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DISARTICULATED REMAINS OF AN ORDOVICIAN METAZOAN FROM THE CEDARBERG FORMATION, SOUTH AFRICA: A RE-INTERPRETATION OF *EOHOSTIMELLA PARVA* KOVÁCS 1986.

by

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ABSTRACT

Small pointed axes previously described as a non-vascular Palaeozoic plant, *Eohostimella parva* Kovács 1986, are assigned to *Siphonacis parva* (Kovács) Chesselet 1990 n. comb. These carbonaceous compressions are indicator fossils for assemblages of *Promissum pulchrum* Kovács 1986, which was initially interpreted as a land plant and is now thought to be a giant conodont. These fossils occur with invertebrates and algae in the Late Ashgillian Soom Shale Member of the Cedarberg Formation, in the Table Mountain Group. *E. parva* has a distinctive internal structure which invalidates its assignment to *Eohostimella* Schopf and casts doubt on its placement in the plant kingdom. Presently these small axes are of uncertain affinity although it seems likely that they are the disarticulated remains of a problematic Ordovician metazoan.

INTRODUCTION

Fossils initially identified as belonging to the genus *Eohostimella* Schopf are found in association with bedding plane assemblages and isolated elements of *Promissum pulchrum* Kovács 1986. The abundant, needle-shaped "*Eohostimella*" *parva* Kovács 1986 is an indicator fossil for the rare assemblages of *P. pulchrum*. The systematic position of the unique *P. pulchrum* has been a contentious issue in palaeontological circles. Its spiny axes were initially interpreted as the remains of a creeping land plant which was either the earliest known vascular plant, or an ancestor of the tracheophytes (Theron and Kovács-Endrödy 1986; Kovács-Endrödy 1986). Theron *et al.* (1990) proposed an entirely different interpretation based on morphological and chemical characteristics. The fossil is now thought to be the remains of a giant conodont. *P. pulchrum* and *"E". parva* co-occur with invertebrates and algae in the Soom Shale Member of the Cedarberg Formation in the Table Mountain Group, which is the lowermost unit of the 8 000m thick, Lower Paleozoic, Cape Supergroup (Tankard *et al.* 1982). The Table Mountain Group is conformably overlain by the Devonian Bokkeveld Group and rests unconformably on the Lower Cambrian Cape Granite Complex, which has been radiometrically dated at 553 + 8 Ma (Cocks & Fortey 1986).

A problematic plant fossil from Lower Silurian deposits in northern Maine was assigned to the new genus *Eohostimella* Schopf *et al.* 1966. *E. heathana* Schopf *et al.* 1966 is characterized by an upright growth habit, a hollow dichotomously branched axis and a unistratose cortex covered by minute spines. Schopf *et al.* (1966) suggested that *Eohostimella* might represent an incipient land plant. This suggestion relies on the erect habit of the plant and the nature of the outer cortex which may have had a mechanical role in maintaining the upright position. This hypothesis is corroborated by analyses of organic chemical constituents which suggest the presence of suberin-cutin and lignin polymers thus implying a "vascular-like" plant chemistry (Niklas 1976).

The work presented here was initially undertaken in preparation to an anatomical investigation of *P. pulchrum*. Since both *"E." parva* and *P. pulchrum* were assumed to have plant affinities, the same preparative techniques were to be used. However, during these preliminary investigations, microscopic tubular structures were found in macerated material of *"E." parva*. This prompted a detailed investigation, the results of which have shown that *"E." parva* should not be assigned to *Eohostimella* Schopf. This has necessitated the erection of a new genus, *Siphonacis* Chesselet 1990, to accommodate this problematic fossil. Morphological details observed in *"E." parva* suggest that individual specimens do not represent the whole organism and cast doubt on the placement of these fossils in the plant kingdom.

GEOLOGICAL SETTING

Lithologically, the Soom Shale Member is a fine-grained, thinly laminated micaceous shale (Cocks *et al.*

1970), which is black when fresh, and rarely exposed (Rust, 1967). It underlies the Disa Member, which constitutes approximately 90% of the Cedarberg Formation and comprises thin-bedded argillaceous dark grey and buff siltstone, fine-grained sandstone and mudstone (Cocks *et al.* 1970).

An age bracket of Upper Ordovician to Lower Silurian (±439 Ma) is estimated for the Soom Shale Member on the basis of invertebrate fossils (Cocks *et al.* 1970) and spore tetrads (Gray *et al.* 1986). The size of spore tetrads described as *Tetrahedraletes* cf. *medinensis*, from the Soom Shale at Swartleikloof, led Gray *et al.* (1986) to suggest an earliest Silurian age, but a late Ordovician age is indicated by chitinozoans from the same locality (Cramer *et al.* 1974). According to Cocks and Fortey (1986) the trilobite *Mucronaspis olini* Temple, from the Soom Shale Member at Buffels Dome in the Hex River Mountains, provides strong evidence for a late Ordovician age for this stratigraphic unit. *Mucronaspis olini* is characteristically of Late Ashgill (Late Rawtheyan or Hirnantian) age and none of the other elements of the fauna contradicts this. In

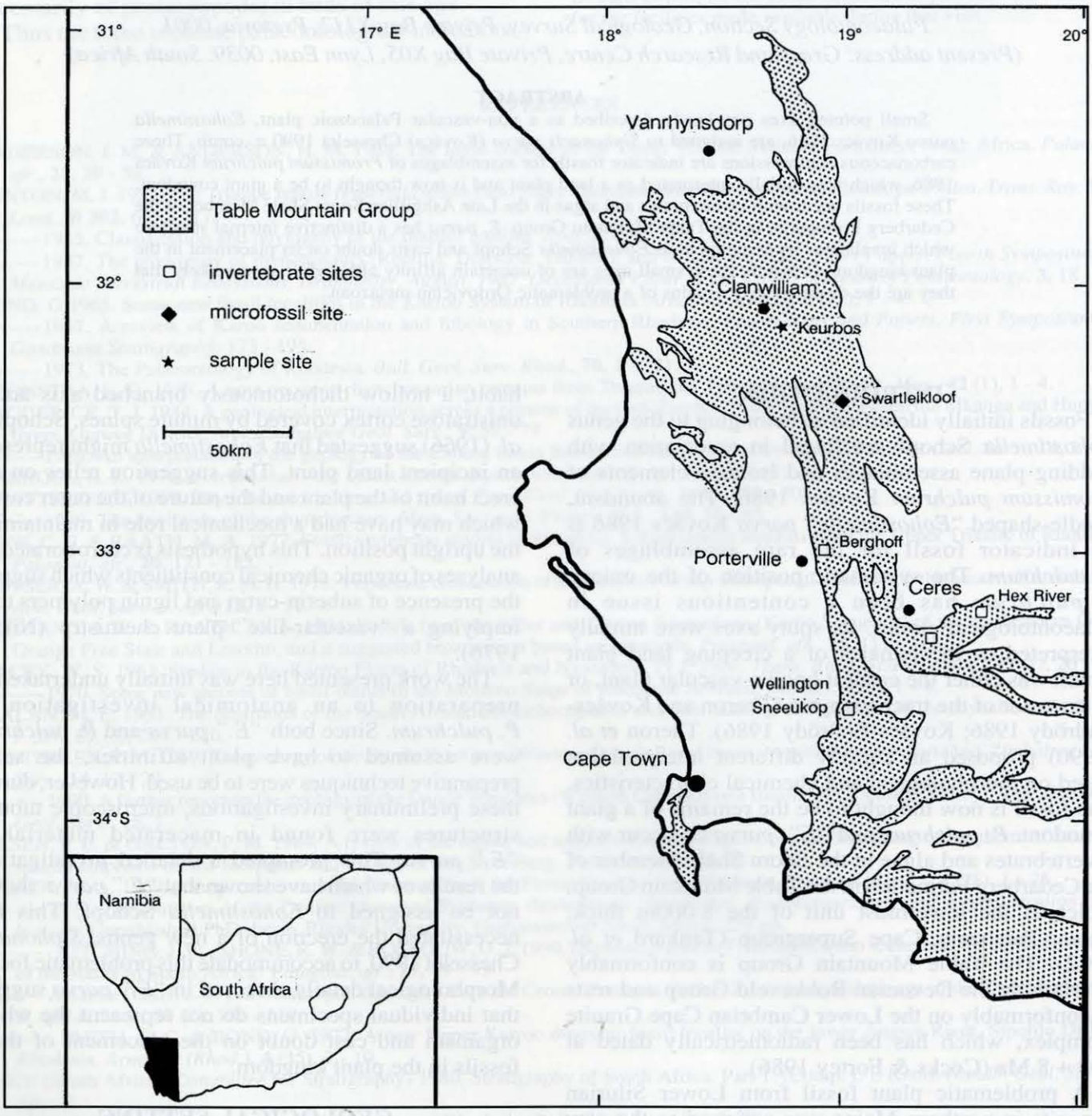

Figure 1. Locality map showing fossil-bearing sites of the Soom Shale Member and the distribution of the Table Mountain Group. (Modified from Theron *et al.* 1990 with permission).

addition, Theron *et al.* (1990) view the late Ordovician age as more likely than the Silurian age for *P. pulchrum*.

The argillaceous sediments of the Cedarberg Formation, in the predominantly arenaceous Table Mountain Group, were deposited during a period of climatic amelioration following the withdrawal of extensive Gondwana ice sheets that were centered in Africa during Ordovician times (Tankard *et al.* 1982). Glaciogenic deposits grade into shales and the presence of varved sediments implies that initial deposition took place in freshwater proglacial lakes (Tankard *et al.* 1982). The varvites are succeeded by fossiliferous sediments in which the absence of varves is attributed by Tankard *et al.* (1982) to sediment mixing and flocculation in brackish or saline water. Gray *et al.* (1986) pointed out that proximity to the sea, and/or marine incursions, is indicated by the presence of chitinozoans and possible marine phytoplankton in

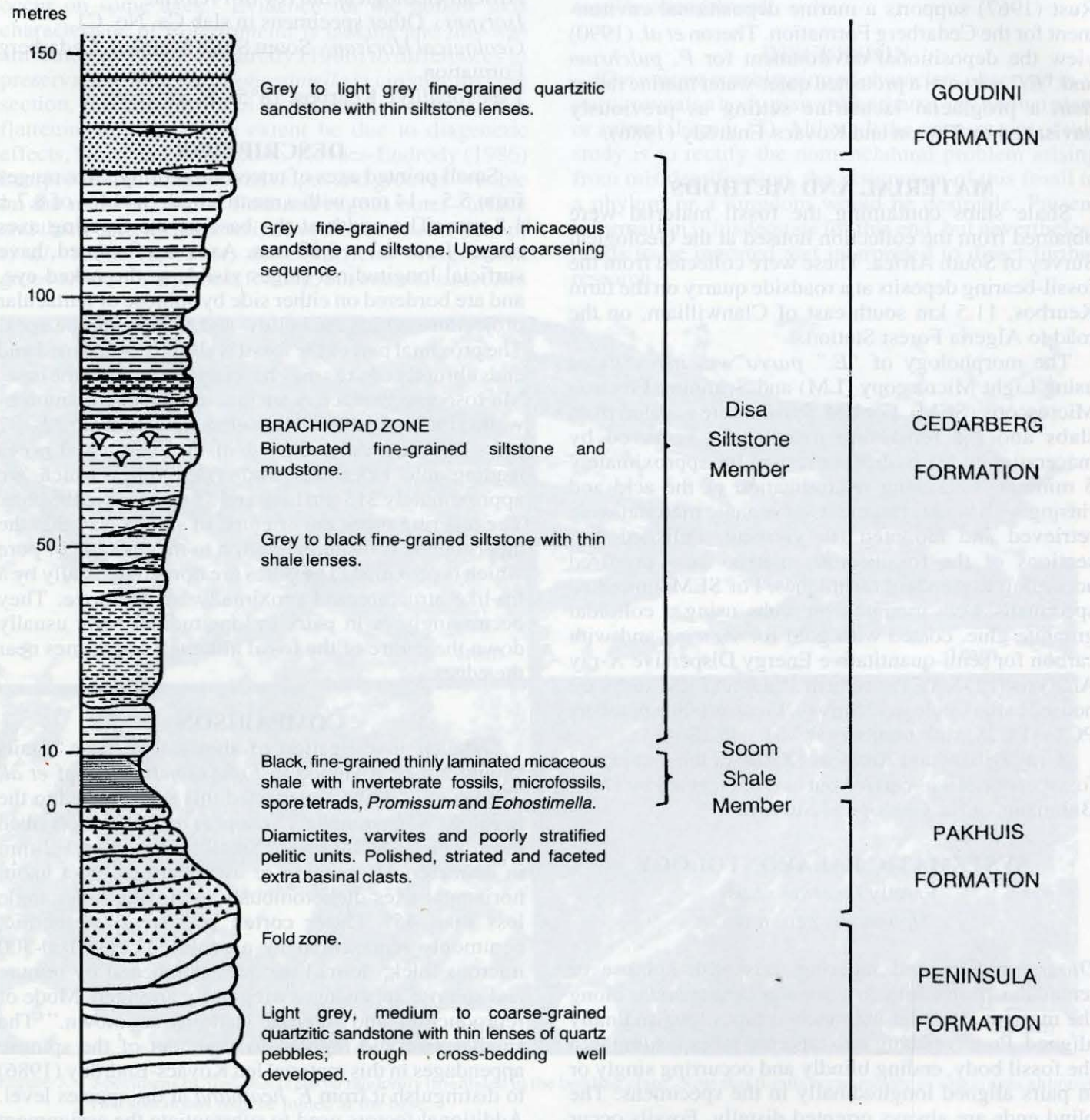

Figure 2. Stratigraphic profile of the Cedarberg Formation. (Modified from Theron *et al.* 1990 with permission).

samples from the Soom Shale Member at Swartleikloof. However, they view the (land plant) spore tetrads, sphaeromorphs and the "absence of normal marine acritarchs" as indicating a possibly "supratidal position during deposition of some of the Soom Shale Member". Trilobites from the base of the Soom Shale Member in the Hex River Mountains (Moore and Marchant, 1981; Cocks and Fortey, 1986) indicate shallow marine conditions. On the basis of lithological evidence as well as the presence of brachiopods in the Disa Member, Rust (1967) supports a marine depositional environment for the Cedarberg Formation. Theron *et al.* (1990) view the depositional environment for *P. pulchrum* and *"E." parva* as a protected quiet-water marine rather than a proglacial lacustrine setting as previously envisaged by Theron and Kovács-Endrödy (1986).

MATERIAL AND METHODS

Shale slabs containing the fossil material were obtained from the collection housed at the Geological Survey of South Africa. These were collected from the fossil-bearing deposits at a roadside quarry on the farm Keurbos, 11.5 km south-east of Clanwilliam, on the road to Algeria Forest Station.

The morphology of *"E." parva* was investigated using Light Microscopy (LM) and Scanning Electron Microscopy (SEM). For LM, fossils were isolated from slabs and the remaining matrix was removed by maceration in 5% hydrofluoric acid for approximately 5 minutes. Following neutralization of the acid and rinsing with water, fragments of organic material were retrieved and mounted for viewing. Polished thin sections of the fossiliferous matrix were prepared according to standard techniques. For SEM, untreated specimens were mounted on stubs using a colloidal graphite glue, coated with gold for viewing and with carbon for semi-quantitative Energy Dispersive X-ray Analysis (EDXA). Permanent slides and EM stubs are housed at the Geological Survey, Pretoria (slide numbers PC1 – PC25, stub numbers PC.S1 – PC.S6).

X-ray Diffraction Analysis (XRD) of the matrix and fossil material was carried out and interpreted by Dr D. Buhmann, at the Geological Survey.

SYSTEMATIC PALAEONTOLOGY

Family *incertae sedis*

Siphonacis gen. nov

Diagnosis Flattened tapering axis with spinose or tentacular projections in a regular arrangement along the margins. Internal unbranched tubes longitudinally aligned. Pores opening into tapering tubes leading into the fossil body, ending blindly and occurring singly or in pairs aligned longitudinally in the specimens. The blind ends are always oriented distally. Fossils occur singly or in pairs in what appears to be an organic connection at the base (or proximal end).

Etymology: *Siphòn* Gr. tube. Refers to the internal structure; *Akis* Gr. a point. Refers to the shape of the fossil.

Siphonacis parva (Kovács) n. comb.

Synonymy. 1986 *Eohostimella parva* Kovács. Kovács-Endrödy (1986) p. 111, pl. 4.1.
Diagnosis: As for genus.
Holotype: C1. V. In the collections of the the South African Geological Survey of Pretoria.
Isotypes: Other specimens in slab Ca. No. C1.
Geological Horizon: Soom Shale Member, Cedarberg Formation.
Type locality: Keurbos, 18°58'E, 32°16'S

DESCRIPTION

Small pointed axes of uncertain affinity. Size ranges from 5.5 – 14 mm with a mean length (n=115) of 8.7 ± 1.8 mm. The width at the base of the tapering axes ranges from 0.3 – 0.08 mm. Axes are flattened, have surficial longitudinal ridges visible to the naked eye, and are bordered on either side by spinose or tentacular projections which are hollow and rounded at the apex. The proximal part of the fossil is slightly broadened and ends abruptly or axes may be joined, in pairs, at the base. Microscopic characters include unbranched, smooth-walled internal tubes of diameters ranging from 22 – 32 µm , longitudinally aligned in the fossil; and pores leading into tapering, blind-ended tubes which are approximately 215 µm long and 35 µm wide at the pore. The tapering tubes are oriented in such a way that the tapering end is distal in relation to the opening or pore which is proximal. The pores are bordered distally by a lip-like structure and proximally by a groove. They occur singly or in pairs in longitudinal rows usually down the centre of the fossil although sometimes near the edges.

COMPARISON

Detailed investigation of shows that these fossils should not be assigned to *Eohostimella* Schopf *et al.* Theron *et al.* (1990) suspected this and referred to the fossil as "*Eohostimella*". Schopf *et al.* (1966) described *Eohostimella* as follows: "Small plants, axes 1-2 mm in diameter, of creeping or ascendant or erect habit, horizontal axes dichotomously branching at an angle less than 45°. Outer cortex persistent, stereomic, commonly represented by a coalified crust 100-300 microns thick; dermal surfaces roughened by minute and spinose appendages irregularly arranged. Mode of reproduction and internal anatomy unknown." The smaller size and regular arrangement of the spinose appendages in this material led Kovács-Endrödy (1986) to distinguish it from *E. heathana* at the species level. Additional factors used to substantiate the assignment of these fossils to *Eohostimella* include the interpretation of superimposed fossils as dichotomously

branched axes and the gradually tapering shape of the fossil. The specific diagnosis for *Eohostimella parva* Kovàcs 1986 p. 112 follows: "Conical axes, 0.5-0.8 mm broad at the base tapering gradually into a long, blunt tip elongated into a point; the axis is more or less 1 cm long. Longitudinal ridges and grooves of different thicknesses and lengths occur on the surface. Minute, spinose appendages in longitudinal rows are confined to one side of the axis. Roundish protuberances of unknown function, at rather regular distances in a row occur on some axes." Evidence for the hollow axis characteristic of *Eohostimella* is lacking and this was attributed by Kovács-Endrödy (1986) to differences in preservation. Whereas *Eohostimella* is circular in cross section, the present fossil is flattened. However, this flattening may to some extent be due to diagenetic effects, burial and compaction. Kovács-Endrödy (1986) interpreted the "longitudinal ridges and grooves" visible on the material as the flattened rugose outer surface and thick cortex characteristic of *Eohostimella* Schopf *et al.* 1966. However, these surficial "ridges and grooves" do not represent folding, but internal structures which have been shown to be smooth-walled tubes and pores leading into tapering tubes. Kovács-Endrödy (1986) noted that the "minute, spinose appendages" are not irregularly arranged as in *Eohostimella* Schopf, nor are they visible on all specimens. Kovács-Endrödy (1986) interprets the uneven distribution of these small spinose structures as their restriction "to one side of the conical axis", rather than to differences in preservation. However, in many specimens the spinose appendages line both edges of the flattened axis in a regular arrangement.

DISCUSSION

The unique combination of characters observed in *S. parva* reveals a body plan unlike that of any known plant or animal (Figure 13). Although the primary aim of this study is to rectify the nomenclatural problem arising from misidentification, the assignment of this fossil to a phylum or a kingdom would be desirable. Present information is inadequate for this end, but nevertheless needs to be reported and interpreted to direct further research.

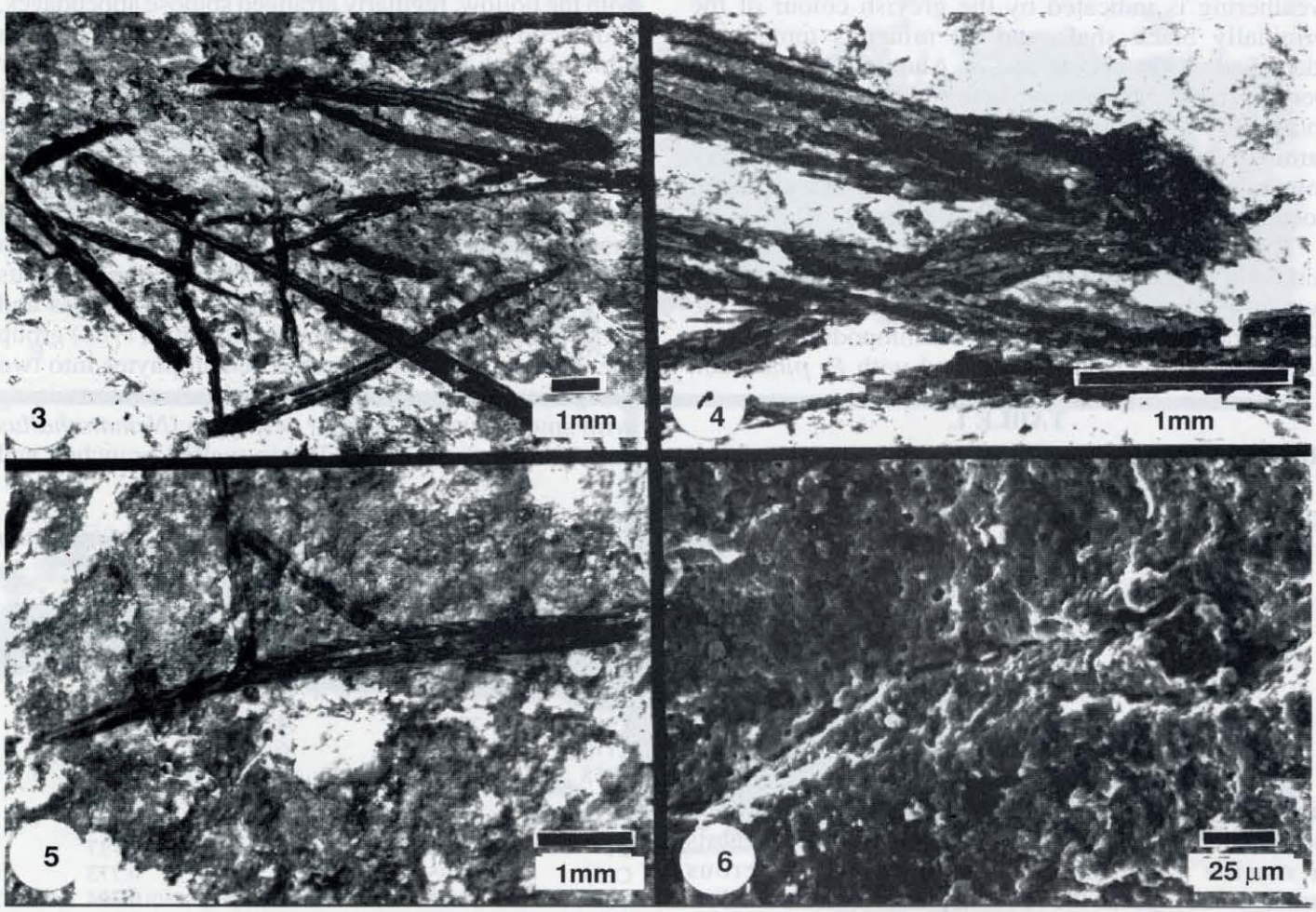

Figure 3. Specimens of *Siphonacis parva* randomly orientated in the bedding plane. Note that fossils occur mostly as single axes although two specimens may be joined at the base.
Figure 4. Two specimens of *Siphonacis parva* which appear to be in organic connection at the base.
Figure 5. A single axis of *Siphonacis parva*. Note minute spinose projections along margin and row of pores in the organic material.
Figure 6. SEM micrograph of pore and tapering tube.

The fossil material is carbonaceous as shown by maceration in hydrofluoric acid. The chemical composition of *S. parva* and the surrounding matrix, as determined by EDXA, is shown in Table 1. The fossil contains higher levels of sulphur than the surrounding matrix (9.9 ± 9.6 for fossil and 3.8 ± 3.3 for matrix) but the high standard deviation indicates some inconsistency in the distribution of sulphur. This sulphur excitation peak is unexplained, but since concomitant higher levels of Fe were not found, the possibility that pyrite may account for the sulphur is excluded. It is also important to note that Theron *et al.* (1990) obtained a sulphur peak in their microprobe analyses of *P. pulchrum* but they did not comment on this result.

X-ray diffraction and petrographic analyses show that the siltstone matrix consists of quartz, muscovite, microcline, an aluminium-rich white mica and two monoclinic micas (polytypes $2M_1$ and 1M), while the fossil contains quartz and mica. The $2M_1$ polytype of mica and the preferred orientation of the shale (F. Hartzer pers. comm.) shows that some metamorphism took place, probably due to deep burial. A degree of weathering is indicated by the greyish colour of the originally black shale and by minerals tentatively identified as Gorceixite and/or Alunite (D. Buhmann pers. comm.). Minor wave action during deposition is indicated by the sometimes disturbed form of the fine laminae in the shale. The accumulation of heavy minerals on bedding planes is indicative of a sediment sorting process (P. Zawada pers. comm.).

The geological context of the Soom Shale Member indicates deposition in an aquatic environment which was probably shallow marine (Theron *et al.* 1990). The association of *S. parva* with brachiopods, trilobites, acritarchs in the Soom Shale and with *P. pulchrum*, unidentified brachiopods, either another conodont or a scolecodonts and a crinoid, at the Keurbos site, suggests a marine environment. In addition, numerous unidentified algae in the bedding planes indicate shallow water, within the photic zone. Furthermore, from the high densities of the fossil in very localized areas of the matrix, their close association with complete conodont assemblages and the relatively quiet depositional environment indicated by preliminary sedimentological observations, it seems likely that the fossils were not transported over large distances. The fossils are randomly orientated in the bedding planes. In slab C.1., which has an area of approximately 190 cm², approximately 150 specimens are preserved together with an assemblage of *P. pulchrum* elements and an unidentified scolecodont or conodont assemblage. Axes also occur singly in some slabs. The range of densities of *S. parva* in the bedding planes is shown in Table 2. Taphonomic studies focusing on the distribution patterns of *S. parva* in the bedding planes would be useful in assessing whether the random orientation of specimens reflects the random dispersion of individuals as would be expected from planktonic life forms, for example, or whether the apparent randomness results from post-mortem disarticulation of a more complex organism.

If the observed morphological details are placed into a functional context, hypotheses regarding the affinities of this enigmatic fossil can be suggested. A small axis bearing a combination of long internal tubes, rows of pores each leading into a blind-ended tube, together with the hollow, regularly arranged spinose appendages, is difficult to interpret functionally as a terrestrial or an aquatic plant. The smooth-walled tubes do not appear to be conducting elements since they do not branch or anastomose. An aquatic plant of such a small size would probably not require vascularization.

An artificial group of plant fossils, the nematophytes, which are grouped on the basis of a structural organization composed of intertwining tubes are known from Silurian (Llandoverian and Wenlockian) deposits (Gray and Boucot 1977; Pratt *et al.* 1978; Niklas and Smocovitis 1983). Niklas and Smocovitis (1983) group the three taxa belonging to the nematophytes into two categories: 1) thin-walled, banded tubes intertwining with smooth-walled tubular cell types (*Nematothallus* and *Nematoplexus*) and; 2) thin-walled branched and

TABLE 1.

Results of EDXA of fossil and matrix showing relative quantities of element oxides (%).

Element Oxides	Sample (n=17) (%)	Matrix (n=6) (%)
MgO	0.607 ± 0.434	0.658 ± 0.483
AlO_3	25.496 ± 5.512	19.312 ± 3.354
SiO_2	51.238 ± 16.168	65.240 ± 7.512
P_2O_5	3.119 ± 1.814	2.315 ± 0.871
SO_3	9.852 ± 9.647	3.767 ± 3.273
K_2O	7.389 ± 1.652	6.612 ± 0.722
CaO	1.575 ± 0.563	1.015 ± 0.125
FeO	0.719 ± 0.221	1.082 ± 0.313

TABLE 2.

Densities (number of specimens per cm²) of *Siphonacis parva* in the bedding planes.

Slab	Area (cm²)	# fossils	number cm-²
C151	-	1	-
C152	-	1	-
C178	49	2	0.041
C260	11.4	2	0.175
C91	20	4	0.200
C119	22.5	6	0.267
C258	42	17	0.405
C251	56	27	0.482
C264	56	38	0.679
C1	190	140	0.737
C259	10.35	8	0.773
C269	31.5	25	0.794
C111	40	39	0.975
C263	4	5	1.250
C262	8	10	1.250
C297	55	78	1.418
C284	60	98	1.633
C111	2	5	2.500

septate tubes intertwined among thicker-walled, large and unbranched tubular elements (*Prototaxites*). In *S. parva* the tubes do not form a plexus, nor are they branched, banded or septate. The possibility that these fossils may be nematophytic is therefore excluded.

If *S. parva* is considered to have animal affinities, what would be the functional implications of the observed morphological details? It seems unlikely that

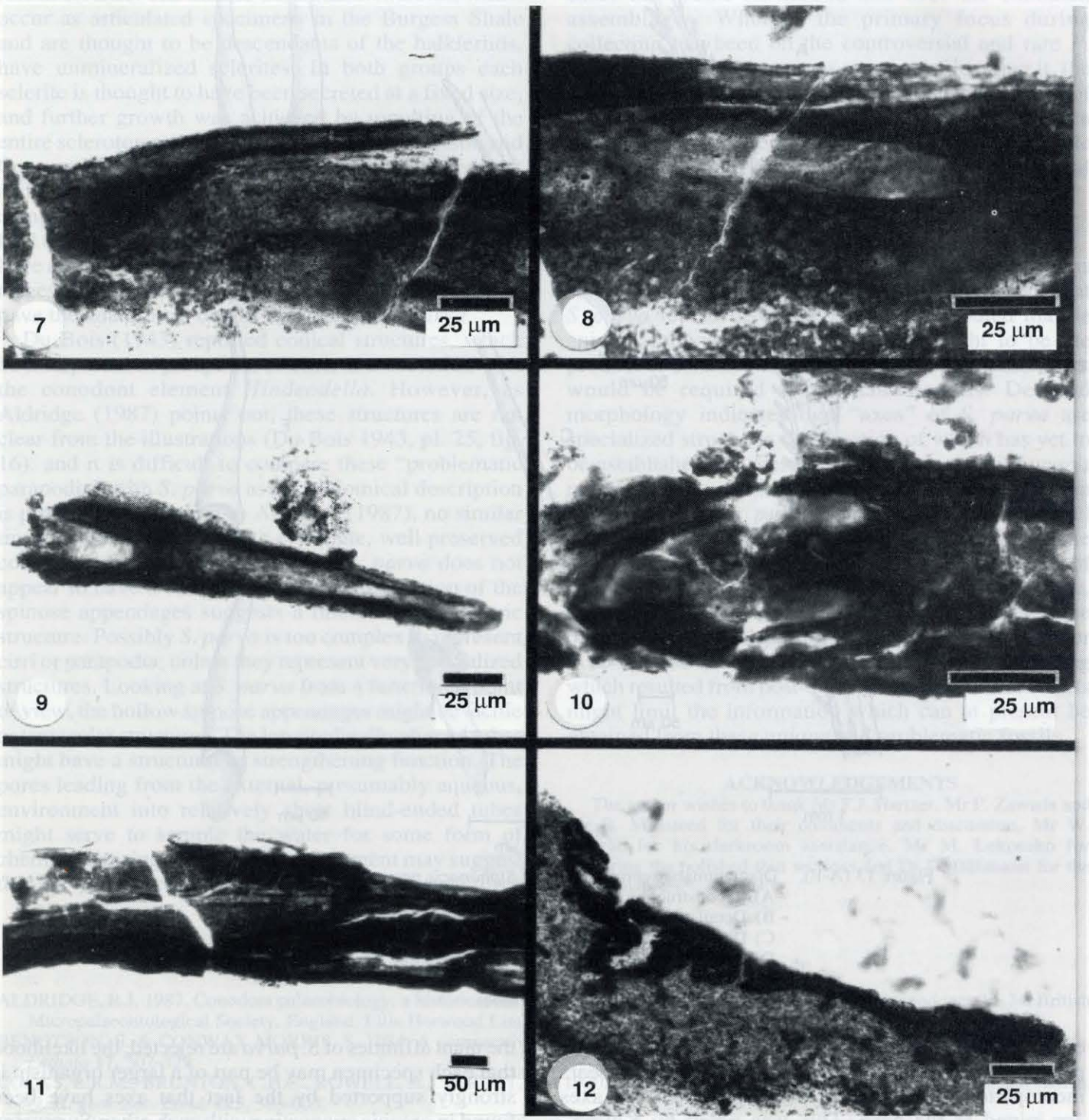

Figure 7. LM micrograph of hollow spinose or tentacular projection at the margin of a macerated fossil.
Figure 8. LM micrograph of spinose projection and lipped pore.
Figure 9. LM micrograph of isolated pore and associated tapering blind-ended tube.
Figure 10. LM micrograph of paired pores and associated tubes. Note groove leading to the pore.
Figure 11. LM micrograph of fragment of macerated carbonaceous material. Note darkened areas showing the positions of smooth-walled internal tubular structures.
Figure 12. LM micrograph of a cross section of *Siphonacis parva*. Note quartz-filled tube and spinose projection.

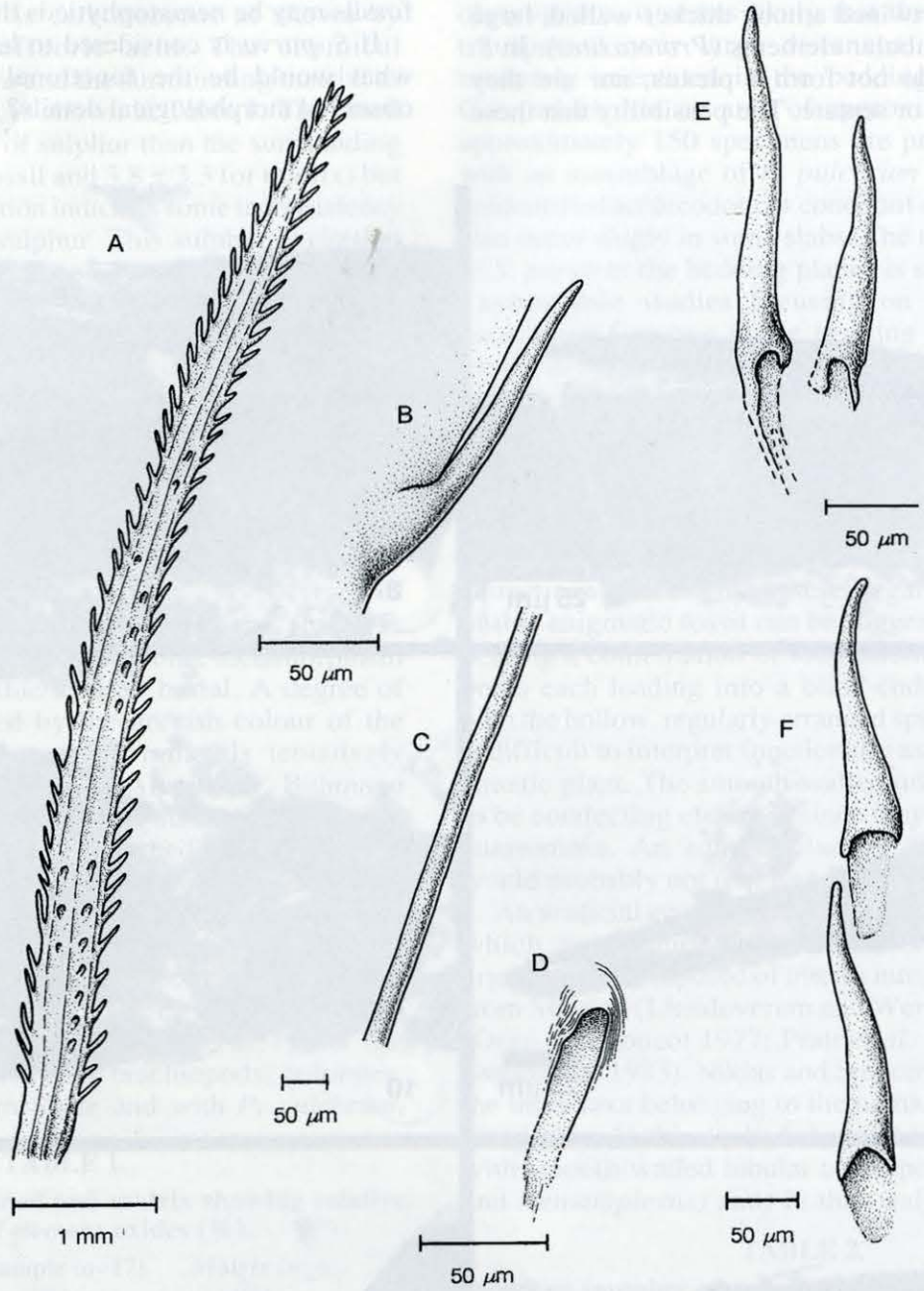

Figure 13 (A-F). Diagrammatic representation of *Siphonacis parva* and structural details.
A) Reconstruction of a whole specimen.
B) Detail of a hollow spinose or tentacular structure.
C) Detail of a smooth-walled tube.
D) Detail of a pore with an elaborate structure on distal side and groove on proximal side.
E) Paired pores and associated tubes.

each specimen represents the whole organism. The proximal end of the fossils, in most cases, appears incomplete and torn; but in a few specimens two axes are joined at the base. This was noted by Kovács-Endrödy (1986) p. 112 who interpreted her observations as follows: "Some of the axes branch dichotomously, and others are attached to one another in such a way that vegetative propagation is indicated. The overwhelming majority of axes without branches might have resulted from the easy separation of branches". If the plant affinities of *S. parva* are rejected, the likelihood that each specimen may be part of a larger organism is strongly supported by the fact that axes have been found in organic connection with each other. Supposing the fossils are disarticulated remains of a larger organism then which part of the hypothetical organism could these fossils be?

A distinctive group of soft-bodied slug-like metazoans is known from the Cambrian Burgess Shale deposits in British Columbia (Conway Morris 1989).

The Lower Cambrian halkieriids are known mainly from disarticulated sclerites composed of calcium carbonate, although articulated specimens are known from Greenland (Conway Morris and Peel 1990). Halkieriid sclerites are thought to have had a primary role in defence. The middle Cambrian wiwaxiids, which occur as articulated specimens in the Burgess Shale and are thought to be descendants of the halkieriids, have unmineralized sclerites. In both groups each sclerite is thought to have been secreted at a fixed size, and further growth was achieved by moulting of the entire sclerotome (Conway Morris 1990; Bengtson and Conway Morris 1984). Whether *S. parva* could represent some form of sclerite is uncertain. The carbonaceous compressions do not contain calcium carbonate (an HCl test showed no reaction). The sclerites of *Wiwaxia* have a "leaf-like" external appearance with longitudinal ridges visible, but it seems unlikely that they would have the anatomical details observed in *S. parva*.

Du Bois (1943) reported conical structures, which he interpreted as parapodia or cirri, in association with the conodont element *Hindeodella*. However, as Aldridge (1987) points out, these structures are not clear from the illustrations (Du Bois 1943, pl. 25, fig. 16), and it is difficult to compare these "problematic parapodia" with *S. parva* as no anatomical description is provided. According to Aldridge (1987), no similar impressions associated with complete, well preserved conodont assemblages are known. *S. parva* does not appear to have a conical shape; the distribution of the spinose appendages suggests a bilaterally symmetric structure. Possibly *S. parva* is too complex to represent cirri or parapodia; unless they represent very specialized structures. Looking at *S. parva* from a functional point of view, the hollow spinose appendages might be tactile or tentacular structures. The longitudinally aligned tubes might have a structural or strengthening function. The pores leading from the external, presumably aqueous, environment into relatively short blind-ended tubes might serve to sample the water for some form of chemical sensing. Such a line of argument may suggest that *S. parva* could represent sensory structures belonging to a soft-bodied animal.

The random orientation of sometimes dense assemblages of *S. parva* contrasts sharply with the often symmetrical arrangement of elements in the bedding plane assemblages of *P. pulchrum*. In some cases the fossils lie around and over the conodont assemblages. Whereas the primary focus during collecting has been on the controversial and rare *P. pulchrum*, using *S. parva* as a means of locating it, the latter has been undercollected and the precise details of their association have not been established. Such data as well as further chemical analyses would be valuable in elucidating the implications of the association of these two fossils.

CONCLUSION

Detailed morphology of *S. parva* indicates that this fossil is not of plant origin and it seems likely that *S. parva* represents remains of a soft-bodied marine animal. Individual specimens are thought to be the product of disarticulation but further taphonomic work would be required to substantiate this. Detailed morphology indicates that "axes" of *S. parva* are specialized structures the function of which has yet to be established. At present the affinities of *Siphonacis parva* are unknown. However, their close association with *Promissum pulchrum*, the similar physical appearance of organic material under LM, some affinities in chemical composition i.e. the presence of a sulphur excitation peak, and their comparable size, suggest that these two fossils could belong to the same organism. This hypothesis would require further investigation and the chemical alteration and flattening which resulted from post-depositional diagenetic effects might limit the information which can at present be obtained from these unique and problematic fossils.

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