

## **of early bryophytes The role of Mid-Palaeozoic mesofossils in the detection**

Dianne Edwards

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The role of Mid-Palaeozoic mesofossils in the **detection of early bryophytes**

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Recently discovered Silurian and Devonian coalified mesofossils provide an additional source of data on Recently discovered Silurian and Devonian coalified mesofossils provide an additional source of data on<br>early embryophytes. Those reviewed in this paper are considered of some relevance to understanding the<br>early history o Recently discovered Silurian and Devonian coalified mesofossils provide an additional source of data on<br>early embryophytes. Those reviewed in this paper are considered of some relevance to understanding the<br>early history o early embryophytes. Those reviewed in this paper are considered of some relevance to understanding the early history of bryophytes while highlighting the difficulties of recognizing bryophytes in often very fragmentary fos early history of bryophytes while highlighting the difficulties of recognizing bryophytes in often very fragmentary fossils. The first group comprises sporophytes in which terminal sporangia contain permanent dyads and tet fragmentary fossils. The first group comprises sporophytes in which terminal sporangia contain<br>permanent dyads and tetrads. Such spores (cryptospores) are similar to those found dispersed in older<br>Ordovician and Silurian s permanent dyads and tetrads. Such spores (cryptospores) are similar to those found dispersed in older<br>Ordovician and Silurian strata, when they are considered evidence for a land vegetation of embryophytes<br>at a bryophyte g Ordovician and Silurian strata, when they are considered evidence for a land vegetation of embryophytes<br>at a bryophyte grade. The phylogenetic significance of plants, where the axes associated with both dyad-<br>and tetrad-co at a bryophyte grade. The phylogenetic significance of plants, where the axes associated with both dyad-<br>and tetrad-containing sporangia are branching, a character state not found in extant bryophytes, is<br>discussed. The se conducting strands include G-type tracheids and a number of novel types of elongate elements not discussed. The second group comprises axial fossils, many with occasional stomata, in which central<br>conducting strands include G-type tracheids and a number of novel types of elongate elements not<br>readily compared with tho conducting strands include G-type tracheids and a number of novel types of elongate elements not<br>readily compared with those of any tracheophyte. They include smooth-walled, evenly thickened elongate<br>elements as well as th readily compared with those of any tracheophyte. They include smooth-walled, evenly thickened elongate<br>elements as well as those with numerous branching  $\pm$  anastomosing projections into the lumen. Some of<br>the latter bea elements as well as those with numerous branching  $\pm$  anastomosing projections into the lumen. Some of<br>the latter bear an additional microporate layer, but the homogenized lateral walls between adjacent cells<br>are never pe the latter bear an additional microporate layer, but the homogenized lateral walls between adjacent cells<br>are never perforate. Such cells, which occur in various combinations in central strands, are compared<br>with the lepto are never perforate. Such cells, which occur in various combinations in central strands, are compared with the leptoids and hydroids of mosses, hydroids of liverworts and presumed water-conducting cells in coeval Lower Dev with the leptoids and hydroids of mosses, hydroids of liverworts and presumed water-conducting cells in coeval Lower Devonian plants such as *Aglaophyton*. It is concluded that lack of information on the chemistry of their coeval Lower Devonian plants such as Aglaophyton. It is concluded that lack of information on the chemistry of their walls hampers sensible assessment of their functions and the affinities of the plants.<br>Finally, a minute fossil, comprising an elongate sporangium in which a central cylindrical cavity<br>containing spores Finally, a minute fossil, comprising an elongate sporangium in which a central cylindrical cavity<br>containing spores and possible elaters terminates in a complex poral dehiscence apparatus, is used to<br>exemplify problems of containing spores and possible elaters terminates in a complex poral dehiscence apparatus, is used to exemplify problems of identifying early bryophytes. It is concluded that further progress necessitates the discovery of exemplify problems of identifying early bryophytes. It is concluded that further progress necessitates the discovery of pre-Upper Silurian fossils with well-preserved anatomy, as well as a re-evaluation of criteria used to

**Keywords:** fossil bryophytes; cryptospores; embryophytes; conducting tissues; phylogeny

### **1. INTRODUCTION**

**The inadequacies of the bryophyte fossil record in eluci-**<br>ating their phylogeny and relationships to tracheophytes THE INTRODUCTION<br>The inadequacies of the bryophyte fossil record in eluci-<br>ating their phylogeny and relationships to tracheophytes<br>relevandary. Its critical reanoraisal has been stimulated The inadequacies of the bryophyte fossil record in eluciting their phylogeny and relationships to tracheophytes relationships that distinctive spaces recorded ating their phylogeny and relationships to tracheophytes<br>re legendary. Its critical reappraisal has been stimulated<br>ecently by suggestions that distinctive spores recorded from Ordovician rocks, which are considered the earliest vidence of land plants, were produced by plants at the om Ordovician rocks, which are considered the earliest<br>vidence of land plants, were produced by plants at the<br>ryophyte grade (Gray 1985; Taylor 1995*a*,*b*, 1997) and by<br>a need to test phylogenetic bypatheses based on clad vidence of land plants, were produced by plants at the ryophyte grade (Gray 1985; Taylor 1995*a*,*b*, 1997) and by<br>the need to test phylogenetic hypotheses based on cladistic<br>abuses of embryophytes (e.g. Mishler *et al.* prophyte grade (Gray 1985; Taylor 1995*a,b*, 1997) and by<br>
a need to test phylogenetic hypotheses based on cladistic<br>
alyses of embryophytes (e.g. Mishler *et al.* 1994). In<br>
a 998 Edwards *et al.* reviewed the record payi 1998, et al. 1999) and the record, paying and the record, paying articular attention to the characters used in such studies The particular attention to the characters used in such studies.<br>
The characters used in such studies.<br>
This paper concentrates on subsequent advances particularly  $\sum_{i=1}^{n}$  and  $\sum_{i=1}^{n}$  articular attention to the characters used in such studies.<br>
This paper concentrates on subsequent advances, particu-<br>
In those involving anatomical and ultrastructural detail articular attention to the characters used in such studies. This paper concentrates on subsequent advances, particu-<br>try those involving anatomical and ultrastructural detail<br>erived from small, coalified fossils predominantly of<br>arly Devonian (Lochkovian) are as an example of the In the involving anatomical and ultrastructural detail<br>
erived from small, coalified fossils predominantly of<br>
larly Devonian (Lochkovian) age as an example of the<br>
otential and frustrations of palaeobotanical contrierived from small, coalified fossils predominantly of<br>
arly Devonian (Lochkovian) age as an example of the<br>
otential and frustrations of palaeobotanical contri-<br>
utions They have been isolated from grey fluvial finearly Devonian (Lochkovian) age as an example of the otential and frustrations of palaeobotanical contri-<br>itions. They have been isolated from grey, fluvial, fine-<br>rained sediments excavated from a stream section north otential and frustrations of palaeobotanical contri-<br>
values. They have been isolated from grey, fluvial, fine-<br>
rained sediments excavated from a stream section north<br>
f Brown Clee Hill Shropshire The mesofossils have If they have been isolated from grey, fluvial, fine-<br>rained sediments excavated from a stream section north<br>f Brown Clee Hill, Shropshire. The mesofossils have<br>lready revealed a ground-bugging vegetation made up rained sediments excavated from a stream section north<br>f Brown Clee Hill, Shropshire. The mesofossils have<br>lready revealed a ground-hugging vegetation made up f Brown Clee Hill, Shropshire. The mesofossils have<br>lready revealed a ground-hugging vegetation made up<br>f plants of diverse affinities in the Late Silurian and<br>arly Devonian (Edwards 1996) They include unequivocal Iready revealed a ground-hugging vegetation made up<br>f plants of diverse affinities in the Late Silurian and<br>larly Devonian (Edwards 1996). They include unequivocal *Phil. Trans. R. Soc. Lond.* B (2000) **355**, 733–755 *733* <sup>755</sup> *733* © 2000 The Royal Society

tracheophytes (e.g. *Cooksonia*; Edwards *et al*. 1992) as well tracheophytes (e.g. *Cooksonia*; Edwards *et al.* 1992) as well<br>as the producers of the spores first recorded in dispersed<br>assemblages in the Ordovician (Wellman *et al.* 1998) tracheophytes (e.g. *Cooksonia*; Edwards *et al.* 1992) as well<br>as the producers of the spores first recorded in dispersed<br>assemblages in the Ordovician (Wellman *et al.* 1998;<br>Edwards *et al.* 1999) The vast majority of t as the producers of the spores first recorded in dispersed<br>assemblages in the Ordovician (Wellman *et al.* 1998;<br>Edwards *et al.* 1999). The vast majority of the mesofossils<br>are axial and sterile. Some bear terminal sporan assemblages in the Ordovician (Wellman *et al.* 1998; Edwards *et al.* 1999). The vast majority of the mesofossils are axial and sterile. Some bear terminal sporangia. Examples of lateral sporangia and axes with enations a Edwards et al. 1999). The vast majority of the mesofossils very rare. Whether or not the sterile axes are all sporo-Examples of lateral sporangia and axes with enations are<br>very rare. Whether or not the sterile axes are all sporo-<br>phytic is uncertain. Many show homoiohydric characters<br>typical of 'nteridonabyte' sporophytes, but in view very rare. Whether or not the sterile axes are all sporophytic is uncertain. Many show homoiohydric characters<br>typical of 'pteridophyte' sporophytes, but in view of<br>similarities in anatomy (e.g. conducting tissues, stomata phytic is uncertain. Many show homoiohydric characters<br>typical of 'pteridophyte' sporophytes, but in view of<br>similarities in anatomy (e.g. conducting tissues, stomata)<br>hetween gametophytes and sporophytes of the Rhynie typical of 'pteridophyte' sporophytes, but in view of<br>similarities in anatomy (e.g. conducting tissues, stomata)<br>between gametophytes and sporophytes of the Rhynie similarities in anatomy (e.g. conducting tissues, stomata)<br>between gametophytes and sporophytes of the Rhynie<br>Chert taxa, *Aglaophyton*, *Nothia* and *Horneophyton*, axial<br>fragments might well derive from gametophytes between gametophytes and sporophytes of the<br>Chert taxa, *Aglaophyton*, *Nothia* and *Horneophytor*<br>fragments might well derive from gametophytes.<br>While these fossils are undoubtedly impornert taxa, Aglaophyton, Nothia and Horneophyton, axial<br>ugments might well derive from gametophytes.<br>While these fossils are undoubtedly important in<br>cumenting past diversity, their value to byvophyte

fragments might well derive from gametophytes.<br>While these fossils are undoubtedly important in<br>documenting past diversity, their value to bryophyte<br>phylogenetic studies especially relating to origins and While these fossils are undoubtedly important in<br>documenting past diversity, their value to bryophyte<br>phylogenetic studies, especially relating to origins and<br>inferred pre-tracheophyte early diversification is somedocumenting past diversity, their value to bryophyte<br>phylogenetic studies, especially relating to origins and<br>inferred pre-tracheophyte early diversification, is some-<br>what limited by their geological age (figure 1). The phylogenetic studies, especially relating to origins and<br>inferred pre-tracheophyte early diversification, is some-<br>what limited by their geological age (figure 1). The inferred pre-tracheophyte early diversification, is somewhat limited by their geological age (figure 1). The Lochkovian examples were formed at a time of major radiations of tracheophytes that occurred some 60 Myr what limited by their geological age (figure 1). The Lochkovian examples were formed at a time of major radiations of tracheophytes that occurred some 60 Myr after the first Ordovician spore records—a time interval Lochkovian examples were formed at a time of major<br>radiations of tracheophytes that occurred some 60 Myr<br>after the first Ordovician spore records—a time interval<br>only 5 Myr shorter than that since the major extinctions radiations of tracheophytes that occurred some 60 Myr<br>after the first Ordovician spore records—a time interval<br>only 5 Myr shorter than that since the major extinctions<br>at the Cretaceous/Tertiary boundary. This fact should only 5 Myr shorter than that since the major extinctions particularly be borne in mind in considering the



5, Trimerophytina.<br>ignificance of the dyad- and tetrad-containing fossils envelope; 3, hilate monads; 4, trilete laevigate monads; 5, ornamented trilete monads; 6, cuticular sheets (cf. *Nematothallus*);<br>sporangial cuticles: 8, stomata: 9, associations of tubes, solid line only indicates presenc Figure 1. Stratigraphic ranges of fossils mentioned in text. 1, permanent (obligate) tetrads  $\pm$  envelope; 2, permanent dyads<br>nvelope; 3, hilate monads; 4, trilete laevigate monads; 5, ornamented trilete monads; 6, cutic nvelope; 3, hilate monads; 4, trilete laevigate monads; 5, ornamented trilete monads; 6, cuticular sheets (cf. *Nematoth*, sporangial cuticles; 8, stomata; 9, associations of tubes, solid line only indicates presence of ba %, sporangial cuticles;<br>1, bifurcating axes of<br>5, Trimerophytina.

eviewed here. The concept that the fossil record shows eviewed here. The concept that the fossil record shows<br>hat the oldest bryophytes were 'contemporaneous with<br>arly vascular plants' (Crandall-Stotler 1986; Frey *et al.*<br>996) will be explored further in this paper. that the oldest bryophytes were 'contemporaly vascular plants' (Crandall-Stotler 1986)<br>1996) will be explored further in this paper. **2.** *IN SITU* **CRYPTOSPORES**

The earliest evidence for the colonization of the land  $\sum_{\text{p}}$  The earliest evidence for the colonization of the land<br>y higher plants (embryophytes) comes from dispersed<br>icrofossil assemblages isolated from Ordovician The earliest evidence for the colonization of the land<br>y higher plants (embryophytes) comes from dispersed<br>icrofossil assemblages isolated from Ordovician<br>Llanvirn) strata (Wellman & Gray this issue) It is in y higher plants (embryophytes) comes from dispersed<br>icrofossil assemblages isolated from Ordovician<br>Llanvirn) strata (Wellman & Gray, this issue). It is in<br>he form of monads and obligate (also termed permanent) icrofossil assemblages isolated from Ordovician Llanvirn) strata (Wellman & Gray, this issue). It is in he form of monads and obligate (also termed permanent) strads and dyads (cryptospores sensu Richardson 1988) Llanvirn) strata (Wellman & Gray, this issue). It is in<br>he form of monads and obligate (also termed permanent)<br>trads and dyads (cryptospores sensu Richardson 1988).<br> $\lambda$  decafossils with *in situ* cryptospores, which migh he form of monads and obligate (also termed permanent)<br>
<sub>c</sub> etrads and dyads (cryptospores sensu Richardson 1988).<br> *Megafossils with in situ* cryptospores, which might be<br>
nticipated on gross morphological and potentially trads and dyads (cryptospores sensu Richardson 1988).<br> *Aegafossils with in situ* cryptospores, which might be nticipated on gross morphological and potentially anato-<br>
aigal grounds to provide more precise evidence of af Legafossils with *in situ* cryptospores, which might be nicipated on gross morphological and potentially anato-<br>ical grounds to provide more precise evidence of affi-<br>ity are first found in the unnermost Silurian and basa nticipated on gross morphological and potentially anato-<br>hical grounds to provide more precise evidence of affi-<br>ity, are first found in the uppermost Silurian and basal Devonian and will be reviewed in some detail here. The resence of polyads in sporangia raises the possibility that

eviewed here. The concept that the fossil record shows trilete or hilate monads before dispersal (see discussion in<br>hat the oldest bryophytes were 'contemporaneous with Edwards et al. 1999). This is difficult to refute whe they are immature, and would have split to become<br>trilete or hilate monads before dispersal (see discussion in they are immature, and would have split to become<br>trilete or hilate monads before dispersal (see discussion in<br>Edwards et al. 1999) This is difficult to refute when such a they are immature, and would have split to become<br>trilete or hilate monads before dispersal (see discussion in<br>Edwards *et al.* 1999). This is difficult to refute when such a<br>limited number of specimens is available for co trilete or hilate monads before dispersal (see discussion in Edwards *et al.* 1999). This is difficult to refute when such a limited number of specimens is available for comparison except that: Edwards *et al.*<br>limited numb<br>except that: (i) almost all the *in situ* taxa can be referred, at least at

- generic level, to the dispersed assemblage at the disp locality; generic level, to the dispersed assemblage at the locality;<br>(ii) with one possible exception (figure 2*j*), transmission<br>electron microscopy (TEM) sections of tetrads do
- (ii) with one possible exception (figure  $2j$ ), transmission<br>electron microscopy (TEM) sections of tetrads do with one possible exception (figure  $2j$ ), transmission<br>electron microscopy (TEM) sections of tetrads do<br>not show the apertural fold that characterizes trilete<br>monads in 'loose' configurations in situ: electron microscopy (TEM) sections of<br>not show the apertural fold that charact<br>monads in 'loose' configurations *in situ*;<br>neither tetrads nor dyads split into not show the apertural fold that characterizes trilete<br>monads in 'loose' configurations *in situ*;<br>(iii) neither tetrads nor dyads split into component<br>elements when they are physically and chemically
- monads in 'loose' configurations *in situ*;<br>neither tetrads nor dyads split into component<br>elements when they are physically and chemically<br>dissociated prior to observation by light microscopy neither tetrads nor dyads split into component<br>elements when they are physically and chemically<br>dissociated prior to observation by light microscopy. elements when they are physically and chemically<br>dissociated prior to observation by light microscopy.<br>In enclosed forms, the persistence of the envelope on

dissociated prior to observation by light incroscopy.<br>In enclosed forms, the persistence of the envelope on<br>dispersal is also conjectural, although even where in TEM<br>sections the layer has a granular and almost discontin-In enclosed forms, the persistence of the envelope on<br>dispersal is also conjectural, although even where in TEM<br>sections the layer has a granular and almost discontin-<br>wous appearance (e.g. figure  $3a$ ) it is remarkably r dispersal is also conjectural, although even where in TEM<br>sections the layer has a granular and almost discontin-<br>uous appearance (e.g. figure 3*g*) it is remarkably resilient

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cale bar = 500 nm. (*k*) Trilayered exospore. Lightest layer to outside. Scale bar =  $100 \text{ nm}$ .<br>*hil. Trans. R. Soc. Lond.* B (2000) <sup>2</sup><br>igure 2. (a–k) North Brown Clee Hill specimens, Shropshire. Lochkovian, Lower Devonian. (a–e,g) SEMs: *Grisellatheca salopensis*.<br>IMW94.76G.1. (a) Entire specimen with bifurcating terminal region. Scale bar = 100 µm. igure 2.  $(a-k)$  North Brown Clee Hill specimens, Shropshire. Lochkovian, Lower Devonian.  $(a-e,g)$  SEMs: *Grisellatheca salopens*<br>
IMW94.76G.1. (*a*) Entire specimen with bifurcating terminal region. Scale bar = 10 µm. (*b*) IMW94.76G.1. (a) Entire specimen with bifurcating terminal region. Scale bar = 100 µm. (b) Surface at bifurcation. Scale<br>ar = 10 µm. (c) In situ tetrad with laevigate surface; ?Cheilotetras. Scale bar = 10 µm. (d) 'Banded  $f_{\text{max}} = 10 \,\mu\text{m}$ . (*c*) In situ tetrad with laevigate surface; ?Cheilotetras. Scale bar = 10 µm. (*d*) 'Banded' tube in fertile region (small<br>from s) and remains of spore tetrad (large arrow). Scale bar = 10 µm. (*e*  $\overrightarrow{O}$  rrows) and remains of spore tetrad (large arrow). Scale bar = 10 µm. (*e*) Longitudinal elements with irregular thickenings<br>
om centre of axis. Scale bar = 10 µm. (*g*) Possible elater. Arrow indicates spore tetr enclosed £attened spore mass. NMW98.23G.3. (*h*) SEM: intact specimen. Arrow indicates possible attachment site. Scale ttached by amorphous material to surface of a *Tortilicaulis* sporangium. NMW96.5G.9. Scale bar = 10  $\mu$ m. (*h*-*k*) ?Cuticle<br>nclosed flattened spore mass. NMW98.23G.3. (*h*) SEM: intact specimen. Arrow indicates possibl nclosed flattened spore mass. NMW98.23G.3. (h) SEM: intact specimen. Arrow indicates possible attachment site. Scale<br>ar = 100 µm. (i) SEM: isolated tetrad. Scale bar = 5 µm. (j,k) TEMs. (j) Part of a tetrad. Arrow indicat ar = 100 µm. (*i*) SEM: isolated tetrad. Scale bar = 5 µm. (*j*,*k*) TEMs. (*j*) Part of a tetrad. A old. Note sections through sporangial covering (top left) are of same optical density as outer cale bar = 500 nm. (*k*)

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**BIOLOGICAL**<br>SCIENCES Figure 3. *In situ* permanent tetrads. (*a*<sup>*-d*</sup>) Discoidal sporangium with *Velatitetras* sp., Ludford Lane, Shropshire. Pridoli, Inner Silurian NMW96 11G 4 (*a*) SEM: intact specimen with non-cellular enclosing layer. P Upper Silurian. NMW96.11G.4. (*a–d* ) Discoidal sporangium with *Velatitetras* sp., Ludford Lane, Shropshire. Pridoli,<br>Jpper Silurian. NMW96.11G.4. (*a*) SEM: intact specimen with non-cellular enclosing layer. Possible att  $\blacktriangleleft$ Jpper Silurian. NMW96.11G.4. (*a*) SEM: intact specimen with non-cellular enclosing layer. Possible attachment at bottom left.<br>cale bar = 100 μm. (*b*) SEM: isolated tetrad with ornamented envelope. Scale bar = 10 μm. ( **ROY** vith faint lamellae, and closely adherent envelope. Arrow indicates position of lumen. Scale bar = 500 nm. (*d*) TEM: sporangial  $\Box$  overing (dark region) and possible remnants of tapetal material. Arrows indicate limits of single spore. Scale bar = 1 µm.<br> $\Box$   $e-g$ ) Axial bifurcating specimen with remnants of terminal sporangium containing *Tetrah* Shropshire. Lochkovian, Lower Devonian. NMW98.23G.2. (*e*) SEM: entire specimen. Arrow indicates sp., North Brown Clee Hill,<br>Shropshire. Lochkovian, Lower Devonian. NMW98.23G.2. (*e*) SEM: entire specimen. Arrow indicates  $\mathcal{L}_{g}$ ) Axial bifurcating specimen with remnants of terminal sporangium containing *Tetrahedraletes* sp., North Brown Clee Hill,<br>
hropshire. Lochkovian, Lower Devonian. NMW98.23G.2. (*e*) SEM: entire specimen. Arrow i PHILOSOPHICAL THE bar **i** hropshire. Lochkovian, Lower Devonian. NMW98.23G.2. (e) SEM: entire specimen. Arrow indicates base of sporangium.<br>
cale bar = 1 mm. (*f*) SEM: *in situ* naked, laevigate, permanent tetrads. Note typical superficia (arrow). Scale bar = 1 mm. (*f*) SEM: *in situ* naked, laevigate, permanent tetrads. Note typical superficial contact lines (arrow). Scale  $\ar = 10 \mu m$ . (*g*) TEM: exospore of two adjacent spores. Note narrow dark layer su  $\sum_{k=1}^{\infty}$  ar = 10 µm. (g) TEM: exospore of two adjacent spores. Note narrow dark layer surrounding each spore, detached in places large arrow). Small arrow indicates lumen. Scale bar = 500 nm. (*h-k*) Fragment with b large arrow). Small arrow indicates lumen. Scale bar = 500 nm. (*h–k*) Fragment with bases of two terminal sporangia. North<br>rown Clee Hill locality. NMW96.11G.3. (*h*) SEM: intact specimen. Scale bar = 100μm. (*i*) SEM: r h) from above. Scale bar = 100  $\mu$ m. (j) SEM: tetrad with granular envelope. Scale bar = 10  $\mu$ m. (k) TEM: poorly preserved Solution physical disruption on extraction and subsequent nitric  $\overline{C}$  physical disruption on extraction and subsequent nitric  $\overline{a}$  is physical disruption on extraction and subsequent nitric cid treatment, such that it appears as a discrete layer in  $\overline{a}$  is the microscopy. Another problem relates to recognition If the physical disruption on extraction and subsequent nitric<br>cid treatment, such that it appears as a discrete layer in<br>ght microscopy. Another problem relates to recognition<br>f a tightly adhering envelope when only scann cid treatment, such that it appears as a discrete layer in<br>ght microscopy. Another problem relates to recognition<br>f a tightly adhering envelope when only scanning<br>lectron microscopy (SEM) studies are possible (e.g. ght microscopy. Another problem relates to recognition  $f$  a tightly adhering envelope when only scanning lectron microscopy (SEM) studies are possible (e.g. *irisellatheca*; figure  $2c$ ).

*lectron* microscopy (SEM) studies are possible (e.g.

## $(a)$  In situ *tetrads*  $\pm$  *envelopes*

(a) In situ *tetrads*  $\pm$  *envelopes*<br>(i) Grisellatheca salopensis *Edwards* et al. *1999* (*figure* 2a-e, g)<br>This single specimen, just 1.54 mm long (*figure* 2*a*) has

(a) In situ *tetrads*  $\pm$  *envelopes*<br>Grisellatheca salopensis *Edwards* et al. 1999 (*figure* 2*a*–e, *g*)<br>This single specimen, just 1.54 mm long (figure 2*a*), has<br>bifurcating terminal sporing region with a distinctiv (i) Grisellatheca salopensis *Edwards* et al. 1999 (*figure* 2a-e, g)<br>This single specimen, just 1.54 mm long (figure 2a), has<br>a bifurcating terminal sporing region with a distinctive,<br>superficial diamond-shaned pattern, This single specimen, just 1.54 mm long (figure 2*a*), has<br>a bifurcating terminal sporing region with a distinctive,<br>superficial diamond-shaped pattern, the only part of the<br>axial structure in which cells are apparent (fi a bifurcating terminal sporing region with a distinctive, superficial diamond-shaped pattern, the only part of the axial structure in which cells are apparent (figure 2*b*).

The unbranched, non-fertile, axial tissues appear dis-The unbranched, non-fertile, axial tissues appear dis-<br>rganized and are now thought to be highly decayed<br> $p_1$  as evidenced by the 'crater'-like eruptions and The unbranched, non-fertile, axial tissues appear dis-<br>rganized and are now thought to be highly decayed<br>p.19) as evidenced by the 'crater'-like eruptions and<br>panded' tubes (figure  $2d f$ ) (Edwards & Richardson rganized and are now thought to be highly decayed<br>p.19) as evidenced by the 'crater'-like eruptions and<br>panded' tubes (figure  $2d_x f$ ) (Edwards & Richardson<br>000) Some longitudinal 'cells' have irregular transverse p.19) as evidenced by the 'crater'-like eruptions and panded' tubes (figure  $2d_x f$ ) (Edwards & Richardson 000). Some longitudinal 'cells' have irregular transverse utgrowths (figure  $2e$ ). Henstic features include the panded' tubes (figure  $2d_x f$ ) (Edwards & Richardson 000). Some longitudinal 'cells' have irregular transverse utgrowths (figure  $2e$ ). Hepatic features include the evigate permanent tetrads and one putative elater 000). Some longitudinal 'cells' have irregular transverse<br>utgrowths (figure 2e). Hepatic features include the<br>ievigate permanent tetrads and one putative elater<br>figures  $2e/a$ ). The latter is a stran-shaned structure utgrowths (figure 2*e*). Hepatic features include the revigate permanent tetrads and one putative elater figures  $2c$ ,*g*). The latter is a strap-shaped structure also aversing the sporting region. It hears superficial tevigate permanent tetrads and one putative elater<br>figures  $2c, g$ ). The latter is a strap-shaped structure<br>aversing the sporing region. It bears superficial<br>dentations forming a herringbone pattern While it is figures  $2c, g$ ). The latter is a strap-shaped structure<br>
aversing the sporing region. It bears superficial<br>
identations forming a herringbone pattern. While it is<br>
ossible that the asymmetric nature of the axis reflects a as aversing the sporing region. It bears superficial<br>dentations forming a herringbone pattern. While it is<br>ossible that the asymmetric nature of the axis reflects a<br>prizontal asymmetrophytic structure with possibly ndentations forming a herringbone pattern. While it is<br>ossible that the asymmetric nature of the axis reflects a<br>orizontal ?gametophytic structure with possibly  $\blacktriangleright$  mbedded sporangia of riccialean type, it is also possible orizontal ?gametophytic structure with possibly<br>
imbedded sporangia of riccialean type, it is also possible<br>
inta it results from incomplete preservation of an erect<br>
decorability at terminal bifurcating sporangium Most Imbedded sporangia of riccialean type, it is also possible<br>Fat it results from incomplete preservation of an erect<br>Forophyte with a terminal bifurcating sporangium. Most<br>Fixes at the locality however fragmentary and degrad A stat it results from incomplete preservation of an erect<br>
a corophyte with a terminal bifurcating sporangium. Most<br>
a stat the locality, however fragmentary and degraded,<br>
a completely surrounded by enidermis or stereome Approphyte with a terminal bifurcating sporangium. Most<br>  $\frac{1}{1}$  xes at the locality, however fragmentary and degraded,<br>  $\frac{1}{1}$  re completely surrounded by epidermis or stereome, s at the locality, however fragmentary and dependence in the tetrad-containing plant.<br>The tetrads themselves have a laevigate surface. e completely surrounded by epidermis or stereome,<br>tures not seen in the tetrad-containing plant.<br>The tetrads themselves have a laevigate surface with<br>mplete continuity, between, adjacent, elements, but

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external containing plant.<br>
The tetrads themselves have a laevigate surface with<br>
omplete continuity between adjacent elements, but<br>
crause they have been examined only by SEM it is The tetrads themselves have a laevigate surface with<br>omplete continuity between adjacent elements, but<br>ecause they have been examined only by SEM, it is<br>mossible to determine whether or not they possess a omplete continuity between adjacent elements, but<br>ecause they have been examined only by SEM, it is<br>mpossible to determine whether or not they possess a<br>losely adhering envelope (and hence belong to ecause they have been examined only by SEM, it is<br>npossible to determine whether or not they possess a<br>losely adhering envelope (and hence belong to mpossible to determine whether or not they possess a<br>losely adhering envelope (and hence belong to<br>*z*<sup>*i*</sup>*datitetras*) or are naked and fused (i.e. without obvious<br>ture and belong to *Cheilatetras*). They are not unlike losely adhering envelope (and hence belong to *Cheilotetras*) or are naked and fused (i.e. without obvious ture and belong to *Cheilotetras*). They are not unlike the strads described in the new fertile specimen (p. 19. *datitetras*) or are naked and fused (i.e. without obvious<br>iture and belong to *Cheilotetras*). They are not unlike the<br>strads described in the new fertile specimen (p.19;<br>gure  $10i-n$ ) although the latter spores show spli ture and belong to *Cheilotetras*). They are not unlike the strads described in the new fertile specimen (p.19; gure  $10j-n$ ) although the latter spores show splits etween the elements extrads described in t<br>gure  $10j-n$  although<br>etween the elements.<br>Sutures are also visil ure  $10j-n$  although the latter spores show splits<br>tween the elements.<br>Sutures are also visible on the laevigate tetrads in a<br>cond bifurcating specimen (figure  $3e-n$ : Edwards *et al.* 

cond bifurcating specimen (figure  $3e-g$ ; Edwards *et al.* 999). They are placed in *Tetrahedraletes medinensis*, a taxon lso found in the earliest Ordovician assemblages. The pores occur in a cun-shaned depression with an 999). They are placed in *Tetrahedraletes medinensis*, a taxon lso found in the earliest Ordovician assemblages. The pores occur in a cup-shaped depression with an irregular parties which is assumed to be part of a sporan lso found in the earliest Ordovician assemblages. The<br>pores occur in a cup-shaped depression with an irregular<br>nargin, which is assumed to be part of a sporangium<br>sympating a naked axis with irregular longitudinal pores occur in a cup-shaped depression with an irregular hargin, which is assumed to be part of a sporangium erminating a naked axis with irregular, longitudinal, argin, which is assumed to be part of a sporangium<br>erminating a naked axis with irregular, longitudinal,<br>uperficial ridges reminiscent of the shrivelled epidermal<br>ells of a rhynionhytoid or tracheophyte. These cells experimenting a naked axis with irregular, longitudinal, uperficial ridges reminiscent of the shrivelled epidermal<br>ells of a rhyniophytoid or tracheophyte. These cells<br>ecome almost square in the vicinity of the spores wher aperficial ridges reminiscent of the shrivelled epidermal<br>ells of a rhyniophytoid or tracheophyte. These cells<br>ecome almost square in the vicinity of the spores, where<br>e sporangial wall itself is many layered. No further ells of a rhyniophytoid or tracheophyte. These cells<br>ecome almost square in the vicinity of the spores, where<br>ne sporangial wall itself is many layered. No further<br>natomical detail was observed ecome almost square in the vicin<br>
are sporangial wall itself is ma<br>
natomical detail was observed.<br>
Two specimens of contrasting Exporangial wall itself is many layered. No further<br>atomical detail was observed.<br>Two specimens of contrasting morphologies and ages<br>ntain unequivocal envelope-enclosed dyads that are

natomical detail was observed.<br>Two specimens of contrasting morphologies and ages<br>ontain unequivocal envelope-enclosed dyads that are<br>signed to Velatitetras (Edwards et al. 1999). In both, the Two specimens of contrasting morphologies and ages<br>ontain unequivocal envelope-enclosed dyads that are<br>signed to *Velatitetras* (Edwards *et al.* 1999). In both, the<br>nucleon is commented The Lockbovian one commises a ontain unequivocal envelope-enclosed dyads that are<br>signed to *Velatitetras* (Edwards *et al.* 1999). In both, the<br>nuclope is ornamented. The Lochkovian one comprises a<br>aked forking axis in which each daughter branch ends signed to *Velatitetras* (Edwards *et al.* 1999). In both, the nyclope is ornamented. The Lochkovian one comprises a aked, forking axis in which each daughter branch ends a generatory sportancium whose smooth surface with Invelope is ornamented. The Lochkovian one comprises a<br>aked, forking axis in which each daughter branch ends<br>at a fragmentary sporangium, whose smooth surface with<br>utlines of enidermal cells contrasts markedly with the 1 a fragmentary sporangium, whose smooth surface with utlines of epidermal cells contrasts markedly with the a fragmentary sporangium, whose smooth surface with<br>utlines of epidermal cells contrasts markedly with the<br>prinkled contours of the axis (figure  $3h-k$ ). Further<br>natomical detail is not preserved. The second example utlines of epidermal cells contrasts markedly with the rinkled contours of the axis (figure  $3h-k$ ). Further natomical detail is not preserved. The second example, Trinkled contours of the axis (figure  $3h-k$ ). Further<br>natomical detail is not preserved. The second example,<br>) nlike the majority of fossils described here, is of late<br>silurian are and was recovered from marginal marine In atomical detail is not preserved. The second example,<br>Unlike the majority of fossils described here, is of late<br>ilurian age and was recovered from marginal marine The parameter of fossils described here, is of late<br>increase and was recovered from marginal marine<br>pacies near Ludlow (figure  $3a-d$ ). It comprises a disc-<br>comprises a disc-<br>comprise the mass encased in a non-cellular hom ilurian age and was recovered from marginal marine<br>acies near Ludlow (figure  $3a-d$ ). It comprises a disc-<br>aped spore mass encased in a non-cellular homoge-<br>equivalent sports of the sport of the sports of the cies near Ludlow (figure  $3a-d$ ). It comprises a disc-<br>happed spore mass encased in a non-cellular homoge-<br>eous layer. SEMs show deep invagination of the<br>nucleon between constituent spores and where it has aped spore mass encased in a non-cellular homoge-<br>eous layer. SEMs show deep invagination of the<br>nvelope between constituent spores and, where it has<br>integrated in this region lagyigate spores beneath eous layer. SEMs show deep invagination of the nyclope between constituent spores and, where it has isintegrated in this region, laevigate spores beneath. FMs of the two kinds of *Velatitetras* suggest that they are nvelope between constituent spores and, where it has<br>isintegrated in this region, laevigate spores beneath.<br>TEMs of the two kinds of *Velatitetras* suggest that they are<br>out closely related. Although in both the exospore i is<br>integrated in this region, laevigate spores beneath.<br>  $\sum_{n=1}^{\infty}$  EMs of the two kinds of *Velatitetras* suggest that they are<br>  $\log$  ot closely related. Although in both the exospore is<br>  $\log$ <br>  $\log$ EMs of the two kinds of *Velatitetras* suggest that they are<br>  $\overline{S}$  ot closely related. Although in both the exospore is<br>
ngle-layered, in the Silurian spores there are traces of<br>
nellation following the spore contours or closely related. Although in both the exospore is ngle-layered, in the Silurian spores there are traces of unellation following the spore contours (figure  $3c$ ) but as vounger ones have a granular exospore (figure  $3k$ ngle-layered, in the Silurian spores there are traces of unellation following the spore contours (figure  $3c$ ) but ne younger ones have a granular exospore (figure  $3k$ ). In imellation following the spore contours (figure  $3c$ ) but<br>ne younger ones have a granular exospore (figure  $3k$ ). In<br>ne latter, the envelope is more electron-dense and tightly<br>dhering its ernament low and irregular. The e are younger ones have a granular exospore (figure 3*k*). In<br>ne latter, the envelope is more electron-dense and tightly<br>dhering, its ornament low and irregular. The ornament dhering, its ornament low and irregular. The ornament *hil. Trans. R. Soc. Lond*. B (2000)

of the Silurian envelope is far more pronounced, its<br>indentations extending almost to the surface of the<br>exospore Again it is closely adherent Towards the outside of the Silurian envelope is far more pronounced, its<br>indentations extending almost to the surface of the<br>exospore. Again it is closely adherent. Towards the outside<br>of the spore mass, the envelope is continuous with the indentations extending almost to the surface of the exospore. Again it is closely adherent. Towards the outside of the spore mass, the envelope is continuous with the innermost layers of the sporangial wall, suggestive of exospore. Again it is closely adherent. Towards the outside<br>of the spore mass, the envelope is continuous with the<br>innermost layers of the sporangial wall, suggestive of<br>involvement of a tanetal layer (forme  $3d$ ) of the spore mass, the envelope is continuous with the innermost layers of the sporangial wall, suggestive of involvement of a tapetal layer (figure  $3d$ ). In the sport of the sport of the space of volvement of a tapetal layer (figure  $3d$ ).<br>In the final example (figure  $2h-k$ ; Edwards *et al.* 1999), vurtesport relationships are less clear-cut. The speciment

section bifurcating specimen (figure 3*e*–g; Edwards *in a* include a middle, lamellated layer (two to three lamellae) cond bifurcating specimen (figure 3*e*–g; Edwards *et al.* 1999). They are placed in *Tetrahedraletes m* In the final example (figure  $2h-k$ ; Edwards *et al.* 1999), cryptospore relationships are less clear-cut. The specimen In the final example (figure  $2h-k$ ; Edwards *et al.* 1999), cryptospore relationships are less clear-cut. The specimen is a discoidal spore mass surrounded by a layer of cuticle, in which puckering to the centre of one su cryptospore relationships are less clear-cut. The specimen<br>is a discoidal spore mass surrounded by a layer of cuticle,<br>in which puckering to the centre of one surface suggests<br>attachment to an axis (figure  $2h$ ). The spor is a discoidal spore mass surrounded by a layer of cuticle,<br>in which puckering to the centre of one surface suggests<br>attachment to an axis (figure  $2h$ ). The spores are in<br>tetrads with propounced invariantions between the in which puckering to the centre of one surface suggests<br>attachment to an axis (figure  $2h$ ). The spores are in<br>tetrads with pronounced invaginations between the units<br>(figure  $2i$ ). Distal surfaces are invaginated. They attachment to an axis (figure  $2h$ ). The spores are in tetrads with pronounced invaginations between the units<br>(figure 2*i*). Distal surfaces are invaginated. They are<br>laevigate or bear fairly evenly spaced but irregularly<br>shaned outgrowths. Spore walls are tri-layered with ea (figure 2*i*). Distal surfaces are invaginated. They are laevigate or bear fairly evenly spaced but irregularly shaped outgrowths. Spore walls are tri-layered with each layer (distinguished by differing electron opacity) laevigate or bear fairly evenly spaced but irregularly<br>shaped outgrowths. Spore walls are tri-layered with each<br>layer (distinguished by differing electron opacity)<br>completely surrounding individual spores (figure  $2i k$ ) shaped outgrowths. Spore walls are tri-layered with each layer (distinguished by differing electron opacity) completely surrounding individual spores (figure  $2j, k$ ). layer (distinguished by differing electron opacity)<br>completely surrounding individual spores (figure  $2j,k$ ).<br>There is a distinct thickening, particularly of the middle<br>layer in the vicinity of the equator and a possible a completely surrounding individual spores (figure  $2j,k$ ).<br>There is a distinct thickening, particularly of the middle layer, in the vicinity of the equator and a possible aper-<br>tural fold at the 'iunctions' of proximal pole There is a distinct thickening, particularly of the middle<br>layer, in the vicinity of the equator and a possible aper-<br>tural fold at the 'junctions' of proximal poles (figure 2*j*).<br>The latter is a characteristic of trilete layer, in the vicinity of the equator and a possible aper-<br>tural fold at the 'junctions' of proximal poles (figure 2*j*).<br>The latter is a characteristic of trilete spores. This feature<br>and the more ready separation of the tural fold at the 'junctions' of proximal poles (figure 2*j*).<br>The latter is a characteristic of trilete spores. This feature<br>and the more ready separation of the tetrad individuals<br>when prepared for TEM and light microsc The latter is a characteristic of trilete spores. This feature<br>and the more ready separation of the tetrad individuals<br>when prepared for TEM and light microscopy (LM) mitiand the more ready separation of the tetrad individuals<br>when prepared for TEM and light microscopy (LM) miti-<br>gate against affinity with cryptospores. However, tri-<br>radiate marks were not apparent in LM Similar exospore when prepared for TEM and light microscopy (LM) mitigate against affinity with cryptospores. However, tri-<br>radiate marks were not apparent in LM. Similar exospore<br>ultrastructure is not seen elsewhere. Three layers reported gate against affinity with cryptospores. However, tri-<br>radiate marks were not apparent in LM. Similar exospore<br>ultrastructure is not seen elsewhere. Three layers reported<br>on the distal exposed surfaces of the Late Ordovici radiate marks were not apparent in LM. Similar exospore<br>ultrastructure is not seen elsewhere. Three layers reported<br>on the distal exposed surfaces of the Late Ordovician/ ultrastructure is not seen elsewhere. Three layers reported<br>on the distal exposed surfaces of the Late Ordovician/<br>Early Silurian dyad *Dyadospora murusattenuata* (type 1)<br>include a middle lamellated layer (two to three la on the distal exposed surfaces of the Late Ordovician/<br>Early Silurian dyad *Dyadospora murusattenuata* (type 1)<br>include a middle, lamellated layer (two to three lamellae)<br>and an inner spiny one and thus are not comparable Early Silurian dyad *Dyadospora murusattenuata* (type 1) include a middle, lamellated layer (two to three lamellae) and an inner spiny one, and thus are not comparable with the ultrastructure in the tetrads here, where tri include a middle, lamellated layer (two to three lamellae)<br>and an inner spiny one, and thus are not comparable with<br>the ultrastructure in the tetrads here, where tri-layering<br>extends around each spore (Taylor 1997) extends around each spore (Taylor 1997). e ultrastructure in the tetrads here, where tri-layering<br>tends around each spore (Taylor 1997).<br>Diversity in ultrastructure also characterizes masses of<br>pooth-walled, naked tetrads recovered from the matrix

smooth-walled, naked tetrads recovered from the matrix. Particularly complex are naked tetrads similar to smooth-walled, naked tetrads recovered from the matrix.<br>
Particularly complex are naked tetrads similar to<br> *Tetrahedraletes*, in which individual monads show some<br>
senaration. The outer third of the exospore is homoge-Particularly complex are naked tetrads similar to<br>*Tetrahedraletes*, in which individual monads show some<br>separation. The outer third of the exospore is homoge-<br>neous the remainder is made un of granules or lamellae *Tetrahedraletes*, in which individual monads show some separation. The outer third of the exospore is homogeneous, the remainder is made up of granules or lamellae (Edwards et al. 1999 first 105–106–113) separation. The outer third of the exospore is homogeneous, the remainder is made up of granules or lamellae (Edwards *et al.* 1999, figs 105, 106, 113).

### **(b) In situ** *dyads*

In one case only, an unbranched axis, 1.2 mm long, is (b) In situ *dyads*<br>In one case only, an unbranched axis, 1.2 mm long, is<br>terminated by a well-defined, beaker-shaped sporangium<br>with intact truncated anex (figures  $4d \ell$ ) Cullulitheca In one case only, an unbranched axis,  $1.2 \text{ mm}$  long, is<br>terminated by a well-defined, beaker-shaped sporangium<br>with intact truncated apex (figures  $4d,e$ ). *Cullulitheca*<br>richardsonii has naked laevigate dyads with a pro *reminated by a well-defined, beaker-shaped sporangium*<br>with intact truncated apex (figures  $4d,e$ ). *Cullulitheca*<br>*richardsonii* has naked laevigate dyads with a pronounced<br>suture and invarianted distal surfaces (figures with intact truncated apex (figures  $4d,e$ ). *Cullulitheca*<br>*richardsonii* has naked laevigate dyads with a pronounced<br>suture and invaginated distal surfaces (figures  $4f,g$ ;<br>Wellman *et al* 1998) enclosed in a sporannium w *richardsonii* has naked laevigate dyads with a pronounced<br>suture and invaginated distal surfaces (figures  $4f,g$ ;<br>Wellman *et al.* 1998) enclosed in a sporangium wall<br>showing no cellular detail. The axis itself has a super suture and invaginated distal surfaces (figures  $4f,g$ ;<br>Wellman *et al.* 1998) enclosed in a sporangium wall<br>showing no cellular detail. The axis itself has a super-<br>ficial shrivelled annearance and also lacks any indicati Wellman *et al.* 1998) enclosed in a sporangium wall showing no cellular detail. The axis itself has a superficial, shrivelled appearance and also lacks any indication of cells. The exospore is homogeneous with no evidenc showing no cellular detail. The axis itself has a super-<br>ficial, shrivelled appearance and also lacks any indication<br>of cells. The exospore is homogeneous, with no evidence<br>of any envelope (figure  $4h$ ) Such spores were a ficial, shrivelled appearance and also lacks any indication<br>of cells. The exospore is homogeneous, with no evidence<br>of any envelope (figure 4*h*). Such spores were assigned to<br>*Duadoshara murudenca* Strother & Traverse eme of cells. The exospore is homogeneous, with no evidence<br>of any envelope (figure 4*h*). Such spores were assigned to<br>*Dyadospora murusdensa* Strother & Traverse emend Burgess<br>& Richardson (1991), although the latter only ra of any envelope (figure 4*h*). Such spores were assigned to *Dyadospora murusdensa* Strother & Traverse emend Burgess & Richardson (1991), although the latter only rarely have distally invaginated surfaces. In contrast a s Dyadospora murusdensa Strother & Traverse emend Burgess<br>& Richardson (1991), although the latter only rarely have<br>distally invaginated surfaces. In contrast a second dyad-<br>containing speciment Eusitheca, fanningiae (figure & Richardson (1991), although the latter only rarely have<br>distally invaginated surfaces. In contrast a second dyad-<br>containing specimen, *Fusitheca fanningiae* (figure 4*i*,*j*;<br>Wellman et al. 1998) has a fusiform terminal distally invaginated surfaces. In contrast a second dyadcontaining specimen, *Fusitheca fanningiae* (figure 4*i,j*; Wellman *et al.* 1998) has a fusiform terminal sporangium at the tip of one branch of an isotomously branc containing specimen, *Fusitheca fanningiae* (figure  $4i,j$ ;<br>Wellman *et al.* 1998) has a fusiform terminal sporangium<br>at the tip of one branch of an isotomously branching<br>naked system (figure  $4i$ ) and the dyads themselves Wellman *et al.* 1998) has a fusiform terminal sporangium<br>at the tip of one branch of an isotomously branching<br>naked system (figure  $4i$ ), and the dyads themselves,<br>although distally invarianted have a closely adherent at the tip of one branch of an isotomously branching<br>naked system (figure  $4i$ ), and the dyads themselves,<br>although distally invaginated, have a closely adherent,<br>thin envelope (figure  $4i$ ) TEM studies reveal a homonaked system (figure  $4i$ ), and the dyads themselves,<br>although distally invaginated, have a closely adherent,<br>thin envelope (figure  $4j$ ). TEM studies reveal a homo-<br>geneous exospore Individual cells could not be seen on although distally invaginated, have a closely adherent, thin envelope (figure  $4j$ ). TEM studies reveal a homogeneous exospore. Individual cells could not be seen on thin envelope (figure  $4j$ ). TEM studies reveal a homogeneous exospore. Individual cells could not be seen on the wrinkled surface of the axis, although the fractured end showed a reticulum of homogenized walls surroundin the wrinkled surface of the axis, although the fractured



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regularly shaped lumina and a central irregular homoregularly shaped lumina and a central irregular homo-<br>enized area. The sporangial wall appears to be single-<br>wered, comprising tubular to spindle-shaped cells with regularly shaped lumina and a central irregular homo-<br>enized area. The sporangial wall appears to be single-<br>ayered, comprising tubular to spindle-shaped cells with<br>niformly thickened lateral walls and some irregular bars enized area. The sporangial wall appears to be single-<br>uyered, comprising tubular to spindle-shaped cells with<br>niformly thickened lateral walls and some irregular bars<br>rossing the lumen. The walls lining the sporangial cav ity a comprising tubular to spindle-shaped cells with niformly thickened lateral walls and some irregular bars<br>rossing the lumen. The walls lining the sporangial cavity<br>reminutely reticulate niformly thickened later<br>rossing the lumen. The v<br>re minutely reticulate.<br>A further hifurcating s Solven the lumen. The walls lining the sporangial cavity<br>A further bifurcating specimen currently being investi-<br>ted by Kate Habrood (Cardiff University) is unique in

re minutely reticulate.<br>A further bifurcating specimen currently being investi-<br>ated by Kate Habgood (Cardiff University) is unique in<br>at the envelope-enclosed dyads are ornamented and the A further bifurcating specimen currently being investi-<br>ated by Kate Habgood (Cardiff University) is unique in<br>at the envelope-enclosed dyads are ornamented and the<br>res bear stomata (figure  $4k-n$ ) Evidence for the two axes bear stomata (Cardiff University) is unique in<br>at the envelope-enclosed dyads are ornamented and the<br>axes bear stomata (figure  $4k^-n$ ). Evidence for the two<br>uard cells is indirect: the stomatal pores are extended at the envelope-enclosed dyads are ornamented and the xes bear stomata (figure  $4k-n$ ). Evidence for the two uard cells is indirect; the stomatal pores are extended to short slits in the position of the common walls and xes bear stomata (figure  $4k-n$ ). Evidence for the two uard cells is indirect; the stomatal pores are extended ito short slits in the position of the common walls and uard cells is indirect; the stomatal pores are extended<br>to short slits in the position of the common walls and<br>there are polar indentations (figure  $4n$ ). TEM sections<br>the state the exospore is homogeneous with superficia to short slits in the position of the common walls and<br>A the are polar indentations (figure  $4n$ ). TEM sections<br>A tow that the exospore is homogeneous with superficial<br>aloni and that these are draned by a uniformly thick The area polar indentations (figure 4*n*). TEM sections<br>The that the exospore is homogeneous with superficial<br>Toni, and that these are draped by a uniformly thick layer<br>Tontaining voids (figure 4*k*). In some examples thi **Example 12** and that the exospore is homogeneous with superficial<br>**Containing voids** (figure 4*k*). In some examples, this layer<br>containing voids (figure 4*k*). In some examples, this layer<br>covers the iunction between the Foni, and that these are draped by a uniformly thick layer<br>
ontaining voids (figure  $4k$ ). In some examples, this layer<br>
overs the junction between the spores, and is hence inter-<br>
overs the junction between the spores, a protaining voids (figure  $4k$ ). In some examples, this layer<br>by overs the junction between the spores, and is hence inter-<br>preted as an envelope. There is no similarly enveloped,<br>pramented, permanent dyad taxon in the dis overs the junction between the spores, and is hence inter-<br>
as an envelope. There is no similarly enveloped,<br>
are numerated, permanent dyad taxon in the dispersed<br>
over record Hilate cryptospores with similar exospore record. There is no similarly enveloped,<br>
ramented, permanent dyad taxon in the dispersed<br>
ore record. Hilate cryptospores with similar exospore<br>
rament at the locality would be placed in *Chelinobilates* Framented, permanent dyad taxon in the dispersed<br>pore record. Hilate cryptospores with similar exospore<br>rament at the locality would be placed in *Chelinohilates*<br>*aridus* (Richardson 1996) but there are no indications pore record. Hilate cryptospores with similar exospore rnament at the locality would be placed in *Chelinohilates oridus* (Richardson 1996), but there are no indications that rnament at the locality would be placed in *Chelinohilates orridus* (Richardson 1996), but there are no indications that the *in situ* examples.

*ridus* (Richardson 1996), but there are no indications<br>natever of splitting in the *in situ* examples.<br>The North Brown Clee locality has yielded some spor-<br>gial cuticles, with adhering permanent dyads. Most that the of splitting in the *in situ* examples.<br>
The North Brown Clee locality has yielded some spor-<br>
permanent dyads. Most<br>
otable is an ovate example with a discrete outline The North Brown Clee locality has yielded some spor-<br>notable is an ovate example with a discrete outline<br>example with a discrete outline<br>example with a discrete outline<br>example  $\frac{1}{2}$ ngial cuticles with adhering permanent dyads. Most<br>otable is an ovate example with a discrete outline<br>?representing a valve) and linear rectangular 'cells', hich bears extremely thin-walled dyads with sporadic Prepresenting a valve) and linear rectangular 'cells', thich bears extremely thin-walled dyads with sporadic reservation of an envelope (figure  $4a$ ,*b*; Wellman *et al*. 1998). The latter is homogeneous and differentiall reservation of an envelope (figure  $4a$ ,*b*; Wellman *et al.* 998). The latter is homogeneous and differentially stains 1 TEM sections (figure  $4c$ ). The exospore itself is also omogeneous except for a zone of voids close 998). The latter is homogeneous and differentially stains<br>
1 TEM sections (figure  $4c$ ). The exospore itself is also<br>
omogeneous except for a zone of voids close to the<br>
1 Homogeneous exospores also characterize groups 1 TEM sections (figure  $4c$ ). The exospore itself is also omogeneous except for a zone of voids close to the imen. Homogeneous exospores also characterize groups f laevigate permanent dyads with some variation in omogeneous except for a zone of voids close to the<br>imen. Homogeneous exospores also characterize groups<br>f laevigate, permanent dyads with some variation in<br>call thickness and degree of invariation of the distal imen. Homogeneous exospores also characterize groups<br>f laevigate, permanent dyads with some variation in<br>rall thickness and degree of invagination of the distal f laevigate, permanent dyads with some variation in *rall thickness and degree of invagination of the distal*<br>urface (Wellman *et al.* 1998). Such ultrastructural<br>niformity is disappointing as spore masses or isolated vall thickness and degree of invagination of the distal<br>urface (Wellman *et al.* 1998). Such ultrastructural<br>niformity is disappointing as spore masses or isolated<br>parameters with hilate dyads i.e. separated cryptospores The sport is disappointing as spore masses or isolated porangia with hilate dyads, i.e. separated cryptospores with large circular contact area lacking a trilete mark niformity is disappointing as spore masses or isolated<br>porangia with hilate dyads, i.e. separated cryptospores<br>vith large circular contact area lacking a trilete mark, porangia with hilate dyads, i.e. separated cryptospores with large circular contact area lacking a trilete mark, now far greater variation. All are laevigate and would be ssigned to *Laevolancis divellomedia* sensu lato—a vith large circular contact area lacking a trilete mark, sp. is homogeneous.<br>
1992 now far greater variation. All are laevigate and would be now far greater variation. All are laevigate and would be<br>signed to *Laevolancis divellomedia* sensu lato—a taxon<br>urrently being further subdivided by J. B. Richardson.<br>Vellman *et al.* (1998) distinguished five broad-exo signed to *Laevolancis divellomedia* sensu lato—a taxon<br>urrently being further subdivided by J. B. Richardson.<br>Vellman *et al.* (1998) distinguished five broad-exospore<br>trastructural types. The only one with an entirely urrently being further subdivided by J. B. Richardson.<br>
Vellman *et al.* (1998) distinguished five broad-exospore<br>
Itrastructural types. The only one with an entirely<br>
omogeneous exospore was recovered from a small Vellman *et al.* (1998) distinguished five broad-exospore ltrastructural types. The only one with an entirely omogeneous exospore was recovered from a small, iscoidal sporangium. The remainder are bilayered in both proximal and distal walls thus contrasting with the iscoidal sporangium. The remainder are bilayered in (i) oth proximal and distal walls thus contrasting with the  $\overline{V}$  *i situ* forms described above where the contact faces show where the contact faces show also show oth proximal and distal walls thus contrasting with the  $\mu$  *situ* forms described above where the contact faces show<br>nly one layer. They also show traces of lamellation, one<br>lyen with white-line-centred lamellae. Preser  $\mathbf{e}_i$  *i situ* forms described above where the contact faces show<br>hy one layer. They also show traces of lamellation, one<br>by with white-line-centred lamellae. Preservation of<br>the delicate structures demonstrates that In delicate structures demonstrates of lamellation, one<br>of the with white-line-centred lamellae. Preservation of<br>a check that the homo-<br>ensity of the walls in the *in situ* permanent dyads and yen with white-line-centred lamellae. Preservation of  $\sum_{n=1}^{\infty}$  of the walls in the *in situ* permanent dyads and atrads from the same locality is not caused by diagnosis The delicate structures demonstrates that the homo-<br>eneity of the walls in the *in situ* permanent dyads and<br>strads from the same locality is not caused by diagenesis.<br>Lowever, such ultrastructural simplicity mirrored in eneity of the walls in the *in situ* permanent dyads and etrads from the same locality is not caused by diagenesis.<br>Iowever, such ultrastructural simplicity, mirrored in arly disnersed taxa such as the Late Ordovician (Ea errads from the same locality is not caused by diagenesis.<br>
Iowever, such ultrastructural simplicity, mirrored in<br>
arly dispersed taxa such as the Late Ordovician/Early<br>
ilurian Tetrahedraletes medinensis (Taylor 1995a) an Iowever, such ultrastructural simplicity, mirrored in<br>arly dispersed taxa such as the Late Ordovician/Early<br>ilurian *Tetrahedraletes medinensis* (Taylor 1995*a*) and<br>legidodradoshara an (Taylor 1996) frustrates attempts to arly dispersed taxa such as the Late Ordovician/Early<br> *Pseudodyadospora* sp. (Taylor 1996) frustrates attempts to<br> *Pseudodyadospora* sp. (Taylor 1996) frustrates attempts to ilurian *Tetrahedraletes medinensis* (<br> *detect affinities using this character.*<br>
detect affinities using this character.

## **(c)** *General discussion on mesofossils with* **in-situ** *cryptospores* (c) General discussion on mesofossils with in-situ<br>cryptospores<br>The mesofossils described here are united in that they

ontain polyads, resembling, at least superficially, the

strata and from rocks extending *ca*. 60 Myr back into the Ordovician. Where subtending structures are preserved, they are naked axes and the sporangia are terminal. Representatives of both dyad- and tetrad-containing Ordovician. Where subtending structures are preserved,<br>they are naked axes and the sporangia are terminal.<br>Representatives of both dyad- and tetrad-containing<br>plants show isotomous branching. Axes are very short in they are naked axes and the sporangia are terminal.<br>Representatives of both dyad- and tetrad-containing<br>plants show isotomous branching. Axes are very short in<br>unbranched representatives and so it is impossible to Representatives of both dyad- and tetrad-containing<br>plants show isotomous branching. Axes are very short in<br>unbranched representatives and so it is impossible to<br>conclude that branching was absent. In one case only viz plants show isotomous branching. Axes are very short in<br>unbranched representatives and so it is impossible to<br>conclude that branching was absent. In one case only, viz<br>Grivellatheca (figure  $2a-e^a$ ) it was speculated that unbranched representatives and so it is impossible to conclude that branching was absent. In one case only, viz *Grisellatheca* (figure  $2a-e,g$ ), it was speculated that the conclude that branching was absent. In one case only, viz<br> *Grisellatheca* (figure  $2a-e,g$ ), it was speculated that the<br>
axial fragment is a gametophyte, with deeply seated<br>
sporancia but this was dismissed as the tissues Grisellatheca (figure  $2a-e,g$ ), it was speculated that the axial fragment is a gametophyte, with deeply seated sporangia, but this was dismissed as the tissues surrounding the spores are superficially quite distinct axial fragment is a gametophyte, with deeply seated<br>sporangia, but this was dismissed as the tissues<br>surrounding the spores are superficially quite distinct<br>from the rest of the specimen. The fossils are therefore all sporangia, but this was dismissed as the tissues<br>surrounding the spores are superficially quite distinct<br>from the rest of the specimen. The fossils are therefore all surrounding the spores are superficially quite distinct<br>from the rest of the specimen. The fossils are therefore all<br>interpreted as sporophytes and derived from plants of<br>small stature. They probably should all be placed i from the rest of the specimen. The fossils are therefore all<br>interpreted as sporophytes and derived from plants of<br>small stature. They probably should all be placed in<br>different genera interpreted as spo<br>small stature. Th<br>different genera. (i) *Comparisons with dispersed spores* In contrast to information on *in situ* spores, the

(i) *Comparisons with dispersed spores*<br>In contrast to information on *in situ* spores, the<br>majority of dispersed spores, particularly from older<br>strata have been described and named from LM studies In contrast to information on *in situ* spores, the majority of dispersed spores, particularly from older strata, have been described and named from LM studies. Combined I M and TEM studies such as those recently majority of dispersed spores, particularly from older<br>strata, have been described and named from LM studies.<br>Combined LM and TEM studies such as those recently<br>undertaken on dispersed spores from the North Brown strata, have been described and named from LM studies.<br>Combined LM and TEM studies such as those recently<br>undertaken on dispersed spores from the North Brown Combined LM and TEM studies such as those recently<br>undertaken on dispersed spores from the North Brown<br>Clee Hill locality are essential for accurate identification<br>(Richardson 1996) This is especially so for distinguishing undertaken on dispersed spores from the North Brown<br>Clee Hill locality are essential for accurate identification<br>(Richardson 1996). This is especially so for distinguishing<br>between fused (sensu Wellman & Richardson 1993) Clee Hill locality are essential for accurate identification<br>(Richardson 1996). This is especially so for distinguishing<br>between fused (sensu Wellman & Richardson 1993)<br>polyads and forms with closely adhering envelopes, an (Richardson 1996). This is especially so for distinguishing<br>between fused (sensu Wellman & Richardson 1993)<br>polyads and forms with closely adhering envelopes, and for deciding whether or not fused or unfused when an polyads and forms with closely adhering envelopes, and<br>for deciding whether or not fused or unfused when an<br>envelope is present. The distally inflated, envelope-<br>enclosed dyads from *Eusithera faminaige* provided a good for deciding whether or not fused or unfused when an envelope is present. The distally inflated, envelope-<br>enclosed dyads from *Fusitheca fanningiae* provided a good<br>illustration for the latter. If fused the dyads would be envelope is present. The distally inflated, envelope-<br>enclosed dyads from *Fusitheca fanningiae* provided a good<br>illustration for the latter. If fused, the dyads would be<br>placed in *Segestreshora laevigata*: if unfused in enclosed dyads from *Fusitheca fanningiae* provided a good<br>illustration for the latter. If fused, the dyads would be<br>placed in *Segestrespora laevigata*; if unfused, in *Abditidyadus illustration for the latter.* If fused, the dyads would be placed in *Segestrespora laevigata*; if unfused, in *Abditidyadus laevigatus*. These spores also superficially resemble the naked *Pseudodyadospan* whose identi placed in *Segestrespora laevigata*; if unfused, in *Abditidyadus*<br>*laevigatus*. These spores also superficially resemble the<br>naked *Pseudodyadospora* whose identification depends on<br>the nature of the contact areas (hidden *laevigatus*. These spores also superficially resemble the nature of the contact areas (hidden in SEM). Ultra-<br>the nature of the contact areas (hidden in SEM). Ultra-<br>structural studies eliminate identity at least with Ash naked *Pseudodyadospora* whose identification depends on<br>the nature of the contact areas (hidden in SEM). Ultra-<br>structural studies eliminate identity, at least, with Ashgill/<br>Llandovery S. membranifera Abditidyadus laevig the nature of the contact areas (hidden in SEM). Ultra-<br>structural studies eliminate identity, at least, with Ashgill/<br>Llandovery *S. membranifera. Abditidyadus laevigatus* ultra-<br>structure is unknown but similarly dated structural studies eliminate identity, at least, with Ashgill/<br>Llandovery *S. membranifera. Abditidyadus laevigatus* ultra-<br>structure is unknown, but similarly dated *Pseudodyadospora*<br>sn is homogeneous Llandovery *S. membranifera. Abditidyadus laevigatus* ultrastructure is unknown, but similarly dated *Pseudodyadospora* sp. is homogeneous.<br>Two specimens contain *in situ* tetrads that are unequistructure is unknown, but similarly dated Pseudodyadospora

permanent or obligate cryptospores recorded from coeval<br>strata and from rocks extending *ca*. 60 Myr back into the<br>Ordovician Where subtending structures are preserved permanent or obligate cryptospores recorded from coeval<br>strata and from rocks extending *ca*. 60 Myr back into the<br>Ordovician. Where subtending structures are preserved,<br>they are naked axes and the sporancia are terminal

vocally membrane-bound and hence would be placed in Two specimens contain *in situ* tetrads that are unequi-<br>vocally membrane-bound and hence would be placed in<br>the dispersed taxon *Velatitetras*, a genus that encompasses<br>both smooth and ornamented envelopes and has been vocally membrane-bound and hence would be placed in<br>the dispersed taxon *Velatitetras*, a genus that encompasses<br>both smooth and ornamented envelopes and has been<br>recorded from the Lower Devonian Neither shows ornathe dispersed taxon *Velatitetras*, a genus that encompasses<br>both smooth and ornamented envelopes and has been<br>recorded from the Lower Devonian. Neither shows orna-<br>ment identical to published spores. The Silurian form both smooth and ornamented envelopes and has been<br>recorded from the Lower Devonian. Neither shows orna-<br>ment identical to published spores. The Silurian form (figure  $3a-d$ ) in the discoidal sporangium is closest to ment identical to published spores. The Silurian form<br>(figure  $3a-d$ ) in the discoidal sporangium is closest to<br>*V. anatoliensis* Steemans, le Herisse & Bozdogan 1996,<br>whose range extends from Ordovician to Early Silurian (figure  $3a-d$ ) in the discoidal sporangium is closest to *V. anatoliensis* Steemans, le Herisse & Bozdogan 1996, whose range extends from Ordovician to Early Silurian.<br>The Lower Devonian examples in sporangia terminating *V. anatoliensis* Steemans, le Herisse & Bozdogan 1996,<br>whose range extends from Ordovician to Early Silurian.<br>The Lower Devonian examples in sporangia terminating<br>a bifurcating axis (figure  $3h/k$ ) have no close counterwhose range extends from Ordovician to Early Silurian.<br>The Lower Devonian examples in sporangia terminating<br>a bifurcating axis (figure  $3h-k$ ) have no close counter-<br>parts in dispersed species. The ultrastructure both of The Lower Devonian examples in sporangia terminating<br>a bifurcating axis (figure  $3h-k$ ) have no close counter-<br>parts in dispersed species. The ultrastructure both of<br>exaspore and envelope of the two in situ forms is quite a bifurcating axis (figure  $3h-k$ ) have no close counter-<br>parts in dispersed species. The ultrastructure both of<br>exospore and envelope of the two *in situ* forms is quite<br>different with only the Silurian form showing trace parts in dispersed species. The ultrastructure both of exospore and envelope of the two *in situ* forms is quite different, with only the Silurian form showing traces of exospore lamellae, but there are no published reports of different, with only the Silurian form showing traces of<br>exospore lamellae, but there are no published reports of<br>similar ultrastructure in dispersed spores. The remaining<br>examples are laevigate. Those of *Grisellatheca* ( exospore lamellae, but there are no published reports of<br>similar ultrastructure in dispersed spores. The remaining<br>examples are laevigate. Those of *Grisellatheca* (figure 2*c*)<br>demonstrate the problems of describing spore similar ultrastructure in dispersed spores. The remaining<br>examples are laevigate. Those of *Grisellatheca* (figure  $2c$ )<br>demonstrate the problems of describing spores solely from<br>SEM studies. If naked, fixed tetrads, they examples are laevigate. Those of *Grisellatheca* (figure  $2c$ )<br>demonstrate the problems of describing spores solely from<br>SEM studies. If naked, fused tetrads, they would be<br>assigned to *Cheilatetras*: if with closely adhe demonstrate the problems of describing spores solely from SEM studies. If naked, fused tetrads, they would be assigned to *Cheilotetras*; if with closely adherent envelope to *Velatitetras*. Laevigrate upfused forms (i.e. SEM studies. If naked, fused tetrads, they would be assigned to *Cheilotetras*; if with closely adherent envelope to *Velatitetras*. Laevigate, unfused forms (i.e. with sutures separating spores) assigned to *Velationalate* assigned to *Cheilotetras*; if with closely adherent envelope<br>to *Velatitetras*. Laevigate, unfused forms (i.e. with sutures<br>separating spores) assigned to *Tetrahedraletes* occur in the to *Velatitetras*. Laevigate, unfused forms (i.e. with sutures separating spores) assigned to *Tetrahedraletes* occur in the bifurcating specimen (figure  $3e-g$ ), and in a number of spore, masses. While ultrastructural stu separating spores) assigned to *Tetrahedraletes* occur in the bifurcating specimen (figure  $3e-g$ ), and in a number of spore masses. While ultrastructural studies have been

seful in demonstrating diversity in these laevigate forms,<br>he most complex exospores, comparable with the lamel-<br>ate exospores of *Dyadospara murusdensa* (Taylor 1995*a*) seful in demonstrating diversity in these laevigate forms,<br>he most complex exospores, comparable with the lamel-<br>ate exospores of *Dyadospora murusdensa* (Taylor 1995*a*,<br>996) and *D. murusattenuata* in part (Taylor 1997), 996) and *D. murusattenuata* in part (Taylor 1997), are in<br>pore masses. The only illustrated ultrastructure from<br>Jpper Ordovician tetrads is from *Tetrahedraletes medinensis*<br>there the exospore is homogeneous (Taylor 1995b pore masses. The only illustrated ultrastructure from<br>Jpper Ordovician tetrads is from *Tetrahedraletes medinensis*<br>there the exospore is homogeneous (Taylor 1995*b*) and<br>thus similar to some of the Lower Devonian examples Ipper Ordovician tetrads is from *Tetrahedraletes medinensis*<br>
there the exospore is homogeneous (Taylor 1995*b*) and<br>
thus similar to some of the Lower Devonian examples<br>
see Edwards *et al.* 1999: figure 3*g*) although here the exospore is homogeneous (Taylor  $1995b$ ) and hus similar to some of the Lower Devonian examples see Edwards et al. 1999; figure  $3g$ ) although an exfobrms. Such comparisons show that while configurations of Such comparisons show that while configurations of

Such comparisons show that while configurations of<br>
the mature spores indicate that the reproductive biology<br>
of the producers remained unchanged from Ordovician to Such comparisons show that while configurations of<br>
the mature spores indicate that the reproductive biology<br>
of the producers remained unchanged from Ordovician to<br>
a lower Devonian times, we have no compelling evidence The mature spores indicate that the reproductive biology<br>
The producers remained unchanged from Ordovician to<br>
Lower Devonian times, we have no compelling evidence<br>
Is yet that the *in situ* spores are conspecific with ea <del>□ f</del> the producers remained unchanged from Ordovician to **□** ower Devonian times, we have no compelling evidence specific with earlier Lower Devonian times, we have no compelling evidence<br>s yet that the *in situ* spores are conspecific with earlier<br>ispersed examples. More evidence is required on the<br>ispersed examples. More evidences in dispersed assembla s yet that the *in situ* spores are conspecific with earlier<br>ispersed examples. More evidence is required on the<br>interacture of cryptospores in dispersed assemblages<br>bless through time especially as limited data from tril is persed examples. More evidence is required on the<br>absorption of cryptospores in dispersed assemblages<br>absorption trilete<br>absorption trilete<br>pores suggest that spore ultrastructure has some taxo-O ltrastructure of cryptospores in dispersed assemblages<br>
hrough time, especially as limited data from trilete<br>
press suggest that spore ultrastructure has some taxo-<br>
inic value, and can show stasis when spore ornament Dhrough time, especially as limited data from trilete pores suggest that spore ultrastructure has some taxoomic value, and can show stasis when spore ornament hanges (e.g. Fanning et al. 1988). pores suggest that spore ultrastru<br>omic value, and can show stasis<br>hanges (e.g. Fanning *et al.* 1988).

## (ii) *A¤nities of the mesofossils Affinities of the mesofos.<br>Spore ultrastructure*

Spore ultrastructure<br>The spores in the mesofossils show none of the lamellate ltrastructure that was used to invoke hepatic, more The spores in the mesofossils show none of the lamellate<br>ltrastructure that was used to invoke hepatic, more<br>recisely sphaerocarpalean, affinity in dispersed dyads<br>com the Asheill/Ordovician (Taylor 1995 $h$  1997) The Itrastructure that was used to invoke hepatic, more<br>recisely sphaerocarpalean, affinity in dispersed dyads<br>com the Ashgill/Ordovician (Taylor 1995*b*, 1997). The<br>sentially homogeneous exospore in the majority is recisely sphaerocarpalean, affinity in dispersed dyads<br>com the Ashgill/Ordovician (Taylor 1995*b*, 1997). The<br>sentially homogeneous exospore in the majority is<br>haracteristic of anthocerotes and bryonsid mosses com the Ashgill/Ordovician (Taylor 1995*b*, 1997). The sentially homogeneous exospore in the majority is haracteristic of anthocerotes and bryopsid mosses, lthough the latter sometimes have a very narrow and ssentially homogeneous exospore in the majority is<br>haracteristic of anthocerotes and bryopsid mosses,<br>lthough the latter sometimes have a very narrow and<br>aconspicuous layer that is basal or within the homogeneous haracteristic of anthocerotes and bryopsid mosses,<br>lthough the latter sometimes have a very narrow and<br>nonspicuous layer that is basal or within the homogeneous<br>art (Brown & Lemmon 1990) If indeed the envelope is It<br>hough the latter sometimes have a very narrow and a<br>conspicuous layer that is basal or within the homogeneous<br>art (Brown & Lemmon 1990). If indeed the envelope is<br>omologous with perispore (Gray 1991; Edwards *et al.*) homogeneous art (Brown & Lemmon 1990). If indeed the envelope is omologous with perispore (Gray 1991; Edwards *et al.* 1999), this is a further similarity with mosses, although erispore also occurs in homosporous ferms, wh omologous with perispore (Gray 1991; Edwards *et al.* 999), this is a further similarity with mosses, although erispore also occurs in homosporous ferns, where, in eneral a thick outer homogeneous layer overlies a lamel-999), this is a further similarity with mosses, although erispore also occurs in homosporous ferns, where, in eneral, a thick, outer homogeneous layer overlies a lamel-<br>ate one (I usardon 1990). However in many spores bot lerispore also occurs in homosporous ferns, where, in eneral, a thick, outer homogeneous layer overlies a lamelate one (Lugardon 1990). However, in many spores, both eneral, a thick, outer homogeneous layer overlies a lamel-<br>te one (Lugardon 1990). However, in many spores, both<br>ryophytic and 'pteridophytic', sporopollenin deposition<br>as obliterated the lamellation present in all develop ate one (Lugardon 1990). However, in many spores, both<br>ryophytic and 'pteridophytic', sporopollenin deposition<br>as obliterated the lamellation present in all developing<br>pores, producing homogenization at maturity. Thus in ryophytic and 'pteridophytic', sporopollenin deposition<br>as obliterated the lamellation present in all developing<br>pores, producing homogenization at maturity. Thus in<br>hese Lower Devonian spores ultrastructure is not useful as obliterated the lamellation present in all developing<br>pores, producing homogenization at maturity. Thus in<br>hese Lower Devonian spores, ultrastructure is not useful in<br>termining broad phylogenetic affinities, although m pores, producing homogenization at maturity. Thus in<br>hese Lower Devonian spores, ultrastructure is not useful in<br>termining broad phylogenetic affinities, although minor<br>ariations in exospore and envelope may be useful in hese Lower Devonian spores, ultrastructure is not useful in<br>etermining broad phylogenetic affinities, although minor<br>ariations in exospore and envelope may be useful in retermining broad phylogenetic affinities, alther ariations in exospore and envelope may between coeval plants. *Spore con¢guration*

Spore configuration<br>It was the tetrad organization of dispersed Ordovician Shore configuration<br>
It was the tetrad organization of dispersed Ordovician<br>
In Silurian spores that led to the hypothesis of their<br>
Mary ophyte affinity (Gray & Boucot 1971; Gray 1985, 1991) It was the tetrad organization of dispersed Ordovician<br>and Silurian spores that led to the hypothesis of their<br>prophyte affinity (Gray & Boucot 1971; Gray 1985, 1991)<br>ased on the retention of this feature in henatics e.g. and Silurian spores that led to the hypothesis of their<br>pryophyte affinity (Gray & Boucot 1971; Gray 1985, 1991)<br>pased on the retention of this feature in hepatics, e.g.<br>hhaencarbos Riccia Cryptothallys and certain mosses *S Selengery Corresponds Sphaerocarpos*, *Riccia*, *Cryptothallus* and certain mosses.<br> *Sphaerocarpos*, *Riccia*, *Cryptothallus* and certain mosses.<br> *Sphaerocarpos*, *Riccia*, *Cryptothallus* and certain mosses. ased on the retention of this feature in hepatics, e.g. phaerocarpos, Riccia, Cryptothallus and certain mosses.<br>
Stant analogues for dyads are far less common but occur<br>
1 bryophytes (e.g. Schuster 1967; Bell 1992), *Selaginella*<br>
Craustein 1930) and ferns (Morzenti 1967; Hicko Xtant analogues for dyads are far less common but occur<br>
1 bryophytes (e.g. Schuster 1967; Bell 1992), *Selaginella*<br>
6 Graustein 1930) and ferns (Morzenti 1967; Hickok & fa<br>
6 Clebowski 1973) In the majority of cases, the a bryophytes (e.g. Schuster 1967; Bell 1992), *Selaginella* & Graustein 1930) and ferns (Morzenti 1967; Hickok & fa Lekowski 1973). In the majority of cases, they result from of bhormal mejosis frequently associated with h Graustein 1930) and ferns (Morzenti 1967; Hickok & Lekowski 1973). In the majority of cases, they result from  $\Omega$  bnormal meiosis, frequently associated with hybridiza-<br>ion and occur together with trilete spores in the s Lekowski 1973). In the majority of cases, they result from<br>
Distancement methods is, frequently associated with hybridiza-<br>
ion, and occur together with trilete spores in the same<br>
parameta Our studies show conclusively t b bnormal meiosis, frequently associated with hybridization, and occur together with trilete spores in the same porangia. Our studies show conclusively that all spores ion, and occur together with trilete spores in the same<br>porangia. Our studies show conclusively that all spores<br>a sporangia are dyads and are not the products of porangia. Our studies show conclusively that all spores a sporangia are dyads and are not the products of reiotic failure. The producers display a type of reproa sporangia are dyads and are not<br>neiotic failure. The producers display<br>uctive biology no longer found today. *Phil. Trans. R. Soc. Lond.* B (2000)

## *Gross morphology*

ate exospores of *Dyadospora murusdensa* (Taylor 1995a, characterize early tracheophytes, e.g. *Cooksonia* (Edwards 996) and *D. murusattenuata* in part (Taylor 1997), are in *et al.* 1992), and a complex of plants produci Isotomously branching axes with terminal sporangia characterize early tracheophytes, e.g. *Cooksonia* (Edwards Isotomously branching axes with terminal sporangia<br>characterize early tracheophytes, e.g. *Cooksonia* (Edwards<br>*et al.* 1992), and a complex of plants producing trilete<br>spores e.g. *Salobella Tortilicaulis* (Edwards *et al* characterize early tracheophytes, e.g. *Cooksonia* (Edwards *et al.* 1992), and a complex of plants producing trilete spores, e.g. *Salopella*, *Tortilicaulis* (Edwards *et al.* 1994) and *Pertonella* (Fanning *et al.* 199 *et al.* 1992), and a complex of plants producing trilete spores, e.g. *Salopella*, *Tortilicaulis* (Edwards *et al.* 1994) and *Pertonella* (Fanning *et al.* 1991), in which xylem anatomy has not been demonstrated and whi spores, e.g. *Salopella, Tortilicaulis* (Edwards *et al.* 1994) and *Pertonella* (Fanning *et al.* 1991), in which xylem anatomy has not been demonstrated and which are therefore termed rhynionhytoid Pertonella (Fanning et al.<br>has not been demonst<br>termed rhyniophytoid.<br>Absence of axial anato has not been demonstrated and which are therefore<br>termed rhyniophytoid.<br>Absence of axial anatomy in the cryptospore-producing

termed rhyniophytoid.<br>Absence of axial anatomy in the cryptospore-producing<br>plants is a major frustration, which will be eased only by<br>the discovery and analysis of further specimens. The Absence of axial anatomy in the cryptospore-producing<br>plants is a major frustration, which will be eased only by<br>the discovery and analysis of further specimens. The<br>finding of stomata on one dyad-containing plant with plants is a major frustration, which will be eased only by<br>the discovery and analysis of further specimens. The<br>finding of stomata on one dyad-containing plant with<br>branching axes and the sterile axes with anomalous the discovery and analysis of further specimens. The finding of stomata on one dyad-containing plant with branching axes and the sterile axes with anomalous conducting tissues  $(n, 7)$  demonstrates some progress finding of stomata on one dyad-containing plant with<br>branching axes and the sterile axes with anomalous<br>conducting tissues (p.7) demonstrates some progress.<br>While clearly premature to place too much emphasis on branching axes and the sterile axes with anomalous<br>conducting tissues (p.7) demonstrates some progress.<br>While clearly premature to place too much emphasis on<br>such preliminary findings the occasion of a symposium conducting tissues  $(p.7)$  demonstrates some progress.<br>While clearly premature to place too much emphasis on<br>such preliminary findings, the occasion of a symposium<br>such as this provides a forum to raise some very tentative While clearly premature to place too much emphasis on such preliminary findings, the occasion of a symposium<br>such as this provides a forum to raise some very tentative<br>hypotheses (admittedly involving too many generaliza-<br>tions) that will be supported or disproved only by the such as this provides a forum to raise some very tentative<br>hypotheses (admittedly involving too many generaliza-<br>tions) that will be supported or disproved only by the<br>discovery of further fossils in Ordovician and Siluria hypotheses (admittedly involving too many generalizations) that will be supported or disproved only by the discovery of further fossils in Ordovician and Silurian rocks rocks. discovery of further fossils in Ordovician and Silurian rocks.<br>Thus considering the affinities of the mesofossils, the

following are, inter alia, possible.

- Illowing are, inter alia, possible.<br>
(i) The plants comprised relict populations of those that<br>
existed in Ordovician times, and bence based on the The plants comprised relict populations of those that existed in Ordovician times, and hence based on the presumed affinities of the  $\frac{in}{d}$  situ cryptospores, are existed in Ordovician times, and hence based on the presumed affinities of the *in situ* cryptospores, are existed in Ordovician times, and hence based on the<br>presumed affinities of the *in situ* cryptospores, are<br>bryophytes with branching sporophytes. Such a<br>hypothesis finds no support in cladistic analyses (e.g. presumed affinities of the *in situ* cryptospores, are<br>bryophytes with branching sporophytes. Such a<br>hypothesis finds no support in cladistic analyses (e.g.<br>Mishler & Churchill 1984) However in *Griellatheca* bryophytes with branching sporophytes. Such a<br>hypothesis finds no support in cladistic analyses (e.g.<br>Mishler & Churchill 1984). However, in *Grisellatheca*,<br>in particular admittedly very poorly preserved axial hypothesis finds no support in cladistic analyses (e.g. Mishler & Churchill 1984). However, in *Grisellatheca*, in particular, admittedly very poorly preserved axial Mishler & Churchill 1984). However, in *Grisellatheca*,<br>in particular, admittedly very poorly preserved axial<br>anatomy finds no similarities with that in later<br>tracheophytes. Those with stomata suggest greater in particular, admittedly very poorly preserved axial<br>anatomy finds no similarities with that in later<br>tracheophytes. Those with stomata suggest greater<br>affinity with mosses than liverworts, raising the anatomy finds no similarities with that in later<br>tracheophytes. Those with stomata suggest greater<br>affinity with mosses than liverworts, raising the<br>possibility that branching evolved early in moss tracheophytes. Those with stomata suggest greater<br>affinity with mosses than liverworts, raising the<br>possibility that branching evolved early in moss affinity with mosses than liverworts, raising the possibility that branching evolved early in moss evolution and was subsequently lost. Anatomical evidence is required to support this possibility that branching evolved<br>evolution and was subsequently lo<br>evidence is required to support this.<br>The spores are plesiomorphic and evolution and was subsequently lost. Anatomical<br>evidence is required to support this.<br>(ii) The spores are plesiomorphic and the plants are<br>stem-group trackeophytes in which branching in
- evidence is required to support this.<br>The spores are plesiomorphic and the plants are<br>stem-group tracheophytes in which branching in<br>sporophytes preceded the separation of spores. Such The spores are plesiomorphic and the plants are<br>stem-group tracheophytes in which branching in<br>sporophytes preceded the separation of spores. Such<br>plants could comprise relict populations of those that stem-group tracheophytes in which branching in<br>sporophytes preceded the separation of spores. Such<br>plants could comprise relict populations of those that sporophytes preceded the separation of spores. Such<br>plants could comprise relict populations of those that<br>existed prior to monad evolution in the latest Ordo-<br>vician or those subsequent to acquisition of stomata plants could comprise relict populations of those that<br>existed prior to monad evolution in the latest Ordo-<br>vician or those subsequent to acquisition of stomata.<br>Support for this hypothesis requires demonstration of existed prior to monad evolution in the latest Ordo-<br>vician or those subsequent to acquisition of stomata.<br>Support for this hypothesis requires demonstration of<br>tracheids in the subtending axes, with or without vician or those subsequent to acquisition of stomata.<br>Support for this hypothesis requires demonstration of<br>tracheids in the subtending axes, with or without stomata.

## **3. CONDUCTING TISSUES IN MESOFOSSILS**

The demonstration that each of the three major clades S. CONDUCTING TISSUES IN MESOPOSSILS<br>The demonstration that each of the three major clades<br>of early vascular plants is characterized by a particular<br>tracheidal architecture august well for the use of anato-The demonstration that each of the three major clades<br>of early vascular plants is characterized by a particular<br>tracheidal architecture augurs well for the use of anato-<br>mical features of water-conducting cells in the assi of early vascular plants is characterized by a particular tracheidal architecture augurs well for the use of anato-<br>mical features of water-conducting cells in the assignment<br>of leafless axial forms at least to a higher ta tracheidal architecture augurs well for the use of anato-<br>mical features of water-conducting cells in the assignment<br>of leafless axial forms at least to a higher taxon (Kenrick<br> $\&$  Crane 1991: Kenrick et al. 1991a b) The mical features of water-conducting cells in the assignment<br>of leafless axial forms at least to a higher taxon (Kenrick<br>& Crane 1991; Kenrick *et al.* 1991*a*,*b*). There is also, but<br>far more limited evidence, suggesting t of leafless axial forms at least to a higher taxon (Kenrick & Crane 1991; Kenrick *et al.* 1991*a,b*). There is also, but far more limited evidence, suggesting that certain species of *Cooksonia*, possessed far simpler co & Crane 1991; Kenrick *et al.* 1991*a,b*). There is also, but far more limited evidence, suggesting that certain species of *Cooksonia* possessed far simpler conducting cells (viz thick-walled tubes with additional interna far more limited evidence, suggesting that certain species of *Cooksonia* possessed far simpler conducting cells (viz<br>thick-walled tubes with additional internal annular thick-<br>enings; Lang 1937; Edwards *et al.* 1992), while the Rhynie<br>Chert *Aglashhyton major*, displays yet anot thick-walled tubes with additional internal annular thick-<br>enings; Lang 1937; Edwards *et al.* 1992), while the Rhynie<br>Chert, *Aglaophyton major*, displays yet another kind, which<br>has been compared with moss hydroids (Edwa enings; Lang 1937; Edwards *et al.* 1992), while the Rhynie Chert, *Aglaophyton major*, displays yet another kind, which has been compared with moss hydroids (Edwards, D. S. 1986). Such tracheary diversity in early vascula Chert, *Aglaophyton major*, displays yet another kind, which<br>has been compared with moss hydroids (Edwards, D. S.<br>1986). Such tracheary diversity in early vascular plants, coupled with information on extant bryophyte conducting

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PHILOSOPHICAL<br>TRANSACTIONS

ssues (e.g. Hébant 1977, 1979) prompted a detailed anatossues (e.g. Hébant 1977, 1979) prompted a detailed anato-<br>ical analysis of sterile, coalified axes, both branched and<br>phranched from Upper Silurian and Lower Devonian ssues (e.g. Hébant 1977, 1979) prompted a detailed anato-<br>ical analysis of sterile, coalified axes, both branched and<br>nbranched from Upper Silurian and Lower Devonian<br>rata, the preliminary results of which are presented he ical analysis of sterile, coalified axes, both branched and<br>nbranched from Upper Silurian and Lower Devonian<br>rata, the preliminary results of which are presented here.<br>The mesofossil fragments are pormally less than 3 mm nbranched from Upper Silurian and Lower Devonian clusters, are continuous with a secondary thickening<br>
Tata, the preliminary results of which are presented here. (figure 5 $e$ ). The vast majority are coalified throughout. A rata, the preliminary results of which are presented here.<br>
The mesofossil fragments are normally less than 3 mm<br>
ong, and a fraction of a millimetre in diameter. They<br>
arely show branching Where superficial features are The mesofossil fragments are normally less than 3 mm<br>ong, and a fraction of a millimetre in diameter. They<br>arely show branching. Where superficial features are<br>civell-preserved outlines of epidermal cells and an ong, and a fraction of a millimetre in diameter. They<br>arely show branching. Where superficial features are<br>cell-preserved, outlines of epidermal cells and an<br>accasional stoma are visible. Two guard cells are rarely arely show branching. Where superficial features are vell-preserved, outlines of epidermal cells and an ccasional stoma are visible. Two guard cells are rarely vell-preserved, outlines of epidermal cells and an ecasional stoma are visible. Two guard cells are rarely<br>vell-defined, but their presence is inferred from polar<br>vell-defined, but their presence is inferred from polar casional stoma are visible. Two guard cells are rarely<br>vell-defined, but their presence is inferred from polar<br>iduations. Stomatal density is thus always very low (cf.<br>dwards 1998). A two- to three-layered stereome may be rell-defined, but their presence is inferred from polar<br>identations. Stomatal density is thus always very low (cf.<br>dwards 1998). A two- to three-layered stereome may be<br>stressed and in a few examples cell walls are preserv rdentations. Stomatal density is thus always very low (cf.<br>dwards 1998). A two- to three-layered stereome may be<br>stressnt, and in a few examples, cell walls are preserved<br>of imperfectly) throughout the axes. Some axes show dwards 1998). A two- to three-layered stereome may be<br>
Fresent, and in a few examples, cell walls are preserved<br>
Fif imperfectly) throughout the axes. Some axes show a<br>
discrete central strand that readily separates from t discrete central strand that readily separates from the discrete central strand that readily separates from the discrete central strand that readily separates from the discrete central strand that readily separates from th  $\Box$  if imperfectly) throughout the axes. Some axes show a<br> $\Box$  iscrete central strand that readily separates from the ples (*a*. 1.2  $\mu$ m) tend to be more irregular in outline and<br>emaining, usually more poorly preserved Fiscrete central strand that readily separates from the<br>emaining, usually more poorly preserved, tissues. In<br>thers, only a variation in anatomy, often acccompanied<br> $\lambda$ y better preservation, marks, the position of central by emaining, usually more poorly preserved, tissues. In thers, only a variation in anatomy, often acccompanied<br>a) y better preservation, marks the position of central<br>anducting tissues. In a very few examples the entire thers, only a variation in anatomy, often acccompanied<br>a) y better preservation, marks the position of central<br>a) onducting tissues. In a very few examples, the entire<br>sil comprises tracheids always of G-type  $\bigcirc$  y better preservation, marks the position of central  $\bigcirc$  onducting tissues. In a very few examples, the entire **(a)** *G-type tracheids*

(a) *G-type tracheids*<br>G-type tracheids (named after the Lower Devonian<br>Gosslingia: Kenrick *et al.* 1991*a*) characterize the<br>external like optimulation of the strain of the strain of the strain of the strain of the strai G-type tracheids (named after the Lower Devonian<br>  $z^{\text{loss}}$  ingia: Kenrick *et al.* 1991*a*) characterize the<br>
osterophyll–lycophyte clade. They were distinguished<br>
osterophyll–lycophyte clade. They were distinguished<br>
ca  $b^2$  *osslingia*: Kenrick *et al.* 1991*a*) characterize the osterophyll-lycophyte clade. They were distinguished ecause the presumed primary wall between convent-<br>and annular and spiral secondary thickenings is osterophyll-lycophyte clade. They were distinguished<br>ecause the presumed primary wall between convent-<br>and annular and spiral secondary thickenings is ecause the presumed primary wall between convent-<br>
and annular and spiral secondary thickenings is<br>
overed by an additional perforated and assumed ligni-<br>
ed layer Configurations of coalified material and pyrite In an anal spiral secondary thickenings is<br>overed by an additional perforated and assumed ligni-<br>ed layer. Configurations of coalified material and pyrite<br>permineralizations of *Gossinaia* were explained in overed by an additional perforated and assumed ligni-<br>ed layer. Configurations of coalified material and pyrite<br>in permineralizations of *Gosslingia* were explained in<br>erms of the relative decay of cellulose and lignin ed layer. Configurations of coalified material and pyrite<br>a permineralizations of *Gasslingia* were explained in<br>erms of the relative decay of cellulose and lignin 1 permineralizations of *Gosslingia* were explained in<br>erms of the relative decay of cellulose and lignin<br>ombined with the bacterial production of pyrite (Kenrick<br>r Edwards 1988) Detailed ultrastructure was deduced by erms of the relative decay of cellulose and lignin<br>
ombined with the bacterial production of pyrite (Kenrick<br>
t Edwards 1988). Detailed ultrastructure was deduced by<br>
process involving acid etching and it revealed that pyr ombined with the bacterial production of pyrite (Kenrick<br>
t Edwards 1988). Detailed ultrastructure was deduced by<br>
process involving acid etching, and it revealed that pyrite<br>
ras precipitated in cell lumens and in spaces t Edwards 1988). Detailed ultrastructure was deduced by<br>process involving acid etching, and it revealed that pyrite<br>vas precipitated in cell lumens and in spaces occupied by process involving acid etching, and it revealed that pyrite vas precipitated in cell lumens and in spaces occupied by elatively biodegradable polymers such as cellulose. Thus ny coalified material remaining in the fossil ( ras precipitated in cell lumens and in spaces occupied by<br>elatively biodegradable polymers such as cellulose. Thus<br>ny coalified material remaining in the fossil (viz<br>econdary thickenings and intervening layer) was interelatively biodegradable polymers such as cellulose. Thus<br>ny coalified material remaining in the fossil (viz<br>econdary thickenings and intervening layer) was inter-<br>reted as once lignified Figure 54 shows a strand of transny coalified material remaining in the fossil (viz<br>econdary thickenings and intervening layer) was inter-<br>reted as once lignified. Figure 5*a* shows a strand of trans-<br>ersely fractured typical G-type tracheids; extra-xylar exendary thickenings and intervening layer) was inter-<br>reted as once lignified. Figure 5a shows a strand of trans-<br>ersely fractured typical G-type tracheids; extra-xylary<br>ssues are largely missing or have been 'condensed' reted as once lignified. Figure  $5a$  shows a strand of transersely fractured typical G-type tracheids; extra-xylary<br>sues are largely missing or have been 'condensed' into a<br>omogenized rind. In this specimen, pyrite occurs only in<br>a tracheary lumina such that the coalified walls com sues are largely missing or have been 'condensed' into a<br>omogenized rind. In this specimen, pyrite occurs only in<br>a tracheary lumina such that the coalified walls comprise<br>oth cellulose and lignin residues and are interpre omogenized rind. In this specimen, pyrite occurs only in<br>a tracheary lumina such that the coalified walls comprise<br>oth cellulose and lignin residues, and are interpreted as a<br>a tore faithful replica of original architectur ne tracheary lumina such that the coalified walls comprise<br>oth cellulose and lignin residues, and are interpreted as a<br>nore faithful replica of original architecture. Comparisons between the two forms of preservation will thus permit ssessment of the extent to which ultrastructure may have etween the two forms of preservation will thus permit<br>sessment of the extent to which ultrastructure may have<br>een affected by permineralization. As analysis of the<br>atter involves destructive acid-etching techniques, these sessment of the extent to which ultrastructure may have<br>
leen affected by permineralization. As analysis of the<br>
letter involves destructive acid-etching techniques, these<br>
loalified specimens allow for the first time deta een affected by permineralization. As analysis of the tuter involves destructive acid-etching techniques, these coalified specimens allow, for the first time, detailed Itter involves destructive acid-etching techniques, these<br>
Coalified specimens allow, for the first time, detailed<br>
escription of individual elements and their spatial rela-) oalified specimens allow, for the first time, detailed<br>
secription of individual elements and their spatial rela-<br>
onships. Here I concentrate on the specimen illustrated in<br>
gures 5 and 6*a-c*. As is characteristic of escription of individual elements and their spatial rela-<br>onships. Here I concentrate on the specimen illustrated in<br>gures 5 and 6*a*<sup> $-c$ </sup>. As is characteristic of the clade as a<br>thole the vylem is not centrarch but shows onships. Here I concentrate on the specimen illustrated in gures 5 and  $6a-c$ . As is characteristic of the clade as a hole, the xylem is not centrarch, but shows a wide range f diameters even in the central part presumably gures 5 and  $6a-c$ . As is characteristic of the clade as a *rhole*, the xylem is not centrarch, but shows a wide range f diameters, even in the central part, presumably effecting the tangency of tracheids (figure 5*a*). Th rhole, the xylem is not centrarch, but shows a wide range f diameters, even in the central part, presumably effecting the tapering of tracheids (figure  $5a$ ). There is no rell-defined zone of 'protoxylem' (insofar as it c f diameters, even in the central part, presumably<br>effecting the tapering of tracheids (figure 5*a*). There is no<br>cell-defined zone of 'protoxylem' (insofar as it can be iden-<br>effecting figure is inferred from a very narro there is no the tapering of tracheids (figure 5*a*). There is no the relation of 'protoxylem' (insofar as it can be idended from a very narrow,  $\overline{O}$  fied in fossils). Its presence is inferred from a very narrow, rell-defined zone of 'protoxylem' (insofar as it can be identifyind in fossils). Its presence is inferred from a very narrow, rushed, peripheral layer in which jumbled fragmentary condary thickenings are apparent. If fied in fossils). Its presence is inferred<br>rushed, peripheral layer in which ji<br>condary thickenings are apparent.<br>Conventional secondary, thickeni ushed, peripheral layer in which jumbled fragmentary<br>condary thickenings are apparent.<br>Conventional secondary thickenings range between<br>nple (figure 5c g) directly attached appular (figure 6c;

strategies the endary thickenings are apparent.<br>Conventional secondary thickenings range between<br>mple (figure  $5c$ ,*g*), directly attached annular (figure  $6c$ ; ensu Bierhorst 1960), to spiral (figure 5b) to reticulate

esofossils and the detection of early bryophytes D. Edwards 741<br>(figure 5*f*). The latter are rare and found towards the (figure  $5f$ ). The latter are rare and found towards the centre. In one tracheid only, globules, singly or in small clusters are continuous with a secondary thickening (figure 5*f*). The latter are rare and found towards the centre. In one tracheid only, globules, singly or in small clusters, are continuous with a secondary thickening (figure 5*e*). The vast majority are coalified throu centre. In one tracheid only, globules, singly or in small<br>clusters, are continuous with a secondary thickening<br>(figure 5*e*). The vast majority are coalified throughout. A<br>few show a small void (triangular in cross sectio clusters, are continuous with a secondary thickening junction with the lateral wall (figure 5*g*). w show a small void (triangular in cross section) at the<br>nction with the lateral wall (figure 5*g*).<br>The secondary thickenings show variation in diameter<br>d distance apart between tracheids but individual trac-

(a)  $G$ -type tracheids<br>
G-type tracheids (named after the Lower Devonian in the functioning plant (see also in *Gosslingia*; Kenrick & junction with the lateral wall (figure 5g).<br>The secondary thickenings show variation in diameter<br>and distance apart between tracheids but individual trac-<br>heids have a uniform appearance. The persistent wall The secondary thickenings show variation in diameter<br>and distance apart between tracheids but individual trac-<br>heids have a uniform appearance. The persistent wall<br>between the secondary thickenings (indeed the latter and distance apart between tracheids but individual tracheids have a uniform appearance. The persistent wall<br>between the secondary thickenings (indeed the latter<br>appear as an integrated part of this wall) is perforated by heids have a uniform appearance. The persistent wall<br>between the secondary thickenings (indeed the latter<br>appear as an integrated part of this wall) is perforated by<br>circular to irregular holes whose size and frequency var between the secondary thickenings (indeed the latter<br>appear as an integrated part of this wall) is perforated by<br>circular to irregular holes whose size and frequency vary<br>between tracheids Uncommon are examples where holes appear as an integrated part of this wall) is perforated by<br>circular to irregular holes whose size and frequency vary<br>between tracheids. Uncommon are examples where holes circular to irregular holes whose size and frequency vary<br>between tracheids. Uncommon are examples where holes<br>are small  $(< 100 \text{ nm})$  and widely spaced. Larger exam-<br>ples  $(a, 12 \text{ nm})$  tend to be more irregular in outline between tracheids. Uncommon are examples where holes<br>are small  $(< 100 \text{ nm})$  and widely spaced. Larger exam-<br>ples  $(aa. 1.2 \mu m)$  tend to be more irregular in outline and<br>may occupy most of the wall such that it tends to bre are small (< 100 nm) and widely spaced. Larger exam-<br>ples  $(aa. 1.2 \mu m)$  tend to be more irregular in outline and<br>may occupy most of the wall such that it tends to break<br>down. Fractured transverse sections (figure  $5b-d$ ) a ples  $(a, 1.2 \mu m)$  tend to be more irregular in outline and may occupy most of the wall such that it tends to break down. Fractured transverse sections (figure  $5b-d$ ) and may occupy most of the wall such that it tends to break<br>down. Fractured transverse sections (figure  $5b-d$ ) and<br>superposed cells (figure  $6a$ ) show that holes in adjacent<br>cells may or may not be coincident and are always o down. Fractured transverse sections (figure  $5b-d$ ) and<br>superposed cells (figure  $6a$ ) show that holes in adjacent<br>cells may or may not be coincident and are always of<br>different size. Thus in some cases there is continuity superposed cells (figure  $6a$ ) show that holes in adjacent cells may or may not be coincident and are always of different size. Thus in some cases there is continuity between lumina of adjacent tracheids (arrows in cells may or may not be coincident and are always of<br>different size. Thus in some cases there is continuity<br>between lumina of adjacent tracheids (arrows in<br>figure 5*bc*). However it is doubted that this was the case different size. Thus in some cases there is continuity<br>between lumina of adjacent tracheids (arrows in<br>figure 5*b*,*c*). However, it is doubted that this was the case<br>in the functioning plant (see also in *Gosslingia*: Ke between lumina of adjacent tracheids (arrows in figure 5*b*,*c*). However, it is doubted that this was the case<br>in the functioning plant (see also in *Gosslingia*; Kenrick &<br>Edwards 1988). Studies of decay of xylem (mainly conifer,<br>e.g. Dunleauy & McQuire 1970; Levy 19 in the functioning plant (see also in *Gosslingia*; Kenrick & Edwards 1988). Studies of decay of xylem (mainly conifer, e.g. Dunleavy & McQuire 1970; Levy 1975) have shown that nit-closing membranes (primary cell wall and Edwards 1988). Studies of decay of xylem (mainly conifer,<br>e.g. Dunleavy & McQuire 1970; Levy 1975) have shown<br>that pit-closing membranes (primary cell wall and<br>middle lamella) are rapidly attacked and removed by e.g. Dunleavy & McQuire 1970; Levy 1975) have shown<br>that pit-closing membranes (primary cell wall and<br>middle lamella) are rapidly attacked and removed by<br>bacteria soon after the death of the plant, thus increasing that pit-closing membranes (primary cell wall and<br>middle lamella) are rapidly attacked and removed by<br>bacteria soon after the death of the plant, thus increasing<br>permeability of the tissue for further infection. It seems middle lamella) are rapidly attacked and removed by<br>bacteria soon after the death of the plant, thus increasing<br>permeability of the tissue for further infection. It seems<br>not unlikely that this process occurred during wate bacteria soon after the death of the plant, thus increasing<br>permeability of the tissue for further infection. It seems<br>not unlikely that this process occurred during waterlogging of the plant fragment prior to burial and fossilizanot unlikely that this process occurred during water-<br>logging of the plant fragment prior to burial and fossiliza-<br>tion. Indeed the presence of such membranes in<br>transpiring plants would have been essential to reduce logging of the plant fragment prior to burial and fossilization. Indeed the presence of such membranes in transpiring plants would have been essential to reduce cavitation cavitation. transpiring plants would have been essential to reduce<br>cavitation.<br>Considering the relationship between the perforated

layer and the thickenings, the schematic reconstruction of Considering the relationship between the perforated<br>layer and the thickenings, the schematic reconstruction of<br>the *Gosslingia* tracheid (Kenrick & Edwards 1988,<br>for 26c) shows the secondary thickenings as inwardly layer and the thickenings, the schematic reconstruction of<br>the *Gosslingia* tracheid (Kenrick & Edwards 1988,<br>fig. 26*c*) shows the secondary thickenings as inwardly<br>directed non-nerforate extensions of the nerforate layer the *Gosslingia* tracheid (Kenrick & Edwards 1988, fig. 26 $\epsilon$ ) shows the secondary thickenings as inwardly directed, non-perforate extensions of the perforate layer, with a core continuous with a layer of presumed cellul fig.  $26c$ ) shows the secondary thickenings as inwardly directed, non-perforate extensions of the perforate layer, with a core continuous with a layer of presumed cellulose, approximately twice as wide as the perforate la directed, non-perforate extensions of the perforate layer, a detached outer layer is not apparent in these coalified approximately twice as wide as the perforate layer. Such<br>a detached outer layer is not apparent in these coalified<br>examples where the perforations extend to the junction<br>between adiacent cells. If correct in assuming the o a detached outer layer is not apparent in these coalified<br>examples where the perforations extend to the junction<br>between adjacent cells. If correct in assuming the original<br>presence of a pit-closing membrane, this suggests examples where the perforations extend to the junction<br>between adjacent cells. If correct in assuming the original<br>presence of a pit-closing membrane, this suggests that the<br>original primary cell wall of the tracheid was v between adjacent cells. If correct in assuming the original<br>presence of a pit-closing membrane, this suggests that the<br>original primary cell wall of the tracheid was very thin,<br>and homogenized with the wall between perfora presence of a pit-closing membrane, this suggests that the original primary cell wall of the tracheid was very thin, and homogenized with the wall between perforations in the intervening layer. In rare specimens where adia original primary cell wall of the tracheid was very thin,<br>and homogenized with the wall between perforations in<br>the intervening layer. In rare specimens where adjacent<br>tracheids have separated in this area, there is some and homogenized with the wall between perforations in<br>the intervening layer. In rare specimens where adjacent<br>tracheids have separated in this area, there is some<br>evidence of grooves in the secondary thickenings the intervening layer. In rare specimens where adjacent<br>tracheids have separated in this area, there is some<br>evidence of grooves in the secondary thickenings<br> $(\text{four 5a})$  possibly demonstrating an originally thicker tracheids have separated in this area, there is some<br>evidence of grooves in the secondary thickenings<br>(figure 5*g*), possibly demonstrating an originally thicker<br>cellulose wall in these examples as in *Gosslingia*. In the evidence of grooves in the secondary thickenings<br>(figure 5*g*), possibly demonstrating an originally thicker<br>cellulose wall in these examples as in *Gosslingia*. In the<br>majority of cases however when viewed from the outsid (figure 5*g*), possibly demonstrating an originally thicker cellulose wall in these examples as in *Gosslingia*. In the majority of cases, however, when viewed from the outside cellulose wall in these examples as in *Gosslingia*. In the majority of cases, however, when viewed from the outside of the cell, the perforate layer is more or less continuous in the vicinity of the tracheids (e.g. figur of the cell, the perforate layer is more or less continuous of the cell, the perforate layer is more or less continuous<br>in the vicinity of the tracheids (e.g. figure  $6a,b$ ). Such<br>observations raise the possibility that the wide zone<br>between the perforated layers in *Gossinnia* is in the vicinity of the tracheids (e.g. figure  $6a,b$ ). Such<br>observations raise the possibility that the wide zone<br>between the perforated layers in *Gosslingia* is at least<br>partially an artefact of pyrite permineralization: observations raise the possibility that the wide zone<br>between the perforated layers in *Gosslingia* is at least<br>partially an artefact of pyrite permineralization: a<br>hypothesis that is currently under experimental investiga between the perforated layers in *Gosslingia* is at least<br>partially an artefact of pyrite permineralization: a<br>hypothesis that is currently under experimental investiga-<br>tion at Cardiff. That the total wall thickness in th partially an artefact of pyrite permineralization: a<br>hypothesis that is currently under experimental investiga-<br>tion at Cardiff. That the total wall thickness in these<br>Lockhovian tracheids is narrower than the coalified la hypothesis that is currently under experimental investiga-<br>tion at Cardiff. That the total wall thickness in these<br>Lochkovian tracheids is narrower than the coalified layer<br>plus pyrite in *Gosslingia* may be of some releva tion at Cardiff. That the total wall thickness in these diminished in that the same taxon is probably not



Figure 5. SEMs: coalified strand with G-type tracheids. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. Name 5. SEMs: coalified strand with G-type tracheids. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian.<br>NMW99.20G.1. (*a*) Fractured cross-section TS. Note homogeneous 'rind' of peripheral tissues. Scale bar =  $\sum_{i=1}^{N}$  IMW99.20G.1. (*a*) Fractured cross-section TS. Note homogeneous 'rind' of peripheral tissues. Scale bar = 10 µm. (*b*) Fractured TS of spiral tracheid. Arrows indicate position of crushed presumed protoxylem. MW99.20G.1. (a) Fractured cross-section TS. Note homogeneous 'rind' of peripheral tissues. Scale bar = 10 µm. (b) Fractured TS. Note in So of spiral tracheid. Arrows indicate position of crushed presumed protoxylem. Scale S of spiral tracheid. Arrows indicate position of crushed presumed protoxylem. Scale bar = 1 µm. (*c*) Fractured TS. Note intacheids and juxtapositioning of the pitting in the interconnecting walls of adjacent tracheids. pparent perforations. Scale bar = 1  $\mu$ m. (*d*) Fractured TS. Tracheid complex at centre of strand. Asterisks indicate possible erminations of tracheids. Scale bar = 5  $\mu$ m. (*e*) Fractured longitudinal section (LS) sho nnular secondary thickenings. Scale bar = 5  $\mu$ m. (*f*) Fractured LS with reticulate pitting. Arrow indicates intervening wall<br>iewed from outside (i.e. by separation of the middle lamella). Scale bar = 10  $\mu$ m. (*g*) Fr erminations of tracheids. Scale bar = 5 µm. (*e*) Fractured longitudinal section (LS) showing unusual globular projections on<br>nullar secondary thickenings. Scale bar = 5 µm. (*f*) Fractured LS with reticulate pitting. Arr mular secondary thickenings. Scale bar = 5 µm. (f) Fractured LS with reticulate pitting. Arrow indicates intervening wall<br>iewed from outside (i.e. by separation of the middle lamella). Scale bar = 10 µm. (g) Fractured LS iewed from outside (i.e. by separation of the midd<br>j ith separation at the middle lamella. Note inter-t:<br>omogeneous in cross-section. Scale bar =  $10 \,\mu m$ .

omogeneous in cross-section. Scale bar =  $10 \mu$ m.<br>avolved. In contrast, Cook & Friedman (1998) have<br>ostulated that the areas of partie within cores of produced. In contrast, Cook & Friedman (1998) have<br>ostulated that the areas of pyrite within cores of<br>econdary thickening and outside the recalcitrant intershow a secondary thickening and outside the recalcitrant inter-<br>enime wall in permineralized G-tune thickenings occurs ostulated that the areas of pyrite within cores of econdary thickening and outside the recalcitrant inter-<br>ening wall in permineralized G-type thickenings occupy

mainly the same regions as the degradation-prone,<br>template layer described in Huberzia tracheids, while mainly the same regions as the degradation-prone,<br>template layer described in *Huperzia* tracheids, while<br>lignified resistant layers correspond to the coalified mainly the same regions as the degradation-prone,<br>template layer described in *Huperzia* tracheids, while<br>lignified resistant layers correspond to the coalified<br>secondary thickenings and intervening layers. Their template layer described in *Huperzia* tracheids, while<br>lignified resistant layers correspond to the coalified<br>secondary thickenings and intervening layers. Their

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Gigure 6. SEMs of presumed conducting tissues. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian.<br>  $P^{1-c}$ ) NMW99.20G.1. (a) Fractured tracheids demonstrating difference in dimensions of pitting in intervening  $a-c$ ) NMW99.20G.1. (*a*) Fractured tracheids demonstrating difference in dimensions of pitting in intervening layers of adjacent ells. Scale bar =  $10 \mu m$ . (*b*) Outside of the tracheid wall as viewed from the middle lamella. Note lack of any major discontinuity  $\sum_{e=0}^{\infty}$  and SMW99.20G.1. (a) Fractured tracheids demonstrating difference in dimensions of pitting in intervening layers of adjacent<br>ells. Scale bar = 10 µm. (*b*) Outside of the tracheid wall as viewed from the mi are less regular and probably interconnected (arrow), and small pits in intervening layer. Scale bar =  $10 \mu m$ . (*c*) Longitudinal fracture where secondary thickenings re less regular and probably interconnected (arrow), sociated with positions of the secondary thickenings. Scale bar = 10 µm. (c) Longitudinal fracture where secondary thickenings<br>re less regular and probably interconnected (arrow), and small pits in intervening layer. Scal re less regular and probably interconnected (arrow), and small pits in intervening layer. Scale bar = 10  $\mu$ m. (*d*) Axial fragme<br>ith central strand. Transversely fractured strand. Surfaces of internal walls of individua ith central strand. Transversely fractured strand. Surfaces of internal walls of individual cells are smooth and extend into lumen,<br>metimes forming an irregular net. NMW99.20G.2. Scale bar = 10 µm.  $(e, f)$  Smooth axis. NMW acture with intact epidermis of cells with evenly thickened walls. Arrow indicates cell magnified in  $(f)$ . Scale bar = 100  $\mu$ m.<br> *f*) Longitudinal fracture of cell with dendritically branched, smooth, wall projections. f) Longitudinal fracture of cell with dendritically branched, smooth, wall projections. Scale bar = 1  $\mu$ m. (g,h) Axis with discrete<br>entral strand. NMW99.20G.4. (g) Irregular fracture showing smooth surface with faint in cale bar = 100  $\mu$ m. (*h*) Fractured TS of strand composed of cells with walls of uniform thickness. Scale bar = 10  $\mu$ m.<br>  $\therefore$ *k*) Longitudinally fractured central cells from smooth axis. NMW99.20G.5. Scale bars = 1 Infaces and globule- to strand-like projections. (*j*) Cell with microperforate layer lining lumen with globular projections.<br>(*i*) Cell with microperforate layer extended into horizontal rod-shaped structures.

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**(b) Cooksonia***-type tracheids* **(** *¢gure 7***j^m)** f) showing microperforate layer covering the projection. Scale bar = 1  $\mu$ m. (f) Transversely fractured cell with complex<br>ortuous' projections. Scale bar = 5  $\mu$ m. (g-i) Axis with enations. NMW99.20G.7. (g) Intact speci h) Stoma. Scale bar = 10 µm. (*i*) Central cell with complex projections in transversely fractured axis. Scale bar = 5 µm.<br> *j*-*m*) Branching axis with one complete tip. NMW99.20G.8. (*j*) Intact specimen. Scale bar = 10  $j-m$ ) Branching axis with one complete tip. NMW99.20G.8. (*j*) Intact specime<br>ip. Scale bar = 50  $\mu$ m. (*l*) Longitudinally fractured central cells, with simple an<br>cale bar = 10  $\mu$ m. (*m*) Stoma on poorly preserved sur

Scale bar =  $10 \mu m$ . (*m*) Stoma on poorly preserved surface. Scale<br>chematic of a G-type tracheid also shows a primary cell<br>call. Infortunately, complete homogenization of the chematic of a G-type tracheid also shows a primary cell<br>vall. Unfortunately, complete homogenization of the vall in the coalified fossils precludes testing of their ypothesis.

(b) Cooksonia-type tracheids (figure 7j-m)<br>Figure 7 shows a bifurcating axial fragment in which a<br>rrower daughter branch terminates as a slight swelling Figure 7 shows a bifurcating axial fragment in which a narrower daughter branch terminates as a slight swelling (figure  $7k$ ). The latter lacks the superficial longitudinal

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FOR FRIED SEEN CHARGES. Trinkling seen on the rest of the specimen, where rare comata are present (figure  $7m$ ), and longitudinally rientated cell walls were not apparent on breaking it vrinkling seen on the rest of the specimen, where rare<br>comata are present (figure  $7m$ ), and longitudinally<br>rientated cell walls were not apparent on breaking it<br>nen Spores could not be identified but it is tempting to omata are present (figure  $7m$ ), and longitudinally rientated cell walls were not apparent on breaking it pen. Spores could not be identified, but it is tempting to onclude that this swollen tip was an immature rientated cell walls were not apparent on breaking it<br>pen. Spores could not be identified, but it is tempting to<br>onclude that this swollen tip was an immature pen. Spores could not be identified, but it is tempting to onclude that this swollen tip was an immature porangium. The fractured proximal end shows cellular reanization except for a couple of elongate longitudinally onclude that this swollen tip was an immature<br>porangium. The fractured proximal end shows cellular<br>rganization except for a couple of elongate longitudinally<br>rights in the couple of elongate longitudinally orangium. The fractured proximal end shows cellular rganization except for a couple of elongate longitudinally rientated elements with transverse, annular thickenings.<br>The cells are narrow  $(< 5 \text{ nm diameter})$  and show no rganization except for a couple of elongate longitudinally<br>rientated elements with transverse, annular thickenings.<br>The cells are narrow  $(< 5 \mu m$  diameter), and show no is rientated elements with transverse, annular thickenings.<br>
The cells are narrow  $(< 5 \mu m$  diameter), and show no<br>
itting in the lateral walls, which are continuous<br>
homogenized) with the thickenings Unfortunately The cells are narrow  $(< 5 \mu m$  diameter), and show no<br>itting in the lateral walls, which are continuous<br>homogenized) with the thickenings. Unfortunately,<br>urber splitting of the specimen failed to provide more itting in the lateral walls, which are continuous<br>homogenized) with the thickenings. Unfortunately,<br>arther splitting of the specimen failed to provide more homogenized) with the thickenings. Unfortunately,<br>arther splitting of the specimen failed to provide more<br>formation on the nature, number or distribution of xther split<br>formation<br>face cells.

Formation on the nature, number or distribution of<br>ese cells.<br>*Comments*: further specimens are clearly needed, but<br>the limited evidence suggests similarities with the such a colls.<br>Comments: further specimens are clearly needed, but<br>ach limited evidence suggests similarities with the<br>cacheids described in *Cooksonia bertoni* from the same **1 Comments:** further specimens are clearly needed, but<br>
acheids described in *Cooksonia pertoni* from the same<br>
leading (Edwards *et al.* 1992) and with those recovered Locality Contract evidence suggests similarities with the cacheids described in *Cooksonia pertoni* from the same<br>(Contract *et al.* 1992) and with those recovered<br>(Contract and a sterile coalified axis from the Unner Silu cacheids described in *Cooksonia pertoni* from the same<br>
cality (Edwards *et al.* 1992) and with those recovered<br>
com a sterile, coalified axis from the Upper Silurian<br>
Whiteliffian) of South Wales The latter are the earl (Edwards *et al.* 1992) and with those recovered come a sterile, coalified axis from the Upper Silurian Whitcliffian) of South Wales. The latter are the earliest emonstrated in an axial fossil (Edwards & Davies 1976) From a sterile, coalified axis from the Upper Silurian<br>Whitcliffian) of South Wales. The latter are the earliest<br>emonstrated in an axial fossil (Edwards & Davies 1976).<br>Awards (1999) suggested that this simple organization Whitcliffian) of South Wales. The latter are the earliest<br>emonstrated in an axial fossil (Edwards & Davies 1976).<br>'dwards (1999) suggested that this simple organization, iz non-perforate, relatively thick-walled cylinder plus futured is ample organization, is non-perforate, relatively thick-walled cylinder plus internal annular thickenings was the primitive integral that secondary wall pitting between thickenings. iz non-perforate, relatively thick-walled cylinder plus<br>that secondary wall pittings was the primitive<br>ype, and that secondary wall pitting between thickenings<br>volved in response to the pressures associated with major For internal annular thickenings was the primitive<br>
ype, and that secondary wall pitting between thickenings<br>
volved in response to the pressures associated with major<br>
vension growth and increased requirements for lateral %, ype, and that secondary wall pitting between thickenings<br>volved in response to the pressures associated with major<br>xtension growth and increased requirements for lateral<br>novement of water volved in response to<br>xtension growth and<br>novement of water. **(c)** *Anomalous conducting cells*

These were all recovered from central parts of axes, are (c) *Anomalous conducting cells*<br>These were all recovered from central parts of axes, are<br>longate and longitudinally aligned, but vary in wall<br>haracters and in associations of the various types. The These were all recovered from central parts of axes, are<br>longate and longitudinally aligned, but vary in wall<br>haracters and in associations of the various types. The<br>se of the term 'secondary thickening' for wall layering longate and longitudinally aligned, but vary in wall<br>haracters and in associations of the various types. The<br>se of the term 'secondary thickening' for wall layering is<br>woulded as there is as yet no information on developme haracters and in associations of the various types. The<br>se of the term 'secondary thickening' for wall layering is<br>voided as there is, as yet, no information on development se of the term 'secondary thickening' for wall layering is<br>voided as there is, as yet, no information on development<br>nd the term has tracheophyte connotations. In many<br>assess the lateral walls of the elongate elements are voided as there is, as yet, no information on development<br>nd the term has tracheophyte connotations. In many<br>ases, the lateral walls of the elongate elements are<br>not about the elongate elements are<br>not probably layered and nd the term has tracheophyte connotations. In many<br>ases, the lateral walls of the elongate elements are<br>ndoubtedly layered and may show extensions, rods that<br>ne or project into the lumen or sometimes folds. They ases, the lateral walls of the elongate elements are ndoubtedly layered and may show extensions, rods that ne or project into the lumen, or sometimes folds. They recalled lumen projections here ndoubtedly layered and may show extensions, rods that<br>ne or project into the lumen, or sometimes folds. They<br>re called lumen projections here.

## (i) *Internally smooth-walled types* (a) *Uniform thickening*<br>(a) *Uniform thickening*<br>les the surface lining

 $\begin{array}{c} \text{(a) Uniform thickening} \\ \text{In these examples, the surface } \text{liming the lumen is} \end{array}$ mooth. Walls of adjacent cells are homogenized and are ot very thick. Such cells are sometimes located at the In these examples, the surface lining the lumen is<br>nooth. Walls of adjacent cells are homogenized and are<br>ot very thick. Such cells are sometimes located at the<br>entre of a strand comprising diverse types (see mooth. Walls of adjacent cells are homogenized and are<br>ot very thick. Such cells are sometimes located at the<br>entre of a strand comprising diverse types (see<br>given  $8c$ ) but in one example (figure  $6a b$ ) are the only the set of a strand comprising diverse types (see agure 8*c*), but in one example (figure 6*g*,*h*) are the only components of a discrete central strand. The surface of entre of a strand comprising diverse types (see<br>gure  $8c$ ), but in one example (figure  $6g$ , $h$ ) are the only<br>omponents of a discrete central strand. The surface of<br>less hort length of naked axis is smooth with broad low Equive 8c), but in one example (figure  $6g,h$ ) are the only *Micropitted*. These fall into two broad categories, both or opponents of a discrete central strand. The surface of with or without projections, that may be flexu represents of a discrete central strand. The surface of<br>also pies marking the elongate, uniformly thickened<br>indermal cells. Stomata are gare. The walls of the The short length of naked axis is smooth with broad, low<br>didlermal cells. Stomata are rare. The walls of the<br>producting cells are approximately the same as those of dges marking the elongate, uniformly thickened<br>pidermal cells. Stomata are rare. The walls of the<br>onducting cells are approximately the same as those of<br>perceptional viewed in SEM at low angles there are pidermal cells. Stomata are rare. The walls of the onducting cells are approximately the same as those of the epidermis. Viewed in SEM at low angles, there are are indications of transverse undulations. The cells are onducting cells are approximately the same as those of<br>the epidermis. Viewed in SEM at low angles, there are<br>one indications of transverse undulations. The cells are<br>olyzonal in fractured transverse section. Longitudinal ne epidermis. Viewed in SEM at low angles, there are<br>ome indications of transverse undulations. The cells are<br>olygonal in fractured transverse section. Longitudinal<br>ceture confirmed that their wide range in diameter ome indications of transverse undulations. The cells are<br>obtgonal in fractured transverse section. Longitudinal<br>cature confirmed that their wide range in diameter<br>obtained in the range in diameter olygonal in fractured transverse section. Longitudinal<br>racture confirmed that their wide range in diameter<br>less from tapering. There is no evidence for any devel-<br>nmental pattern exacture confirmed<br>
exults from tapering<br>
pmental pattern.<br>
Comments: clongs France comments: There is no evidence for any devel-<br>mental pattern.<br>*Comments*: elongate cells with smooth, pitted or non-<br>reforate lateral walls characterize moss hydroids in

pmental pattern.<br>
Comments: elongate cells with smooth, pitted or non-<br>
erforate lateral walls characterize moss hydroids in Comments: elongate cells with smooth, pitted or non-<br>erforate lateral walls characterize moss hydroids in<br>eneral, although the thinner facets, generally quoted as<br>xraing by hydrolysis but now interpreted as resulting erforate lateral walls characterize moss hydroids in eneral, although the thinner facets, generally quoted as resulting by hydrolysis, but now interpreted as resulting *Phil. Trans. R. Soc. Lond.* B (2000) *Phil. Trans. R. Soc. Lond.* B (2000)

from post-mortem cell extension, i.e. without chemical<br>heakdown (I igrone *et al.*, this issue), are not represented from post-mortem cell extension, i.e. without chemical<br>breakdown (Ligrone *et al.*, this issue), are not represented<br>as thinner walls in the fossils (Hébant 1974) from post-mortem cell extension, i.e. witho<br>breakdown (Ligrone *et al.*, this issue), are not<br>as thinner walls in the fossils (Hébant 1974).<br>Elongate, cells, with uniformly, thickened eakdown (Ligrone *et al.*, this issue), are not represented<br>thinner walls in the fossils (Hébant 1974).<br>Elongate cells with uniformly thickened walls also<br>cur in the central regions of axes of Rhynie Chert taxa

as thinner walls in the fossils (Hébant 1974).<br>Elongate cells with uniformly thickened walls also<br>occur in the central regions of axes of Rhynie Chert taxa, Elongate cells with uniformly thickened walls also<br>occur in the central regions of axes of Rhynie Chert taxa,<br>*Aglaophyton* (Edwards, D. S. 1986), while in *Nothia* (El-<br>Saadawy & Lacey 1979) the preserved water-conducting occur in the central regions of axes of Rhynie Chert taxa,<br>Aglaophyton (Edwards, D. S. 1986), while in *Nothia* (El-<br>Saadawy & Lacey 1979) the preserved water-conducting<br>cells are described as 'narrow with no detectable th *Aglaophyton* (Edwards, D. S. 1986), while in *Nothia* (El-Saadawy & Lacey 1979) the preserved water-conducting cells are described as 'narrow with no detectable thick-<br>ening or pitting' although the walls are more intens Saadawy & Lacey 1979) the preserved water-conducting<br>cells are described as 'narrow with no detectable thick-<br>ening or pitting', although the walls are more intensely coloured than in the rest of the tissues apart from the epidermis.

#### (b) *Lumen projections*

Here the surface lining the lumen is again smooth (i.e. not pitted or perforate) but bears various kinds of projections.

pitted or perforate) but bears various kinds of projections.<br>*Dendritic*. The unbranched single specimen has a smooth<br>surface with longitudinal ridges, but is unusual in that the *Dendritic*. The unbranched single specimen has a smooth surface with longitudinal ridges, but is unusual in that the enidermis although preserved is inconspicuous because *Dendritic*. The unbranched single specimen has a smooth surface with longitudinal ridges, but is unusual in that the epidermis, although preserved, is inconspicuous because cortical cells are also preserved, and there is surface with longitudinal ridges, but is unusual in that the<br>epidermis, although preserved, is inconspicuous because<br>cortical cells are also preserved, and there is no well-<br>defined central strand (figure 6e). The latter c epidermis, although preserved, is inconspicuous because<br>cortical cells are also preserved, and there is no well-<br>defined central strand (figure 6*e*). The latter contains at<br>least two cells with numerous irregular lumen pr cortical cells are also preserved, and there is no well-<br>defined central strand (figure  $6e$ ). The latter contains at<br>least two cells with numerous irregular lumen projections<br>that are much branched and completely lack an defined central strand (figure  $6e$ ). The latter contains at<br>least two cells with numerous irregular lumen projections least two cells with numerous irregular lumen projections<br>that are much branched and completely lack any order<br>(figure 6*f*). They may stand free or be adpressed to the<br>cell wall, and are so numerous that the latter are di that are much branched and completely lack any order (figure  $6f$ ). They may stand free or be adpressed to the cell wall, and are so numerous that the latter are difficult to see but do not appear to contain pits (figure  $6f$ ). They may stand free or be adpressed to the cell wall, and are so numerous that the latter are difficult to see, but do not appear to contain pits.

*Comments*: these bizarre cells have no counterparts in extant or coeval plants. Fungal contamination remains a possibility.

*Fretwork*. In these examples the projections may be robust Fretwork. In these examples the projections may be robust<br>or fine, show limited branching and fusion, and may<br>traverse the lumen (figure  $8f$ ) as well as looking like Fretwork. In these examples the projections may be robust<br>or fine, show limited branching and fusion, and may<br>traverse the lumen (figure  $8f$ ) as well as looking like<br>tracheidal annular to pitted secondary thickenings (fi or fine, show limited branching and fusion, and may<br>traverse the lumen (figure  $8f$ ) as well as looking like<br>tracheidal annular to pitted secondary thickenings (figure<br> $8h$ ). The latter are continuous (homogenized) with t traverse the lumen (figure  $8f$ ) as well as looking like tracheidal annular to pitted secondary thickenings (figure  $8h$ ). The latter are continuous (homogenized) with the lateral walls. These examples, some of which show great 8*h*). The latter are continuous (homogenized) with the lateral walls. These examples, some of which show great complexity (e.g. figure 8*k*), come from a central strand of diverse composition (figure 8*c*) in contrast wit lateral walls. These examples, some of which show great<br>complexity (e.g. figure 8*k*), come from a central strand of<br>diverse composition (figure 8*c*) in contrast with similar<br>cells but with less regular thickenings in fi complexity (e.g. figure  $8k$ ), come from a central strand of diverse composition (figure  $8c$ ) in contrast with similar cells, but with less regular thickenings in figure  $6d$  where all the cells are the same. Figure  $8l$ diverse composition (figure  $8c$ ) in contrast with similar cells, but with less regular thickenings in figure  $6d$  where all the cells are the same. Figure  $8l, m$  shows a central strand limited by a thick homogeneous rind cells, but with less regular thickenings in figure  $6d$  where all the cells are the same. Figure  $8l, m$  shows a central strand limited by a thick homogeneous rind, where all the cells although of varying diameter are char all the cells are the same. Figure  $\delta l$ , *m* shows a central strand limited by a thick homogeneous rind, where all the cells, although of varying diameter, are characterized by fine + branched projections strand limited by a thick hom<br>cells, although of varying dia<br>fine ± branched projections.<br>*Comments:* comparisons Ils, although of varying diameter, are characterized by<br>  $c \pm$  branched projections.<br> *Comments*: comparisons with transfer cells may be<br>
propriate here although 'large-scale' pitting is absent

fine  $\pm$  branched projections.<br>Comments: comparisons with transfer cells may be<br>appropriate here, although 'large-scale' pitting is absent<br>in lateral walls in these examples *Comments*: comparisons with the appropriate here, although 'large-sin lateral walls in these examples.

in lateral walls in these examples.<br>*Micropitted*. These fall into two broad categories, both<br>with or without projections, that may be flexuous or *Micropitted*. These fall into two broad categories, both with or without projections, that may be flexuous or straight depending on whether or not the perforate layer Micropitted. These fall into two broad categories, both with or without projections, that may be flexuous or straight, depending on whether or not the perforate layer readily separates from the common homogenized wall with or without projections, that may be flexuous or<br>straight, depending on whether or not the perforate layer<br>readily separates from the common homogenized wall<br>between elements Figure 8g shows an example of a sepastraight, depending on whether or not the perforate layer<br>readily separates from the common homogenized wall<br>between elements. Figure 8*g* shows an example of a sepa-<br>rated layer  $ca$  300 nm thick that is extended into a readily separates from the common homogenized wall<br>between elements. Figure 8g shows an example of a sepa-<br>rated layer *ca*. 300 nm thick that is extended into a<br>?hollow, rod-shaped projection. The perforations, *ca*. 40between elements. Figure 8g shows an example of a separated layer *ca*. 300 nm thick that is extended into a ?hollow, rod-shaped projection. The perforations, *ca*. 40–90 nm diameter, may be simple or surrounded by a narrow rim (figure 8*i*). The latter example also shows Phollow, rod-shaped projection. The perforations,  $ca$ .  $40-90$  nm diameter, may be simple or surrounded by a narrow rim (figure 8*i*). The latter example also shows occasional small globular outgrowths similar to forms 90 nm diameter, may be simple or surrounded by a narrow rim (figure  $8i$ ). The latter example also shows occasional small globular outgrowths similar to forms that dominate the lumen surface of adjacent elements narrow rim (figure 8*i*). The latter example also shows<br>occasional small globular outgrowths similar to forms<br>that dominate the lumen surface of adjacent elements<br> $(f_{\text{curve}} - 8i)$ . It has not yet been possible to determine occasional small globular outgrowths similar to forms<br>that dominate the lumen surface of adjacent elements<br>(figure 8*j*). It has not yet been possible to determine<br>whether or not the perforations are in identical positions that dominate the lumen surface of adjacent elements (figure  $\frac{8j}{5}$ ). It has not yet been possible to determine whether or not the perforations are in identical positions in adjacent cells (i.e. comparable with pit pa (figure  $8j$ ). It has not yet been possible to determine<br>whether or not the perforations are in identical positions<br>in adjacent cells (i.e. comparable with pit pairs) but this<br>seems unlikely. The common homogenized wall i whether or not the perforations are in identical positions<br>in adjacent cells (i.e. comparable with pit pairs) but this<br>seems unlikely. The common homogenized wall is usually far less prominent than that illustrated in figure 8g. In no



 $\text{ar} = 10 \,\mu\text{m}$ . (*m*) Close up of cells with fine smooth strands traversing lumen. Scale bar = 1  $\mu$ m.<br>*hil. Trans. R. Soc. Lond.* B (2000) Figure 8. SEMs of presumed conducting cells. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. (*a*<sup>*k*</sup>) Unbranched smooth coalified axis. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian.<br>(*a*<sup>*k*</sup>) Unbranched smooth coalified axis. NMW96.30G.1. (*a*) Transverse fracture showing stereome and central s Figure 8. SEMs of presumed conducting cells. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian.<br>  $\gamma^{2-k}$ ) Unbranched smooth coalified axis. NMW96.30G.1. (*a*) Transverse fracture showing stereome and central  $\sigma$  a-k) Unbranched smooth coalified axis. NMW96.30G.1. (a) Transverse fracture showing stereome and central strand with <br>
'ell-preserved cells. Scale bar = 100 µm. (*b*) Evenly thickened smooth-walled cells to centre of vell-preserved cells. Scale bar = 100  $\mu$ m. (*b*) Evenly thickened smooth-walled cells to centre of central strand. Arrows indicate wo adjacent cells with additional layer with smooth surface. Scale bar = 1  $\mu$ m. (*c*) wo adjacent cells with additional layer with smooth surface. Scale bar = 1 µm. (c) Oblique longitudinal fracture showing<br>mooth central cells surrounded by those with internal thickenings. Scale bar = 10 µm. (d) Junction b actured cells. To the left, the microperforate lining layer also occurs on projections into the lumen. To the right, cells with small ranular projections on layer lining lumen. Scale bar = 1 µm. (*e*) Rare smooth projecti niformly thickened walls. Scale bar = 1  $\mu$ m. (f) TS cell with complex smooth projections forming a fretwork. Scale bar = 1  $\mu$ m.<br>g) Chaotic appearance in transversely fractured cells produced when microperforate layer per informly thickened walls. Scale bar = 1  $\mu$ m. (*f*) TS cell with complex smooth projections forming a fretwork. Scale bar = *g*) Chaotic appearance in transversely fractured cells produced when microperforate layer b <sup>*g*</sup>) Chaotic appearance in transversely fractured cells produced when microperforate layer becomes detached. Note that pits enetrate the latter (arrows). Scale bar = 1  $\mu$ m. (*i*) Transversely orientated superficial th ar = 10  $\mu$ m. (*i*) Microperforate layer magnified to show rimmed pits and some globules. Scale bar = 1  $\mu$ m. (*j*) Predominantly lobules on surface. Scale bar = 1  $\mu$ m. (*k*) Complex thickenings to margin of strand. S ar = 10 µm. (*i*) Microperforate layer magnified to show rimmed pits and some globules. Scale bar = 1 µm. (*j*) Predominant<br>lobules on surface. Scale bar = 1 µm. (*k*) Complex thickenings to margin of strand. Scale bar = lobules on surface. Scale bar = 1 µm. (*k*) Complex thickenings to margin of strand. Scale bar = 1 ith small discrete central strand. NMW99.20G.9. (*l*) TS complete strand limited by irregular h ar = 10 µm. (*m*) Close up

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xample are adjacent walls completely perforate such that xample are adjacent walls completely perforate such that<br>djacent lumens are in continuity. In rare, as yet not fully<br>westigated examples, the projections are convoluted but xample are adjacent walls completely perforate such that<br>djacent lumens are in continuity. In rare, as yet not fully<br>vestigated examples, the projections are convoluted, but<br>varingly branched and may occupy a considerable diacent lumens are in continuity. In rare, as yet not fully<br>overtigated examples, the projections are convoluted, but<br>paringly branched and may occupy a considerable<br>olume of the lumen (figure  $Re f$ ). In others they are volume of the lumen ( $\theta$ <sub>gy</sub>) are convoluted, but paringly branched and may occupy a considerable olume of the lumen (figure  $\theta$ e,*f*). In others they are dressed to the lumen wall appearing similar to paringly branched and may occupy a considerable<br>olume of the lumen (figure  $\theta e_x f$ ). In others they are<br>dpressed to the lumen wall, appearing similar to<br>econdary thickenings (figure  $6k$ ). They occur in short olume of the lumen (figure  $\partial e_x f$ ). In others they are<br>dpressed to the lumen wall, appearing similar to<br>econdary thickenings (figure  $6k$ ). They occur in short<br>example in a unique example dpressed to the lumen wall, appearing similar to econdary thickenings (figure  $6k$ ). They occur in short engths of unbranched axes and also in a unique example condary thickenings (figure 6*k*). They occur in short<br>ingths of unbranched axes and also in a unique example<br>aring short, apically incomplete enations (figure 7*g*,*i*),<br>there stomata are also present (figure 7*b*). In t example stop in a unique example<br>aring short, apically incomplete enations (figure  $7g_i$ ),<br>there stomata are also present (figure  $7h$ ). In the second<br>are of wall thickening there is no senaration of a perforearing short, apically incomplete enations (figure  $7g_i$ ), there stomata are also present (figure  $7h$ ). In the second ype of wall thickening, there is no separation of a perfor-There stomata are also present (figure 7*h*). In the second ype of wall thickening, there is no separation of a perforte layer and the pores are not parallel-sided but expand,  $\blacktriangleright$  ich that in section they appear as mi ype of wall thickening, there is no separation of a perforte layer and the pores are not parallel-sided but expand,<br>
i uch that in section they appear as minute bordered pits,<br>
ilthough pit pairs are not present (figure 7*a*). The<br>
illontours of exposed surfaces reflect the shape Let that in section they appear as minute bordered pits,<br>Although pit pairs are not present (figure 7a). The<br>Alontours of exposed surfaces reflect the shape of the<br>Anderlying cavities (figure 7d). In addition there are in Ithough pit pairs are not present (figure 7*d*). The<br>Iontours of exposed surfaces reflect the shape of the<br>Inderlying cavities (figure 7*d*). In addition there are indi-<br>Didual globules and groups of smooth + spherical st Funderlying cavities (figure 7*d*). In addition there are indi-<br>idual globules and groups of smooth  $\pm$  spherical struc-<br>lures that may extend into the lumen as chains (figures 6*i* Inderlying cavities (figure 7*d*). In addition there are indi-<br>idual globules and groups of smooth  $\pm$  spherical struc-<br>into the lumen as chains (figures 6*i*) and 7*h*). Adiacent to elements of this type are those idual globules and groups of smooth  $\pm$  spherical struc-<br>ires that may extend into the lumen as chains (figures 6*i*) and 7*b*). Adjacent to elements of this type are those<br>interval well-defined pores but where the inter lacking well-defined pores, but where the internal surface<br>in  $7b$ ). Adjacent to elements of this type are those<br>incidence internal surface<br>ears a reticulum with hevilled edges (figure  $7c$ ). It is and 7*b*). Adjacent to elements of this type are those internal surface ears a reticulum with bevilled edges (figure 7*c*). It is enting to conclude that this is an immature wall teking well-defined pores, but where the internal surface ears a reticulum with bevilled edges (figure  $7c$ ). It is empting to conclude that this is an immature wall.

### (iii) *General comments on functions of cells from comparative anatomy*

Combinations of the various types of presumed (iii) *General comments on functions of cells from comparative*<br> $anatory$ <br>Combinations of the various types of presumed<br>onducting elements described above suggest that diver-Combinations of the various types of presumed<br>onducting elements described above suggest that diver-<br>ty in structure might be related to differences in<br>unction. The most instructive in this respect was the onducting elements described above suggest that diver-<br>ty in structure might be related to differences in<br>inction. The most instructive in this respect was the<br>rand described by Edwards et al. (1998) in an axial ty in structure might be related to differences in inction. The most instructive in this respect was the rand described by Edwards *et al.* (1998) in an axial, parently astomatiferous specimen lacking branching approximation. The most instructive in this respect was the rand described by Edwards  $et al.$  (1998) in an axial, pparently astomatiferous, specimen lacking branching rand described by Edwards *et al.* (1998) in an axial, pparently astomatiferous, specimen lacking branching ut with a prominent stereome. Additional illustrations re presented here (figure  $8a-k$ ). The central strand pparently astomatiferous, specimen lacking branching<br>ut with a prominent stereome. Additional illustrations<br>re presented here (figure  $8a-k$ ). The central strand<br>omnrised at least four cell types, although these may ut with a prominent stereome. Additional illustrations<br>re presented here (figure  $8a-k$ ). The central strand<br>omprised at least four cell types, although these may<br>sterarade (figure  $8b$ ). Its centre is occupied by tubular re presented here (figure  $8a-k$ ). The central strand<br>omprised at least four cell types, although these may<br>itergrade (figure  $8b$ ). Its centre is occupied by tubular<br>lements with essentially smooth (figure  $8c$ ) but someomprised at least four cell types, although these may<br>itergrade (figure 8*c*), Its centre is occupied by tubular<br>lements with essentially smooth (figure 8*c*), but some-<br>mes gently transversely undulating walls (figure 8 tergrade (figure 8*b*). Its centre is occupied by tubular lements with essentially smooth (figure 8*e*), but some-<br>mes gently transversely undulating walls (figure 8*e*), thich in section have a completely uniform feature lements with essentially smooth (figure  $8c$ ), but somemes gently transversely undulating walls (figure  $8e$ ), water-conducting cells is a possibility, but they are far less<br>  $\phi$  hich in section have a completely uniform, featureless regular than tracheidal secondary thicken hich in section have a completely uniform, featureless<br>ppearance, because adjacent walls are homogenized<br>figure 8*b*). Figure 8*e* shows a unique smooth projection.<br>The surrounding cells again have imperforate walls, but ppearance, because adjacent walls are homogenized figure 8*b*). Figure 8*e* shows a unique smooth projection.<br>The surrounding cells again have imperforate walls, but<br>are are extended into smooth rods, sometimes branched<br>r anastomosing and traversing the lumen (figure 8*f* The surrounding cells again have imperforate walls, but<br>are are extended into smooth rods, sometimes branched<br>are anastomosing and traversing the lumen (figure 8*f*), or<br>a adiacent and are continuous with the lateral walls lies are extended into smooth rods, sometimes branched<br>
r anastomosing and traversing the lumen (figure  $8f$ ), or<br>
e adjacent and are continuous with the lateral walls. In<br>
is respect they are similar to secondary thicken r anastomosing and traversing the lumen (figure  $8f$ ), or<br>e adjacent and are continuous with the lateral walls. In<br>is respect they are similar to secondary thickenings figure  $8h$ ). The most complex arrangement is shown in is respect they are similar to secondary thickenings<br>figure  $8h$ ). The most complex arrangement is shown in<br>gure  $8k$ . Elements with detaching microperforate layers<br>cur to the outside of the strand where projections are figure  $8h$ ). The most complex arrangement is shown in gure  $8k$ . Elements with detaching microperforate layers cur to the outside of the strand, where projections are stranged and sometimes appear, quite disorganized gure 8k. Elements with detaching microperforate layers<br>cur to the outside of the strand, where projections are<br>xtensive, and sometimes appear quite disorganized<br>ligning  $g(x, a)$ . Inferences on the functions of the elements ccur to the outside of the strand, where projections are<br>xtensive, and sometimes appear quite disorganized<br>ligure  $8c$ ,*g*). Inferences on the functions of the elements<br>or the hampered by lack of information on the chemis The stensive, and sometimes appear quite disorganized<br>
(algure  $8c$ ,g). Inferences on the functions of the elements<br>
(b) re hampered by lack of information on the chemistry of<br>
(b) re walls In coalified compression fossil The means of the elements<br>  $\sum_{n=1}^{\infty}$  re hampered by lack of information on the chemistry of<br>  $\sum_{n=1}^{\infty}$  re walls. In coalified compression fossils of tracheo-<br>
by the preservation of conducting elements is relate The hampered by lack of information on the chemistry of<br>the walls. In coalified compression fossils of tracheo-<br>hytes, preservation of conducting elements is related to<br> $\}$  energies of the recalcitrant polymer lignin. Phl he walls. In coalified compression fossils of tracheohytes, preservation of conducting elements is related to<br>ne presence of the recalcitrant polymer lignin. Phloem is<br>ot preserved in such fossils. However, the presence of a<br>ider range of cell types in these mesofossils lead a presence of the recalcitrant polymer lignin. Phloem is<br>ot preserved in such fossils. However, the presence of a<br>ider range of cell types in these mesofossils leads to the<br>ossibility, that, predominantly, cellulose, cell, ot preserved in such fossils. However, the presence of a<br>
vider range of cell types in these mesofossils leads to the<br>
ossibility that predominantly cellulose cell walls are<br>  $\sum$  reserved This may denend on wall thicknes rider range of cell types in these mesofossils leads to the ossibility that predominantly cellulose cell walls are  $\Omega$  reserved. This may depend on wall thickness (e.g. in a creame) or even presence of pop-lignin polyphe ossibility that predominantly cellulose cell walls are<br>  $\overline{S}$  reserved. This may depend on wall thickness (e.g. in a<br>  $\overline{S}$  recome) or even presence of non-lignin polyphenols (e.g.<br>  $\overline{S}$  recomes on charactery of reserved. This may depend on wall thickness (e.g. in a creome) or even presence of non-lignin polyphenols (e.g.  $\pm$  e discussion on chemistry of the stereome in *Psilophyton* the functions of the stereome in *Psilophyton*<br>awsonii, Edwards *et al.* 1997). In any event, inferences on<br>ne functions of the cells should not be constrained by<br>reconcentions based on trackeophyte anatomy. awsonii, Edwards et al. 1997). In any event, infer<br>ne functions of the cells should not be constrated reconceptions based on tracheophyte anatomy. reconceptions based on tracheophyte anatomy.<br>*hil. Trans. R. Soc. Lond.* B (2000)

of fossils and the detection of early bryophytes D. Edwards 747<br>The featureless, smooth, relatively thin-walled cells The featureless, smooth, relatively thin-walled cells<br>whose length exceeds  $200 \mu m$ , seen in the centre of the<br>specimen and entirely composing the central strand are The featureless, smooth, relatively thin-walled cells<br>whose length exceeds  $200 \mu m$ , seen in the centre of the<br>specimen and entirely composing the central strand, are<br>closest to bydroids of mosses. The latter as in the fo whose length exceeds  $200 \mu m$ , seen in the centre of the specimen and entirely composing the central strand, are closest to hydroids of mosses. The latter, as in the fossils, are usually strongly tangering with no pitting specimen and entirely composing the central strand, are<br>closest to hydroids of mosses. The latter, as in the fossils,<br>are usually strongly tapering with no pitting or perforaclosest to hydroids of mosses. The latter, as in the fossils,<br>are usually strongly tapering with no pitting or perfora-<br>tions. They are almost invariably surrounded by leptoids.<br>The thinner walls (facets) in moss hydroids are usually strongly tapering with no pitting or perforations. They are almost invariably surrounded by leptoids.<br>The thinner walls (facets) in moss hydroids (e.g. Hébant<br>1974) have not been seen in the fossils, although l tions. They are almost invariably surrounded by leptoids.<br>The thinner walls (facets) in moss hydroids (e.g. Hébant<br>1974) have not been seen in the fossils, although longitud-<br>inally fractured walls of the strand entirely c The thinner walls (facets) in moss hydroids (e.g. Hébant 1974) have not been seen in the fossils, although longitudinally fractured walls of the strand entirely composed of these elements show periodic lens-shaped thickeni 1974) have not been seen in the fossils, although longitud-<br>inally fractured walls of the strand entirely composed of<br>these elements show periodic lens-shaped thickenings<br>corresponding to the undulations noted above. Such inally fractured walls of the strand entirely composed of<br>these elements show periodic lens-shaped thickenings<br>corresponding to the undulations noted above. Such walls<br>adiacent to the lumina also bear irregular films, poss these elements show periodic lens-shaped thickenings<br>corresponding to the undulations noted above. Such walls<br>adjacent to the lumina also bear irregular films, possibly corresponding to the undulations noted above. Such walls<br>adjacent to the lumina also bear irregular films, possibly<br>the residues of cell contents. Uniform wall width charac-<br>terizes the central cells of *Aglaobhyton major* adjacent to the lumina also bear irregular films, possibly<br>the residues of cell contents. Uniform wall width charac-<br>terizes the central cells of *Aglaophyton major*, where an<br>inner core of elongate thin-walled cells lacki the residues of cell contents. Uniform wall width characterizes the central cells of *Aglaophyton major*, where an inner core of elongate thin-walled cells lacking inter-<br>cellular spaces is surrounded by a cylinder of simi terizes the central cells of *Aglaophyton major*, where an<br>inner core of elongate thin-walled cells lacking inter-<br>cellular spaces is surrounded by a cylinder of similar tissue but with thicker walls. In a re-evaluation of the cellular spaces is surrounded by a cylinder of similar tissue but with thicker walls. In a re-evaluation of the central strand of *Aglaophyton*, D. S. Edwards (1986) concluded that (i) the innermost cells were comparable tissue but with thicker walls. In a re-evaluation of the central strand of  $Aglaophyton$ , D. S. Edwards (1986) concluded that (i) the innermost cells were comparable with polytrichaceous hydroids: (ii) they were surrounded central strand of *Aglaophyton*, D. S. Edwards (1986)<br>concluded that (i) the innermost cells were comparable<br>with polytrichaceous hydroids; (ii) they were surrounded<br>by stereids with a presumed structural role: and (iii) t concluded that (i) the innermost cells were comparable<br>with polytrichaceous hydroids; (ii) they were surrounded<br>by stereids with a presumed structural role; and (iii) the<br>outermost tissue, had similarities with moss lentoi with polytrichaceous hydroids; (ii) they were surrounded<br>by stereids with a presumed structural role; and (iii) the<br>outermost tissue had similarities with moss leptoids.<br>However, it should be emphasized that such an arrang by stereids with a presumed structural role; and (iii) the outermost tissue had similarities with moss leptoids.<br>However, it should be emphasized that such an arrangeoutermost tissue had similarities with moss leptoids.<br>However, it should be emphasized that such an arrange-<br>ment has no extact counterpart in extant bryophytes<br>(Edwards 1993) The strand of smooth, thin-walled cells However, it should be emphasized that such an arrange-<br>ment has no extact counterpart in extant bryophytes<br>(Edwards 1993). The strand of smooth, thin-walled cells<br>described here is closer in wall dimensions to those ment has no extact counterpart in extant bryophytes<br>(Edwards 1993). The strand of smooth, thin-walled cells<br>described here is closer in wall dimensions to those<br>surrounding the central zone of putative hydroids. The (Edwards 1993). The strand of smooth, thin-walled cells described here is closer in wall dimensions to those surrounding the central zone of putative hydroids. The described here is closer in wall dimensions to those<br>surrounding the central zone of putative hydroids. The<br>spheres frequently recorded in the two central tissues and<br>also in transfusion cells of *Aglaophyton* (Remy & Hass surrounding the central zone of putative hydroids. The spheres frequently recorded in the two central tissues and also in transfusion cells of *Aglaophyton* (Remy & Hass 1996) and regarded by some as silica artefacts (see spheres frequently recorded in the two central tissues and<br>also in transfusion cells of *Aglaophyton* (Remy & Hass<br>1996) and regarded by some as silica artefacts (see discus-<br>sion in Edwards D. S. 1986: Edwards 1993) have also in transfusion cells of *Aglaophyton* (Remy & Hass 1996) and regarded by some as silica artefacts (see discussion in Edwards, D. S. 1986; Edwards 1993), have not 1996) and regarded by some as silica artefacts (see discussion in Edwards, D. S. 1986; Edwards 1993), have not been seen in these smooth-walled, coalified fossils although spherical structures are present in cells with sion in Edwards, D. S. 1986; Edwards 1993), have not<br>been seen in these smooth-walled, coalified fossils<br>although spherical structures are present in cells with<br>lumen projections. The cells with smooth internal projecbeen seen in these smooth-walled, coalified fossils<br>although spherical structures are present in cells with<br>lumen projections. The cells with smooth internal projec-<br>tions are not so readily compared favourably with although spherical structures are present in cells with<br>lumen projections. The cells with smooth internal projec-<br>tions are not so readily compared favourably with lumen projections. The cells with smooth internal projections are not so readily compared favourably with modern analogues. A structural role for the projections in water-conducting cells is a possibility but they are far tions are not so readily compared favourably with<br>modern analogues. A structural role for the projections in<br>water-conducting cells is a possibility, but they are far less<br>regular than tracheidal secondary thickenings modern analogues. A structural role for the proj<br>water-conducting cells is a possibility, but they a<br>regular than tracheidal secondary thickenings. regular than tracheidal secondary thickenings.<br>(iv) *Comparisons of micropitted cells* 

*deriand data isomera in presence of non-lignin polyphenols (e.g.* coalified fossils here, the microporate layer of the S-type  $\alpha$  discussion on chemistry of the stereome in *Psilophyton* tracheid would be comparable wi A microporate layer lining the lumen characterizes (iv) Comparisons of micropitted cells<br>
A microporate layer lining the lumen characterizes<br>
S-type tracheids (Kenrick *et al.* 1991*a*), now considered<br>
diagnostic of the Rhynionsida including *Rhynia guynne*-A microporate layer lining the lumen characterizes<br>S-type tracheids (Kenrick *et al.* 1991*a*), now considered<br>diagnostic of the Rhyniopsida, including *Rhynia gwynne-*<br>*raughanii* and *Stockmansella* spp (Kenrick & Crane *S*-type tracheids (Kenrick *et al.* 1991*a*), now considered diagnostic of the Rhyniopsida, including *Rhynia gwynne-vaughanii* and *Stockmansella* spp. (Kenrick & Crane 1991; Kenrick *et al.* 1991*b*). In the original de diagnostic of the Rhyniopsida, including *Rhynia gwynne-vaughanii* and *Stockmansella* spp. (Kenrick & Crane 1991;<br>Kenrick *et al.* 1991*b*). In the original descriptions based on demineralized pyrite permineralizations of *Sennicaulis* **Kenrick et al. 1991b**). In the original descriptions based on demineralized pyrite permineralizations of *Sennicaulis* hippocrepiformis, the coalified underlying material occu-<br>pying the position of the primary wall and h demineralized pyrite permineralizations of *Sennicaulis*<br>*hippocrepiformis*, the coalified underlying material occu-<br>pying the position of the primary wall and helical<br>'econdary' thickenings was described as spongy (Kenric hippocrepiformis, the coalified underlying material occupying the position of the primary wall and helical 'secondary' thickenings was described as spongy (Kenrick et al. 1991a). It was suggested that the decay resistance pying the position of the primary wall and helical 'secondary' thickenings was described as spongy (Kenrick *et al.* 1991*a*). It was suggested that the decay resistance of the 'secondary' thickenings was described as spongy (Kenrick *et al.* 1991*a*). It was suggested that the decay resistance of the microporate layer might be due to impregnation with an 'aromatic non-nolygaccharide component' *et al.* 1991*a*). It was suggested that the decay resistance of the microporate layer might be due to impregnation with an 'aromatic non-polysaccharide component' (possibly lignin).<br>A similar explanation would be appropri microporate layer might be due to impregnation with an 'aromatic non-polysaccharide component' (possibly lignin).<br>A similar explanation would be appropriate for the coali-<br>fied residues in the spongy layer, but whether the %the farmulation is a component of the space of the coalisation in the spaces of the spaces in the spaces in the spaces were filled with air, fluid or degradable polysaccharides A similar explanation would be appropriate for the coali-<br>fied residues in the spongy layer, but whether the spaces<br>were filled with air, fluid or degradable polysaccharides<br>such as cellulose or bemicellulose remains conje fied residues in the spongy layer, but whether the spaces<br>were filled with air, fluid or degradable polysaccharides<br>such as cellulose or hemicelluloes remains conjectural. The<br>pores did not extend through this layer, por w were filled with air, fluid or degradable polysaccharides<br>such as cellulose or hemicelluloes remains conjectural. The<br>pores did not extend through this layer, nor was a middle such as cellulose or hemicelluloes remains conjectural. The<br>pores did not extend through this layer, nor was a middle<br>lamella detected. Comparing such organization with the<br>coalified fossils here, the microporate layer of pores did not extend through this layer, nor was a middle lamella detected. Comparing such organization with the coalified fossils here, the microporate layer of the S-type tracheid would be comparable with the inner porat lamella detected. Comparing such organization with the coalified fossils here, the microporate layer of the S-type tracheid would be comparable with the inner porate layer<br>and the sponsy zone with homogenized adjacent wall coalified fossils here, the microporate layer of the S-type tracheid would be comparable with the inner porate layer<br>and the spongy zone with homogenized adjacent walls,<br>which could have been of less uniform composition in the<br>living plant but homogenized on diagenesis. The pores i and the spongy zone with homogenized adjacent walls, which could have been of less uniform composition in the living plant but homogenized on diagenesis. The pores in

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Pitted and possibly perforate walls characterize the he coalified fossils lack any regular helical thickenings.<br>
Pitted and possibly perforate walls characterize the<br>
ydroids of gametophytes of metzgerialean liverworts<br>
Hébant 1977: Frey et al. 1996). The Symbhyggyng type ha Pitted and possibly perforate walls characterize the ydroids of gametophytes of metzgerialean liverworts  $Hébant 1977$ ; Frey *et al.* 1996). The *Symphyogyna* type has the elements of the *symphyogyna* type has Hébant 1977; Frey et al. 1996). The *Symphyogyna* type has een described as most tracheid-like, in that the elongate, Hébant 1977; Frey *et al.* 1996). The *Symphyogyna* type has<br>veen described as most tracheid-like, in that the elongate,<br>very narrow hydroids have walls of uneven thickness.<br>like *et al.* (1996) and Ligrone & Duckett (199 Freen described as most tracheid-like, in that the elongate,<br>Frey narrow hydroids have walls of uneven thickness.<br>Frey *et al.* (1996) and Ligrone & Duckett (1996) have<br>Freently confirmed that the thick wall is cellulose First ery narrow hydroids have walls of uneven thickness.<br>First equal is cellulose, the thick wall is cellulose,<br>Figure that the thick wall is cellulose,<br> $\sum_{r=1}^{\infty}$  is cellulose, First *al.* (1996) and Ligrone & Duckett (1996) have<br>
"ecently confirmed that the thick wall is cellulose,<br>  $\int$  rimary and non-layered, with pits situated at the bases<br>  $\int$  f oblique slit-shaned denressions *ca* 0.3 um of ecently confirmed that the thick wall is cellulose,<br>
for oblique, slit-shaped depressions, *ca*. 0.3 µm diameter,<br>
and a produced around plasmodesmata Perforated Finary and non-layered, with pits situated at the bases<br>
f oblique, slit-shaped depressions,  $ca$ . 0.3  $\mu$ m diameter,<br>
f ond produced around plasmodesmata. Perforated<br>
ramples are probably artefacts of preparation They ar  $\bigcirc$  of oblique, slit-shaped depressions, *ca*. 0.3  $\mu$ m diameter,<br>  $\bigcirc$  nd produced around plasmodesmata. Perforated<br>  $\left\{\n\begin{array}{l}\n\text{samples are probably artefacts of preparation. They are}\n\end{array}\n\right\}$  hus totally unlike any tracheids or the cells described In the produced around plasmodesmata. Perforated xamples are probably artefacts of preparation. They are hus totally unlike any tracheids or the cells described ere In contrast, the SEMs of internal surfaces of xamples are probably artefacts of preparation. They are<br>hus totally unlike any tracheids or the cells described<br>ere. In contrast, the SEMs of internal surfaces of<br>redominantly the end walls (not lateral walls) of ere. In contrast, the SEMs of internal surfaces of redominantly the end walls (not lateral walls) of ere. In contrast, the SEMs of internal surfaces of redominantly the end walls (not lateral walls) of *Iaplomitrium* and *Takakia* look similar to some of the internative degree of the sigmonitied forms (Hébant 1979; Burr redominantly the end walls (not lateral walls) of<br> *Haplomitrium* and *Takakia* look similar to some of the<br>
icropitted forms (Hébant 1979; Burr *et al.* 1974; Ligrone<br> *t al*, this issue) The cells themselves are slightly *d fallomitrium* and *Takakia* look similar to some of the icropitted forms (Hébant 1979; Burr *et al.*, 1974; Ligrone *t al.*, this issue). The cells themselves are slightly more longate than the surrounding parenchymat icropitted forms (Hébant 1979; Burr *et al.* 1974; Ligrone or stomatiferous, on the chemical composition of cell  $t$  *al.*, this issue). The cells themselves are slightly more walls and, most importantly, on fertile parts t al., this issue). The cells themselves are slightly more<br>longate than the surrounding parenchymatous cells, and<br>he non-layered walls are only slightly thicker (cf. the<br>inhly elongate thick-walled cells in  $Sumbbvavna$ ). Héb longate than the surrounding parenchymatous cells, and<br>he non-layered walls are only slightly thicker (cf. the<br>ighly elongate, thick-walled cells in *Symphyogyna*). Hébant<br>1973) considered the *Hablamitrium* pits as truly he non-layered walls are only slightly thicker (cf. the ighly elongate, thick-walled cells in *Symphyogyna*). Hébant 1973) considered the *Haplomitrium* pits as truly perforate nd arising from enlarged plasmodesmata. Such ighly elongate, thick-walled cells in *Symphyogyna*). Hébant 1973) considered the *Haplomitrium* pits as truly perforate nd arising from enlarged plasmodesmata. Such perfo-1973) considered the *Haplomitrium* pits as truly perforate<br>
nd arising from enlarged plasmodesmata. Such perfo-<br>
ated 'pit pairs' have not been seen in the fossils. In<br> *Fakakia* pores also occur in pairs and are derived nd arising from enlarged plasmodesmata. Such perfo-<br>ated 'pit pairs' have not been seen in the fossils. In<br>*Takakia*, pores also occur in pairs and are derived from sp<br>desmodesmata but are much smaller (I igrone *et al*, t ated 'pit pairs' have not been seen in the fossils. In *Takakia*, pores also occur in pairs and are derived from lasmodesmata, but are much smaller (Ligrone *et al.*, this sugare). The speciment described here (figure  $8a-k$ *fakakia*, pores also occur in pairs and are derived from specimen demonstrates the kinds of problems encountered lasmodesmata, but are much smaller (Ligrone *et al.*, this in trying to provide unequivocal evidence for ea dasmodesmata, but are much smaller (Ligrone *et al.*, this sue). The specimen described here (figure  $8a-k$ ), with entral strand composed of cells comparing favourably *i*th moss-like bydroids surrounded by cells with lume sue). The specimen described here (figure  $8a-k$ ), with entral strand composed of cells comparing favourably *i*th moss-like hydroids surrounded by cells with lumen rejections, some of which are micronitted raises the entral strand composed of cells comparing favourably<br> *i*th moss-like hydroids surrounded by cells with lumen<br>
rojections, some of which are micropitted, raises the<br>
ossibility that the latter since not obviously structura rith moss-like hydroids surrounded by cells with lumen rojections, some of which are micropitted, raises the ossibility that the latter, since not obviously structural, rojections, some of which are micropitted, raises the ossibility that the latter, since not obviously structural, zere involved with food conduction. However, the orga-<br>ization of moss lentoids is far simpler with thickene ossibility that the latter, since not obviously structural,<br>
vere involved with food conduction. However, the orga-<br>
ization of moss leptoids is far simpler, with thickened but<br>
and the presence of many vere involved with food conduction. However, the orga-<br>ization of moss leptoids is far simpler, with thickened but<br>ndifferentiated lateral walls and the presence of many,<br>netimes enlarged plasmodesmata in the end walls ization of moss leptoids is far simpler, with thickened but<br>ndifferentiated lateral walls and the presence of many,<br>netimes enlarged, plasmodesmata in the end walls.<br>Nere are no perforated end walls comparable with those ndifferentiated lateral walls and the presence of many,<br>metimes enlarged, plasmodesmata in the end walls.<br>There are no perforated end walls comparable with those<br>angiosperm sieve plates (Hébant 1977: Scheirer 1980) imetimes enlarged, plasmodesmata in the end walls.<br>There are no perforated end walls comparable with those<br>a angiosperm sieve plates (Hébant 1977; Scheirer 1980), but the inclined end walls do resemble the simple sieve reas of sieve cells in certain ferns (Stevenson 1974). In the inclined end walls do resemble the simple sieve<br>reas of sieve cells in certain ferns (Stevenson 1974).<br>Lecently discovered hepatic, food-conducting cells in<br>the complex (Ligrang & Duckett 1994: Asterella) and reas of sieve cells in certain ferns (Stevenson 1974).<br>
decently discovered hepatic, food-conducting cells in<br>
oth complex (Ligrone & Duckett 1994: *Asterella*) and<br>
limple (Ligrone *et al*, this issue) thalloid liverworts seently discovered hepatic, food-conducting cells in oth complex (Ligrone & Duckett 1994: *Asterella*) and limple (Ligrone *et al.*, this issue) thalloid liverworts have the same cytological organization as lentoids with Toth complex (Ligrone & Duckett 1994: *Asterella*) and<br>
limple (Ligrone *et al.*, this issue) thalloid liverworts have<br>
the same cytological organization as leptoids, with<br>
tensively thickened walls and highly structured limple (Ligrone *et al.*, this issue) thalloid liverworts have<br>the same cytological organization as leptoids, with<br>xtensively thickened walls and highly structured plasmo-<br>espath. The latter are sometimes associated with the same cytological organization as leptoids, with<br>attensively thickened walls and highly structured plasmo-<br>esmata. The latter are sometimes associated with depres-<br>ions and hence are comparable with primary pit fields stensively thickened walls and highly structured plasmo-<br>esmata. The latter are sometimes associated with depres-<br>esmand hence are comparable with primary pit fields, esmata. The latter are sometimes associated with depres-<br>ions and hence are comparable with primary pit fields,<br>ut there are no indications of perforations in living cells<br>I irrone *et al*, this issue) ions and hence are comparent there are no indication<br>Ligrone *et al.*, this issue).<br>Perhaps the most striking t there are no indications of perforations in living cells<br>igrone *et al.*, this issue).<br>Perhaps the most striking similarities of the cells with<br>mplex internal projections are with embryon<br>by

Ligrone *et al.*, this issue).<br>Perhaps the most striking similarities of the cells with<br>projections are with embryophyte<br>ransfer cells (Pate & Gunning 1972; Gunning 1977) Perhaps the most striking similarities of the cells with<br>
projections are with embryophyte<br>
ransfer cells (Pate & Gunning 1972; Gunning 1977).<br>
uthough from TEMs the architecture of the cell wall  $\Omega$  omplex internal projections are with embryophyte ransfer cells (Pate & Gunning 1972; Gunning 1977).<br>  $\Omega$  architecture of the cell wall architecture of the cell wall ransfer cells (Pate & Gunning 1972; Gunning 1977).<br>
Ilthough from TEMs the architecture of the cell wall<br>
ngrowths is difficult to comprehend, SEM preparations involving an enzyme-etching method reveal a complex, hree-dimensional branching and anastomous structure,

lasmodesmata-derived, were longer and were much shows transfer cells adjacent to the xylem in a legume nore evenly and densely spaced  $(16 \mu m^{-2})$ . The micropo- root nodule). Such preparations also show primary pit possibly even more complex than those described here but<br>in the same size range (e.g. Briarty 1974, where fig. 9-2 possibly even more complex than those described here but<br>in the same size range (e.g. Briarty 1974, where fig. 9-2<br>shows transfer cells adjacent to the xylem in a legume possibly even more complex than those described here but<br>in the same size range (e.g. Briarty 1974, where fig. 9-2<br>shows transfer cells adjacent to the xylem in a legume<br>root nodule). Such preparations also show primary pi in the same size range (e.g. Briarty 1974, where fig. 9-2 shows transfer cells adjacent to the xylem in a legume<br>root nodule). Such preparations also show primary pit<br>fields of irregular shape (restricted to the cell wall<br>proper) quite uplike the small circular pits in the fossil proper), such preparations also show primary pit<br>fields of irregular shape (restricted to the cell wall<br>proper), quite unlike the small, circular pits in the fossil<br>that occur on an additional inner layer of the wall as we fields of irregular shape (restricted to the cell wall<br>proper), quite unlike the small, circular pits in the fossil<br>that occur on an additional inner layer of the wall as well<br>as on the projections. In that transfer cells proper), quite unlike the small, circular pits in the fossil<br>that occur on an additional inner layer of the wall as well<br>as on the projections. In that transfer cells are widespread<br>today at the junctions between gametophy that occur on an additional inner layer of the wall as well<br>as on the projections. In that transfer cells are widespread<br>today at the junctions between gametophytes and sporophytes in bryophytes and `pteridophytes' (Pate & today at the junctions between gametophytes and sporo-<br>phytes in bryophytes and 'pteridophytes' (Pate &<br>Gunning 1972; Ligrone *et al.* 1993) and occur between<br>gametophytic cortical cells and zygote in *Coleochaete* phytes in bryophytes and 'pteridophytes' (Pate & Gunning 1972; Ligrone *et al.* 1993) and occur between gametophytic cortical cells and zygote in *Coleochaete* (Graham & Wilcox 1983) it is most likely that they Gunning 1972; Ligrone *et al.* 1993) and occur between<br>gametophytic cortical cells and zygote in *Coleochaete*<br>(Graham & Wilcox 1983), it is most likely that they<br>existed in early embryonhytes and that elongate cells of gametophytic cortical cells and zygote in *Coleochaete* (Graham & Wilcox 1983), it is most likely that they existed in early embryophytes and that elongate cells of similar labyrinthian construction were involved not in (Graham & Wilcox 1983), it is most likely that they<br>existed in early embryophytes and that elongate cells of<br>similar labyrinthian construction were involved, not in<br>water transport, but as part of a food-conducting tissue existed in early embryophytes and that elongate cells of<br>similar labyrinthian construction were involved, not in<br>water transport, but as part of a food-conducting tissue<br>system However, the preservation of cells with such similar labyrinthian construction were involved, not in<br>water transport, but as part of a food-conducting tissue<br>system. However, the preservation of cells with such<br>delicate extensions of the cellulose cell wall in coalif water transport, but as part of a food-conducting tissue<br>system. However, the preservation of cells with such<br>delicate extensions of the cellulose cell wall in coalified<br>fossils stretches credulity even in a locality with system. However, the preservation of cells with such delicate extensions of the cellulose cell wall in coalified fossils stretches credulity even in a locality with fossils showing such exceptional preservation. Neverthele delicate extensions of the cellulose cell wall in coalified<br>fossils stretches credulity even in a locality with fossils<br>showing such exceptional preservation. Nevertheless,<br>these new fossils do exhibit strands of diverse c fossils stretches credulity even in a locality with fossils<br>showing such exceptional preservation. Nevertheless,<br>these new fossils do exhibit strands of diverse cells, for the<br>most part not readily nor exactly matched by t showing such exceptional preservation. Nevertheless,<br>these new fossils do exhibit strands of diverse cells, for the<br>most part not readily nor exactly matched by those in<br>extant conducting cells. More information is now nee these new fossils do exhibit strands of diverse cells, for the most part not readily nor exactly matched by those in extant conducting cells. More information is now needed most part not readily nor exactly matched by those in<br>extant conducting cells. More information is now needed<br>on the nature of the axes, e.g. whether or not branching<br>or stomatiferous, on the chemical composition of cell extant conducting cells. More information is now needed<br>on the nature of the axes, e.g. whether or not branching<br>or stomatiferous, on the chemical composition of cell<br>walls and most importantly on fertile parts, be they on the nature of the axes, e.g. whether or not branching<br>or stomatiferous, on the chemical composition of cell<br>walls and, most importantly, on fertile parts, be they<br>gametophytic or sporophytic gametophytic or sporophytic.

### **4. RECOGNITION OF EARLY BRYOPHYTES: A CASE HISTORY**

**THE FORTH THE FOLLOWING STATE STATES. A CASE**<br> **HISTORY**<br>
The following account of a solitary, very fragmentary<br>
recimen demonstrates the kinds of problems encountered SPORT<br>The following account of a solitary, very fragmentary<br>specimen demonstrates the kinds of problems encountered<br>in trying to provide unequivocal evidence for early bryo-The following account of a solitary, very fragmentary<br>specimen demonstrates the kinds of problems encountered<br>in trying to provide unequivocal evidence for early bryo-<br>phytes in the fossil record specimen demonstrates the kinds of problems encountered

### **(a)** *Description* **(** *¢gures 9 and 10***)**

The coalified axial fragment,  $ca. 600 \,\mu m$  long and  $130 \,\mu m$  wide, has a saucer-shaped expansion at one end The coalified axial fragment,  $ca$ .  $600 \mu m$  long and  $130 \mu m$  wide, has a saucer-shaped expansion at one end that is presumed to be the distal (figure  $9a-d$ ). The axial part shows gross striction and irregular longitudina 130  $\mu$ m wide, has a saucer-shaped expansion at one end<br>that is presumed to be the distal (figure  $9a-d$ ). The axial<br>part shows gross striation and irregular, longitudinal<br>ridging suggestive of some shrinkage. Its surface part shows gross striation and irregular, longitudinal<br>ridging, suggestive of some shrinkage. Its surface also has part shows gross striation and irregular, longitudinal<br>ridging, suggestive of some shrinkage. Its surface also has<br>some transverse ribbing, but microscopically is generally<br>smooth except for occasional small, crater-like b ridging, suggestive of some shrinkage. Its surface also has<br>some transverse ribbing, but microscopically is generally<br>smooth except for occasional, small, crater-like bodies<br>that are more prominent on the terminal expansio some transverse ribbing, but microscopically is generally<br>smooth except for occasional, small, crater-like bodies<br>that are more prominent on the terminal expansion<br>(figure  $9a$ ) At the proximal fractured surface, the axis smooth except for occasional, small, crater-like bodies<br>that are more prominent on the terminal expansion<br>(figure 9*g*). At the proximal fractured surface, the axis is that are more prominent on the terminal expansion<br>(figure 9g). At the proximal fractured surface, the axis is<br>limited by a superficial homogeneous layer, *ca*. 3.0  $\mu$ m<br>thick extended into longitudinal ridges (figure 9e) (figure 9*g*). At the proximal fractured surface, the axis is limited by a superficial homogeneous layer,  $ca$ . 3.0  $\mu$ m thick, extended into longitudinal ridges (figure 9*e*), although near the margins there are structur limited by a superficial homogeneous layer,  $ca$ .  $3.0 \mu m$ <br>thick, extended into longitudinal ridges (figure  $9e$ ),<br>although near the margins, there are structures suggestive<br>of thick-walled epidermal cells, whose inner wal thick, extended into longitudinal ridges (figure  $9e$ ), although near the margins, there are structures suggestive of thick-walled epidermal cells, whose inner walls are thinner than the outer Unfortunately this area is d although near the margins, there are structures suggestive<br>of thick-walled epidermal cells, whose inner walls are<br>thinner than the outer. Unfortunately, this area is disor-<br>ganized and it is impossible to detect any furthe of thick-walled epidermal cells, whose inner walls are thinner than the outer. Unfortunately, this area is disorganized and it is impossible to detect any further cell layers although irregular voids may be evidence for th thinner than the outer. Unfortunately, this area is disor-<br>ganized and it is impossible to detect any further cell<br>layers, although irregular voids may be evidence for this<br>(figure  $9e$ ). There are no indications of a dis ganized and it is impossible to detect any further cell layers, although irregular voids may be evidence for this<br>(figure  $9e$ ). There are no indications of a distinct cuticle.<br>The central area is occupied by a number of compressed,<br>smooth-walled, bodies, with, rounded, topogr (figure  $9e$ ). There are no indications of a distinct cuticle.<br>The central area is occupied by a number of compressed,<br>smooth-walled bodies with rounded topography and<br>some adhering grapules (figure  $9e$ ). These are spore The central area is occupied by a number of compressed,<br>smooth-walled bodies with rounded topography and<br>some adhering granules (figure 9*e*). These are spore<br>tetrads The avis widens to 330 um distally. The surface smooth-walled bodies with rounded topography and<br>some adhering granules (figure  $9e$ ). These are spore<br>tetrads. The axis widens to  $330 \,\mu m$  distally. The surface some adhering granules (figure  $9e$ ). These are spore<br>tetrads. The axis widens to  $330 \mu m$  distally. The surface<br>ridging is not present on the expanded bevelled margin,<br>although the presumed cuticle itself is continuous o tetrads. The axis widens to  $330 \mu m$  distally. The surface ridging is not present on the expanded bevelled margin, although the presumed cuticle itself is continuous over the rim (form  $10a/c$ ) where it becomes irregularly ridging is not present on the expanded bevelled margin, although the presumed cuticle itself is continuous over the rim (figure  $10a-c$ ), where it becomes irregularly frag-<br>mented Where it bas broken away a reticulum of although the presumed cuticle itself is continuous over the<br>rim (figure  $10a-c$ ), where it becomes irregularly frag-<br>mented. Where it has broken away, a reticulum of<br>shallow isodiametric cells is seen below (asterisk in rim (figure  $10a-c$ ), where it becomes irregularly fragmented. Where it has broken away, a reticulum of shallow, isodiametric cells is seen below (asterisk in

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**b**ars ≤ 10. SEMs: unnamed specimen. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. NMW99.20G.10. Scale ars = 10 μm except (*a*). (*a*) Intact specimen with terminal expansion. Scale bar = 100 μm. (*b*) T Solution of the tetrad within hollow central area with terminal expansion. Scale bar = 100  $\mu$ m. (*b*) Terminal expansion from above.<br>
Note tetrad within hollow central area with incomplete lobed collar. (*c*) Same viewe  $\alpha$  ars = 10 µm except (*a*). (*a*) Intact specimen with terminal expansion. Scale bar = 100 µm. (*b*) Terminal expansion from about the looked collar continuity of superficial layer (?cuticle). (*e*) Fractured base of a Superficial thin hollow central area with incomplete lobed collar. (*c*) Same viewed from side. Note collar and possible elater<br>arrow). (*d*) Terminal expansion from below demonstrating continuity of superficial layer (?c sports). (*d*) Terminal expansion from below demonstrating continuity of superficial layer (?cuticle). (*e*) Fractured base of<br>Pecimen. Note superficial thick walls and tetrads (arrows). (*f*) Surface of terminal expansion elater lodged between collar and surface of terminal expansion ( $f$ ) Surface ore, end of ?elater (arrow) and periclinal fracture through epidermis later lodged between collar and surface of terminal expansion (top).

ater longed between conar and surface of terminal expansion (i)<br>gure 9*f*). From above, the central area of the terminal<br>expansion is seen as a hollow cylinder (now compressed) gure 9 $f$ ). From above, the central area of the terminal<br>Departsion is seen as a hollow cylinder (now compressed)<br> $\frac{1}{2}$ , 135 um diameter and lined by an irregular, ridged wall gure  $9f$ ). From above, the central area of the terminal<br>  $2 \times 135 \mu m$  diameter and lined by an irregular, ridged wall<br>  $2 \times 135 \mu m$  diameter and lined by an irregular, ridged wall<br>  $2 \times 135 \mu m$  evidence for distinct cell Expansion is seen as a hollow cylinder (now compressed)<br>  $\lambda$ . 135  $\mu$ m diameter and lined by an irregular, ridged wall<br>
icking any evidence for distinct cells, although the<br>
interest serves it comprised a layer of thick  $\alpha$ . 135 µm diameter and lined by an irregular, ridged wall icking any evidence for distinct cells, although the actured surface suggests it comprised a layer of thick-<br>valled cells with small lumens (figure 10 $e$ ). Its acking any evidence for distinct cells, although the microscopically smooth, except for adhering irregular

particles. Distally, the central cavity is limited by a very<br>smooth singulike structure that is marginally and particles. Distally, the central cavity is limited by a very<br>smooth, ring-like structure that is marginally and<br>centrifurally lobed with rounded contours (figures 96.6) particles. Distally, the central cavity is limited by a very smooth, ring-like structure that is marginally and centrifugally lobed with rounded contours (figures  $9b,c$  and  $10a-d$ ). It has not been possible to demonstrate centrifugally lobed with rounded contours (figures  $9b,c$ <br>and  $10a-d$ ). It has not been possible to demonstrate conti-<br>muity between this 'collar' and the ridged interior of the<br>cavity Indeed, the lobed edge overlaps the ce and  $10a-d$ ). It has not been possible to demonstrate continuity between this 'collar' and the ridged interior of the cavity. Indeed, the lobed edge overlaps the centripetally sloping margin that becomes increasingly disor nuity between this 'collar' and the ridged interior of the cavity. Indeed, the lobed edge overlaps the centripetally sloping margin that becomes increasingly disorganized in

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Figure 10. SEMs: unnamed specimen. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. NMW99.20G.10. Scale bars  $\frac{1}{2}$  igure 10. SEMs: unnamed specimen. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. NMW99.20G.10.<br>Cale bars = 10 µm, except in (*g*), (*i*) and (*p*). (*a*<sup>*-c*)</sup> Longitudinally fractured sport 10. SEMs: unnamed specimen. North Brown Clee Hill, Shropshire. Lochkovian, Lower Devonian. NMW99.20G.10.<br>Cale bars = 10 µm, except in  $(g)$ ,  $(i)$  and  $(p)$ .  $(a-c)$  Longitudinally fractured terminal expansion showing re porangial wall. (*d*) Fragmented inner surface of the 'axis' just below the collar. Note smooth longitudinal ridging and adhering<br>etrads. Arrow indicates possible elater. (*e*) Transverse fracture of hollow cylinder at bas porangial wall. (d) Fragmented inner surface of the 'axis' just below the collar. Note smooth longitudinal ridging and adhering<br>etrads. Arrow indicates possible elater. (*e*) Transverse fracture of hollow cylinder at base trads. Arrow indicates possible elater. (*e*) Transverse fracture of hollow cylinder at base of terminal expansion showing lack of<br>  $\hat{f}$  by cellular detail (outside at top) in cylinder surrounding the spores. (*f*) Pos we cellular detail (outside at top) in cylinder surrounding the spores. (f) Possible elater. (g,h) Close-up of surface of elater in f). (g) Scale bar = 1  $\mu$ m. (*i*) Fractured elater. Internal thickening indicated by arr f). (g) Scale bar = 1 µm. (i) Fractured elater. Internal thickening indicated by arrow. Scale bar = 1 µm. ( $j-l,n$ ) Intact tetrads<br>vith predominantly smooth surface to ?envelope. Note some indications of separation particul tetrad with debris obliterating exposed proximal surfaces. ( *<sup>p</sup>*) Part of (*m*) magni¢ed showing microgranular surface and possible urface of exotic monad with triradiate<br>
etrad with debris obliterating exposed<br>
dhering bacteria. Scale bar = 5 µm.

theiring bacteria. Scale bar = 5  $\mu$ m.<br>
his area. However, the isolated fragment illustrated in<br>
gure  $10a-c$  shows that the superficial sloughing off layer his area. However, the isolated fragment illustrated in gure  $10a-c$  shows that the superficial sloughing-off layer f the terminal expansion is continuous with the lower his area. However, the isolated fragment illustrated in gure  $10a-c$  shows that the superficial sloughing-off layer f the terminal expansion is continuous with the lower nexposed surface of the recurved flap, while its exp urface is continuous with the thick walls forming the

gure  $10a-c$  shows that the superficial sloughing-off layer superficial layer (figure  $10a-c$ ). In contrast, the cells of the f the terminal expansion is continuous with the lower surface of the terminal expansion have thin  $\sum_{n=1}^{\infty}$  inner periclinal and anticlinal walls of the cells of the superficial layer (figure  $10a-c$ ). In contrast, the cells of the inner periclinal and anticlinal walls of the cells of the superficial layer (figure  $10a$ <sup>-*c*</sup>). In contrast, the cells of the lower surface of the terminal expansion have thinner inner periclinal and anticlinal walls of the cells of the superficial layer (figure  $10a-c$ ). In contrast, the cells of the lower surface of the terminal expansion have thinner walls but it is impossible to determine if th superficial layer (figure  $10a-c$ ). In contrast, the cells of the than one layer of cells in this region. The superficial cells

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FIFT CREAR CREAR CREAR CREAR CREAR CREAR CREAR CREAR TO THE PROPERTY OF THE PROPERTY OF SUITS AND THE PLACE OF THE PLA re more or less isodiametric in surface view on tu become more elongate on the lower surface.<br>Adhering to the sides of the hollow cylinder are E more or less isodiametric in surface view on the edge,<br>t become more elongate on the lower surface.<br>Adhering to the sides of the hollow cylinder are tetrads<br>spores (figure  $10d e$ ). Occasional tetrads and a monad

ut become more elongate on the lower surface. In both cases, the spores are monads with triradiate<br>Adhering to the sides of the hollow cylinder are tetrads marks. The spores described here are in tetrads and in<br>f spores (f **BIOLOGICAL**<br>SCIENCES Adhering to the sides of the hollow cylinder are tetrads<br>
f spores (figure  $10d,e$ ). Occasional tetrads and a monad<br>
ith triradiate apertural fold also occur on the rim<br>
figure  $9b$  f) together with a short cylindrical str f spores (figure  $10d,e$ ). Occasional tetrads and a monad<br>ith triradiate apertural fold also occur on the rim<br>figure  $9b, f$ ), together with a short, cylindrical structure<br>ith broad superficial grooves (figure  $9b$ ) and a l *i*th triradiate apertural fold also occur on the rim figure  $9b$ ,  $f$ ), together with a short, cylindrical structure *i*th broad, superficial grooves (figure  $9b$ ), and a longer  $-$ ut less 'complete' tubular structure wi figure  $9b, f$ ), together with a short, cylindrical structure<br>ith broad, superficial grooves (figure  $9b$ ), and a longer<br>ut less 'complete' tubular structure with no obvious<br>nerficial details except for faint sporadic broa The broad, superficial grooves (figure 9*h*), and a longer<br>in the less 'complete' tubular structure with no obvious<br>perficial details except for faint sporadic broad ridges<br>figure  $10f-h$ ). The former is interpreted as a c The less 'complete' tubular structure with no obvious<br>perficial details except for faint sporadic broad ridges<br>figure 10*f*<sup>-*h*</sup>). The former is interpreted as a cast of a<br>ructure with internal ridging. The tetrads (figu perficial details except for faint sporadic broad ridges<br>figure  $10f-h$ ). The former is interpreted as a cast of a<br>ructure with internal ridging. The tetrads (figure  $10j-n$ <br> $\frac{1}{2}$ ,  $\frac{31 \text{ um}}{28-35 \text{ um}}$ ;  $n=7$ ) in dia figure 10*f-h*). The former is interpreted as a cast of a ructure with internal ridging. The tetrads (figure  $10j-n$ ) *n*. 31  $\mu$ m (28–35  $\mu$ m; *n* = 7) in diameter are essentially ructure with internal ridging. The tetrads (figure  $10j-n$ )<br>
z. 31  $\mu$ m (28–35  $\mu$ m;  $n = 7$ ) in diameter are essentially<br>  $\pm$  nooth-walled, but with some adhering granules. *i*. 31  $\mu$ m (28–35  $\mu$ m; *n* = 7) in diameter are essentially nooth-walled, but with some adhering granules.<br>Figure 10*k* shows an exceptional specimen where the alranules are more or less evenly spaced. Using crypto- $\bullet$  nooth-walled, but with some adhering granules.<br> $\bullet$  igure 10*k* shows an exceptional specimen where the ranules are more or less evenly spaced. Using cryptosigure  $10k$  shows an exceptional specimen where the larger values are more or less evenly spaced. Using crypto-<br>spore terminology, they are fused in the sense that in the largerity there is no line marking the junction b  $\Box$  ranules are more or less evenly spaced. Using crypto-<br>  $\Box$  pore terminology, they are fused in the sense that in the<br>  $\Box$  pajority there is no line marking the junction between ajority there is no line marking the junction between<br>
dividual components, and the junction between three<br>
by a depressed  $\pm$  triangular area.<br>
Lowever all specimens show indications of splitting into dividual components, and the junction between three<br>Doores is marked by a depressed  $\pm$  triangular area.<br>Iowever, all specimens show indications of splitting into<br>marate components (e.g. figure 10/*n*). The latter have a individual components, and the junction between three Soores is marked by a depressed  $\pm$  triangular area.<br>Iowever, all specimens show indications of splitting into<br>parate components (e.g. figure  $10l,n$ ). The latter have a<br>ronounced equatorial thickening accentuated by inva Iowever, all specimens show indications of splitting into parate components (e.g. figure  $10l,n$ ). The latter have a ronounced equatorial thickening accentuated by invagimounced equatorial thickening accentuated by invagiated distal surfaces. One specimen shows evidence of<br>process complete separation but, unfortunately, detritus<br>becures the criginal contact areas and any haptetynic ated distal surfaces. One specimen shows evidence of<br>pore complete separation but, unfortunately, detritus<br>bscures the original contact areas and any haptotypic<br>estures (figure  $10a$ ). The monad with distinct trivaliate ated distal surfaces. One specimen shows evidence of for the separation but, unfortunately, detritus<br>bscures the original contact areas and any haptotypic<br>atures (figure  $10b$ ). The monad with distinct triradiate<br>ark in figure  $10b$  is unlikely to be related to the tetrads bscures the original contact areas and any haptotypic extures (figure  $10\rho$ ). The monad with distinct triradiate nark in figure  $10\rho$  is unlikely to be related to the tetrads rank in figure  $10\dot{p}$  is unlikely to be related to the tetrads<br>s it has a minute granular ornament on all surfaces. The<br>gure also shows adhering putative bacteria, but whether<br>get are recent or very ancient contaminant s it has a minute granular ornament on all surfaces. The<br>gure also shows adhering putative bacteria, but whether<br>nese are recent or very ancient contaminants cannot be<br>ecided I suspect the former s it has a minute granular ornament on all surfaces. The gure also shows adhering puta<br>nese are recent or very anciencided. I suspect the former.

### **(b)** *Discussion*

The nature of terminal expansion is conjectural. Is it he sporangium? Or is it part of a complex terminal The nature of terminal expansion is conjectural. Is it<br>ne sporangium? Or is it part of a complex terminal<br>ehiscence structure of an elongate sporangium? The<br>resumed hollow ?cuticle-lined cylindrical structure is e sporangium? Or is it part of a complex terminal<br>ehiscence structure of an elongate sporangium? The<br>resumed hollow, ?cuticle-lined cylindrical structure is<br>uite unlike anything else encountered in the Lochkovian ehiscence structure of an elongate sporangium? The<br>resumed hollow, ?cuticle-lined cylindrical structure is<br>uite unlike anything else encountered in the Lochkovian<br>semblage or indeed elsewhere. It is certainly not a resumed hollow, ?cuticle-lined cylindrical structure is<br>uite unlike anything else encountered in the Lochkovian<br>semblage, or indeed elsewhere. It is certainly not a<br>onventional axis with central strand, and the presence of uite unlike anything else encountered in the Lochkovian<br>ssemblage, or indeed elsewhere. It is certainly not a<br>onventional axis with central strand, and the presence of<br>organism the presumed provimal end suggests the whole ssemblage, or indeed elsewhere. It is certainly not a<br>onventional axis with central strand, and the presence of<br>ores in the presumed proximal end suggests the whole<br>virture was fertile. It is tempting to compare the <sup>2</sup>cut bores in the presumed proximal end suggests the whole<br>tructure was fertile. It is tempting to compare the ?cutiproces in the presumed proximal end suggests the whole<br>intervals fertile. It is tempting to compare the ?cuti-<br>ularized layer lining the cavity as homologous with the<br>properties produced by the tanetum in a variety The sport was fertile. It is tempting to compare the ?cuti-<br>ularized layer lining the cavity as homologous with the<br>produced by the tapetum in a variety<br>f I ower Devonian plants e  $\alpha$  Resilities (Edwards et al. orangial linings produced by the tapetum in a variety f Lower Devonian plants, e.g. *Resilitheca* (Edwards *et al.* 1995) and *Psilophyton* (Banks *et al.* 1975). Such an interpretation (viz elongate sporangium with distal dehis-(995) and *Psilophyton* (Banks *et al.* 1975). Such an inter-<br>retation (viz elongate sporangium with distal dehis-<br>rence) finds no counterpart in extant embryophytes.<br>Lowever elongate sporangia characterize the Anthoceroretation (viz elongate sporangium with distal dehis-<br>lence) finds no counterpart in extant embryophytes.<br>Lowever, elongate sporangia characterize the Anthocero- $\Gamma$  ence) finds no counterpart in extant embryophytes.<br>
Iowever, elongate sporangia characterize the Anthocero-<br>
les, where the central part of the sporangium is<br>
counied by a columella that produces the pseudoelaters Iowever, elongate sporangia characterize the Anthocero-<br>Jales, where the central part of the sporangium is<br>cupied by a columella that produces the pseudoelaters. Jales, where the central part of the sporangium is<br>
ccupied by a columella that produces the pseudoelaters.<br>
ince this region has already decomposed in the mature<br>
corangium it is broadly similar to the fossil. A major ccupied by a columella that produces the pseudoelaters.<br>Since this region has already decomposed in the mature<br>orangium, it is broadly similar to the fossil. A major<br>ifference relates to debiscence. In anthocerotes, the wa ince this region has already decomposed in the mature<br>
porangium, it is broadly similar to the fossil. A major<br>
ifference relates to dehiscence. In anthocerotes, the wall<br>
elits into two valves. In the fossil, the recurve splits into the fossil. A major<br>ifference relates to dehiscence. In anthocerotes, the wall<br>of the recurved lobed<br>of the recurved lobed<br>of the recurved lobed<br>of the recurved lobed<br>of the surface of the terminal ifference relates to dehiscence. In anthocerotes, the wall<br>plits into two valves. In the fossil, the recurved lobed<br>ollar is an extension of the surface of the terminal<br>pransion which probably initially formed the roof of plits into two valves. In the fossil, the recurved lobed<br>ollar is an extension of the surface of the terminal<br>xpansion, which probably initially formed the roof of the<br>corangial cavity but then split centrifugally and curv ollar is an extension of the surface of the terminal<br>
xpansion, which probably initially formed the roof of the<br>  $\bigcirc$  orangial cavity but then split centrifugally and curved<br>
utwards producing a large central pore for sp really spansion, which probably initially formed the roof of the<br>Dorangial cavity but then split centrifugally and curved<br>utwards, producing a large central pore for spore<br>scape. Distal poral debiscence is rare in early la porangial cavity but then split centrifugally and curved<br>utwards, producing a large central pore for spore<br>scape. Distal poral dehiscence is rare in early land<br>lants being recorded only in a bifurcating cylindrical utwards, producing a large central pore for spore<br>scape. Distal poral dehiscence is rare in early land<br>lants, being recorded only in a bifurcating cylindrical<br>organism containing Emphanisharites of micromatus from he Welsh Borderland locality and in *Horneophyton* 

(Edwards & Richardson  $(2000)$  and discussion therein).<br>In both cases, the spores are monads with triradiate<br>marks. The spores described here are in tetrads and in (Edwards & Richardson  $(2000)$  and discussion therein).<br>In both cases, the spores are monads with triradiate<br>marks. The spores described here are in tetrads and in<br>some cases resemble permanent tetrads, with no sutures In both cases, the spores are monads with triradiate<br>marks. The spores described here are in tetrads and in<br>some cases resemble permanent tetrads, with no sutures<br>between individual monads. In this state, they would be marks. The spores described here are in tetrads and in<br>some cases resemble permanent tetrads, with no sutures<br>between individual monads. In this state, they would be<br>assigned to the dispersed taxon *Cheilotetras*. Most hav some cases resemble permanent tetrads, with no sutures<br>between individual monads. In this state, they would be<br>assigned to the dispersed taxon *Cheilotetras*. Most have<br>laevigate distal surfaces—the irregular adhering part between individual monads. In this state, they would be assigned to the dispersed taxon *Cheilotetras*. Most have laevigate distal surfaces—the irregular, adhering particles may demonstrate microbial activity or may be ext assigned to the dispersed taxon *Cheilotetras*. Most have laevigate distal surfaces—the irregular, adhering particles may demonstrate microbial activity or may be extra-<br>exosporal residues They are not considered a part of laevigate distal surfaces—the irregular, adhering particles<br>may demonstrate microbial activity or may be extra-<br>exosporal residues. They are not considered a part of wall<br>ornament. However, as is the case with the *in situ* may demonstrate microbial activity or may be extra-<br>exosporal residues. They are not considered a part of wall<br>ornament. However, as is the case with the *in situ* tetrads<br>illustrated in figures 2 and 3 some show indicatio ornament. However, as is the case with the *in situ* tetrads illustrated in figures 2 and 3, some show indications of ornament. However, as is the case with the *in situ* tetrads illustrated in figures 2 and 3, some show indications of separation, with remarkably 'clean' fracture lines.<br>Frustratingly in the one showing most separation illustrated in figures 2 and 3, some show indications of<br>separation, with remarkably 'clean' fracture lines.<br>Frustratingly, in the one showing most separation<br>(figure 10a) happtotypic features are obscured by debris. It Frustratingly, in the one showing most separation (figure 10*o*), haptotypic features are obscured by debris. It is tempting to relate these tetrads to examples thought to Frustratingly, in the one showing most separation<br>(figure 10*0*), haptotypic features are obscured by debris. It<br>is tempting to relate these tetrads to examples thought to<br>demonstrate henatic affinities in Ordovician and S (figure 10 $\sigma$ ), haptotypic features are obscured by debris. It<br>is tempting to relate these tetrads to examples thought to<br>demonstrate hepatic affinities in Ordovician and Silurian<br>early land plants, or possibly to consid demonstrate hepatic affinities in Ordovician and Silurian<br>early land plants, or possibly to consider them as being demonstrate hepatic affinities in Ordovician and Silurian<br>early land plants, or possibly to consider them as being<br>produced by relict populations of the plants that first<br>evolved separation of tetrads for dispersal in the early land plants, or possibly to consider them as being<br>produced by relict populations of the plants that first<br>evolved separation of tetrads for dispersal in the Late<br>Ordovician/Early Silurian (Steemans et al. 1996). As produced by relict populations of the plants that first<br>evolved separation of tetrads for dispersal in the Late<br>Ordovician/Early Silurian (Steemans *et al.* 1996). Asso-<br>ciated with the spores are two structures one tubula evolved separation of tetrads for dispersal in the Late<br>Ordovician/Early Silurian (Steemans *et al.* 1996). Asso-<br>ciated with the spores are two structures, one tubular and<br>one a cast, that may be elaters. The cast of a tu Ordovician/Early Silurian (Steemans *et al.* 1996). Asso-<br>ciated with the spores are two structures, one tubular and<br>one a cast, that may be elaters. The cast of a tubular<br>lumen has spiral or annular depressions that are ciated with the spores are two structures, one tubular and<br>one a cast, that may be elaters. The cast of a tubular<br>lumen has spiral or annular depressions that are broad one a cast, that may be elaters. The cast of a tubular<br>lumen has spiral or annular depressions that are broad<br>and deep, presumably reflecting internal thickenings of a<br>tubular structure (figure  $9b$ ). Similarities to trac lumen has spiral or annular depressions that are broad<br>and deep, presumably reflecting internal thickenings of a<br>tubular structure (figure 9*h*). Similarities to tracheids and<br>the 'banded' tubes initially assigned to nemat and deep, presumably reflecting internal thickenings of a<br>tubular structure (figure  $9h$ ). Similarities to tracheids and<br>the 'banded' tubes initially assigned to nematophytes<br>(Lang  $1937$ ) are obvious but in the latter th tubular structure (figure  $9h$ ). Similarities to tracheids and<br>the 'banded' tubes initially assigned to nematophytes<br>(Lang 1937) are obvious, but in the latter, the thickenings the 'banded' tubes initially assigned to nematophytes (Lang 1937) are obvious, but in the latter, the thickenings<br>are narrower and more closely spaced. The longer, flat-<br>tened tubular structure shows only faint indications (Lang 1937) are obvious, but in the latter, the thickenings<br>are narrower and more closely spaced. The longer, flat-<br>tened tubular structure shows only faint indications of<br>internal thickenings of diverse widths (figure  $1$ are narrower and more closely spaced. The longer, flat-<br>tened tubular structure shows only faint indications of<br>internal thickenings of diverse widths (figure 10*h*), inter-<br>pretation being hampered by external adhering fr tened tubular structure shows only faint indications of internal thickenings of diverse widths (figure  $10h$ ), inter-<br>pretation being hampered by external adhering fragments internal thickenings of diverse widths (figure  $10h$ ), inter-<br>pretation being hampered by external adhering fragments<br>and internal growth of pyrite. Their identification as<br>elaters is based on their position and gross sim pretation being hampered by external adhering fragments<br>and internal growth of pyrite. Their identification as<br>elaters is based on their position and gross similarities<br>with extant forms demonstrated as possessing recalcit and internal growth of pyrite. Their identification as<br>elaters is based on their position and gross similarities<br>with extant forms, demonstrated as possessing recalcitrant<br>polymers and hence with enhanced fossilization pot elaters is based on their position and gross similarities<br>with extant forms, demonstrated as possessing recalcitrant<br>polymers and hence with enhanced fossilization potential with extant forms, demonstrated as possessing recalcitrant polymers and hence with enhanced fossilization potential (Kroken *et al.* 1996). Their position may also be considered evidence for their being residues of a bryop polymers and hence with enhanced fossilization potential (Kroken *et al.* 1996). Their position may also be considered evidence for their being residues of a bryophyte spor-<br>angial wall, although the length of the tubular (Kroken *et al.* 1996). Their position may also be considered evidence for their being residues of a bryophyte spor-<br>angial wall, although the length of the tubular one does<br>not support this. That they are pathogenic, as ered evidence for their being residues of a bryophyte spor-<br>angial wall, although the length of the tubular one does not support this. That they are pathogenic, as proposed<br>for tubes with much smaller and closely spaced thicken-<br>ings mentioned elsewhere in this paper (p.5), is for tubes with much smaller and closely spaced thickenfor tubes with much smaller and closely spaced thicken-<br>ings mentioned elsewhere in this paper (p.5), is<br>discounted on their size and their isolation from any form<br>of the debris that characterizes microbial films However ings mentioned elsewhere in this paper (p.5), is<br>discounted on their size and their isolation from any form<br>of the debris that characterizes microbial films. However,<br>cratering of the cuticle associated with decay is prese discounted on their size and their isolation from any form<br>of the debris that characterizes microbial films. However,<br>cratering of the cuticle associated with decay is present on<br>the surface of the expanded region of the debris that characterizes microbial films. However, cratering of the cuticle associated with decay is present on the surface of the expanded region.

Thus, although in this small specimen hepatic characthe surface of the expanded region.<br>Thus, although in this small specimen hepatic characters may be present, its overall organization finds no<br>counterpart in extant liverworts. Its proposed debiscence Thus, although in this small specimen hepatic characters may be present, its overall organization finds no counterpart in extant liverworts. Its proposed dehiscence mechanism is unique. On the other hand, it cannot be ters may be present, its overall organization finds no<br>counterpart in extant liverworts. Its proposed dehiscence<br>mechanism is unique. On the other hand, it cannot be<br>demonstrated to be a tracheophyte either counterpart in extant liverworts. Its proposed dehiscence<br>mechanism is unique. On the other hand, it cannot be<br>demonstrated to be a tracheophyte either.

## **5. RECOGNITION OF BRYOPHYTE SPOROPHYTES IN**<br>THE FOSSIL BECOPP N OF BRYOPHYTE SPORO<br>THE FOSSIL RECORD

## **(a)** *Unbranched sporophytes*

scape. Distal poral dehiscence is rare in early land inal sporangia borne singly on short lengths of lants, being recorded only in a bifurcating cylindrical unbranched axes. In longer specimens, branching is porangium cont THE FUSSIL RECURD<br>
(a) *Unbranched sporophytes*<br>
The unequivocal demonstration of absence of<br>
anching in a fragmentary fertile sporophyte presents (a) *Unbranched sporophytes*<br>The unequivocal demonstration of absence of<br>branching in a fragmentary fertile sporophyte presents<br>insuperable problems. The majority of fertile specimens branching in a fragmentary fertile sporophyte presents<br>insuperable problems. The majority of fertile specimens recovered from this Lochkovian locality comprise terminsuperable problems. The majority of fertile specimens<br>recovered from this Lochkovian locality comprise term-<br>inal sporangia borne singly on short lengths of<br>unbranched axes. In longer specimens, branching is recovered from this Lochkovian locality comprise term-<br>inal sporangia borne singly on short lengths of<br>unbranched axes. In longer specimens, branching is<br>sometimes preserved What is needed is a large number of inal sporangia borne singly on short lengths of<br>unbranched axes. In longer specimens, branching is<br>sometimes preserved. What is needed is a large number of<br>specimens of varying length all of which have specimens of varying length, all of which have

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*exuberans*, where large obovate- to club-shaped sporangia erminate uphranched axes at least 12 cm long. Some rock nbranched axes. This was the case for *Sponogonites*<br>*suberans*, where large obovate- to club-shaped sporangia<br>erminate unbranched axes at least 12 cm long. Some rock<br>urfaces show parallel alignment of these axes and suberans, where large obovate- to club-shaped sporangia<br>erminate unbranched axes at least 12 cm long. Some rock<br>urfaces show parallel alignment of these axes, and<br>lthough the irregular coalified film that Andrews (1960) erminate unbranched axes at least 12 cm long. Some rock<br>urfaces show parallel alignment of these axes, and<br>lthough the irregular coalified film that Andrews (1960) urfaces show parallel alignment of these axes, and<br>lthough the irregular coalified film that Andrews (1960)<br>hought represented a thalloid gametophyte merely over-<br>es the bases of the axes. S explerans remains the most lthough the irregular coalified film that Andrews (1960)<br>hought represented a thalloid gametophyte merely over-<br>es the bases of the axes, *S. exuberans* remains the most<br>compelling earliest fossil bryophyte candidate. The hought represented a thalloid gametophyte merely over-<br>es the bases of the axes, *S. exuberans* remains the most<br>ompelling earliest fossil bryophyte candidate. The axes<br>and of uniform width in the bases of the axes, *S. exuberans* remains the most ompelling earliest fossil bryophyte candidate. The axes and *Sporogonites* are very straight and of uniform width, uch that they give the impression of great rigidi ompelling earliest fossil bryophyte candidate. The axes<br>
a *Spongonites* are very straight and of uniform width,<br>
uch that they give the impression of great rigidity as is<br>
und in the setae of mosses. Stomata at the base a *Sporogonites* are very straight and of uniform width,<br>uch that they give the impression of great rigidity as is<br>bund in the setae of mosses. Stomata at the base of the<br>porangium and a possible but equivocal columella uch that they give the impression of great rigidity as is<br>bund in the setae of mosses. Stomata at the base of the<br>porangium and a possible, but equivocal columella bund in the setae of mosses. Stomata at the base of the porangium and a possible, but equivocal columella<br> **Halle 1916, 1936; Edwards** *et al.* **1998) reinforce moss**<br> **Highland Halle** (1916) concluded that it was a porangium and a possible, but equivocal columella<br>  $\bullet$ Halle 1916, 1936; Edwards *et al.* 1998) reinforce moss<br>  $\bullet$  ffinity, although Halle (1916) concluded that it was a<br>
decreasing of the Bryophyta of a reneralized typ Halle 1916, 1936; Edwards *et al.* 1998) reinforce n<br>Finity, although Halle (1916) concluded that it was<br>porangium of the Bryophyta of a 'generalized' type. Finity, although Halle (1916) concluded that it was a<br>prangium of the Bryophyta of a 'generalized' type.<br>Consistent absence of branching accompanied by axial<br>isting prompted (Edwards 1979) to postulate bryophyte

Aporangium of the Bryophyta of a 'generalized' type.<br>
Consistent absence of branching accompanied by axial<br>
wisting prompted (Edwards 1979) to postulate bryophyte<br>
alpossibly henatic) affinity for Unner Silurian Tertilicau (possible) Consistent absence of branching accompanied by axial<br>
wisting prompted (Edwards 1979) to postulate bryophyte<br>
possibly hepatic) affinity for Upper Silurian *Tortilicaulis*<br>
parameter of twisting in wisting prompted (Edwards 1979) to postulate bryophyte<br>
possibly hepatic) affinity for Upper Silurian *Tortilicaulis*<br>
demonstration of twisting in<br>
ilurian sterile branching axes at another locality and the The parameter of the particle affinity for Upper Silurian *Totilicaulis*<br>
Subsequent demonstration of twisting in<br>
ilurian sterile branching axes at another locality and the<br>
iscovery of Lower Devonian specimens (Edwards discovery of Lower Devonian specimens (Edwards *et al.* 1994) with similarly shaped sporangia with trilete spores and twisting in both axes and sporangia weakens broad iscovery of Lower Devonian specimens (Edwards *et al.* 994) with similarly shaped sporangia with trilete spores nd twisting in both axes and sporangia, weakens bryo-994) with similarly shaped sporangia with trilete spores<br>nd twisting in both axes and sporangia, weakens bryo-<br>byte affinity for the older specimens, but anatomical<br>vidence in the latter is essential to establish that the nd twisting in both axes and sporangia, weakens bryo-<br>byte affinity for the older specimens, but anatomical<br>vidence in the latter is essential to establish that the same<br>enus is involved where  $\frac{1}{2}$  in the latte enus is involved. **(b)** *Sporangial characters*

(**b**) **Sporangial characters**<br>These were reviewed at length by Edwards *et al.* (1998). (b) *Sporangial characters*<br>These were reviewed at length by Edwards *et al*<br>Ay comments here are thus not comprehensive.<br>Spore configurations provide evidence for the *e* 

Ay comments here are thus not comprehensive.<br>Spore configurations provide evidence for the existence *Ay* comments here are thus not comprehensive.<br>Spore configurations provide evidence for the existence<br>f plants at a bryophyte grade in the Ordovician/Silurian<br>Gray 1985) and their ultrastructure points to sphaero-Spore configurations provide evidence for the existence<br>f plants at a bryophyte grade in the Ordovician/Silurian<br>Gray 1985) and their ultrastructure points to sphaero-<br>arralean affinity (Taylor 1997). The value of similar f plants at a bryophyte grade in the Ordovician/Silurian<br>Gray 1985) and their ultrastructure points to sphaero-<br>arpalean affinity (Taylor 1997). The value of similar<br>arms when preserved in sporancia remains more contro-Gray 1985) and their ultrastructure points to sphaero-<br>arpalean affinity (Taylor 1997). The value of similar<br>preserved in sporangia remains more controarpalean affinity (Taylor 1997). The value of similar<br>prms when preserved in sporangia remains more contro-<br>ersial, particularly where the producers have branching<br>poronbytes. The demonstration of elaters in sporancia between preserved in sporangia remains more contro-<br>ersial, particularly where the producers have branching<br>porophytes. The demonstration of elaters in sporangia<br>could strengthen the existence of henatics. To date, there ersial, particularly where the producers have branching<br>porophytes. The demonstration of elaters in sporangia<br>vould strengthen the existence of hepatics. To date, there<br>re two possible in situ records but much larger numb porophytes. The demonstration of elaters in sporangia<br>vould strengthen the existence of hepatics. To date, there<br>re two possible *in situ* records, but much larger numbers<br>f elaters per sporangium are required to allow mor ould strengthen the existence of hepatics. To date, there etailed analysis. Kroken *et al*.'s (1996) suggestion that f elaters per sporangium are required to allow more<br>etailed analysis. Kroken *et al.*'s (1996) suggestion that<br>one of the banded tubes in the dispersed record might<br>declaters deserves further attention etailed analysis. Kroken *et al*'s (199) one of the banded tubes in the disp<br>  $\begin{bmatrix} e \\ e \end{bmatrix}$  elaters deserves further attention.<br>
There is a considerable amount of me of the banded tubes in the dispersed record might<br>elaters deserves further attention.<br>There is a considerable amount of information on the<br>nstruction of the sporancium wall including possible

e elaters deserves further attention.<br>There is a considerable amount of information on the<br>onstruction of the sporangium wall, including possible apetal layers and dehiscence mechanisms, in early racheophytes and rhyniophytoids where spores are onstruction of the sporangium wall, including possible<br>apetal layers and dehiscence mechanisms, in early<br>racheophytes and rhyniophytoids where spores are<br>lmost all trilete. A few examples have sporangial apetal layers and dehiscence mechanisms, in early<br>racheophytes and rhyniophytoids where spores are<br>limost all trilete. A few examples have sporangial<br>tiomata a character shared with certain mosses but they racheophytes and rhyniophytoids where spores are<br>all most all trilete. A few examples have sporangial<br>tomata, a character shared with certain mosses, but they<br>be rarely concentrated near the base of the sporancium are rate in the rarely concentrated near the base of the sporangium<br>are rarely concentrated near the base of the sporangium<br>of the sporangium of<br>sporangium of the sporangium of the sporangium of<br>sporangium of the sporangi (Edwards, a character shared with certain mosses, but they  $\bigcup$  re rarely concentrated near the base of the sporangium  $\bigcap$  Edwards *et al.* 1996). I doubt it would be possible to ) re rarely concentrated near the base of the sporangium<br>Edwards *et al.* 1996). I doubt it would be possible to<br>distinguish a bryophyte using only sporangial wall char-<br>term particularly in the absence of complex debisce Edwards *et al.* 1996). I doubt it would be possible to istinguish a bryophyte using only sporangial wall char-<br>cters, particularly in the absence of complex dehiscence<br>rechanisms found in mosses. The recent suggestions t istinguish a bryophyte using only sporangial wall char-<br>cters, particularly in the absence of complex dehiscence<br>nechanisms found in mosses. The recent suggestions that<br>ifferentially thickened walls of cells from certain m cters, particularly in the absence of complex dehiscence<br>rechanisms found in mosses. The recent suggestions that<br>ifferentially thickened walls of cells from certain moss<br>nd liverwort sporancia that survive acetolysis are s rechanisms found in mosses. The recent suggestions that<br>ifferentially thickened walls of cells from certain moss<br>nd liverwort sporangia that survive acetolysis are similar<br>at the banded (i.e. differentially thickened) tube ifferentially thickened walls of cells from certain moss<br>nd liverwort sporangia that survive acetolysis are similar<br> $\frac{1}{2}$  the banded (i.e. differentially thickened) tubes found<br> $\frac{1}{2}$  Silurian and Devonian sediment nd liverwort sporangia that survive acetolysis are similar<br>
<sup>2</sup> the banded (i.e. differentially thickened) tubes found<br>
<sup>2</sup> a Silurian and Devonian sediments (Kroken *et al.* 1996)<br>
<sup>2</sup> mands further testing To date, all t the banded (i.e. differentially thickened) tubes found<br>a Silurian and Devonian sediments (Kroken *et al.* 1996)<br>emands further testing. To date, all the examples recov-<br>red in our studies are long and radially symmetrical a Silurian and Devonian sediments (Kroken *et al.* 1996) emands further testing. To date, all the examples recovred in our studies are long and radially symmetrical when other associated with wefts of smaller tubes. In th emands further testing. To date, all the examples recov-<br>red in our studies are long and radially symmetrical<br>ubes, often associated with wefts of smaller tubes. In the<br>resofossils at this I ower Devonian locality individu red in our studies are long and radially symmetrical<br>ubes, often associated with wefts of smaller tubes. In the<br>resofossils at this Lower Devonian locality, individual<br>ells in the sporangial wall may be thickened usually t ubes, often associated with wefts of smaller tubes. In the resofossils at this Lower Devonian locality, individual<br>ells in the sporangial wall may be thickened, usually to

different degrees in anticlinal and periclinal walls, but not different degrees in anticlinal and periclinal walls, but not spirally. Kroken *et al.* also suggested that some of the dispersed sheets, with reticulate patterning reflecting different degrees in anticlinal and periclinal walls, but not<br>spirally. Kroken *et al.* also suggested that some of the<br>dispersed sheets with reticulate patterning reflecting<br>underlying cellular organization which are ofte spirally. Kroken *et al.* also suggested that some of the dispersed sheets with reticulate patterning reflecting underlying cellular organization, which are often considered cuticles of the *Nematothallus* complex also der dispersed sheets with reticulate patterning reflecting<br>underlying cellular organization, which are often consid-<br>ered cuticles of the *Nematothallus* complex, also derive underlying cellular organization, which are often considered cuticles of the *Nematothallus* complex, also derive from bryophyte sporangia. We have recently shown that the chemical composition of such cuticles differs from ered cuticles of the *Nematothallus* complex, also derive<br>from bryophyte sporangia. We have recently shown that<br>the chemical composition of such cuticles differs from<br>those of tracheophytes in that they are predominantly from bryophyte sporangia. We have recently shown that<br>the chemical composition of such cuticles differs from<br>those of tracheophytes in that they are predominantly<br>aromatic rather than alinhatic (Edwards *et al.* 1996) They the chemical composition of such cuticles differs from<br>those of tracheophytes in that they are predominantly<br>aromatic rather than aliphatic (Edwards *et al.* 1996). They<br>thus have a different source from sporancial cuticle those of tracheophytes in that they are predominantly<br>aromatic rather than aliphatic (Edwards  $et al.$  1996). They<br>thus have a different source from sporangial cuticles<br>recorded often with adhering trilete spores but somearomatic rather than aliphatic (Edwards *et al.* 1996). They<br>thus have a different source from sporangial cuticles<br>recorded, often with adhering trilete spores, but some-<br>times dyads (figure 4a) from Wenlock and younger thus have a different source from sporangial cuticles<br>recorded, often with adhering trilete spores, but some-<br>times dyads (figure 4*a*) from Wenlock and younger<br>sediments. As mentioned earlier we need to know more recorded, often with adhering trilete spores, but some-<br>times dyads (figure  $4a$ ) from Wenlock and younger sediments. As mentioned earlier, we need to know more<br>about the precise chemistry of tissues in extant fossils and<br>indeed in bryophytes, although whether such information sediments. As mentioned earlier, we need to know more<br>about the precise chemistry of tissues in extant fossils and<br>indeed in bryophytes, although whether such information<br>will be of value in detecting affinities in view of about the precise chemistry of tissues in extant fossils and<br>indeed in bryophytes, although whether such information<br>will be of value in detecting affinities in view of the effects<br>of diagenesis on complex aromatic molecul indeed in bryophytes, although whether such information<br>will be of value in detecting affinities in view of the effects<br>of diagenesis on complex aromatic molecules remains<br>uncertain (see discussion in Ewbank *et al*, 1997 will be of value in detecting affinities in view of the of diagenesis on complex aromatic molecules uncertain (see discussion in Ewbank *et al.* 1997). **(c)** *Axial anatomical features*

(c) *Axial anatomical features*<br>The various kinds of conducting cells described here,<br>hough difficult to interpret in terms of function (c) *Axial anatomical features*<br>The various kinds of conducting cells described here,<br>although difficult to interpret in terms of function,<br>demonstrate the potential of such fossils to preserve hyvoalthough difficult to interpret in terms of function, demonstrate the potential of such fossils to preserve bryoalthough difficult to interpret in terms of function,<br>demonstrate the potential of such fossils to preserve bryo-<br>phyte tissues. Structures less likely to be preserved are<br>prizoids. These are preserved by silica in the Rhy demonstrate the potential of such fossils to preserve bryophyte tissues. Structures less likely to be preserved are prizoids. These are preserved by silica in the Rhynie Chert and are unicellular (see review in Edwards 199 phyte tissues. Structures less likely to be preserved are thizoids. These are preserved by silica in the Rhynie Chert and are unicellular (see review in Edwards 1993) in both tracheophytes (e.g. *Rhynia Trichopherophyton*) rhizoids. These are preserved by silica in the Rhynie<br>Chert and are unicellular (see review in Edwards 1993)<br>in both tracheophytes (e.g. *Rhynia*, *Trichopherophyton*) and<br>*Aslaophyton* which is one of the few Rhynie Chert *Aglaophyton*, which is one of the few Rhynie Chert taxon<br>*Aglaophyton*, which is one of the few Rhynie Chert taxon<br>*Aglaophyton*, which is one of the few Rhynie Chert taxon<br>reputed to have some bryophyte characters. The o in both tracheophytes (e.g. *Rhynia, Trichopherophyton*) and *Aglaophyton*, which is one of the few Rhynie Chert taxon reputed to have some bryophyte characters. The other is *Herneobhyton* which has columellate sporancia *Aglaophyton*, which is one of the few Rhynie Chert taxon<br>reputed to have some bryophyte characters. The other is<br>*Horneophyton*, which has columellate sporangia with<br>complex poral debiscence structures (e.g. Eggert 1974) reputed to have some bryophyte characters. The other is<br> *Horneophyton*, which has columellate sporangia with<br>
complex poral dehiscence structures (e.g. Eggert 1974)<br>
terminating otherwise homoiohydric aerial axes Indeed Horneophyton, which has columellate sporangia with<br>complex poral dehiscence structures (e.g. Eggert 1974)<br>terminating otherwise homoiohydric aerial axes. Indeed,<br>the absence of unequivocal bryophytes in the Rhynie complex poral dehiscence structures (e.g. Eggert 1974)<br>terminating otherwise homoiohydric aerial axes. Indeed,<br>the absence of unequivocal bryophytes in the Rhynie<br>terrestrial ecosystems, which have been so intensively terminating otherwise homoiohydric aerial axes. Indeed,<br>the absence of unequivocal bryophytes in the Rhynie<br>terrestrial ecosystems, which have been so intensively<br>researched is a major mystery especially as bryophytes the absence of unequivocal bryophytes in the Rhynie terrestrial ecosystems, which have been so intensively researched, is a major mystery, especially as bryophytes can be pioneering colonizers on highly stressed substrates researched, is a major mystery, especially as bryophytes<br>can be pioneering colonizers on highly stressed substrates<br>in modern hot-spring analogues (e.g. New Zealand;<br>Rurns 1997) can be pionee<br>in modern h<br>Burns 1997).

#### **6. CONCLUDING REMARKS**

'We see what we know'—our searches for evidence for fossil bryophytes are constrained by data based on extant We see what we know'—our searches for evidence for<br>fossil bryophytes are constrained by data based on extant<br>representatives. The fossil record of bryophytes is very<br>poor compared with other plant groups although fossil bryophytes are constrained by data based on extant<br>representatives. The fossil record of bryophytes is very<br>poor compared with other plant groups, although<br>occasional records (e.g. *Najadita*) provide tantalizing representatives. The fossil record of bryophytes is very<br>poor compared with other plant groups, although<br>occasional records (e.g. *Naiadita*) provide tantalizing<br>combinations of characters not seen in extant form poor compared with other plant groups, although<br>occasional records (e.g. *Naiadita*) provide tantalizing<br>combinations of characters not seen in extant form<br>(Hemsley 1989) An alternative approach is prompted by occasional records (e.g. *Naiadita*) provide tantalizing<br>combinations of characters not seen in extant form<br>(Hemsley 1989). An alternative approach is prompted by<br>Mishler & Churchill's (1985) reconstruction of a number combinations of characters not seen in extant form<br>(Hemsley 1989). An alternative approach is prompted by<br>Mishler & Churchill's (1985) reconstruction of a number<br>of archetynes based on shared homologies. Thus, for (Hemsley 1989). An alternative approach is prompted by<br>Mishler & Churchill's (1985) reconstruction of a number<br>of archetypes based on shared homologies. Thus, for<br>example the archetype of land plants was reconstructed Mishler & Churchill's (1985) reconstruction of a number<br>of archetypes based on shared homologies. Thus, for<br>example, the archetype of land plants was reconstructed<br>as a thalloid gametophyte with single sessile sporancium of archetypes based on shared homologies. Thus, for<br>example, the archetype of land plants was reconstructed<br>as a thalloid gametophyte with single sessile sporangium<br>and that for the moss-tracheophyte clade as a radially example, the archetype of land plants was reconstructed<br>as a thalloid gametophyte with single sessile sporangium<br>and that for the moss-tracheophyte clade as a radially<br>symmetrical leafless branched gametophyte with as a thalloid gametophyte with single sessile sporangium<br>and that for the moss-tracheophyte clade as a radially and that for the moss-tracheophyte clade as a radially<br>symmetrical, leafless, branched gametophyte with<br>conducting tissues and stomata. A coalified fossil of the<br>latter might appear as a collection of branching axes with symmetrical, leafless, branched gametophyte with<br>conducting tissues and stomata. A coalified fossil of the<br>latter might appear as a collection of branching axes with<br>a single terminal sporancium. Here, the single sporanci conducting tissues and stomata. A coalified fossil of the latter might appear as a collection of branching axes with a single terminal sporangium. Here, the single sporangium and perhaps the demonstration of a discontinuity of a single terminal sporangium. Here, the single sporangium and perhaps the demonstration of a discontinuity of some sort at the sporophyte/gametophyte junction would provide good evidence for a fossil bryophyte in the gium and perhaps the demonstration of a discontinuity of<br>some sort at the sporophyte/gametophyte junction would<br>provide good evidence for a fossil bryophyte in the<br>absence of anatomy, but demands a new approach to the some sort at the sporophyte/gametophyte junction would<br>provide good evidence for a fossil bryophyte in the<br>absence of anatomy, but demands a new approach to the<br>examination of existing material. The recent palaeoprovide good evidence for a fossil bryophyte in the absence of anatomy, but demands a new approach to the examination of existing material. The recent palaeo-botanical research reported here indicates that the fossil examination of existing material. The recent palaeo-

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**PHILOSOPHICAL**<br>TRANSACTIONS

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ecord is now producing new combinations of characters ecord is now producing new combinations of characters<br>nd novel character states, and makes the search for new<br>nd older fossiliferous horizons imperative. The ecord is now producing new combinations of characters<br>nd novel character states, and makes the search for new<br>nd older fossiliferous horizons imperative. The<br>producian/Silurian dispersed spore record also demands nd novel character states, and makes the search for new<br>nd older fossiliferous horizons imperative. The<br>dividently branched spore record also demands<br>urther investigation of the kind initiated by Taylor (e.g. nd older fossiliferous horizons imperative. The brdovician/Silurian dispersed spore record also demands arther investigation of the kind initiated by Taylor (e.g. Prodiction Silurian dispersed spore record also demands<br>arther investigation of the kind initiated by Taylor (e.g.<br>995*a*,*b*, 1997). It is quite remarkable that in a time<br>aterval that is hypothesized to have seen the eme interval that is hypothesized to have seen the emergence fluorence is approximately that is hypothesized to have seen the emergence of liverworts and mosses there is apparent stasis in terms 995*a*, $b$ , 1997). It is quite remarkable that in a time iterval that is hypothesized to have seen the emergence fliverworts and mosses, there is apparent stasis in terms of named taxa in composition of dispersed spore as iterval that is hypothesized to have seen the emergence f liverworts and mosses, there is apparent stasis in terms f named taxa in composition of dispersed spore assemf liverworts and mosses, there is apparent stasis in terms<br>
if named taxa in composition of dispersed spore assem-<br>
lages (Wellman 1996), apart from the appearance of<br>
ionads Superficial organent shows little of the divers f named taxa in composition of dispersed spore assemlages (Wellman 1996), apart from the appearance of nonads. Superficial ornament shows little of the diversity expredict later in the Silurian and Devonian (probably lages (Wellman 1996), apart from the appearance of<br>ionads. Superficial ornament shows little of the diversity<br>ecorded later in the Silurian and Devonian (probably<br>syndained by the presence of envelopes) but investigations ionads. Superficial ornament shows little of the diversity ecorded later in the Silurian and Devonian (probably  $\blacktriangleright$  xplained by the presence of envelopes), but investigations ecorded later in the Silurian and Devonian (probably<br>splained by the presence of envelopes), but investigations<br>of ultrastructure in the same species through time might<br>deveal evidence of change reveal and by the presence of<br>The diffusive change.<br>The contract change.

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### *Discussion*

**Discussion**<br>P. Kenrick (*Department of Palaeontology*, *The Natural History*<br>*Museum London UK*) Sporophyte branching is completely **Discussion**<br> **P. Kenrick (Department of Palaeontology, The Natural History**<br> *Museum, London, UK*). Sporophyte branching is completely<br>
absent in the normal course of development of modern P. Kenrick (*Department of Palaeontology, The Natural History Museum, London, UK*). Sporophyte branching is completely absent in the normal course of development of modern liverworts hornworts and mosses. The absence of ap *Museum, London, UK*). Sporophyte branching is completely absent in the normal course of development of modern liverworts, hornworts and mosses. The absence of apical absent in the normal course of development of modern<br>liverworts, hornworts and mosses. The absence of apical<br>growth during the ontogeny of these groups (except for<br>very limited apical cell divisions in mosses) explains why liverworts, hornworts and mosses. The absence of apical<br>growth during the ontogeny of these groups (except for<br>very limited apical cell divisions in mosses) explains why<br>this is the case and indicates that their sporophyte growth during the ontogeny of these groups (except for<br>very limited apical cell divisions in mosses) explains why<br>this is the case and indicates that their sporophytes were

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ever branched. Furthermore, the lack of a sporophyte ever branched. Furthermore, the lack of a sporophyte eneration in the charophycean algal ancestors of land lants is consistent with the idea that the earliest land ever branched. Furthermore, the lack of a sporophyte<br>eneration in the charophycean algal ancestors of land<br>lants is consistent with the idea that the earliest land<br>lants would have had very simple, unbranched sporoeneration in the charophycean algal ancestors of land<br>lants is consistent with the idea that the earliest land<br>lants would have had very simple, unbranched sporo-<br>bytes How does one reconcile these data with fossil lants is consistent with the idea that the earliest land<br>lants would have had very simple, unbranched sporo-<br>hytes. How does one reconcile these data with fossil<br>vidence indicating that sporophytic branching is plesiolants would have had very simple, unbranched sporo-<br>hytes. How does one reconcile these data with fossil<br>vidence indicating that sporophytic branching is plesio-<br>perspectively for embryon bytes as a whole? vidence indicating that sporophytic branching is plesio-<br>norphic for embryophytes as a whole?

orphic for embryophytes as a whole?<br>
D. Edwards. Dr Kenrick refers to the very limited<br>
produce a presented in my paper for sporophytic evidence presented in my paper for sporophytic<br>anching in plants containing dyads and tetrads. These vidence presented in my paper for sporophytic ranching in plants containing dyads and tetrads. These

fossils come from Lower Devonian rocks; we have no<br>megafossil evidence for the polyad producers before this.<br>They may well have lacked sporophytic branching The fossils come from Lower Devonian rocks; we have no<br>megafossil evidence for the polyad producers before this.<br>They may well have lacked sporophytic branching. The<br>presence of polyads in the Lower Devonian plants may megafossil evidence for the polyad producers before this.<br>They may well have lacked sporophytic branching. The<br>presence of polyads in the Lower Devonian plants may<br>just indicate the retention of a stem-group bryophytic They may well have lacked sporophytic branching. The<br>presence of polyads in the Lower Devonian plants may<br>just indicate the retention of a stem-group bryophytic<br>character. Evidence for the nature of conducting cells in presence of polyads in the Lower Devonian plants may<br>just indicate the retention of a stem-group bryophytic<br>character. Evidence for the nature of conducting cells in<br>these fossils would help to resolve this issue just indicate the retention of a stem-group<br>character. Evidence for the nature of condu-<br>these fossils would help to resolve this issue.<br>The possibility of loss of sporophytic b aracter. Evidence for the nature of conducting cells in<br>see fossils would help to resolve this issue.<br>The possibility of loss of sporophytic branching in<br>wonbytes deserves further consideration and is one that

these fossils would help to resolve this issue.<br>The possibility of loss of sporophytic branching in<br>bryophytes deserves further consideration and is one that The possibility of loss of sporophytic branching in<br>bryophytes deserves further consideration and is one that<br>might be appropriately addressed in a functional geno-<br>mics programme bryophytes deserves<br>might be appropria<br>mics programme.