The late Ordovician Soom Shale Lagerstätte: an extraordinary post-glacial fossil and sedimentary record

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Abstract: Fossils of the Late Ordovician Soom Shale Lagerstätte are characterized by exceptional preservation of their soft tissues in clay minerals. The low-diversity community lived in an unusual cold-water setting, dominated by anoxic bottom waters, in the immediate aftermath of the Hirnantian glaciation. Giant conodonts represented by complete tooth sets, and one with trunk musculature and liver preserved, unarmoured jawless fish, lobopods and enigmatic taxa are some of the more important fossils. Furthermore, this Lagerstätte also preserves biomineralized Ordovician taxa such as brachiopods, orthoconic nautiloids and trilobites. It is important in capturing the only known examples of many taxa, extending temporal ranges of others and providing a unique glimpse of a post-glacial refugium, at a time when other Lagerstätten are unknown.

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The late Ordovician Soom Shale Lagerstätte, Western Cape Province, South Africa has produced an array of marine fossils, many of which preserve spectacular details of their soft (i.e. nonbiomineralized) tissues. Anatomical features usually lost rapidly after death, through scavenging or decomposition, such as eyes, gills, muscles and livers, are preserved. Some of the fossil assemblage is typical of a shallow marine Ordovician setting, such as brachiopods, trilobites and orthoconic nautiloids. However, other taxa, such as the naraoiid *Soomaspis* (Fortey & Theron 1995), a marine lobopodian (Whittle *et al.* 2009) and undescribed taxa including a naked agnathan (jawless fish) and a multi-segmented enigmatic fossil would not seem out of place in a Cambrian Lagerstätte (Selden & Nudds 2004). Thus, the Soom Shale appears to chronicle surviving taxa from the Cambrian radiation together with more conventional Ordovician taxa, with aspects of their soft part anatomy preserved.

The Soom Shale Lagerstätte is distinctive in several ways: the host shale itself is conspicuous as the only fine-grained lithology in a 3000 m thick sequence of dominantly arenaceous rocks; the fossils record life in a cold-water, glacially influenced marine setting in the immediate aftermath of a mass extinction and major glaciation; the mode of preservation is the inverse of the 'normal' fossil record: in the Soom Shale the hard, biomineralized components of animals are demineralized, and are often comparatively poorly preserved, whereas nonbiomineralized decay-prone anatomy is frequently preserved in exquisite detail. This uniqueness, however, does not diminish the significance and importance of the fossil assemblage from this deposit. As well as recording the earliest and latest known examples of several taxa, thus extending the known temporal ranges of several organisms, the Soom Shale also preserves several taxa unrecorded elsewhere, adding to our knowledge of end-Ordovician biodiversity and ecology. Finally, as well as exceptional fossil preservation, the lithology itself constitutes an undisturbed and probably continuous archive of depositional processes and climate change during and immediately after the dramatic collapse of the Hirnantian (latest Ordovician) glaciation.

The first fossil discovery in the Soom Shale was in 1981, when a team of geologists from the Geological Survey of South Africa (now Council for Geoscience), guided by Johannes Theron, were searching for potential biostratigraphical markers. The team focused on the Cedarberg Formation, the most prominent argillaceous unit in a thick sequence of Palaeozoic sandstones. In the basal member of the Cedarberg Formation, the Soom Shale Member, they discovered several centimetre-sized spiky elements, which occurred together in loose bundles. These fossils were first published as the earliest record of vascular land plants or their ancestors (Kovács-Endrödy 1986). However, this interpretation was overturned and the fossils were convincingly shown to be bedding plane assemblages of conodonts (Theron *et al.* 1990). Subsequently, the search for additional fossil material has been spearheaded by Johannes Theron and Dick Aldridge (to whom this paper is dedicated) and this yielded a variety of taxa, many with soft tissues preserved.

Location, stratigraphy and age

The Soom Shale Member and overlying Disa Siltstone Member together form the Cedarberg Formation of the Table Mountain Group, part of the Cape Supergroup (Figs 1 and 2). To date, fossils in the Soom Shale Member have been found across a geographically wide area: an age-diagnostic mucronaspidine trilobite in the Hex River Mountains (Cocks & Fortey 1986) as well as the typical Hirnantian brachiopod fauna from Wellington to Porterville (Fig. 1). The principal fossil site for exceptional preservation in the Soom Shale Member is at Keurbos farm.

The Cedarberg Formation forms a conspicuous recessive, laterally persistent, marker horizon (about 120 m thick), among predominantly arenitic units of the Table Mountain Group (Fig. 1b). The Soom Shale Member is about 10–15 m thick and is underlain by the glacially derived Pakhuis Formation (Aldridge *et al.* 2001). Upwards it merges with the thinly bedded Disa Siltstone Member composed of alternating mudstone and siltstone.

The Cedarberg Formation contains the only datable fossils in the entire Table Mountain Group, a succession of latest Cambrian to Early Devonian age (Rust, 1967). The highest resolution dating of the Soom Shale Member (and also the Cedarberg Formation) is provided by chitinozoans (*Spinachitina* and its morphotypes). The presence of *S. oulebsiri* restricts the age to a 1 myr interval of late
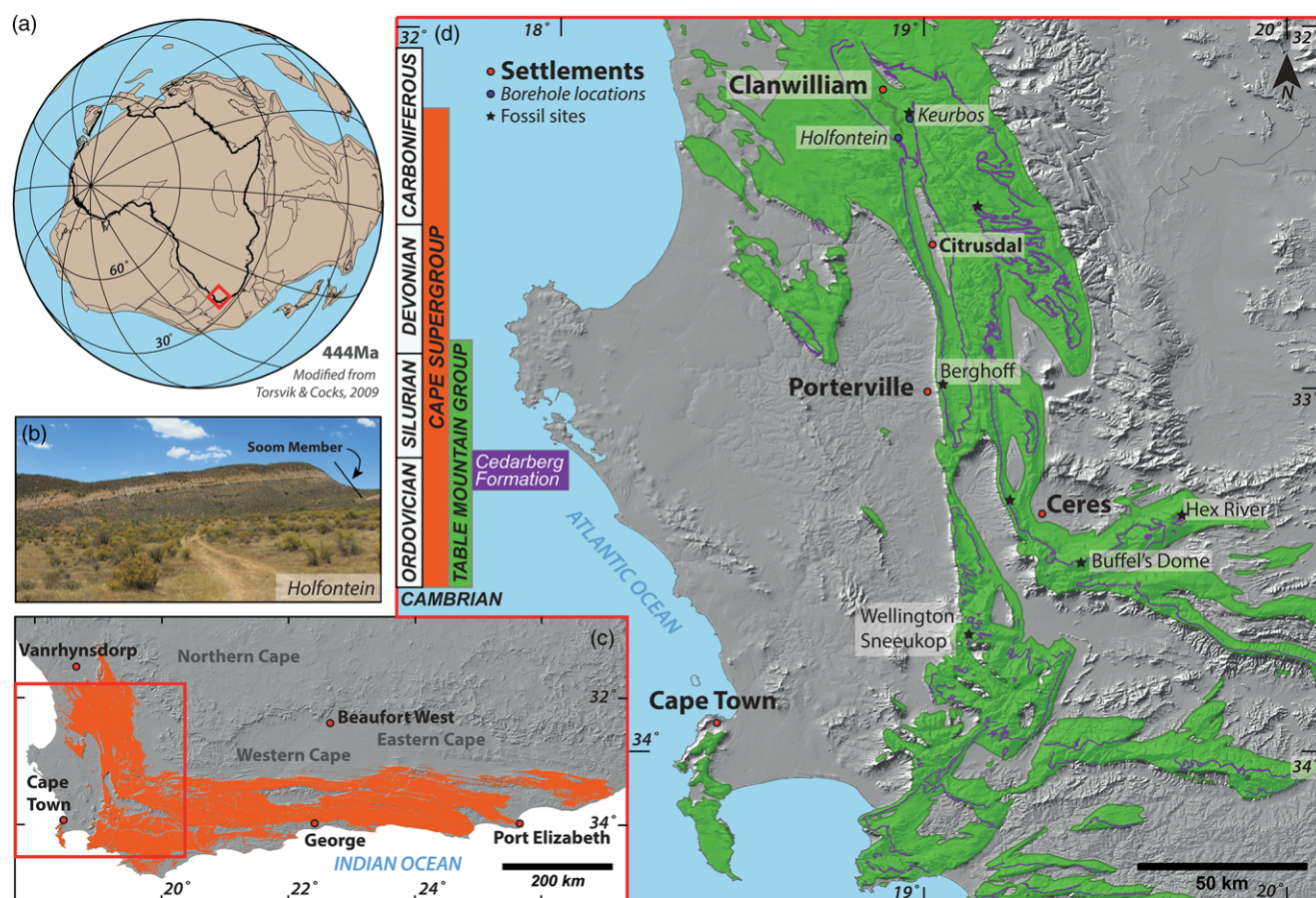
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Fig. 1. (**a**) Palaeogeographical reconstruction for *c.* 444 Ma, showing that the palaeolatitude of the southernmost portion of South Africa was 30 – 45°S. (**b**) In outcrop the Soom Shale Member is distinctive and typically occurs as a recessive marker (here at Holfontein). (**c**) The outcrop of the Cape Supergroup in South Africa. The red box shows limits of map in (**d**). (**d**) Outcrop of the Table Mountain Group, and Cedarberg Formation showing fossil-bearing localities.

Hirnantian to Rhuddanian time (Vandenbroucke *et al.* 2009). The absence of *S. fragilis* chitinozoans suggests that it underlies Silurian (Rhuddanian) strata. Thus, a late Hirnantian age is most likely (Vandenbroucke *et al.* 2009).

The end-Ordovician glaciation, extinction and the Soom Shale

During the Hirnantian an extensive, but short-lived, glaciation, centred on the South Pole, is widely considered to be the leading cause of the second largest extinction event in the Phanerozoic (Sepkoski 1996). The precise mechanisms that caused up to 85% of marine species to become extinct are still debated (see Harper *et al.* 2014) but it is clear that the event had two phases (e.g. Sheehan 2001; Sutcliffe *et al.* 2000). The first is associated with the onset of glaciation (Delabroye & Vecoli 2010); the second was prompted by the melting of the Gondwanan ice sheet, which led to glacioeustatic rise (Berry *et al.* 1995; Brenchley *et al.* 1995; Sheehan 2001) and extensive black shale deposition (Armstrong & Coe 1997; Delabroye & Vecoli 2010). A large continental ice sheet extended outwards from central Africa (Beuf *et al.* 1971; Deynoux 1985; Sutcliffe *et al.* 2000), possibly as far south as the Western Cape Province, which was situated *c.* 30 – 45°S at the time (Sutcliffe *et al.* 2000; Torsvik & Cocks 2009; Fig. 1). Although the late Ordovician was certainly a cold environment in South Africa, there is debate on the extent to which ice sheets influenced the deposition of the Pakhuis Formation and associated Peninsula Formation 'Fold Zone' (Backeberg & Rowe 2009; Blignault & Theron 2010, 2011; Rowe & Backeberg 2011). The distinctive lithologies of the Pakhuis Formation comprise sandy diamictites, sandstones and rarely varved mudrocks with dropstones. Piedmont

glaciers, resulting from late Ordovician orogeny, are also implicated in Pakhuis Formation deposition (Young *et al.* 2004). The Soom Shale directly overlies the Pakhuis Formation with a gradational contact; indeed, within the lowermost metre of the Soom Shale diamict-like layers occur sporadically. The main part of the Soom Shale Member is composed of alternating laminae of mud and silt lacking evidence of bioturbation, which were deposited during post-glacial transgression (Gabbott 1998; Aldridge *et al.* 2001). High molybdenum abundance and carbon, sulphur and iron geochemistry point to a dominantly anoxic and at times euxinic basin (Fig. 2; Gabbott 1998). Thus, together the Pakhuis and Cedarberg Formations provide a continuous lithological record of the rapid collapse of the ice sheet in South Africa, and subsequent climatic amelioration. However, the Soom Shale sediments suggest a lingering glacial influence (see Box 1).

The Soom Shale preserves some taxa of the distinctive Hirnantian brachiopod fauna (Bassett *et al.* 2009). Elsewhere, this fauna is known to have survived the first extinction phase across high to moderate latitudes but the fauna disappeared almost entirely during the second extinction phase, except in a couple of refugia (Rong & Harper 1988; Harper *et al.* 2014). It is possible that the Soom Shale represents such a refugium, but in a localized postglacial cold-water setting (Sheehan 2001).

The fauna of the Soom Shale

Vertebrates

The Soom Shale is perhaps most famous for conodonts. The remains of this taxon exemplify the quality of preservation, the
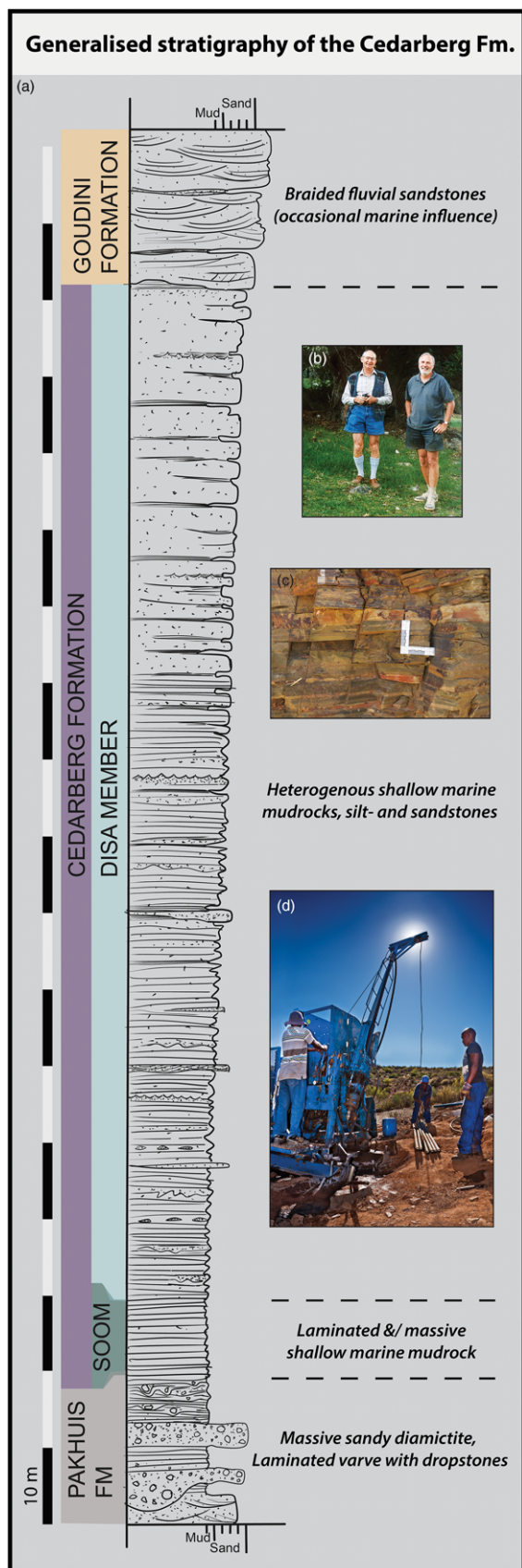
Fig. 2. (**a**) Schematic stratigraphic log of the Cedarberg Formation showing the lower and upper contacts with the glacial Pakhuis and braided fluvial Goudini Formations, respectively. The upward-coarsening Cedarberg Formation is subdivided into the lower Soom and Upper Disa Members, both deposited in a shallow marine environment. (**b**) Dick Aldridge (right) and Hannes Theron. (**c**) Typical exposure of weathered Soom Shale sediment. (**d**) Drill rig at Holfontein.

unusual composition of the fossils and that Soom taxa are often anatomically peculiar members of their kind. Conodonts are mostly represented in the fossil record by millimetre-sized phosphatic elements recovered after acid preparation of rocks from Cambrian to Late Triassic age; they are the teeth of otherwise nonbiomineralized jawless fish (Aldridge *et al.* 1986). Rarely, these phosphatic elements occur as natural assemblages reflecting the morphology and topology of the conodont tooth-set, albeit collapsed into two dimensions on the bedding plane. The Soom Shale preserves hundreds of bedding plane assemblages of conodonts, which can be seen on the shale surface with the naked eye. All are from the priniodontid order; those of the taxon *Promissum pulchrum* form a significant proportion of the fossils collected from the Lagerstätte (Aldridge *et al.* 2013). They are both the most complex conodont apparatus known (Aldridge *et al.* 1995) and the largest, with single elements up to 25 mm long (Fig. 4c). A second taxon, *Notiodella keblon*, was the first 17-element apparatus discovered from the fossil record (Theron *et al.* 1990; Aldridge *et al.* 2013). Interestingly, both taxa preserve complete tooth-sets more frequently than single elements, which is rare in the fossil record. This suggests that once the carcasses were deposited on the seafloor they lay undisturbed by physical or biological disturbance. Many of these bedding plane assemblages also preserve the eyes of the animal as either dark, carbonaceous rings or circles, or as silvery films of clay minerals (Aldridge & Theron 1993; Gabbott 1998).

As well as eyes, a single specimen of *Promissum pulchrum* also preserves aspects of the body (Fig. 4d). The preserved part of the Soom Shale conodont is 109 mm long, although the posterior portion is missing from the edge of the slab; scaling using complete animals from Scotland (see below) suggests that *Promissum pulchrum* would have been *c.* 40 cm in length (compared with 4 cm for the Scottish specimens).

Only four localities worldwide record conodont soft tissues. In the Silurian, one locality preserves a remnant of the trunk (Smith *et al.* 1987), another locality the eyes (von Bitter *et al.* 2007), whereas in the Carboniferous Granton Shrimp Bed of Scotland (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993) and the Soom Shale more details of the animal head and trunk are preserved. There are several specimens of conodonts in the Granton Shrimp Bed showing a long slender body with eyes, trunk musculature and a notochord, along with other features including a ray-supported caudal fin (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993). The Soom Shale conodont preserves eyes, V-shaped muscle blocks and a ventrally positioned dark patch of material interpreted to be the liver (Gabbott *et al.* 1995). Scanning electron microscopy of small samples of the eye and V-shaped muscle blocks showed them to comprise fibres of *c.* 5 μm diameter, which were interpreted to represent, in the eyes, extrinsic eye musculature, and in the trunk, muscle fibres (Gabbott *et al.* 1995). However, subsequent analyses of these fibres across the entire animal show that they are all similarly oriented, which may point towards an alternative explanation: fibrous clay minerals may have precipitated on the position of the eyes and muscle blocks in a manner similar to that postulated for late diagenetic–metamorphic clays on Burgess Shale fossils (see Butterfield *et al.* 2007; Page *et al.* 2008). Regardless of how muscle blocks and other soft tissue anatomy were preserved in the Soom Shale, specimen anatomy from both the Granton Shrimp Bed and the Soom Shale conodonts demonstrates a vertebrate affinity. They are shown cladistically to be more derived than either hagfishes or lampreys (both nonbiomineralized taxa) because they possess a mineralized dermal skeleton (e.g. Donoghue *et al.* 2000; Sansom *et al.* 2010).

The only other possible vertebrates in the Soom Shale are the remains of naked and completely unbiomineralized agnatha, the largest of which is about 11 cm in length (Aldridge *et al.* 2001) showing excellent preservation of the eyes, branchial structures and possibly the liver. This taxon is being described.

Box 1. The Soom Shale Member sediment

In most respects the Soom Member appears to be a typical black, finely laminated mudrock, deposited by dilute density currents, and intercalated with a hemipelagic component. However, closer inspection reveals a unique sedimentary facies, which has been interpreted to indicate a pervasive aeolian influence.

The Soom Shale is composed of two facies that are laminated on a millimetre to submillimetre scale. The homogeneous facies is represented by fine- to medium-grained silt-bearing mudstone that is a few millimetres thick (Fig. 3a, d and g). It occasionally shows normal grading and is sometimes associated with a grain-thick layer enriched in slightly coarser material. The laminated facies consists of two components: a homogeneous mudstone that seems to represent thinner layers of the homogeneous facies, and a distinctive dark, organic-rich layer, containing coarse-silt grains that frequently occur in discontinuous layers and clusters (Fig. 3b–e and g), although isolated grains also occur (Fig. 3f). The grains in the laminated facies are significantly larger than grains in the homogeneous facies, and it is their size distribution that has provided clues to their origin. The 'outsized' grains are characteristic of loess, being *c.* 35 µm in mean diameter, and it has been suggested that wind transported this glacially produced 'dust' out to sea. This material may have fertilized the upper waters, stimulating algal production; the grains may have then become bound by algae either in the water column or on the seafloor (see Gabbott *et al.* 2010). However, there are a number of significantly larger grains (100 – 150 µm) within clusters and it is possible that this size fraction was blown across seasonal sea ice: a similar process occurs today on the McMurdo Ice Shelf, Antarctica (see Atkins & Dunbar, 2009).
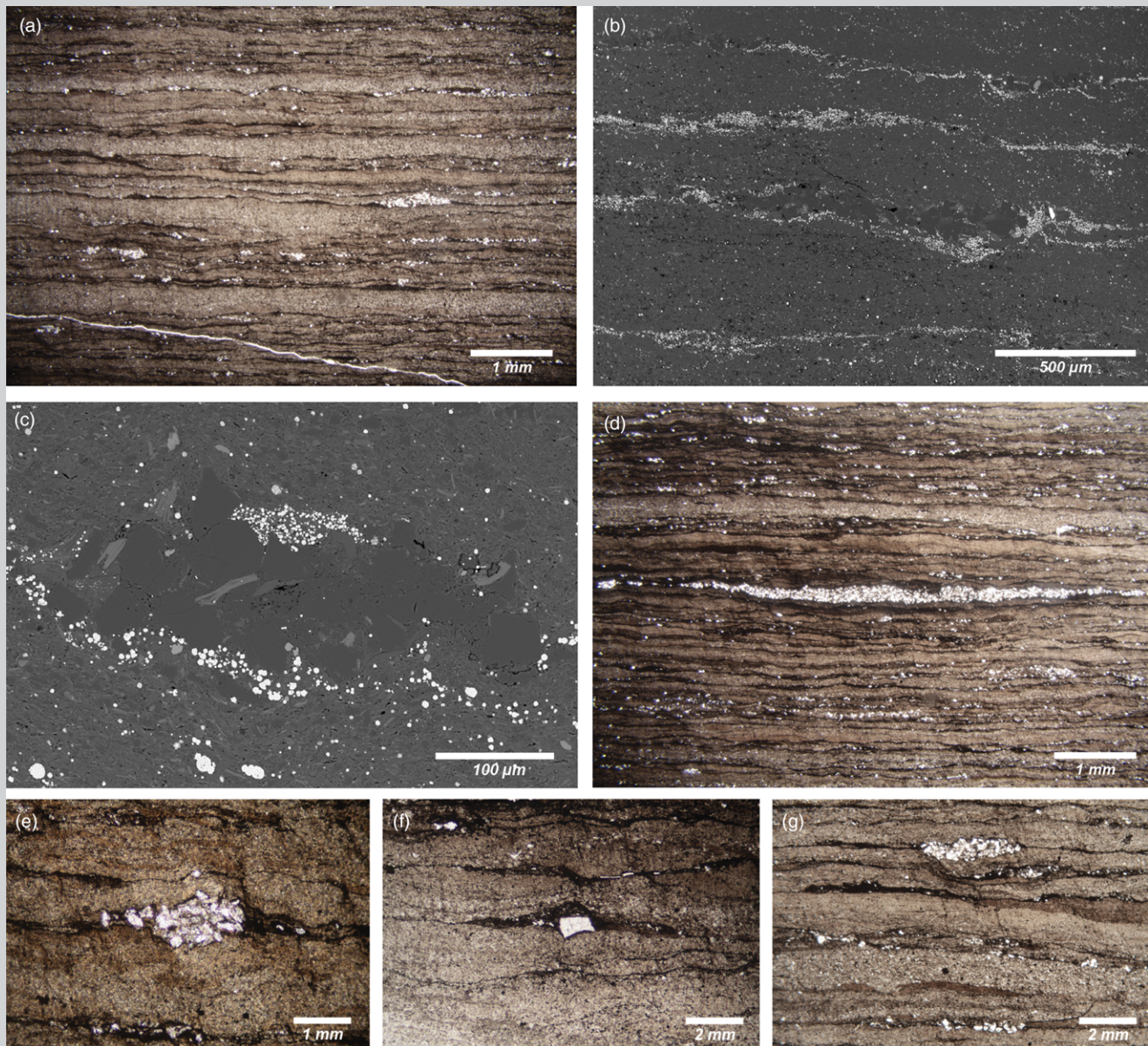

Fig. 3. Typical textural and compositional features of the Soom Shale sediment. (**a**)–(**g**) are petrographic images and (**b**) and (**c**) are scanning electron microscope backscattered electron images. (**a**) Typical intercalated homogeneous facies (four lighter layers) and dark, organic-rich laminated facies. The white patches represent clusters of quartz grains (see also (**c**), (**d**), (**e**) and (**g**)), which almost exclusively occur within the dark, organic-rich layers of the laminated facies. (**b**) Intercalated homogeneous and laminated facies. Here, pyrite framboids and microcrystals (bright grains) are confined to the laminated facies, probably precipitating within the organic-rich layers. In the centre of the image a cluster of large quartz grains (dark grey) occurs, bounded below by a pyrite-rich layer. (**c**) A cluster of grains in the laminated facies, comprising dominantly quartz (dark grey) with a few large clay grains (elongate, light grey grains); pyrite (bright grains) occurs around the cluster and denotes the likely position of organic matter (algae?). (**d**) An elongate cluster of quartz grains in the laminated facies. (**e**) Small, tightly packed quartz cluster. (**f**) A large and isolated quartz grain within a thin organic-rich layer. (**g**) Homogeneous facies (bottom) and laminated facies (top); within the latter lighter, brown lenses and layers occur; these are composed of mud.

Arthropods

Arthropods are the most diverse group represented in the Soom Shale; trilobites, naraoiids, eurypterids, ostracods and caryocarids have been identified (Braddy *et al.* 1995, 1999; Aldridge *et al.* 2001; Gabbott *et al.* 2003; Whittle *et al.* 2007), along with a selection of unidentified specimens (Whittle 2007). Muscles, gut traces and lamellate book gills are preserved in eurypterid specimens (Fig. 4b; *Onychopterella augusti*), the presence of four pairs of book-gills supporting a sister group relationship between eurypterids and scorpions (Braddy *et al.* 1995, 1999). Whittle *et al.* (2009) identified a lobopodian from the Soom Shale providing a link between Cambrian lobopodians from sites such as the Burgess Shale and Chengjiang and younger forms from the Silurian and Carboniferous. A fossil belonging to a group more typically associated with Cambrian strata is the uncalcified arthropod *Soomaspsis splendida* Fortey & Theron 1995. This taxon has a cephalic shield and pygidium of roughly equal size between which are three thoracic segments (with possibly a fourth concealed beneath the cephalic shield); like other primitive, uncalcified trilobites it is in the Naraoiidae family. Myodocope ostracods (*Myodoprimigenia fistuca*) are found in the Soom Shale in exclusive association with orthoconic cephalopods, suggesting that they fed on cephalopod carrion as epibenthic scavengers (Gabbott *et al.* 2003). The morphology, including a weakly mineralized, thin flexible shell and pronounced rostrum and rostal incisure, most strongly suggest an ostracod that lived off the seafloor, perhaps being nektobenthic. The caryocarid *Soomicaris cedarbergensis* is an extremely rare component of the Soom Shale fauna but it is important as it extends the geographical, ecological and temporal range of the family and provides the only evidence of a zooplanktonic constituent to the Soom Shale biota, as no graptolites have been found (Whittle *et al.* 2009; Racheboeuf & Crasquin 2010).

Molluscs

The most common molluscs recovered from the Soom Shale are orthoconic nautiloids, the shells of which occur as moulds with some relief, after being completely demineralized. The specimens preserve a possible stomach and an unambiguous radula, which consists of up to 26 transverse rows with five simple tooth-like elements in each row (Gabbott 1999). Radulae are a key synapomorphy of the Mollusca and provide important phylogenetic and ecological information, but they are rarely preserved. For example, from the entire Lower Palaeozoic succession, radulae occur in the early Cambrian Mahto Formation, Alberta, Canada (Butterfield 2008) and are interpreted in both *Wiwaxia* and *Odontogriphus* from the Burgess Shale (Caron *et al.* 2006; but see Butterfield 2006, for an alternative view). In the Silurian there are two occurrences (Mehl 1984; Sutton *et al.* 2006).

Other molluscs include incomplete specimens of a bellerophontid monoplacophoran belonging to the family Sinuitidae, tentatively identified as *Bucanella* sp., and specimens of infaunal deposit feeding nuculanacean bivalves, attributed to *Concavodonta* (Cocks & Fortey 1986). All are extremely rare.

Annelids

Scolecodonts are the small (usually less than 1 mm) complex jaw apparatuses of polychaete annelid worms, which are usually recovered as single elements after microfossil processing. In the Soom Shale scolecondonts occur as complete sets of elements that comprise jaw apparatuses on the bedding planes, a rarity in the fossil record. What makes them more important, however, is that the record of Ordovician scolecondonts from Gondwana is poor, being

mostly based on either single-element taxa or records of 'scolecodonts' with no accompanying taxonomic treatment (Hints *et al.* 2015). Scolecondonts described from the Soom Shale were low in diversity and were identified as probable mochtyellids and xanioprionids (*Synaptogenys* and *Xanioprion*?) (Whittle *et al.* 2008). No associated soft tissue remains have been found.

Brachiopods

The four brachiopod genera (three Linguliformea and one Rhynchonelliformea) described from the Soom Shale have been identified as members of the distinctive world-wide late Ordovician *Hirnantia* Fauna (Bassett *et al.* 2009). Rarely soft tissue preservation occurs. For example, in *K. cedarbergensis* 3D preservation of the pedicle represents the earliest documented, and possibly the only record of this kind for Palaeozoic discinoids; its structure is similar to that of Recent lingulids. *Trematis taljaardi* preserves bands of periostracum on the flanks of the pedicle notch.

Enigmatics

The most frequently found fossil in the Soom Shale is its most enigmatic. Carbonaceous compressions of small (typically 5–15 mm in length and 1–2 mm in maximum width) pointed axes occur on bedding planes singly, as a few specimens together and as dense masses (Fig. 4f,g). They do not show any consistency in orientation, but are commonly found in association with conodont assemblages. The axes are mostly straight, although flexed and folded, and even sinuous specimens are known. Parallel to their long axes are a series of longitudinal lines (usually four or five) with relief, and small sets of depressions running between them. Another morphotype of the same fossil has small, paired projections orthogonal to the main axes. They were originally described by Kovács-Endrödy (1986) as the remains of a non-vascular land plant and given the designation *Eohostimella parva*. Subsequently, Chesselet (1992) reinterpreted these structures as possible disarticulated remains of a problematic Ordovician metazoan and renamed them as *Siphonacis parva*. However, there is little evidence to constrain what these common fossils are.

The largest fossil in the Soom Shale is of a multisegmented (*c.* 45 segments) animal some 380 mm long and 140 mm wide (Aldridge *et al.* 2001). The animal is a bilaterian as evinced by its obvious cardinal axes and bilateral symmetry. There are two very well-preserved specimens with complex, well-defined anatomical features, which overlap in the main body. The body margin is characterized by imbricating flaps, one per segment, which are similar, although less robust in appearance, to those in anomalocariids (e.g. Daley 2013). This fossil awaits a full description.

There are also many other soft-bodied fossils with unknown affinities, which have yet to be identified, and others that are represented by a single occurrence where a tentative assignment awaits confirmation through discovery of other specimens (Aldridge *et al.* 2001; Whittle 2007). One such occurrence is an unidentified arthropod with inwardly directed appendages of two distinct types: one is multiarticulate and biramous; the other is paddle-shaped with setiferous terminations (Fig. 4e).

Algae and plankton

Although not constituting 'exceptional preservation', algae and phytoplankton form an important component of the Soom Shale, being at the base of the food chain (Fig. 4a). Almost all of the bedding surfaces of the Soom Shale are covered with algae, which probably constituted the greatest biomass of the biota (Gabbott 1998). It is not known whether the algae lived on the seafloor
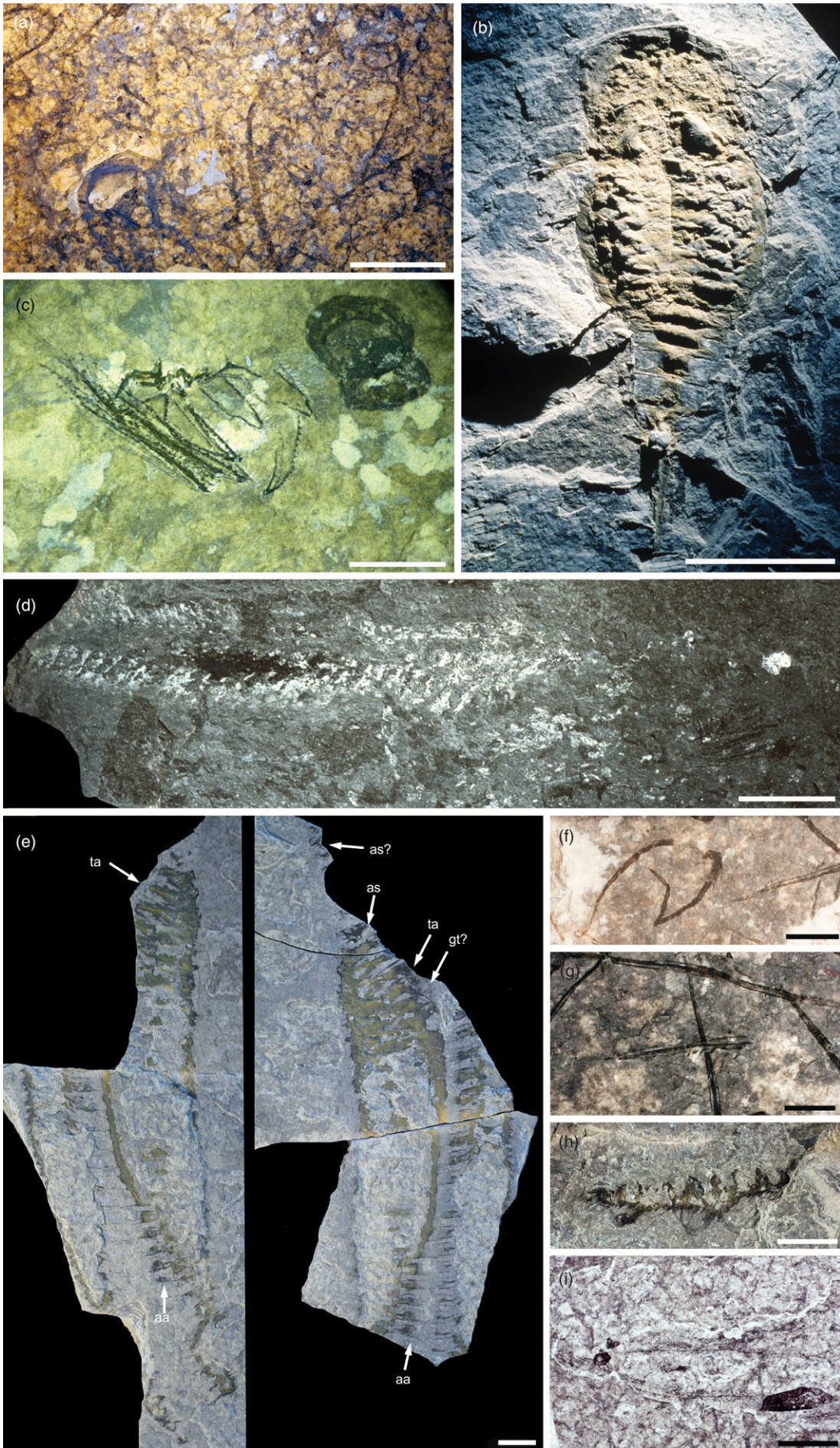
forming a mat, or in the water column, but their intimate association with large quartz grains may indicate the latter (see Box 1). Phytoplankton have been recognized in the form of leiospheres, sphaeromorphs and spherical bodies attributed to the Prasinophyta, a group of green algae (Tappan 1980; Gray *et al.* 1986). Acritarchs (Gray *et al.* 1986; Aldridge *et al.* 2001) and small spore tetrads (Cocks & Fortey 1986; Gray *et al.* 1986) also occur.

Chitinozoans are recorded after standard palynological preparation (Cramer *et al.* 1974; Vandenbroucke *et al.* 2009) but can also be seen on bedding planes with a hand lens. Here they occur as scattered individuals, in linked chains, in aggregated masses and with associated organic envelopes interpreted to be cocoons (Gabbott *et al.* 1998).

Palaeoecology

The parallel-laminated Soom Shale Member sediment lacks clear bioturbation, although extremely rarely there may be some surficial disturbance and there are possible pelletal textures. Unsurprisingly then, the fauna of the Soom Shale preserves no infauna, except for a handful of extremely small (<5 mm long) lingulid brachiopods. These are bedding-parallel and may have been transported in, or more probably they colonized during brief periods of bottom and pore water oxygenation, dying as juveniles when anoxia was re-established. There is a paucity of sessile epibenthos, accounting to some extent for the low-diversity fauna when compared with other marine, shallow-water Ordovician communities such as those in north Wales and Scotland (Selden & Nudds 2012). Occasional single, but more commonly clusters of brachiopods occur on bedding planes, unassociated with orthoconic nautiloids, demonstrating occasional bottom water oxygenation, but such occurrences are rare. Gregarious nektobenthos include lobopods, eurypterids, naraoiids, ostracods and trilobites. Evidently, bottom waters were oxygenated for periods of time.

The fully motile nekton niche is represented by orthoconic nautiloids (including their pseudoplanktic brachiopods), conodonts and agnathans. As in many Lagerstätten the record of zooplankton is impoverished but a caryocaridid represents a mesopelagic taxon that was probably an active swimmer (Vannier *et al.* 2003; Whittle *et al.* 2007).

There are several taxa associated with the orthoconic nautiloids. Brachiopods and cornulitids are found on the orthocones; the aligned, adaperturally opening cornulitids suggest that attachment and growth occurred during the life of the orthocone, and size distribution analysis of the brachiopods also indicated colonization within the lifetime of the orthocone (Gabbott 1999). The presence of ostracods in the body chambers of orthocones suggests a benthic, or possibly nektobenthic scavenging mode of life, feeding on cephalopod carrion (Gabbott *et al.* 2003).

There are taxa that are conspicuously missing from the fauna and their absence provides some indication of the environment. For example, that there are no echinoderms, gastropods and bivalves is best explained through a persistently anoxic or euxinic seafloor, with brief interludes of oxygenation; there is no evidence of a soupy substrate prohibiting benthic colonization. Graptolites are another fossil group notable for their absence, particularly because, in all other records worldwide of carycarids (present in the Soom Shale) they co-occur with graptolites, both being cosmopolitan constituents of Ordovician plankton (Whittle *et al.* 2007). Therefore the absence of graptolites in the Soom Shale is puzzling. Non-preservation is unlikely; perhaps a cold-water setting precluded them.

Five categories of bromalite have been identified from the deposit based on shape, content and internal structure (Aldridge *et al.* 2006). The presence of crushed discinoid valves in several bromalite occurrences demonstrates that an effective durophagous predator was present in the Soom Shale community. Furthermore, the presence of broken conodont elements in other specimens provides evidence that there was some tiering within the predatory trophic level (Aldridge *et al.* 2006).

Taphonomy

The fossils of the Soom Shale show virtually no evidence of transport and the spine-like *Siphonacis parva*, which would have been very susceptible to even weak currents, demonstrates alignment only in rare instances. The disarticulation and scavenging of remains is also not apparent. Carcasses were delivered rapidly to a relatively cold and often anoxic (and intermittently euxinic) seafloor, where they may have been rapidly buried by either distal turbidites or algal material (Gabbott *et al.* 2010).

In the Soom Shale original biominerals such as aragonite (orthoconic nautiloids), calcite (trilobites) and even apatite (conodont elements and brachiopods) are lost. Morphology is either recorded as a mould or replicated by clays, alunite group minerals and rarely quartz (Gabbott 1998). The nonbiomineralized tissues occur either as clays (usually illites) or as carbonaceous films, with more labile tissues exhibiting the former and more recalcitrant tissues the latter preservation modes. This unusual mode of preservation where soft tissues have apparently undergone clay mineralization (Gabbott 1998; Gabbott *et al.* 2001) has since been recorded in other deposits (e.g. Zhu *et al.* 2005; Callow & Brasier 2009; Anderson *et al.* 2011; Cai *et al.* 2012; Wacey *et al.* 2014). However, although rapid stabilization of decaying tissues and their replacement by alumino-silicates was postulated by Gabbott (1998), the complex diagenetic and anchizone metamorphism experienced by the Soom Shale makes it challenging to disentangle the role, if any, of clays in preservation. Whether they undertook an active role in decay retardation, and directly replaced the tissues, or whether they are diagenetic or metamorphic artefacts is unknown. In the Burgess Shale alumino-silicates are found on many taxa and are thought to have been the result of volatilization of carbonaceous material during metamorphism, which allowed clay mineral growth in voids (Butterfield *et al.* 2007; Page *et al.* 2008). However, convincing instances of aluminosilicification of organic matter, and fossils, are known (Wacey *et al.* 2014) as are records of bacterial mediation of clay mineralization (e.g. Urrutia & Beveridge 1994; Fiore *et al.* 2011). Furthermore, clay minerals are seen to attach to lobster eggs in decay

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Fig. 4. (**a**) Frequently, bedding planes are covered with algal strands. Scale bar represents 10 mm. (**b**) The eurypterid *Onychopterella augusti* Braddy *et al.* 1995, showing preservation of muscles associated with appendages; GSSA C373a. Scale bar represents 20 mm. (**c**) The eyes and apparatus of *Promissum pulchrum* Kovács-Endrödy 1986; GSSA C351b. Scale bar represents 5 mm. (**d**) Body fossil of *Promissum pulchrum*, anterior to the right. The V-shaped muscle blocks, liver (dark elongate patch on body), eye (silver circle to the right) and apparatus (below the eye) should be noted; GSSA C721b. Scale bar represents 10 mm. (**e**) Ventral surface of enigmatic arthropod (part on left and counterpart on right; anterior to the top); GSSA C1707. Appendages are directed inwards towards the centre of the organism. The appendages and general morphology of the fossil can be compared with crustaceans but a definitive identification cannot be confirmed based on this single incomplete fossil (Whittle 2007). ta, thoracic appendages; aa, abdominal appendages; as, anterior structures; gt, possible gut trace. (**f**) *Siphonacis parva* showing typical straight (right) and bent (left) morphotypes; GSSA C520. Scale bar represents 2.5 mm. (**g**) *Siphonacis parva* showing small projections from the central axis on one specimen; GSSA C935. Scale bar represents 2.5 mm. (**h**) Segmented and lobed enigmatic fossil; GSSA C509; Scale bar represents 5 mm. (**i**) Possible agnatha; two subcircular dark patches are eyes and the dark trapezoid is possibly the liver. Scale bar represents 5 mm.

experiments (Martin *et al.* 2004). More work is required to determine precisely the nature of the clays in the Soom Shale.

A range of geochemical redox proxies, including Mo abundance and Fe, S and C relationships, indicate that the Soom Shale was a dominantly anoxic and occasionally euxinic environment (Gabbott 1998). Loss of carbonate biominerals is attributed to low-pH waters produced by the decomposition of copious organic matter. However, extremely low pH values are required for dissolution of apatite and this may have been facilitated by Fe becoming limiting to pyrite formation, allowing a build-up of H_2S in pore and bottom waters. The occasional oxidation of such water may have produced acidity sufficient to demineralize apatite (Gabbott 1998). In a core of black, unweathered Soom Shale, a few conodont elements have been recovered and these demonstrate demineralization, so at least in these cases recent weathering cannot be invoked to account for mineral loss. However, the extent to which this is the case across the deposit is not tested.

Conclusions

Fossils are rare and difficult to find in the Soom Shale but the endeavour is worth while because the fauna provides us with an unmatched view of Late Ordovician ecology in a unique environment. The remains of hundreds of conodont bedding plane assemblages, many with associated eyes, and a single specimen with the trunk preserved, first brought attention to the Soom Shale. However, it is likely to be the description of enigmatic taxa that will ensure that this Lagerstätte continues to add significantly to palaeobiological reconstructions of the biosphere of the end-Ordovician, a time of dramatic biotic upheaval.

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References

Aldridge, R.J. & Theron, J.N. 1993. Conodonts with preserved soft tissues from a new Ordovician *Konservat-Lagerstätte*. *Journal of Micropalaeontology*, **12**, 113–117, http://doi.org/10.1144/jm.12.1.113

Aldridge, R.J., Briggs, D.E.G., Clarkson, E.N.K. & Smith, M.P. 1986. The affinities of conodonts—new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia*, **19**, 279–291.

Aldridge, R.J., Briggs, D.E.G., Smith, M.P., Clarkson, E.N.K. & Clark, N.D.L. 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 405–421.

Aldridge, R.J., Purnell, M.A., Gabbott, S.E. & Theron, J.N. 1995. The apparatus architecture and function of *Promissum pulchrum Kovacs-Endrody* (Conodonta, Upper Ordovician) and the prioniodontid plan. *Philosophical Transactions of the Royal Society of London, Series B*, **347**, 275–291.

Aldridge, R.J., Gabbott, S.E. & Theron, J.N. 2001. The Soom Shale. *In*: Briggs, D.E.G. & Crowther, P.R. (eds) *Palaeobiology II*. Blackwell, Oxford, 340–342.

Aldridge, R.J., Gabbott, S.E., Siveter, L.J. & Theron, J.N. 2006. Bromalites from the Soom Shale Lagerstätte (Upper Ordovician) of South Africa: palaeoecological and palaeobiological implications. *Palaeontology*, **49**, 857–871.

Aldridge, R.J., Murdock, D.J.E., Gabbott, S.E. & Theron, J.N. 2013. A 17-element conodont apparatus from the Soom Shale Lagerstätte (Upper Ordovician), South Africa. *Palaeontology*, **56**, 261–276.

Anderson, E.P., Schiffbauer, J.D. & Xiao, S. 2011. Taphonomic study of Ediacaran organic-walled fossils confirms the importance of clay minerals and pyrite in Burgess Shale-type preservation. *Geology*, **39**, 643–646.

Armstrong, H.A. & Coe, A.L. 1997. Deep-sea sediments record the geophysiology of the late Ordovician glaciation. *Journal of the Geological Society, London*, **154**, 929–934, http://doi.org/10.1144/gsjgs.154.6.0929

Atkins, C.B. & Dunbar, G.B. 2009. Aeolian sediment flux from sea ice into Southern McMurdo Sound, Antarctica. *Global and Planetary Change*, **69**, 133–141.

Backeberg, N.R. & Rowe, C.D. 2009. Mega-scale (~50 m) Ordovician load casts at De Balie, South Africa: Possible sediment fluidization by thermal destabilisation. *South African Journal of Geology*, **112**, 187–196.

Bassett, M.G., Popov, L.E., Aldridge, R.J., Gabbott, S.E. & Theron, J.N. 2009. Brachiopoda from the Soom Shale Lagerstätte (Upper Ordovician, South Africa). *Journal of Paleontology*, **83**, 614–623.

Berry, W.B.N., Quinby-Hunt, M.S. & Wilde, P. 1995. Impact of Late Ordovician glaciation–deglaciation on marine life. *In*: Stanley, S.M. (ed.) *Studies in Geophysics: Effects of Past Global Change on Life*. National Academy Press, Washington, DC, 34–46.

Beuf, S., Biju-Duval, B., de Charpal, O., Rognon, P., Gariel, O. & Bennacef, A. 1971. *Les grès du Paléozoïque inférieur au Sahara*. Technip, Paris.

Blignault, H. & Theron, J.N. 2010. Reconstruction of the Ordovician Pakhuis Ice Sheet, South Africa. *South African Journal of Geology*, **113**, 335–360.

Blignault, H. & Theron, J.N. 2011. Reply to the discussion by C. D. Rowe and N. R. Backeberg on the paper 'Reconstruction of the Ordovician Pakhuis Ice Sheet, South Africa' by H. J. Blignault and J. N. Theron. *South African Journal of Geology*, **114**, 103–104.

Braddy, S.J., Aldridge, R.J. & Theron, J.N. 1995. A new eurypterid from the Late Ordovician Table Mountain Group, South Africa. *Palaeontology*, **38**, 563–581.

Braddy, S.J., Aldridge, R.J., Gabbott, S.E. & Theron, J.N. 1999. Lamellate book-gills in a late Ordovician eurypterid from the Soom Shale, South Africa: support for a eurypterid–scorpion clade. *Lethaia*, **32**, 72–74.

Brenchley, P.J., Carden, G.A.F. & Marshall, J.D. 1995. Environmental changes associated with the 'first strike' of the Late Ordovician mass extinction. *Modern Geology*, **20**, 69–82.

Briggs, D.E.G., Clarkson, E.N.K. & Aldridge, R.J. 1983. The conodont animal. *Lethaia*, **16**, 1–14.

Butterfield, N.J. 2006. Hooking some stem group 'worms': fossil lophotrochozoans in the Burgess Shale. *BioEssays*, **28**, 1161–1166.

Butterfield, N.J. 2008. An early Cambrian radula. *Journal of Paleontology*, **82**, 543–554.

Butterfield, N.J., Balthasar, U. & Wilson, L.A. 2007. Fossil diagenesis in the Burgess Shale. *Palaeontology*, **50**, 537–543.

Cai, Y., Schiffbauer, J.D., Hua, H. & Xiao, S. 2012. Preservational modes in the Ediacaran Gaojiashan Lagerstätte: Pyritization, aluminosilicification, and carbonaceous compression. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **326**, 109–117.

Callow, R.H. & Brasier, M.D. 2009. A solution to Darwin's dilemma of 1859: exceptional preservation in Salter's material from the late Ediacaran Longmyndian Supergroup, England. *Journal of the Geological Society, London*, **166**, 1–4, http://doi.org/10.1144/0016-76492008-095

Caron, J.-B., Scheltema, A.H., Schander, C. & Rudkin, D. 2006. A soft-bodied mollusc with radula from the Middle Cambrian Burgess Shale. *Nature*, **442**, 159–163.

Chesselet, P. 1992. Disarticulated remains of an Ordovician metazoan from the Cedarberg Formation, South Africa: a re-interpretation of *Eohostimella parva* Kovács 1986. *Palaeontology Africana*, **29**, 11–20.

Cocks, L.R.M. & Fortey, R.A. 1986. New evidence on the South African Lower Palaeozoic: age and fossils reviewed. *Geological Magazine*, **123**, 437–444.

Cramer, F.H., Rust, I.C. & Diez De Cramer, M.D.C.R. 1974. Upper Ordovician chitinozoans from the Cedarberg Formation of South Africa. Preliminary note. *Geologische Rundschau*, **63**, 340–345.

Daley, A.C. 2013. Anomalocaridids. *Current Biology*, **23**, 860–861.

Delabroye, A. & Vecoli, M. 2010. The end-Ordovician glaciation and the Hirnantian Stage: a global review and questions about Late Ordovician event stratigraphy. *Earth-Science Reviews*, **98**, 269–282.

Deynoux, M. 1985. Terrestrial or waterlain glacial diamictites? Three case studies from the late Precambrian and late Ordovician glacial drifts in West Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **51**, 97–141.

Donoghue, P.C.J., Fortey, P.L. & Aldridge, R.J. 2000. Conodont affinity and chordate phylogeny. *Biological Reviews*, **75**, 191–251.

Fiore, S., Dumontet, S., Huertas, F.J. & Pasquale, V. 2011. Bacteria-induced crystallization of kaolinite. *Applied Clay Science*, **53**, 566–571.

Fortey, R.A. & Theron, J.N. 1995. A new Ordovician arthropod, *Soomaspis*, and the agnostid problem. *Palaeontology*, **37**, 841–861.

Gabbott, S.E. 1998. Taphonomy of the Ordovician Soom Shale Lagerstätte: an example of soft tissue preservation in clay minerals. *Palaeontology*, **41**, 631–667.

Gabbott, S.E. 1999. Orthoconic cephalopods and associated fauna from the Late Ordovician Soom Shale Lagerstätte, South Africa. *Palaeontology*, **42**, 123–148.

Gabbott, S.E., Aldridge, R.J. & Theron, J.N. 1995. A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature*, **374**, 800–803.

Gabbott, S.E., Aldridge, R.J. & Theron, J.N. 1998. Chitinozoan chains and cocoons from the Upper Ordovician Soom Shale Lagerstätte, South Africa: implications for affinity. *Journal of the Geological Society, London*, **155**, 447–452, http://doi.org/10.1144/gsjgs.155.3.0447

Gabbott, S.E., Norry, M.J., Aldridge, R.J., & Theron, J.N. 2001. Preservation of Fossils in Clay Minerals; a Unique Example from the Upper Ordovician Soom Shale, South Africa. *Proceedings of the Yorkshire Geological and Polytechnic Society*, **53**, 237–244. http://doi.org/10.1144/pygs.53.3.237

Gabbott, S.E., Siveter, D.J., Aldridge, R.J. & Theron, J.N. 2003. The earliest myodocopes: ostracodes from the late Ordovician Soom Shale Lagerstätte of South Africa. *Lethaia*, **36**, 151–160.

Gabbott, S.E., Zalasiewicz, J., Aldridge, R.J. & Theron, J.N. 2010. Eolian input into the Late Ordovician postglacial Soom Shale, South Africa. *Geology*, **38**, 1103–1106.

Gray, J., Theron, J.N. & Boucot, A.J. 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geological Magazine*, **123**, 445–454.

Harper, D.A., Hammarlund, E.U. & Rasmussen, C.M. 2014. End Ordovician extinctions: a coincidence of causes. *Gondwana Research*, **25**, 1294–1307.

Hints, O., Paris, F. & Al-Hajri, S. 2015. Late Ordovician scoleocodonts from the Qusaiba-1 core hole, central Saudi Arabia, and their paleogeographical affinities. *Review of Palaeobotany and Palynology*, **212**, 85–96, http://doi.org/10.1016/j.revpalbo.2014.08.013

Kovács-Endrödy, E. 1986. The earliest known vascular plant, or a possible ancestor of vascular plants in the flora of the Lower Silurian Cedarberg Formation, Table Mountain Group, South Africa. *Annals of the Geological Survey of South Africa*, **20**, 93–118.

Martin, D., Briggs, D.E.G. & Parkes, R.J. 2004. Experimental attachment of sediment particles to invertebrate eggs and the preservation of soft-bodied fossils. *Journal of the Geological Society, London*, **161**, 735–738, http://doi.org/10.1144/0016-764903-164

Mehl, J. 1984. Radula und Fangarme bei *Michelinoceras* sp. aus dem Silur von Bolivien. *Paläontologische Zeitschrift*, **58**, 211–229.

Page, A., Gabbott, S.E., Wilby, P.R. & Zalasiewicz, J.A. 2008. Ubiquitous Burgess Shale-style 'clay templates' in low-grade metamorphic mudrocks. *Geology*, **36**, 855–858.

Racheboeuf, P.R. & Crasquin, S. 2010. The Ordovician caryocaridid phyllocarids (Crustacea): diversity and evolutionary tendencies. *Neues Jahrbuch für Geologie und Paläontologie*, **257**, 237–248.

Rong, J.-Y. & Harper, D.A.T. 1988. A Global Synthesis of the Latest Ordovician Hirnantian Brachiopod Fauna. *Transactions of the Royal Society of Edinburgh: Earth and Environmental Science*, **79**, 383–402.

Rowe, C.D. & Backeberg, N.R. 2011. Discussion on: Reconstruction of the Ordovician Pakhuis Ice Sheet, South Africa by H. J. Blignault and J. N. Theron. *South African Journal of Geology*, **114**, 95–102.

Rust, I.C. 1967. *On the sedimentation of the Table Mountain Group in the Western Cape Province*. PhD dissertation, Stellenbosch University.

Sansom, R.S., Freedman, K., Gabbott, S.E., Aldridge, R.J. & Purnell, M.A. 2010. Taphonomy and affinity of an enigmatic Silurian vertebrate, Jamoytius kerwoodi White. *Palaeontology*, **53**, 1393–1409. http://doi.org/10.1111/j.1475-4983.2010.01019

Selden, P. & Nudds, J. 2004. The Soom Shale. *In*: Selden, P. & Nudds, J. (eds) *Evolution of Fossil Ecosystems*. Manson, London, 29–36.

Selden, P. & Nudds, J. 2012. The Soom Shale. 2nd edition. *In*: Selden, P. & Nudds, J. (eds) *Evolution of Fossil Ecosystems*. Academic Press, London, 42–52.

Sepkoski, J.J. 1996. Patterns of Phanerozoic extinction: a perspective from global data bases. *In*: Walliser, O.H. (ed.) *Global Events and Event Stratigraphy in the Phanerozoic*. Springer, Berlin, 35–51.

Sheehan, P.M. 2001. The Late Ordovician Mass Extinction. *Annual Review of Earth and Planetary Sciences*, **29**, 331–364.

Smith, M., Briggs, D. & Aldridge, R. 1987. A conodont animal from the lower Silurian of Wisconsin, USA, and the apparatus architecture of panderodontid conodonts. *In*: Aldridge, R.J. (ed.) *Palaeobiology of Conodonts*. Ellis Horwood, Chichester, 91–104.

Sutcliffe, O.E., Dowdeswell, J.A., Whittington, R.J., Theron, J.N. & Craig, J. 2000. Calibrating the Late Ordovician glaciation and mass extinction by the eccentricity cycles of Earth's orbit. *Geology*, **28**, 967–970.

Sutton, M.D., Briggs, D.E.G., Siveter, D.J. & Siveter, D.J. 2006. Fossilized soft tissues in a Silurian platyceratid gastropod. *Proceedings of the Royal Society of London, Series B*, **273**, 1039–1044.

Tappan, H. 1980. *The Paleobiology of Plant Protists*. W. H. Freeman, San Francisco, CA.

Theron, J.N., Rickards, R.B. & Aldridge, R.J. 1990. Bedding plane assemblages of *Promissum pulchrum*, a new giant Ashgill conodont from the Table Mountain Group, South Africa. *Palaeontology*, **33**, 359–378.

Torsvik, T.H. & Cocks, L.R.M. 2009. BugPlates: Linking biogeography and palaeogeography, http://www.geodynamics.no/Web/Content/Software

Urrutia, M.M. & Beveridge, T.J. 1994. Formation of fine-grained metal and silicate precipitates on a bacterial surface (*Bacillus subtilis*). *Chemical Geology*, **116**, 261–280.

Vandenbroucke, T.R.A., Gabbott, S.E., Paris, F., Aldridge, R.J. & Theron, J.N. 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. *Journal of Micropalaeontology*, **28**, 53–66, http://doi.org/10.1144/jm.28.1.53

Vannier, J., Racheboeuf, P.R., Brussa, E.D., Williams, M., Rushton, A.W.A., Servais, T. & Siveter, D.J. 2003. Cosmopolitan arthropod zooplankton in the Ordovician seas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 173–191.

von Bitter, P.H., Purnell, M.A., Tetreault, D.K. & Stott, C.A. 2007. Eramosa Lagerstatte—Exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating organisms (Silurian, Ontario, Canada). *Geology*, **35**, 879–882.

Wacey, D., Saunders, M. *et al.* 2014. Enhanced cellular preservation by clay minerals in 1 billion-year-old lakes. *Scientific Reports*, **4**: 5841, 11.

Whittle, R.J. 2007. *Systematics, taphonomy and palaeoecology of selected invertebrates from the Late Ordovician Soom Shale Lagerstätte, South Africa*. PhD thesis, University of Leicester.

Whittle, R.J., Gabbott, S.E., Aldridge, R.J. & Theron, J.N. 2007. Taphonomy and palaeontology of a Late Ordovician caryocaridid from the Soom Shale Lagerstätte, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 383–397.

Whittle, R.J., Gabbott, S.E., Aldridge, R.J. & Theron, J.N. 2008. Late Ordovician (Hirnantian) scolecodont clusters from the Soom Shale Lagerstätte, South Africa. *Journal of Micropalaeontology*, **27**, 147–159, http://doi.org/10.1144/jm.27.2.147

Whittle, R.J., Gabbott, S.E., Aldridge, R.J. & Theron, J.N. 2009. An Ordovician lobopodian from the Soom Shale Lagerstätte, South Africa. *Palaeontology*, **52**, 561–567.

Young, G.M., Minter, W.E.L. & Theron, J.N. 2004. Geochemistry and palaeogeography of upper Ordovician glaciogenic sedimentary rocks in the Table Mountain Group, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **214**, 323–345.

Zhu, M.-y., Babcock, L. E. & Steiner, M. 2005. Fossilization modes in the Chengjiang Lagerstätte (Cambrian of China); testing the roles of organic preservation and diagenetic alteration in exceptional preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**, 31–46.