

PRESERVATION OF SOFT TISSUES IN SILURIAN GRAPTOLITES FROM LATVIA

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ABSTRACT. The contractile stalks of graptoloid zooids are preserved as organic carbon residues in thecae of the middle Llandovery graptoloid graptolites *Rastrites geinitzii* and *Neolagarograptus?* sp. from the Aizpute-41 core, Latvia. The contractile stalks are surrounded by equant pyrite crystals, resulting in three-dimensional preservation of the graptolite rhabdosomes, and are associated with sediment of similar composition to, and derived from, the adjacent matrix. Matrix entered the thecae after pyrite crystal growth and filled some of the space left by collapse of the contractile stalks and some intercrystalline cavities; other space is partially infilled by diagenetic minerals. The contractile stalks are parallel-sided and occupy up to one-half the metathecal width, which is not inconsistent, assuming post-mortem shrinkage, with the suggestion that graptoloid zooids filled their thecal tubes in life. The location of the preserved soft tissues, towards the distal ends of the metathecae, is very different from that predicted by decay experiments on the extant pterobranch hemichordate *Rhabdopleura*; the latter's soft tissues may thus not be a reliable analogue for those of these Silurian graptoloids.

KEY WORDS: soft tissues, graptoloids, Silurian, Latvia.

ONE of the most remarkable features of graptoloid graptolites is that their soft tissues are virtually unknown. This seems particularly surprising considering that they occur in profusion in sedimentary strata ('graptolitic shales') interpreted to have accumulated under low oxygen conditions such as those that have favoured exceptional preservation in, for example, the Middle Cambrian Burgess Shale. This lack of soft tissue preservation has meant that fundamental questions regarding graptoloid biology and palaeoautecology have remained unanswered.

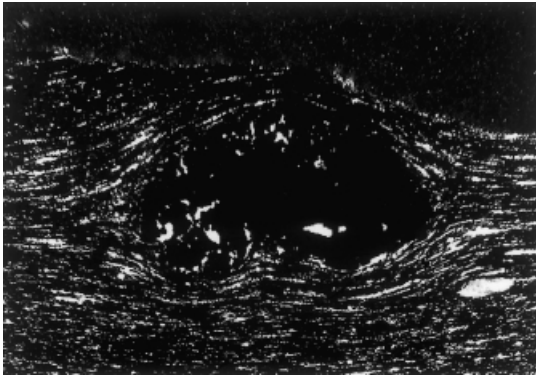
The purpose of this paper is to record the occurrence of soft tissue preservation in two graptoloid graptolite species from the Llandovery of Latvia.

PREVIOUS RECORDS OF SOFT TISSUE IN GRAPTOLITES

Previous records of graptolite soft tissue are largely limited to the anisograptid genus *Psigraptus* from the Tremadoc of northern Canada (Jackson 1967) and Tasmania (Rickards and Stait 1984; Rickards *et al.* 1991) in which pyritized (in some cases subsequently limonitized) stolons and zooids have been recognised. Bjerreskov (1994, p. 219) has also described pyritized 'circular and oval forms present in a few thecae [that] may represent remnants of the bodies or stalks of zooids'. Her illustrated material of *Monoclimacis* sp. was from the Telychian (upper Llandovery) of Bornholm, Denmark. Bjerreskov's (1978) previous attempts at 'finding traces of the unknown soft parts' using X-rays were unsuccessful: 'Despite the large number of graptolites examined no definite shapes and details of the soft parts have been revealed during this investigation' (Bjerreskov 1978, p. 467).

MATERIAL AND METHODS

All of the specimens are preserved on a single bedding surface. The material examined comprises a core chip [graptolites on this are numbered 341-24 and 345-2-8 (*Rastrites geinitzii*), 341-27 (*Neolagarograptus?* sp.), and 341-30 (*Metaclimacograptus orientalis*)], a thin section (345-1), and pieces of core



TEXT-FIG. 1. Thin section, 345-1, showing three-dimensional preservation of *Rastrites geinitzii* (see also Text-fig. 5C); note the irregularly shaped and distributed cavities; $\times 30$.

mounted on SEM stubs (graptolites on the core chips, all *R. geinitzii*, are numbered 345-11–16). All material is housed in the Institute of Geology, Tallinn Technical University, Tallinn, Estonia.

The material is from the Dobe Formation at a depth of 973.83 m in the Aizpute-41 core, western Latvia. This was drilled in the 1960s and has been the subject of a recent integrated biostratigraphical study (Loydell *et al.* 2003). The core slab bears several specimens of *Rastrites geinitzii* Törnquist (Text-figs 2–3), a single proximal end of *Neolagarograptus?* sp. (Text-fig. 2), a single specimen of *Metaclimacograptus orientalis* (Obut and Sobolevskaya) and small fragments of other, indeterminate graptoloids. A sample from 40 mm higher in the core bears '*Demirastrites*' *pectinatus* (Richter), indicating the upper *triangulatus* or the *magnus* graptolite Biozone of the lower Aeronian (middle Llandovery).

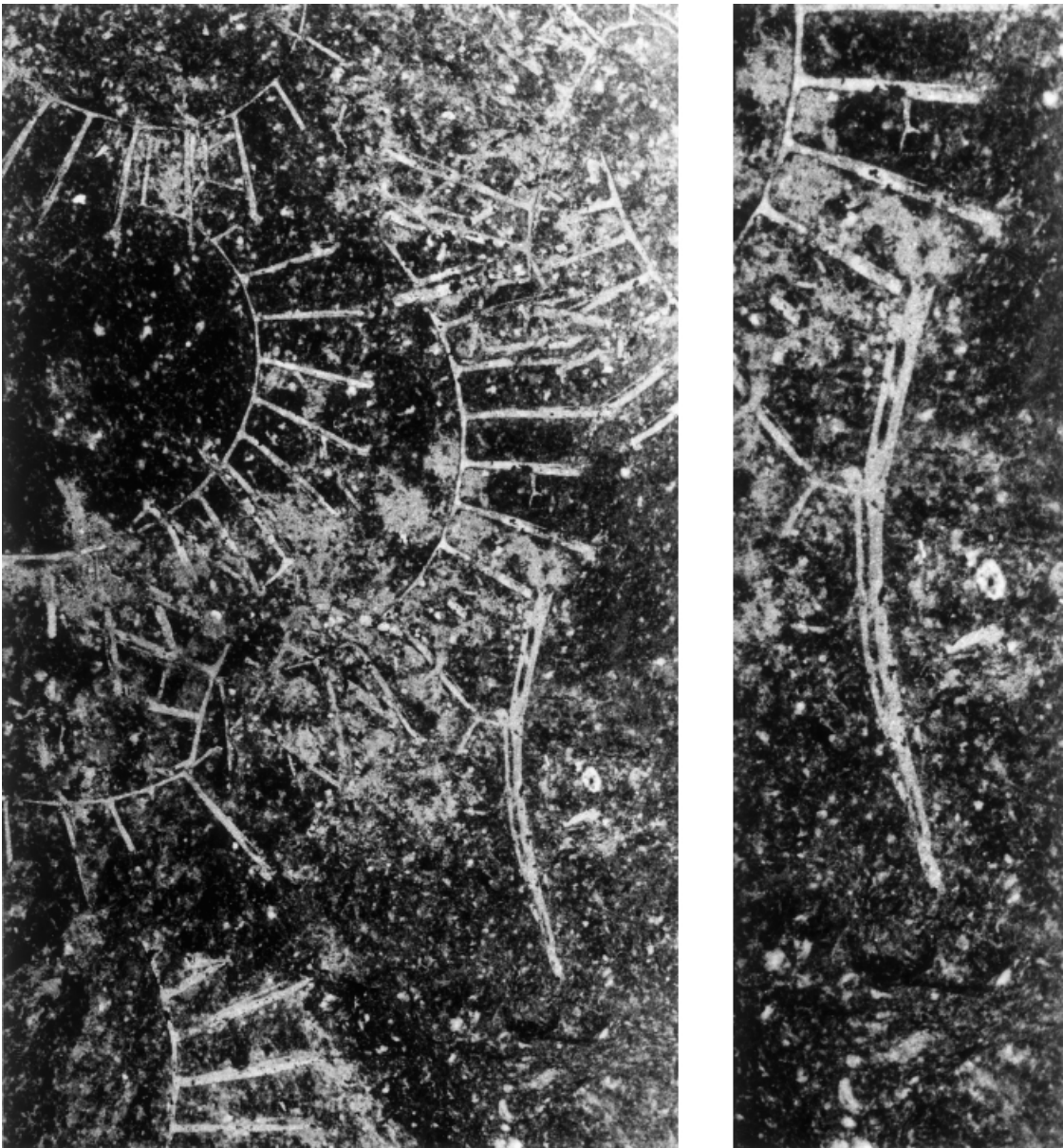
The material was examined at the University of Portsmouth using light microscopes and a JEOL JSM-6100 SEM using both secondary (SE) and back-scattered electrons (BSE) on specimens coated with gold-palladium. Elemental analyses were performed at the University of Bristol using a Hitachi S3500N SEM equipped with an EDAX Phoenix Energy Dispersive Spectrometer operating at 10 kV.

PRESERVATION

All of the graptolites are preserved in three dimensions (Text-figs 1, 5c). Only in the specimen of *Metaclimacograptus orientalis* (Loydell *et al.* 2003, fig. 4p) and a few of the thecae of *Rastrites geinitzii* (e.g. Text-fig. 5c) has the slab split around the exterior of the graptolite. In all other cases the graptolite rhabdosomes have split in two down their middle. Such an occurrence is extremely rare, the usual situation in three-dimensionally preserved material being, upon splitting of a slab, the presence of a 'part' bearing the graptolite periderm, usually infilled with pyrite, and a 'counterpart' bearing an external mould (see figures in e.g. Sudbury 1958; Hutt 1975).

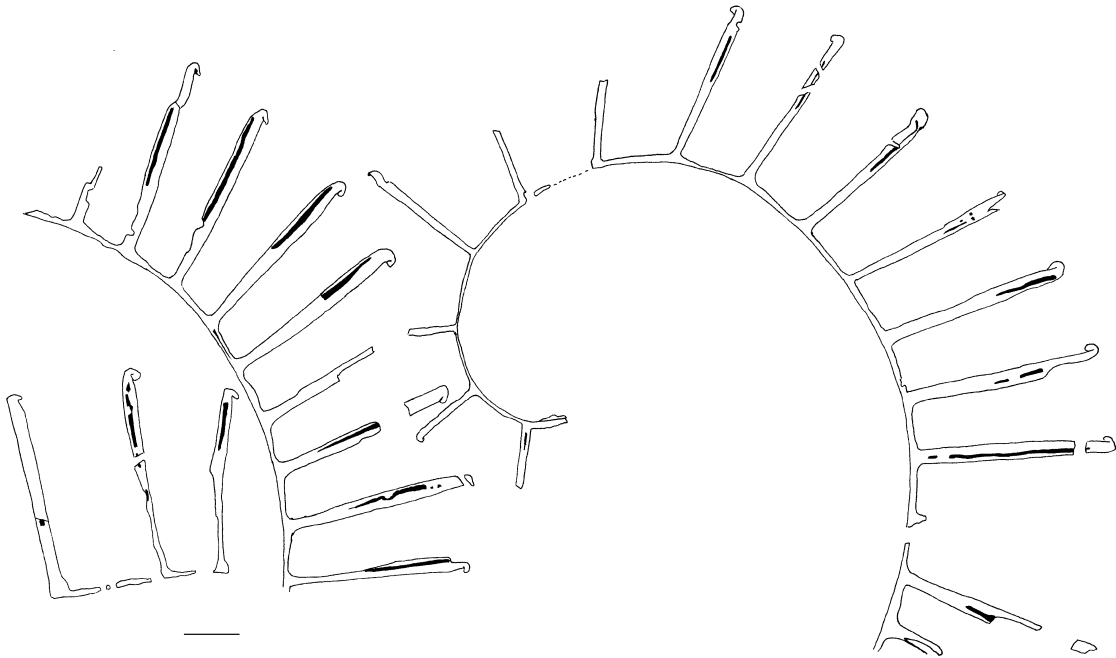
Mineralogy of rhabdosome infill

Pyrite infills most of the rhabdosome. A few larger, irregularly shaped, cavities and some of the interstitial space between pyrite crystals remain open (Text-fig. 1). The remaining space was infilled after precipitation of the pyrite by clay minerals or diagenetic minerals (including calcite, sphalerite and galena). Elemental mapping (Text-fig. 4) indicates that the clay minerals are of similar composition to, and presumably derived from, the adjacent matrix. The pyrite is in the form of euhedral crystals (Text-fig. 5A) with a diameter of up to 10 μm , some of which are embedded in the graptolite periderm (Text-fig. 5B) in a manner similar to that described for pyrite microcrysts by Underwood and Bottrell (1994, fig. 2e). The three-dimensional nature of the rhabdosomes indicates that these pyrite crystals are early diagenetic. Such rhabdosome-filling, 'early euhedral (equant) pyrite' (*sensu* Underwood and Bottrell 1994) is rare; it was not observed by Bjerreskov (1991, 1994) and Underwood (1992) in their studies of pyrite diagenesis



TEXT-FIG. 2. A, soft tissue preservation in *Rastrites geinitzii* (341-24 and 345-2-8) and *Neolagarograptus?* sp. (341-27); $\times 5.4$. B, close-up of *Neolagarograptus?* sp.; note preservation of soft tissue in sicularia, th1 and th2; $\times 8.6$.

in graptolites. Underwood and Bottrell (1994), however, provided two examples: within a low relief 'didymograptid' from the Llanvirn of Newfoundland; and in the middle Ordovician Viola Limestone of Oklahoma, in which the pyrite is associated with calcite spar. In contrast with the Aizpute-41 specimens, Bjerreskov (1991, 1994) found that microcrystalline pyrite and framboids were the earliest precipitated pyrite forms, with euhedral pyrite growing at a later stage (when there was reduced access to sea water; Raiswell 1982).



TEXT-FIG. 3. Soft tissue within metathecae of *Rastrites geinitzii* (341-24, 345-9-10). Note the consistent position of the soft tissue towards the dorsal side of the metatheca. Scale bar represents 1 mm.

Preservation of graptolite soft tissues

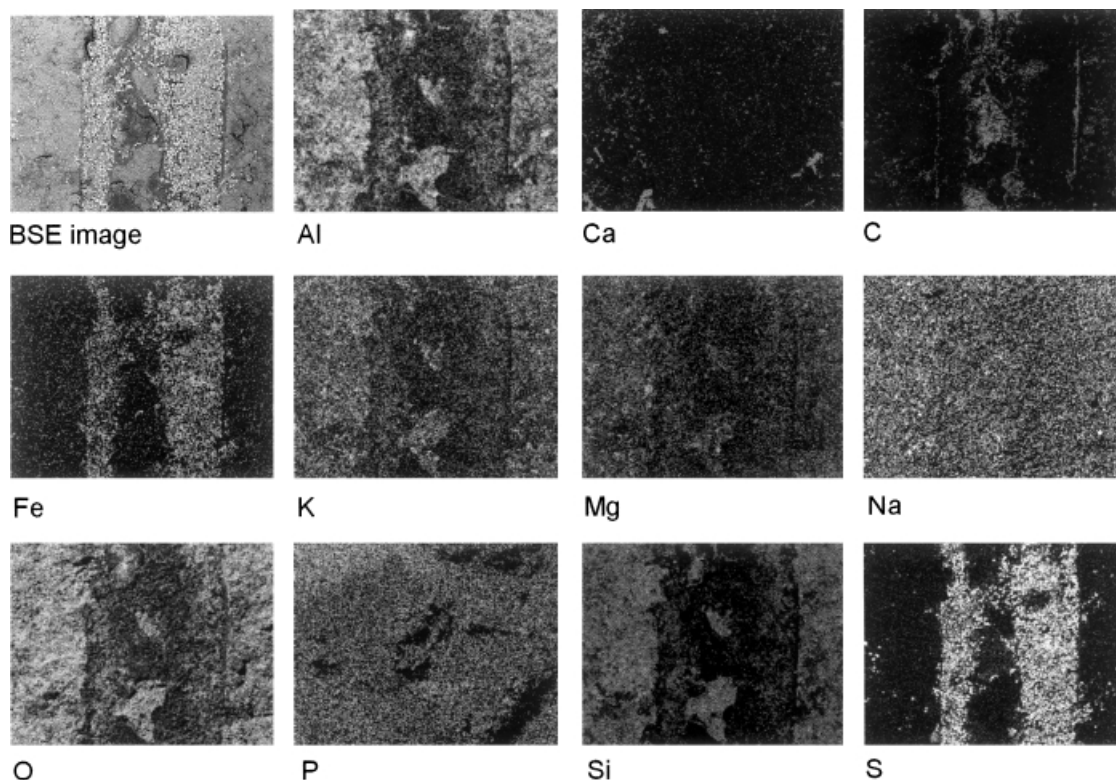
Graptoloid soft tissues are preserved in many thecae (see details below); SEM examination and elemental mapping (Text-fig. 4) indicates that these are preserved as two-dimensional organic carbon residues. This is the first record of carbonized soft tissue preservation in graptoloids.

The soft tissues occur within the sicula and thecae of the specimen of *Neolagarograptus?* sp. (Text-fig. 2), and within more than 70 thecae of 12 *Rastrites geinitzii* rhabdosomes (Pl. 1; Text-figs 2-3). The soft tissues are in all cases enclosed by pyrite crystals (Pl. 1, fig. 2). In *Neolagarograptus?* sp. the soft tissue is situated towards the dorsal side of, and occupies approximately half the width of the thecae (Text-fig. 2). In the *R. geinitzii* metathecae the soft tissues occur consistently towards the dorsal (i.e. distal) side, but are not attached to the dorsal metathecal wall; they comprise one-quarter to one-third of the metathecal width (Text-fig. 3). The lateral margins of the soft tissues are sharply defined and their breadth is constant. Although the plane of splitting is broadly bedding-parallel, only subtle variations in its vertical position would be required to leave the soft tissues either obscured by overlying pyrite, or retained in the counterpart. There is, however, no evidence in any of the specimens for the soft tissues extending beyond either the thecal aperture, or past the proximal part of each theca into the common canal. The length of soft tissue observed in each theca is likely to correspond to that preserved.

Like the later infill of interstitial space in the surrounding pyrite, the soft tissues are associated with clay minerals of identical composition to, and presumably derived from, the adjacent matrix (Text-fig. 4), and more rarely, diagenetic minerals, including calcite, sphalerite and galena. The cavities within the pyrite have highly irregular outlines, vary in position between thecae, lack any continuity along the length of the thecae and are never associated with carbonaceous material.

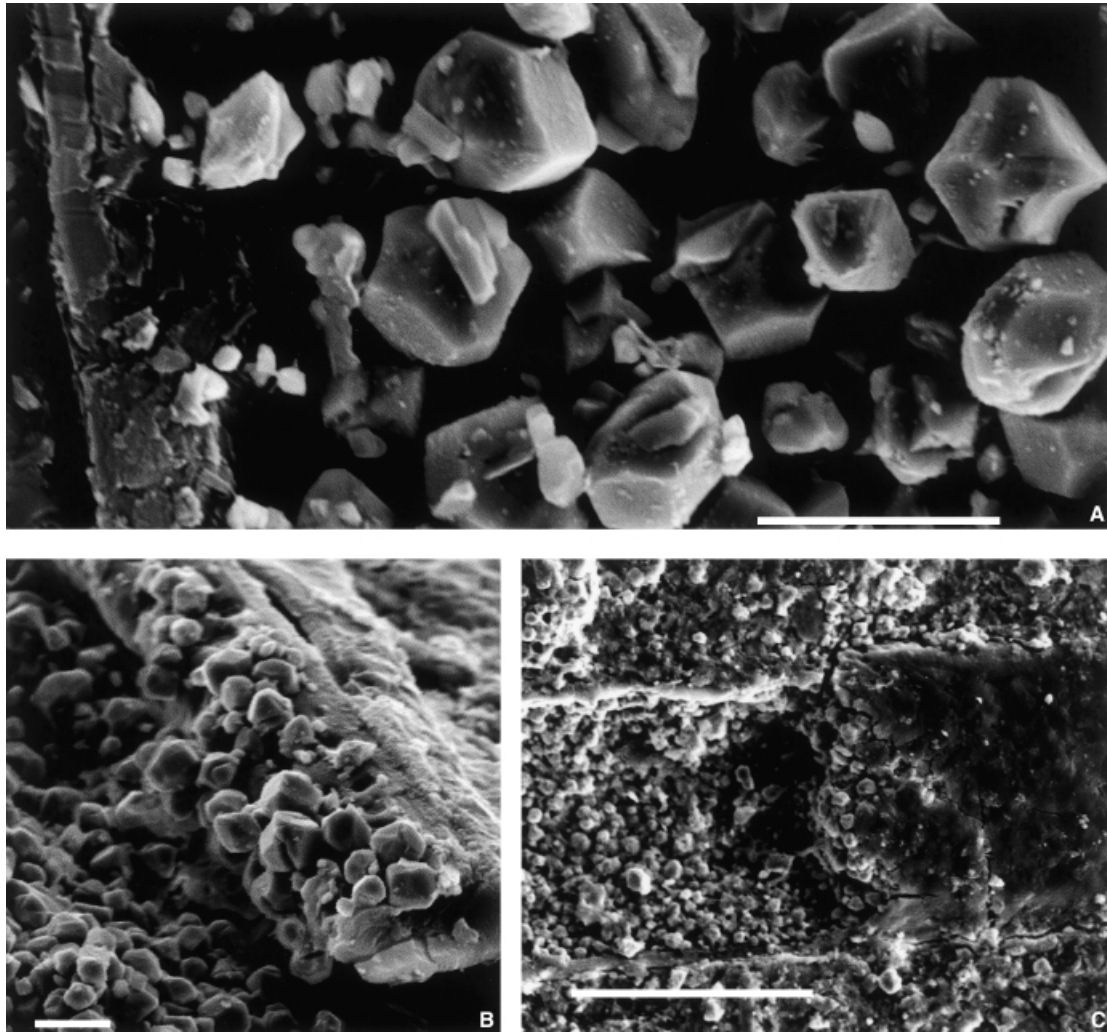
Interpreted sequence of events

The interpreted sequence of biostratinomic and early diagenetic events is as follows.



TEXT-FIG. 4. Elemental maps of part of a *Rastrites geinitzii* metatheca (that figured in Pl. 1, fig. 4; 345-16). On the BSE (backscattered electron = atomic number contrast) image the brightest areas are pyrite, the darkest the soft tissues preserved as an organic carbon residue, and the pale grey areas are matrix.

1. Death of graptolite, before or upon which the zooids may have contracted into the thecae (see below).
2. Moderately rapid sinking of rhabdosomes to the sea-floor during which decay of the most labile tissues was initiated. Bjerreskov (1991) concluded that graptolites in an outer shelf environment probably reached the sea bottom within less than six days. Such rapid sinking of graptoloid graptolites is suggested by their distribution patterns. In the Silurian, different assemblages characterize inner to mid shelf, outer shelf, and basinal environments (e.g. Loydell 2001). Such differences would not be retained if their residence time in the water column was long; currents would redistribute the graptolites laterally.
3. Precipitation of euhedral pyrite crystals within most of the void space inside the graptoloid rhabdosomes. As this is responsible for the three-dimensional preservation of the rhabdosomes it was initiated shortly after the graptolites settled on the sea bottom, and before the periderm lost its structural strength.
4. Collapse of the soft tissues into two-dimensional structures, presumably as a result of decay-induced loss of their structural strength, occurred after precipitation of the pyrite: pyrite surrounds the soft tissues entirely, but does not infill the space created by their collapse.
5. Partial infill of remaining space [the 'channels' formed by collapse of the soft tissues (Pl. 1, fig. 4), spaces between individual pyrite crystals and larger scale cavities] by sediment, and diagenetic minerals including calcite, sphalerite and galena. The relative timing of the precipitation of the different minerals and the infiltration of sediment is unknown. It is, however, considered more likely that sediment infiltration would have occurred first; this sediment is chemically identical to, and presumably derived from the adjacent matrix, and thus would have been most easily remobilized when its fluid content was high, i.e. when at or near the sediment-water interface.

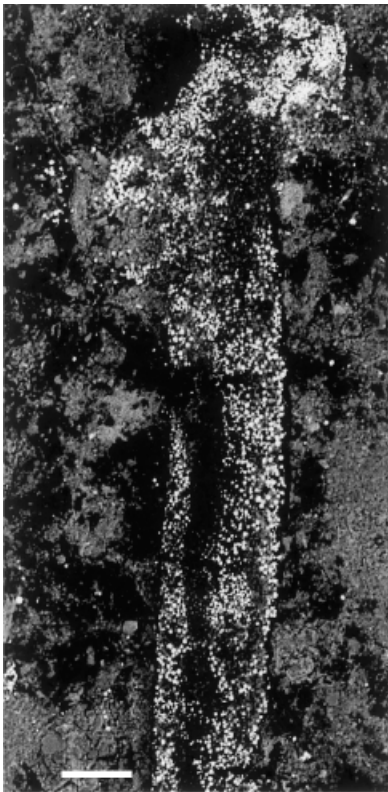


TEXT-FIG. 5. Preservation of *Rastrites geinitzii*; Aizpute-41 core, Latvia. A–B, 345-11. A, pyrite crystals within protheca. B, pyrite crystals embedded in nema. C, 345-12, graptolite periderm infilled with pyrite crystals; this is a rare example of the core splitting around the graptolite (to the right) rather than through the middle (to the left). Scale bars represent 10 μm (A–B) or 100 μm (C). All are SE (secondary electron) images.

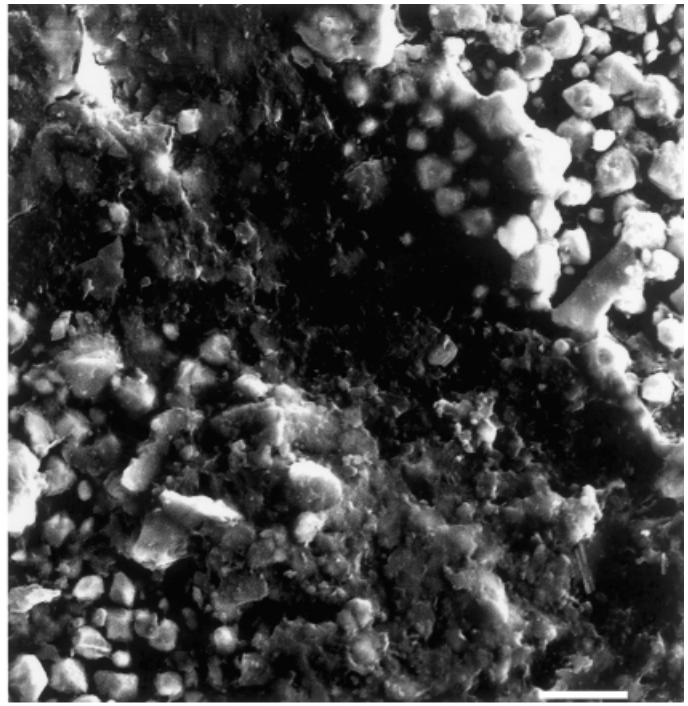
EXPLANATION OF PLATE 1

Figs 1–4. Soft tissue preservation in *Rastrites geinitzii*; Aizpute-41 core, Latvia. 1, 3–4, BSE images. 1, 345-13; metatheca showing soft tissue. 3, 345-15; mesial part of rhabdosome; all thecae contain soft tissue. 4, 345-16; close-up of part of metatheca (see Text-fig. 4 for elemental maps). 2, 345-14; SE image; close-up of soft tissue, underlain (top right) and overlain (bottom left) by pyrite crystals. Scale bars represent 100 μm (figs 1, 4), 10 μm (fig. 2) or 1 mm (fig. 3). On the BSE image the brightest areas are pyrite, the darkest are the soft tissues preserved as an organic carbon residue, and the pale grey areas are matrix. In 4 the matrix contains some elongate calcium carbonate grains (spicules?).

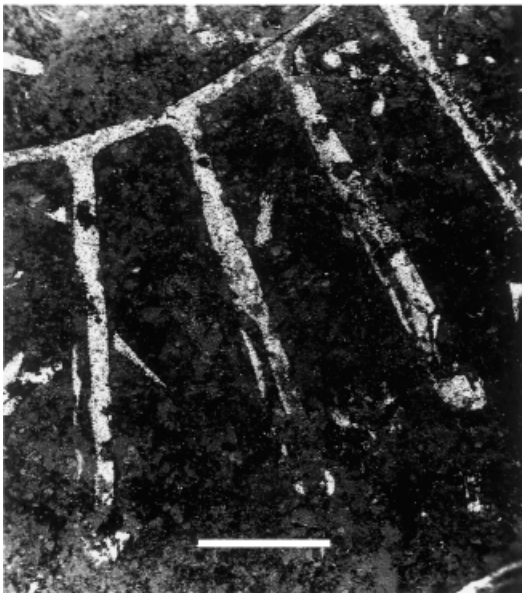
PLATE 1



1



2



3



4

LOYDELL, graptolite soft tissue

DISCUSSION

Preservation

There are no obvious aspects of their taphonomic history that explain why soft tissues are preserved in these graptoloids. The mode of deposition (vertical settling as opposed to entombment within a depositing event bed), the host lithology (dark grey shales) and the depositional environment (outer shelf) are the same as in many other assemblages of graptoloids. The texture of the pyrite infill of the rhabdosome is uncommon, but not previously unknown. Euhedral pyrite growth does, however, require reduced access to seawater (Raiswell 1982); there are two other notable features.

Firstly, pyrite is not restricted to within the rhabdosome; extensive discontinuous patches occur elsewhere on the surface of the slab (Text-fig. 2). These patches are particularly well developed, and the density of pyrite highest, in the vicinity of the graptoloids (Text-fig. 2A; note that the counterpart does not have patches where they are absent on the part illustrated). Secondly, the density of graptoloids on the surface of splitting is high; overlapping graptoloids are not separated vertically by a thin layer of sediment.

Assuming that the rate at which individual graptoloid rhabdosomes accumulated on the sea floor was constant (cf. seasonal mass mortalities), the rate of sedimentation may have been reduced temporarily. Alternatively, it is possible that these graptolites reached the sea bottom *en masse* and more rapidly than normal (enhancing the likelihood of soft-tissue preservation) because they became trapped within a descending marine snow aggregate. These sink today at rates of up to a few hundreds of metres per day (Lampitt 1996, p. 103).

A reduced rate of sedimentation may have facilitated the development of a microbial film or shroud locally on the sediment surface and, especially, over the graptoloids. The association of soft tissue preservation and surficial microbial films is proven in a variety of different environments; mat decay can lead to early diagenetic precipitation of a variety of minerals, including pyrite (Schieber 1999; Noffke 2000). The effects of being embedded in an organic-rich marine snow may have been similar; see Jones *et al.* (2002). The infiltration of sediment into the rhabdosome would occur after decay of the microbial film or the marine snow; the patches of pyrite on the surface of the specimen would then represent their degraded remains. The presence of either the marine snow aggregate or a microbial mat would satisfy Raiswell's (1982) requirement of reduced access to seawater for euhedral pyrite growth.

Interpretation of the preserved soft tissues

The most widely accepted model of graptoloid anatomy is based on the biology of the extant hemichordate *Rhabdopleura*: the zooid body was connected to the equivalent of the pectocaulus in *Rhabdopleura* and the stolon of dendroids by a contractile stalk which in *Rhabdopleura* is a solid muscular structure (Stebbing and Dilly 1972, p. 445) as opposed to a fluid-filled tube.

In experimentally decayed specimens of *Rhabdopleura*, the zooids usually retracted into the thecae prior to death but some died projecting out of their aperture (Briggs *et al.* 1995). Interpretation of the soft tissues in the Aizpute-41 core is therefore complicated by the fact that the position of the zooids at the time of death is not known. The soft tissues are, however, elongate and parallel-sided, as would be expected from a collapsed tube or cylinder (Briggs and Williams 1981); this geometry implies that they are more likely to be either the contractile stalk or stolon, than the terminal, broadly ovoid, zooid. By analogy with the anatomy of dendroid graptolites and *Rhabdopleura*, the stolon would not have extended beyond the proximal part of each theca. It is therefore most probable that the soft tissues correspond to the equivalent of the contractile stalk, the terminal part of which, including the zooid, decayed completely.

Independent of environmental conditions, the sequence in which organisms decay is similar; successively more recalcitrant tissues remain with time. Exceptionally preserved fossils in which labile, but not more recalcitrant tissues, are preserved are known. Musculature is preserved (in calcium phosphate) in most specimens of *Myoscolex* recovered from the Emu Bay Shale (Lower Cambrian, Australia), but examples in which the (organically preserved) cuticle is also preserved are more rare (Briggs and Nedin 1997). The preferential preservation of more labile tissues, however, requires their replication in

authigenic minerals, not, as herein, preservation of the original tissues as degraded carbonaceous residues. Thus, it is reasonable to interpret the contractile stalks as having had greater recalcitrance than other (unpreserved) tissues. On this basis, the actual zooids and the equivalent of the stolon system of dendroids were composed of more labile tissues, and have not been preserved. The absence of the latter is the more surprising; other than the periderm, the stolon system is the only part of dendroid graptolites to be commonly preserved. The stolon and tubes of *Rhabdopleura* exhibited no obvious morphological change during ten weeks of decay under anoxic and oxygen-limited conditions (Briggs *et al.* 1995), and tended to retain their structural integrity. The zooids (both the zooid body and contractile stalk), however, decayed rapidly (becoming unrecognisable within a week), although vestiges remained for a period of weeks. The contractile stalks in the Aizpute-41 graptoloids clearly had some resistance to decay; their collapse into two-dimensional residues did not occur until after precipitation of the pyrite (see above).

Rhabdopleura, therefore, may not provide the perfect analogue for the soft tissues of graptoloids. Perhaps the differences between *Rhabdopleura* and graptoloids predicted by their comparative taphonomy may reflect their different ecologies. *Rhabdopleura* is benthic with a fairly randomly organised coenocium, rather than planktic and very precise in its geometry. Reducing the density of the stolon system in graptoloids (and, in the process, its preservation potential) may have served as an aid to buoyancy.

The dimensions of the graptolite zooid

Sudbury (1991) provided estimates for zooid size in a number of graptoloids, based upon measurements of fuselli and cortical bandages and the assumption that these structures were produced by the cephalic shield of pterobranch-like zooids. Sudbury (1991, p. 381) noted that the 'zooids are small compared with the size of the thecae'. Rigby and Sudbury (1995), on the other hand, noted that there is a measurable relationship between coenecium increment width and the cephalic shield length of the rhabdopleuran zooid responsible for its production. Again based on the assumption that graptolites constructed their rhabdosomes in the same manner as pterobranchs, Rigby and Sudbury (1995) suggested that 'the graptolite zooid would have completely filled its tube'.

Because of the likelihood of significant shrinkage of soft tissues during the later stages of decay, it seems reasonable to assume that the dimensions of the contractile stalks in the Aizpute-41 specimens described herein are their *minimum* dimensions when the graptolite colony was alive. These preserved dimensions do not support Sudbury's (1991) 'small zooid' suggestion, but, allowing for post-mortem shrinkage, are not inconsistent with Rigby and Sudbury's (1995) 'tube-filling' scenario.

Sudbury's (1991, fig. 3) illustrations showed zooids, based on extant *Rhabdopleura*, with long, narrow stalks (approximately 5 per cent of the width of the metatheca) terminating in a zooidal 'body' approximately four times the width of the stalk. Similarly, Durman and Sennikov's (1993) illustrations of Middle Cambrian *Rhabdopleura* indicate that the 'stalks' preserved in this fossil material were approximately one-fifth the zooidal width and very narrow in comparison with the width of the zooidal tubes. Thus the width (between one-quarter and one-half of the metathecal width) of the contractile stalks in the Aizpute-41 graptoloids is very different from that in *Rhabdopleura*.

CONCLUSIONS

Soft tissues preserved as organic carbon residues occur in two Silurian graptoloid species from the Aizpute-41 core, Latvia. Their preservation requires an as yet unidentified processes. Rapid sinking, followed by inhibition of decay, both of which may have resulted from entrapment within a marine snow aggregate, and the latter via development of a microbial mat on the sea floor, are possible factors.

The size and location of the preserved soft tissues are consistent with the suggestion that zooids filled their tubes, but suggest that in these two Silurian graptoloid species the soft tissues were rather different from those of the extant pterobranch *Rhabdopleura*, the zooids of which are those most often used in graptolite life reconstructions.

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