1896), Arenig; Norway
G) Gurley 1896, Arenig-Llanvim; North America
H) Bulman 1931, Caradoc; South America
I) Ruedemann 1934, Middle Ordovician; North America
J) Moberg and Segerberg 1906, Tremadoc; Sweden
K) New species, Ashgill; South Africa

A)-J) Stratigraphical distribution data from Vannier *et al* 2003

### *Caryocaris* sp. nov.

*Caryocaris* sp. nov. has strongly convex dorsal and ventral margins, a short, pronounced horn-like rostrum anteriorly, and a smooth posterior margin. This combination of features differs from all other known species of *Caryocaris*.
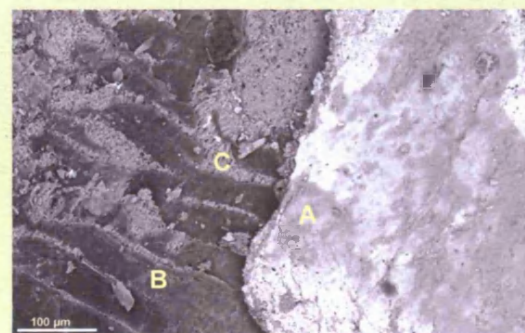


Dorsal hinge line
Anterior    Posterior
rostrum    smooth posterior margin
Ventral border    doublure
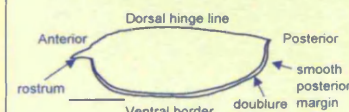


Above and below, part and counterpart of specimen of *Caryocaris* sp. nov.
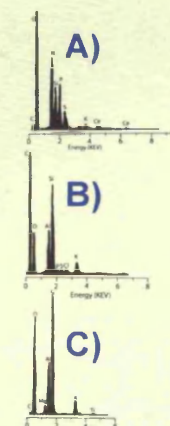
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### Taphonomy



Scanning electron micrograph (above) and spectra (right) for the three layers of the carapace of a specimen of *Caryocaris* sp. nov. (A) alunite and mixed clay signature, (B) carbon and clay signature and (C) illite signature.



A) 
B) 
C) 

epicuticle
exocuticle
endocuticle

A through-thickness SEM micrograph of the cuticle of the crustacean *Homarus americanus* (Raabe *et al.* 2005).

Carapaces from the Soom Shale show three different areas of preservation: (A) Al, P, S and Ce are accounted for by alunite group minerals, Si, Al and K indicate the presence of a clay mineral (probably illite); (B) Mixture of carbon and clay mineral (Al, Si, and K); (C) K, Al and Si probably also represent illite. In the Soom Shale, illite is known to replace originally labile tissues whereas more recalcitrant structures are preserved as carbon (Gabbott, 1998).

In the arthropod exoskeleton, the most labile layer is the inner endocuticle (above, right). The middle exocuticle is high in protein and can be strengthened by calcium carbonate or calcium phosphate and is the most recalcitrant of the layers. We suggest that the illitic composition represents the inner endocuticle (C), carbon preserves the exocuticle (B) and alunite group minerals may, therefore, replace the outer epicuticle (A).

## Implications

Until this discovery, orthoconic cephalopods were the only animals identified from the Soom Shale that clearly lived high in the water column. This is the first record of a zooplanktonic life habit from the Soom Shale. All other caryocaridids have been found in association with graptolites none of which have been found preserved in the Soom Shale, making this occurrence of *Caryocaris* unusual. The ecology of this exceptionally preserved fauna is more complicated and the fauna more diverse than originally thought and the temporal range of the Caryocarididae has been extended by approximately 10 million years.

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# Enigmatic fossils from the Soom Shale Lagerstätte South Africa

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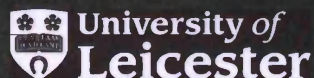
*Rowan J. Whittle, Richard J. Aldridge and Sarah E. Gabbott*
Department of Geology, University of Leicester, UK, LE1 7RH Contact: rjw35@le.ac.uk
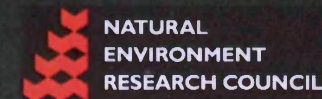
The Upper Ordovician Soom Shale conservation Lagerstätte preserves soft tissues through clay mineral replacement, as well as retaining organic remains. Fossil bearing localities occur around Clanwilliam in the Cedarberg Mountains north of Cape Town. Some of the earliest muscle fibres in the fossil record are preserved at this locality (Gabbott *et al.* 1995). Fossils such as orthocones, eurypterids, trilobites and brachiopods are present (Aldridge *et al.* 2003). However, the Soom Shale preserves several soft-bodied fossils that are currently enigmatic. Taxonomy and taphonomy are being employed to assign these fossils to their respective phyla.
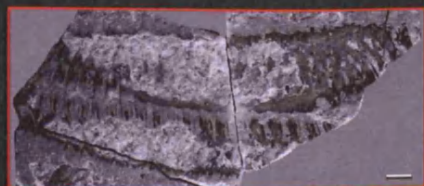

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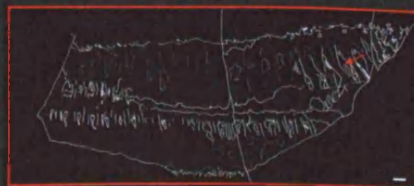

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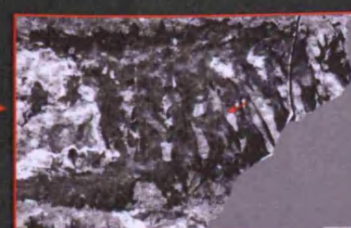

Scale bar = 1 mm

Segmented

Appendages – multiarticulate and possibly biramous ( ↙ )

Arthropod: Crustacean or Chelicerate?


Scale bar = 2 mm

**Segmented**

Gently tapering towards end

Central line down length of fossil, from which lines extend perpendicularly to margin of fossil ( ↙ )


Scale bar = 2 mm
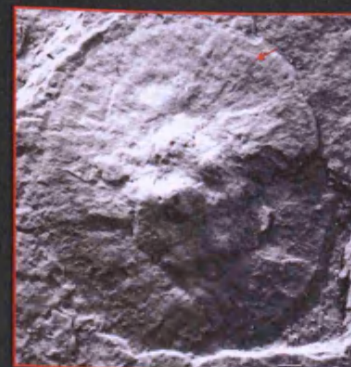
Carbonised spines with central ridge structure

Spinose projections occur ( ↙ )

Many examples in Soom Shale

Originally interpreted as remains of a creeping land plant (Kovács-Endrödy 1986) then re-interpreted as metazoan spines (Chesselet 1992)
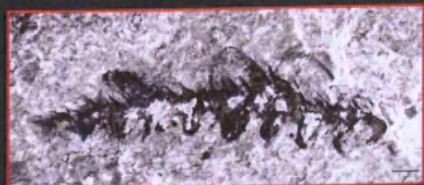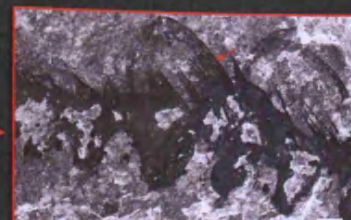

Scale bar = 1 mm

Distinct central area with approximately 4 raised domes

Radial linear structures extend from margin of central area to edge of fossil ( ↙ )

Medusoid ?

Sedimentary structure?


Scale bar = 3 mm


Scale bar = 1 mm


Scale bar = 2 mm

Side A (A)- 9-11 lobes

Side B (B)- 3 attenuated arcs and 25 angled spines

Some spines extend into the arcs ( ↙ )

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APPENDIX VIII: SEM EDX DATA

DVD CONTENTS:

*Caryocaris*

Medusoid

Scolecodonts

Lobopods

Arthropods

Enigmatic Organisms

Other Soom Shale Fossils