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Article *in* Botanical Gazette · September 1991

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0006-8071/91/5203-0010$02.00

WATER-CONDUCTING CELLS IN EARLY FOSSIL LAND PLANTS: IMPLICATIONS FOR THE EARLY EVOLUTION OF TRACHEOPHYTES

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Wall structure in the water-conducting cells of *Rhynia gwynne-vaughanii* and *Asteroxylon mackiei* from the Lower Devonian Rhynie Chert was examined and compared using thin sections and scanning electron microscopy of etched sections. Although the internal thickenings of these cells are superficially similar in both plants, there are significant differences in other aspects of wall structure. The tracheids of *A. mackiei* are shown to be of a basic type (G-type) that is common in some early land plant fossils such as zosterophylls and lycopods, and they are comparable to protoxylem elements in some extant 'pteridophytes'. The "tracheids" of *R. gwynne-vaughanii* are more similar to another kind of water-conducting cell (S-type) that combines certain features of tracheids and moss hydroids. The S-type cell is known from two other Lower Devonian sporophytes, *Stockmansella langii* and *Huvenia kleui,* supporting recent suggestions that these three taxa form a natural group. S-type cells are also found in the gametophyte *Sciadophyton* sp. as well as two taxa, *Sennicaulis hippocrepiformis* and *Taeniocrada dubia,* for which reproductive structures are unknown. The water-conducting tissues of other early land plants are briefly reviewed and detailed reconstructions of the S-type and G-type cell are provided. A preliminary cladistic analysis focusing on the Rhyniophytina of Banks results in the recognition of a 'protracheophyte' grade, as well as a small clade, the Rhyniaceae, comprising *Rhynia, Stockmansella,* and *Huvenia.* If the tracheid-like features of S-type and G-type cells are regarded as homologous, then the Rhyniaceae are resolved as the basal clade that forms the sister group to all other tracheophytes. The occurrence of a more or less isomorphic alternation of generations in some Devonian 'protracheophytes' and the Rhyniaceae implies that the gametophytes of all extant 'pteridophytes' are phylogenetically reduced.

Introduction

The exceptionally well-preserved Lower Devonian silicified plants from Rhynie, Scotland, have strongly influenced ideas of plant evolution for more than 70 yr and are central to the widely accepted classification of early vascular plants established by BANKS (1968, 1975). Even though the Rhynie Chert substantially postdates the earliest evidence of a land flora based on both microfossils (Upper Ordovician: GRAY and BOUCOT 1977; GRAY et al. 1982; RICHARDSON and MCGREGOR 1986; NØHR-HANSEN and KOPPELHUS 1988) and megafossils (late Wenlock, middle Silurian: EDWARDS et al. 1983), the four taxa originally described by KIDSTON and LANG (1917, 1920*a*, 1920*b*; *Asteroxylon mackiei, Rhynia gwynne-vaughanii, Horneophyton lignieri,* and *Rhynia major,* now transferred to *Aglaophyton* [EDWARDS 1986]) still provide some of the most complete data currently available on the structure and biology of early land plants (TAYLOR 1981, 1988; STEWART 1983; GENSEL and ANDREWS 1984; CHALONER 1988). The genus *Rhynia,* in particular, has been widely discussed and has frequently been used as a model for the anatomy and morphology of a typical early 'pteridophyte.'

Recent studies of the Rhynie Chert plants have further clarified various aspects of their morphology and anatomy (LYON 1964; EGGERT 1974; EL-SAADAWY and LACEY 1979*a*, 1979*b*; EDWARDS 1980, 1986), but a surprising result has been the recognition that the water-conducting cells of *Aglaophyton major* lack the distinctive lignified thickenings characteristic of tracheids and in this respect are more similar to the hydroids of mosses (EDWARDS 1986). Differentially thickened, water-conducting cells also are absent from another Rhynie Chert plant, *Nothia aphylla,* which was described originally as the possible fertile parts of *A. mackiei* (KIDSTON and LANG 1920*b*; LYON 1964; EL-SAADAWY and LACEY 1979*a*). All extant tracheophytes possess tracheids and a branched sporophyte, but *Aglaophyton* and *Nothia* demonstrate that the occurrence of these two features is decoupled in certain fossil taxa thus raising significant questions concerning the nature of the 'bryophyte'-'pteridophyte' transition. In this paper we provide new data that are relevant to this issue and focus on *R. gwynne-vaughanii* and *A. mackiei* as part of a detailed survey of the water-conducting cells in early land plants. These data are necessary to facilitate comparisons with the tracheids of extant 'pteridophytes' and functionally similar cells in sporophytes and gametophytes of 'bryophytes' (KENRICK and EDWARDS 1988; KENRICK et al. 1991*a*, 1991*b*).

The presence of tracheids is one of several characters that distinguish vascular plants from 'bryophytes', and in a paleobotanical context the absence of these cells has been used to exclude *A. major* and *N. aphylla* from the Rhyniophytina of Banks (EDWARDS and EDWARDS 1986; TAYLOR 1988). However, the metaxylem of many early

Manuscript received March 1991; revised manuscript received May 1991.

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vascular plants is not typical of that in extant 'pteridophytes' because it is composed exclusively of annular or helically thickened cells in which "conventional" pitting does not occur (KENRICK and EDWARDS 1988). Such cells have been termed tracheids by analogy to early formed protoxylem in extant taxa, which often has annular or helical thickenings. Recent analyses of pyritized Lower Devonian material have recognized two distinct types of superficially similar annular or helically thickened cell that have markedly different wall structures. "G-type" cells (KENRICK et al. 1991*a*) have a two-layered cell wall composed of a decay-resistant inner layer (next to the cell lumen) and a nonresistant outer layer. The inner wall layer is continuous between the thickenings where it is perforated by numerous simple pits. "S-type" cells (KENRICK et al. 1991*a*) have a very thin, continuous, decay-resistant inner layer and an enigmatic "spongy" outer layer that is particularly well developed at the thickenings. Both over and between the thickenings the inner layer is perforated by numerous minute pores. The terms G-type and S-type are abbreviations of *Gosslingia*-type and *Sennicaulis*-type after the fossil plants from which these cells were described originally.

The G-type cell is very similar to the early formed protoxylem tracheids in *Lycopodium* and *Equisetum,* but the S-type cell differs significantly from the tracheids of any extant plant and in certain features resembles the water-conducting cells of some extant 'bryophytes' such as *Takakia lepidozioides, Pallavicinia lyellii,* and *Hymenophyton flabellatum* (HÉBANT 1977, 1979). The descriptions and comparisons presented here show that the water-conducting cells of *A. mackiei* are of the G-type while the 'tracheids' of *R. gwynne-vaughanii* are comparable to S-type cells. Because both plants are from the same locality and are similarly preserved in silica, these significant differences in cell wall structure are unlikely to be due to preservational effects. The evolutionary significance of plants with S-type cells is discussed based on preliminary cladistic hypotheses of relationships among early land plants.

Material and methods

The silicified remains of *Rhynia gwynne-vaughanii* and *Asteroxylon mackiei* are from the famous Lower Devonian chert near the village of Rhynie, Scotland (TAYLOR 1981; STEWART 1983; GENSEL and ANDREWS 1984). The age of the Rhynie outlier, including the chert beds, is not well constrained. The spore assemblage from the chert and associated sediments yields forms that resemble those from other Scottish Lower Old Red Sandstone facies of probable Pragian (Siegenian) to Emsian age (RICHARDSON 1967; WESTOLL 1977).

Axes were identified as *R. gwynne-vaughanii* following the diagnoses given by KIDSTON and LANG (1920*a*) and more recently by EDWARDS (1986). Care was taken not to confuse *R. gwynne-vaughanii* and *Aglaophyton major. Rhynia gwynne-vaughanii* is smaller, has internally ornamented water-conducting tissue, adventitious as well as truly dichotomous branching, and characteristic hemispherical projections on the axis surface. Not all of these features were visible in every axis examined, but the water-conducting cells illustrated here were observed in axes with the characteristic hemispherical projections and are similar to previously illustrated material of *R. gwynne-vaughanii* figured by KIDSTON and LANG (1917, pl. 7, fig. 48) and EDWARDS (1986, fig. 3).

Axes were identified as *A. mackiei* following the descriptions given by KIDSTON and LANG (1920*b*) and LYON (1964). Water-conducting cells were observed in leafy axes possessing the characteristic actinostele. Similar cells were illustrated by KIDSTON and LANG (1920*b,* pl. 10, figs. 77–79), LANG and COOKSON (1931, pl. 13, fig. 43) and LEMOIGNE and ZDEBSKA (1980, pl. 3, figs. 18–20).

The cell walls of both plants were examined in thin section. This method was preferred over the peel technique because etching results in damage to the delicate remains of the cell wall and loss of some of the preserved organic material. Such effects are particularly clear in the SEM preparations of *R. gwynne-vaughanii* (see below). One thin section contained approximately seven axes of *R. gwynne-vaughanii* and another, approximately four axes of *A. mackiei* in longitudinal section. Detailed analyses of these two sections were compared with observations from other thin sections, peels, and published photographs of the Rhynie chert material. Sections were examined and photographed using a Leitz Dialux 20 photomicroscope. To improve resolution, coverslips were removed and the surface of the sections examined directly using a 100× oil immersion objective lens. Measurements of cell wall dimensions (fig. 1; table 1) were taken from thin sections.

Specimens were prepared for scanning electron microscopy (SEM) by etching in 40% hydrofluoric acid followed by rinsing in distilled water. The length of etch varied between ca. 5 and 20 min, depending on the specimen. Etched sections of *A. mackiei* are relatively robust and were air dried; the etched conducting cells of *R. gwynne-vaughanii* are more delicate and were critical point dried. The specimens were mounted directly on to stubs, gold coated and scanned using an AMRAY 1810 scanning electron microscope.

Phylogenetic hypotheses and ideas of character evolution were evaluated using PAUP 3.0 (DAVID L. SWOFFORD, Illinois Natural History Service,

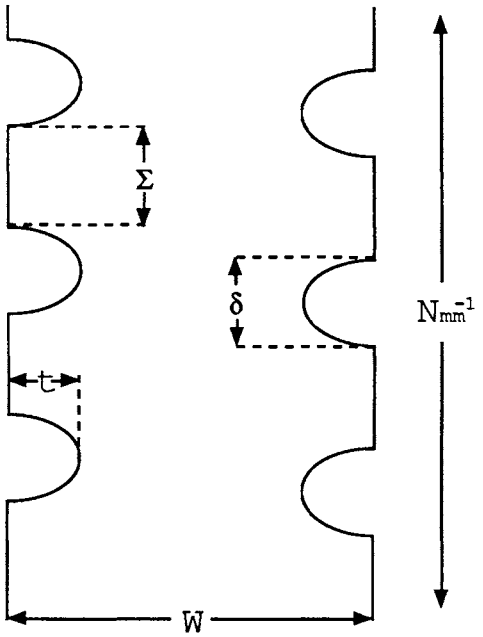


FIG. 1.—Diagrammatic representation of median longitudinal section through water-conducting cell with helical or annular thickening showing measurements made. δ = thickness of thickening at the base; Σ = distance between gyres; t = distance thickening protrudes into cell lumen; W = maximum cell lumen diameter; Nmm^{-1} = the number of gyres or thickenings mm^{-1}.

Champaign) on an Apple Macintosh IIcx (see fig. 26; Appendix). The MULPARS option was used to save all equally parsimonious trees generated by the BANDB (Branch and Bound) option, which is guaranteed to find the most parsimonious solution for a given set of data. Throughout the text, groups thought to be paraphyletic are indicated by single quotes.

Descriptions

ASTEROXYLON MACKIEI

The elongate cells making up the xylem of *A. mackiei* superficially appear to have scalariform thickenings (figs. 2, 4), but detailed examination shows that, even in the largest cells, thickenings are annular or helical with only occasional direct connections between adjacent annular bars (figs. 2–5, 8). The false impression of scalariform thickenings is given by tangential sections through the cell wall in which the annular thickenings are seen in plan view (figs. 2, 4). In median longitudinal section the thickenings appear as small dark peg-like protrusions into the cell lumen (figs. 3, 5). Detailed measurements of wall ornamentation (fig. 1) are given in table 1.

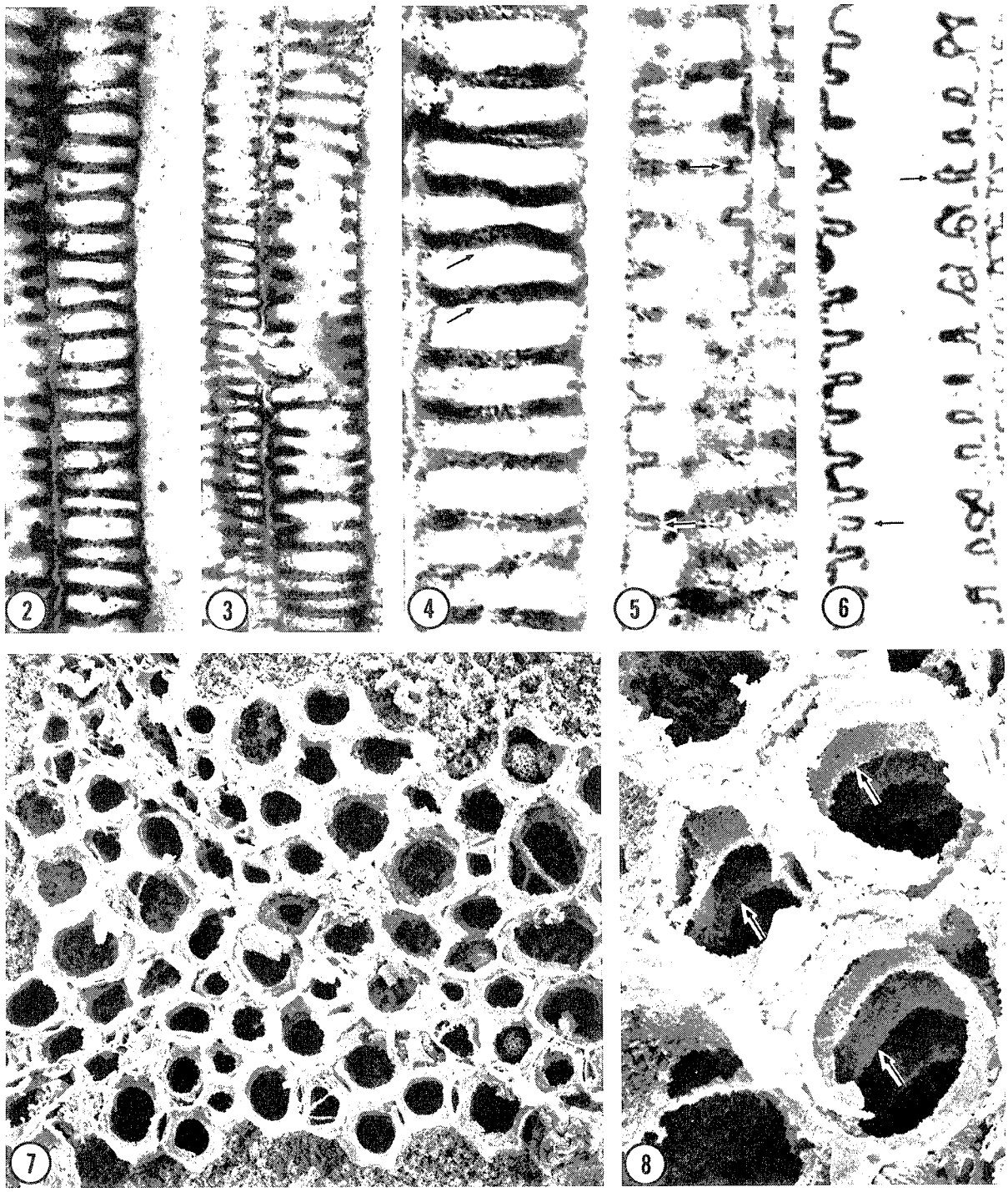
In median section the cell wall is clearly two-layered: the outer layer of each cell appears translucent, but the layer adjacent to the cell lumen is dark, opaque, and typically ca. 0.5 μm thick (fig. 5). This is a consistent feature of the cell wall. In smaller cells, the interior of the annular thick-

TABLE 1

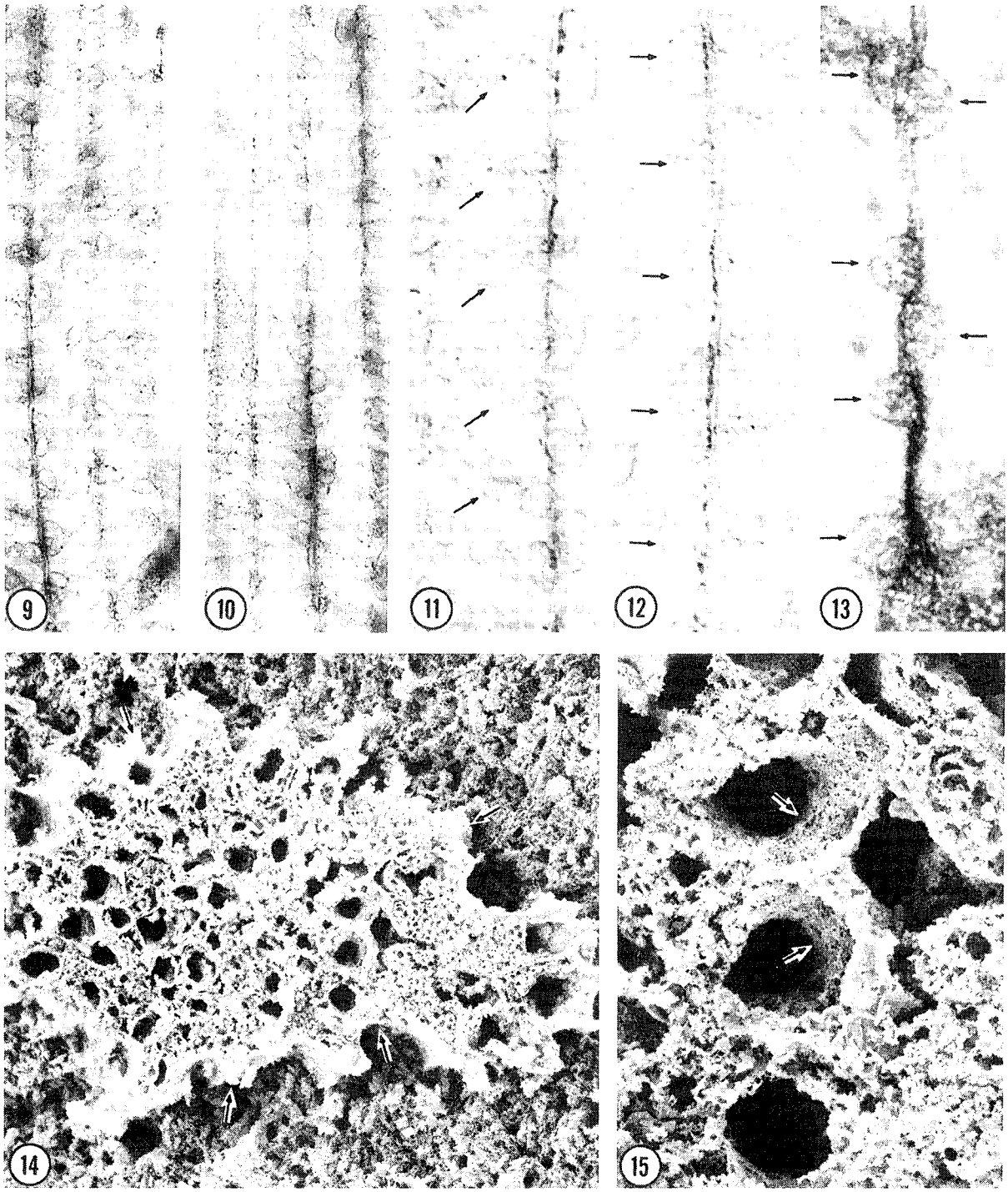
COMPARISON OF WATER-CONDUCTING CELLS IN GOSSLINGIA BRECONENSIS AND ASTEROXYLON MACKIEI WITH S-TYPE CELLS IN THE SIX TAXA SO FAR RECORDED WITH THIS FEATURE

Taxon	References	Phase of life cycle	Type	Thickening	Spongy layer	Microporate inner wall layer	δ	Σ	t	W	Nmm^{-1}
G. breconensis	*a, b*	Sporophyte	G-type	Annular + helical	None	None	3.0	2.7	4.1	34.0	156
A. mackiei	*c*	Sporophyte	G-type	Annular + helical	None	None	3.0	4.7	5.3	29.2	130
Sennicaulis hippocrepiformis	*b*	?	S-type	Helical	✓	✓	11.2	17.4	9.8	34.5	36
Taeniocrada dubia	*d*	?	S-type	Helical	✓	✓	?	?	?	?	?
Rhynia gwynne-vaughanii	*c*	Sporophyte	S-type	Helical	✓	*	10.7	4.5	6.0	20.6	61
Stockmansella langii	*e, f*	Sporophyte	S-type	Helical	?	✓	†	19.7	†	29.2	34
Huvenia kleui	*f*	Sporophyte	S-type	Helical	?	✓	†	15.6	†	26.4	45
Sciadophyton sp.	*f, g*	Gametophyte	S-type	Helical	?	✓	†	18.7	†	27.8	40

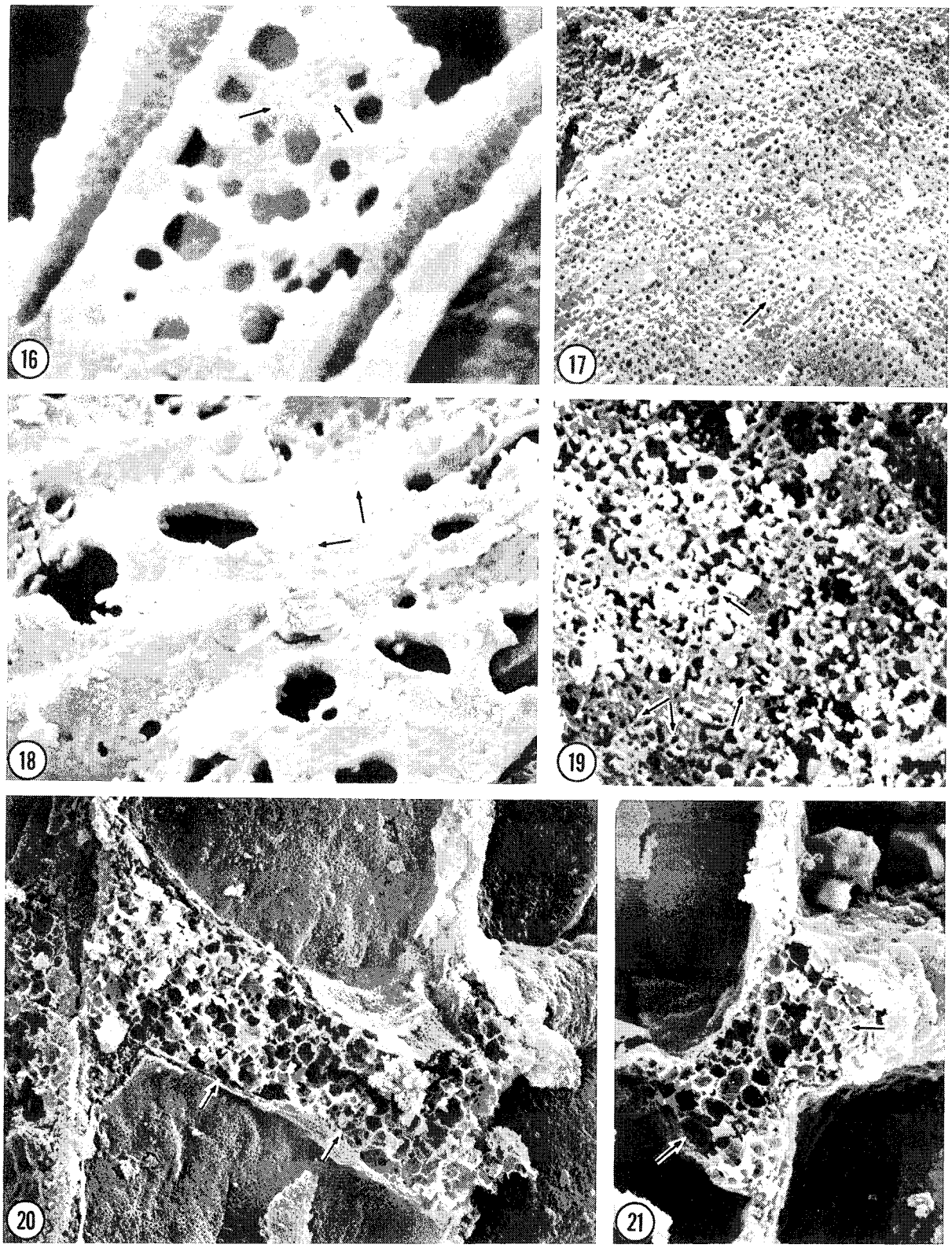
NOTE.—For explanation of cell wall measurements (δ, Σ, t, W, mean values in μm), see fig. 1. The number of measurements for each taxon and each category varied considerably and depended on the quality and quantity of material available for study. For *S. hippocrepiformis, G. breconensis, A. mackiei,* and *R. gwynne-vaughanii,* the number of individual measurements for each wall dimension varied between 44 and 122 taken from 10 or more cells for each taxon; for the other three taxa in which measurements were possible, only three or four cells were measured, yielding 30–40 measurements. Evidence for S-type structure: ✓ = feature present; ? = unknown or feature not observed; † = material too poorly preserved for useful measurements; * = there is some evidence for this feature (cf. figs. 17, 19 in this paper). *a* = KENRICK and EDWARDS (1988). *b* = KENRICK et al. (1991*a*). *c* = this paper. *d* = HUEBER (1982). *e* = FAIRON-DEMARET (1985, 1986). *f* = KENRICK et al. (1991*b*). *g* = REMY et al. (1980).



FIGS. 2–8.—Figs. 2–5, Longitudinal thin sections of the water-conducting cells of *Asteroxylon mackiei*. Fig. 2, Tangential section showing thickenings in plan view; × 532. Fig. 3, Median section showing thickenings in section; × 532. Fig. 4, Detail of thickenings in plan view. Two thickenings are arrowed; × 1,055. Fig. 5, Detail of thickenings in section view. Arrows indicate two examples of peg-like nature of thickenings; × 1,055. Fig. 6, Polished median longitudinal thick section of a water-conducting cell of *Gosslingia breconensis* showing thickenings in section view. Arrows indicate two examples of peg-like nature of thickening; ca. × 1,055. Figs. 7, 8, Scanning electron micrographs of the etched water-conducting cells of *Asteroxylon mackiei*. Fig. 7, Metaxylem; × 285. Fig. 8, Annular or helical thickenings in three adjacent cells, × 1,050.



FIGS. 9–15.—Figs. 9–12, Longitudinal thin sections of the water-conducting cells of *Rhynia gwynne-vaughanii.* Fig. 9, Thickenings in plan view and section; × 532. Fig. 10, Thickenings in plan view and section; × 532. Fig. 11, Detail of the thickening in plan view. Arrows indicate gyres; × 1,055. Fig. 12, Detail of thickening in section view. Each section through a gyre is arrowed; × 1,055. Fig. 13, Polished longitudinal thick section of wall of two adjacent water-conducting cells in *Sennicaulis hippocrepiformis* showing shape of helical thickening in section. Each section through a gyre is arrowed; ca. × 1,055. Figs. 14, 15, Scanning electron micrographs of the etched water-conducting cells of *Rhynia gwynne-vaughanii.* Fig. 14, Whole xylem strand. Arrows indicate outer edge of strand; × 285. Fig. 15, Thickening (arrows) plunges downward in a helix in two adjacent cells; × 1,050.



FIGS. 16–21.—Figs. 16–19, Detail of the cell walls of etched water-conducting cells; × 6,500. Fig. 16, *Gosslingia breconensis.* Large perforations in coalified layer between annular wall thickenings viewed from outside the cell. Note also the very fine scale indentations (arrows) on the surface of the coalified material and inside the hollow thickenings. Fig. 17, *Sennicaulis hippocrepiformis.* Microporate wall layer. A micropore is arrowed. Fig. 18, *Asteroxylon mackiei.* Large perforations in coalified layer between annular wall thickenings viewed from inside the cell. Note also the very fine scale indentations (arrows) on the surface of the coalified material. Fig. 19, *Rhynia gwynne-vaughanii.* Presumed microporate wall layer with small lumps of insoluble white material obscuring surface. Arrows indicate small pores and possible fibrous texture (lower left). Figs. 20, 21, Detail of spongy structure inside the helical thickenings of *Sennicaulis hippocrepiformis.* Fig. 20, Plan view with inner microporate layer removed from over thickening revealing underlying spongy structure; × 2,900. Fig. 21, Section view of thickening in two adjacent cells showing spongy interior; × 3,400.

enings (fig. 5; peg-like protrusions in section) is also translucent resulting in a hollow appearance, but in larger cells the thickenings may be completely opaque (fig. 3). Scanning electron micrographs of etched cells illustrate the morphology of the dark, opaque layer (figs. 7, 8, 18). Internal thickenings are visible in all cells (figs. 7, 8) and between thickenings the inner layer is perforated by pores or simple pits of varying size but with a maximum diameter of about 5 μm (fig. 18). Also visible on the surface of this layer are numerous, very fine indentations.

Rhynia gwynne-vaughanii

The elongate cells that make up the water-conducting strand of *R. gwynne-vaughanii* each have a single large helical thickening (figs. 9–12, 14, 15). The helical arrangement can be observed both by focusing through cells with a light microscope and by scanning electron microscopy of etched cells (figs. 14, 15). Frequent reversals in tilt of the gyres are evident in all cells (figs. 9–11). In median longitudinal section, thickenings appear as distinct hemispherical projections into the cell lumen (figs. 9, 10, 12). The base of the thickening (the junction with the thinner part of the wall) may be very broad (fig. 12), but the overall size of the thickening decreases toward either end of the cell. Detailed measurements of wall ornament (fig. 1) are given in table 1.

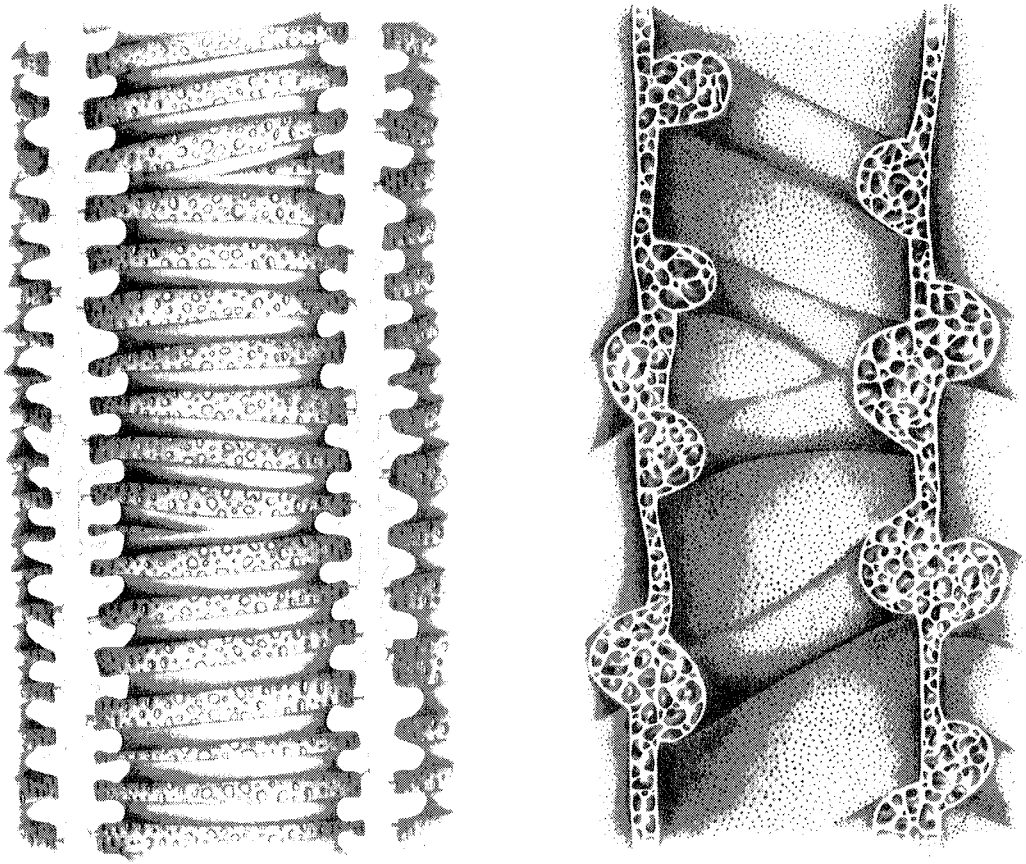
In median section the composition of the cell wall is distinctive and consistent in all cells examined. The thickenings and the adjacent thinner parts of the wall are translucent (figs. 9–12). The interior of the thickenings has a spongy texture that is evident in plan (fig. 11) and section view (fig. 12). The lacunae in the spongy layer appear quite large (fig. 11: ca. 4.5 μm diameter), but small lacunae are also abundant, although more difficult to resolve (fig. 12). There is an extremely thin inner opaque layer that bounds the thickening and lines the inner surface of the cell (figs. 12, 15, 19). The thickness of this layer proved impossible to measure accurately from thin sections and SEMs, but conservative estimates place it between 100 and 300 nm thick. The ultrastructure of the thin layer is poorly preserved in etched SEM preparations (fig. 19), but the consistent morphology of fragments of this inner layer indicates a microporate or fibrous texture (fig. 19). Better preserved material is needed to establish the structure of this layer more precisely.

Comparisons

Asteroxylon mackiei

The water-conducting cells of *A. mackiei* resemble the G-type cell originally described from pyritized material of *Gosslingia breconensis* (Kenrick and Edwards 1988; Kenrick et al. 1991*a*). A longitudinal section through one such cell preserved in pyrite (fig. 6) and a reconstruction of the G-type cell wall (fig. 22) are illustrated for comparison. This cell type has indirectly or directly attached, annular or helical thickenings (*sensu* Bierhorst 1960). Indirect attachments are formed by sheets of coalified material with simple pits that stretch between adjacent thickened bars (figs. 16, 22). The cell wall is two-layered: a relatively thick, discontinuous, coalified inner layer underlies a mineralized outer layer from which coalified material is absent. The layering of the cell wall in the pyritized cells of *G. breconensis* (fig. 6) and the silicified cells of *A. mackiei* (fig. 5) is identical. The internal dark coalified layer is similar in both plants, whereas the outer translucent layer of the wall in *A. mackiei* corresponds exactly to the pyritized layer in the wall of *G. breconensis,* even to the extent of occurring within the thickenings. The thickenings in the two plants are also of similar overall size (table 1), morphology, and shape in section (figs. 5, 6). Simple pits of similar morphology are found between thickenings and numerous very fine indentations occur on the surface of the coalified remains in both plants (figs. 16, 18).

It has been argued that certain features of this cell wall, particularly the simple pits between thickenings, are a result of preservational processes and are of no structural or taxonomic significance. Hartman (1981), working on pyritized material, concluded that these pits were caused by pyrite crystal growth, while Lemoigne and Zdebska (1980), working with silicified cells, attributed them to biological decay or alteration of the wall by silica. However, the characteristic G-type cell wall has now been identified in several taxa that are variously preserved (Kenrick and Edwards 1988, table 2): *Drepanophycus spinaeformis* preserved in calcium carbonate concretions (Grierson and Hueber 1967), *Barinophyton citrulliforme* preserved in limonite (Brauer 1980), *Baragwanathia abitibiensis* preserved as nonmineralized coalified material (Hueber 1983), *G. breconensis* preserved in pyrite (Kenrick and Edwards 1988), *Taeniocrada stilesvillensis* preserved in pyrite (Taylor 1986), and *A. mackiei* preserved in silica (Lemoigne and Zdebska 1980; this paper). We argue that the consistent appearance of these cell walls in various preservation states is good evidence that the pits between thickenings and other wall features have a structural rather than a diagenetic origin. Kenrick and Edwards (1988) concluded that the distribution of coalified material within the G-type cell wall reflects the distribution of decay-resistant chemicals. Thus, in *Gosslingia* the coalified part of the wall can be thought of as a 'lignified' layer, and the pyritized part as a more readily decomposed



FIGS. 22, 23.—Reconstructions of G-type and S-type water-conducting cells; × 1,000. Fig. 22 (left), Median section through the G-type water-conducting cell ('tracheid') of *Gosslingia breconensis* (KENRICK and EDWARDS 1988). The cell wall is two-layered. A decay-resistant inner layer (represented as white in section view) makes up most of the thickening and is continuous with a pitted sheet between thickenings. The decay-resistant layer underlies a nonresistant outer layer (represented as gray in section view). Fig. 23 (right), Median section through the S-type water-conducting cell ('tracheid') of *Sennicaulis hippocrepiformis* (KENRICK et al. 1991*a*). The cell wall is two-layered. A very thin resistant inner layer (represented as white in section view) lines the entire inner surface of the cell and is perforated by numerous plasmodesmata derived pores. The resistant inner layer underlies a semi-resistant outer layer (spongy in section view).

"nonlignified" layer. The simple pits between thickenings are perforations through a sheet of "lignified" wall material (figs. 16, 22). Comparable sheets or strands of lignified wall material also have been described from the tracheids of other fossil taxa. Strands of secondary wall material that stretch across pit apertures are found in several lycopods, such as *Eskdalia variabilis* (ROWE 1988), *Lepidodendron* (WESLEY and KUYPER 1951), *Lepidophloios* and *Stigmaria* (CICHAN et al. 1981), and *Minarodendron cathaysiense* (LI 1990), and in the trimerophyte *Psilophyton dawsonii* (HARTMAN and BANKS 1980).

Certain aspects of the wall of G-type cells are comparable to features in the tracheids of extant pteridophytes. The occurrence of minor vertical strands of wall material between major more or less transversely oriented annular or helical strands is widespread among vascular plants (BIERHORST 1960, p. 300). In the Equisetaceae and Ophioglossaceae such strands occur between annular thickenings in the protoxylem, and although less extensive they may be comparable to the sheet of secondary wall material with simple pits that stretches between thickenings in the G-type cell. In addition, the cores of the thickenings in the protoxylem and early formed metaxylem of *Lycopodium* are nonlignified or weakly lignified (BIERHORST 1960, p. 252, fig. 21), as is also inferred for many of the thickenings in G-type cells.

Among extinct taxa, in addition to *G. breconensis,* the G-type cell wall is common in the Zosterophyllophytina Banks (KENRICK and EDWARDS 1988, table 2) and closely related fossil plants such as *Barinophyton citrulliforme,* and the lycopods *Drepanophycus spinaeformis* and *Baragwanathia abitibiensis.* The identification of this cell type in the lycopod-like plant *A. mackiei* is consistent with these previous observations.

RHYNIA GWYNNE-VAUGHANII

The water-conducting cells of *R. gwynne-vaughanii* closely resemble the S-type cell, originally described from limonitic and pyritized material of *Sennicaulis hippocrepiformis* (KENRICK et al. 1991*a*), except that they are noticeably narrower (table 1: W). A longitudinal section through the wall of one such cell preserved in limonite (fig. 13), SEMs of the etched helical thickening (figs. 20, 21), and a reconstruction of the S-type cell wall (fig. 23) are illustrated for comparison. S-type cells in both *R. gwynne-vaughanii* and *S. hippocrepiformis* are elongate, each with a large simple helical thickening that shows frequent reversals in direction of the gyres. The hemispherical shape of the thickening in section is similar in both *S. hippocrepiformis* (fig. 13) and *R. gwynne-vaughanii* (fig. 12), although in the latter the distance between gyres (Σ) is smaller and more comparable to that in G-type cells. In both plants the coalified wall is clearly two-layered and a thin continuous inner layer (next to the cell lumen) overlies a thick spongy later that is particularly pronounced in the thickenings (figs. 11, 12, 20, 21, 23; KENRICK et al. 1991*a*). In *Sennicaulis* the inner layer is well preserved and perforated by numerous micropores. These micropores average about 100 nm diameter and occur with a density of about 16 μm^{-2}, and the thickness of the microporate layer is estimated as between 100 nm and 200 nm (figs. 17, 20, 21). In *R. gwynne-vaughanii* the morphology of the inner layer is not easily observed (fig. 19) because etching the delicate, silicified cell walls proved difficult. This material does not survive the etching process as well as that preserved in limonite or pyrite, and only one of the many conducting strands that were etched remained relatively intact (fig. 14). The thin layer lining the cell lumen (fig. 19) has pores of variable size and shape, and has more of a fibrous appearance than the equivalent layer in *S. hippocrepiformis* (fig. 17).

As with the G-type cell, we argue that the features of the S-type cell have a structural basis and cannot be dismissed as a result of preservation or decay. Three lines of argument support this conclusion. First, features of the S-type cell such as the spongy wall layer cannot be attributed to a single mineralization process because they have been observed in pyrite, limonite, and silica (table 1). Second, S-type and G-type cells are markedly and consistently different from each other when preserved in the same minerals at the same localities. At Brecon Beacons Quarry, both cell types are preserved in pyrite and limonite (KENRICK et al. 1991*a*), and in the Rhynie Chert they are preserved in silica (this paper). Third, the microporate layer of the S-type cell wall, not seen in G-type cells, is directly comparable to the microporate wall in the water-conducting cells of some extant 'bryophytes'.

While helical thickenings are common in the early formed protoxylem of vascular plants, the "spongy" internal structure of thickenings in S-type cells and the thin microporate inner wall layer have not been recorded from the tracheids of any extant 'pteridophyte'. However, the microporate layer of S-type cells is remarkably similar to the cell wall of the water-conducting cells of the moss *Takakia lepidozioides* as well as the liverworts *Pallavicinia lyellii* and *Hymenophyton flabellatum* (HÉBANT 1979, figs. 2, 4, 5). The walls in these plants have plasmodesmata-derived micropores of similar size and density to those in the fossil suggesting a similar function and underlying developmental process (KENRICK et al. 1991*a*). According to HÉBANT (1979), a preliminary survey of the water-conducting cells of 'bryophytes' indicates that such a microporate wall is more characteristic of hepatics than mosses, but a more detailed survey of a greater range of taxa needs to be completed.

The S-type cell was characterized initially from sterile axis fragments assigned to *S. hippocrepiformis* (KENRICK et al. 1991*a*), and similar water-conducting cells are known from ribbon-like axes with stomata called *Taeniocrada dubia* (Dawson's rhizomata of *Psilophyton princeps* [HUEBER 1982]). The morphology of both these plants is poorly understood and their reproductive structures are unknown. More recently (KENRICK et al. 1991*b*), S-type cells have been identified in two better known Lower Devonian taxa, *Stockmansella langii* (FAIRON-DEMARET 1985, 1986) and *Huvenia kleui* (HASS and REMY 1991). Both plants are characterized by fusiform sporangia attached to shallow concave "pads of tissue" that are arranged laterally on the main axes or terminally on short subordinate lateral branches. A distinct coaly layer at the point of attachment of the sporangium to the axis serves as an abscission layer for empty sporangia in *S. langii* and possibly also in *R. gwynne-vaughanii*. In *H. kleui* sporangia are rarely abscised, and this layer is interpreted as a means of isolating empty sporangia (HASS and REMY 1991). Unless these unusual features reflect the abscission of a very simple sporophyte consisting of a single sporangium, all three of these plants are most straightforwardly interpreted as branched sporophytes. This interpretation is further supported by their general similarity to *Aglaophyton major* and 'trimerophytes' such as *Psilophyton dawsonii* that are unequivocal sporophytes, as well as by the continuity of the vascular strand through the pad of tissue into the base of the sporangium in *R. gwynne-vaughanii* (EDWARDS 1980) and *H. kleui* (HASS and REMY 1991).

In addition to the sporophytes discussed above,

the S-type cell also has been recorded from *Sciadophyton* sp. (KENRICK et al. 1991*b*), which is probably a gametophyte (REMY et al. 1980; REMY 1982). Axes of this plant are dichotomously branched, are ribbon-like, and bear terminal disk or cup-shaped structures with small circular marks on the surface. These disks or cups are interpreted as gametangiophores based on their similarity in shape, size, and position to unequivocal gametangiophores from the Rhynie Chert. In the gametophytes *Lyonophyton rhyniensis* (REMY and REMY 1980; REMY and HASS 1991*a*), *Kidstonophyton discoides* (REMY and HASS 1991*b*), and *Langiophyton mackiei* (REMY and HASS 1991*c*) from the Rhynie Chert, the gametangiophore is a terminal disk-like or cup-shaped structure with antheridia or archegonia on the upper surface. The position and size of the antheridia in *L. rhyniensis* and *K. discoides* are comparable to the small circular marks on the cup-shaped structures of *Sciadophyton* sp. (REMY et al. 1980; REMY 1982).

Discussion

EARLY FOSSIL HISTORY OF WATER-CONDUCTING CELLS

Four distinct kinds of water-conducting cell have now been recognized *in situ* within branched sporophytes described from the Lower Devonian (figs. 24, 25): (1) unornamented elongated cells are found in the sporophytes *Aglaophyton major* and *Nothia aphylla* as well as the gametophytes *Lyonophyton rhyniensis* and *Kidstonophyton discoides,* all of which are known only from the Rhynie Chert; (2) S-type cells (fig. 23) are known from the sporophytes *Rhynia gwynne-vaughanii, Stockmansella langii,* and *Huvenia kleui,* as well as the gametophyte *Sciadophyton* sp., and *Sennicaulis hippocrepiformis* and *Taeniocrada dubia* for which reproductive structures are unknown; (3) G-type cells (fig. 22) are widespread in the sporophytes of zosterophylls and early lycopods (see above); and (4) tracheids with unequivocal scalariform pitting are first documented clearly in *Psilophyton dawsonii.* Despite substantial evidence of pre-Devonian land plants (fig. 25) there are no unequivocal records of S-type or G-type conducting cells prior to the Pragian, and pitted tracheids are not recorded until the Emsian. Because S-type and G-type cells also are easily mistaken for sclariform pitted elements, details of "tracheids" reported from other Pragian and Emsian fossils such as *Horneophyton lignieri* (HASS, personal communication), and also those mentioned by KENRICK and EDWARDS (1988), require reevaluation. Prior to the Pragian, differentially thickened water-conducting cells have been recorded twice in sterile axes associated with plants of *Cooksonia*-type morphology (LANG 1937; EDWARDS and DAVIES 1976), but in neither case are the cells sufficiently well preserved to determine accurately their wall structure.

The almost simultaneous appearance in the fossil record of unornamented water-conducting cells with S-type and G-type cells (figs. 24, 25) is probably strongly influenced by taphonomic factors. Plant tissues are most commonly preserved in the mineral pyrite, or its oxidation products, but preservation of nonlignified cell walls is comparatively rare in such material. The only records of unornamented water-conducting cells in the Devonian are in the exceptionally well-preserved silicified plants of the Rhynie Chert (e.g., *Nothia* and *Aglaophyton*; fig. 24). In the earlier well-preserved *Cooksonia*-type plants from the Lochkovian in which stomata and thick-walled sterome are documented, there is apparently no cellular preservation in the inner part of the axis. The absence of preserved water-conducting tissues in these plants suggests a relatively undifferentiated water-conducting system. Of the cells that survive the pyritization process, the S-type and G-type appear simultaneously in the upper Lochkovian or lower Pragian and are found at an increasing number of localities through the Pragian and Emsian (fig. 24). Trends in these data should be interpreted with caution because they are based mainly on a restricted range of well-studied lo-

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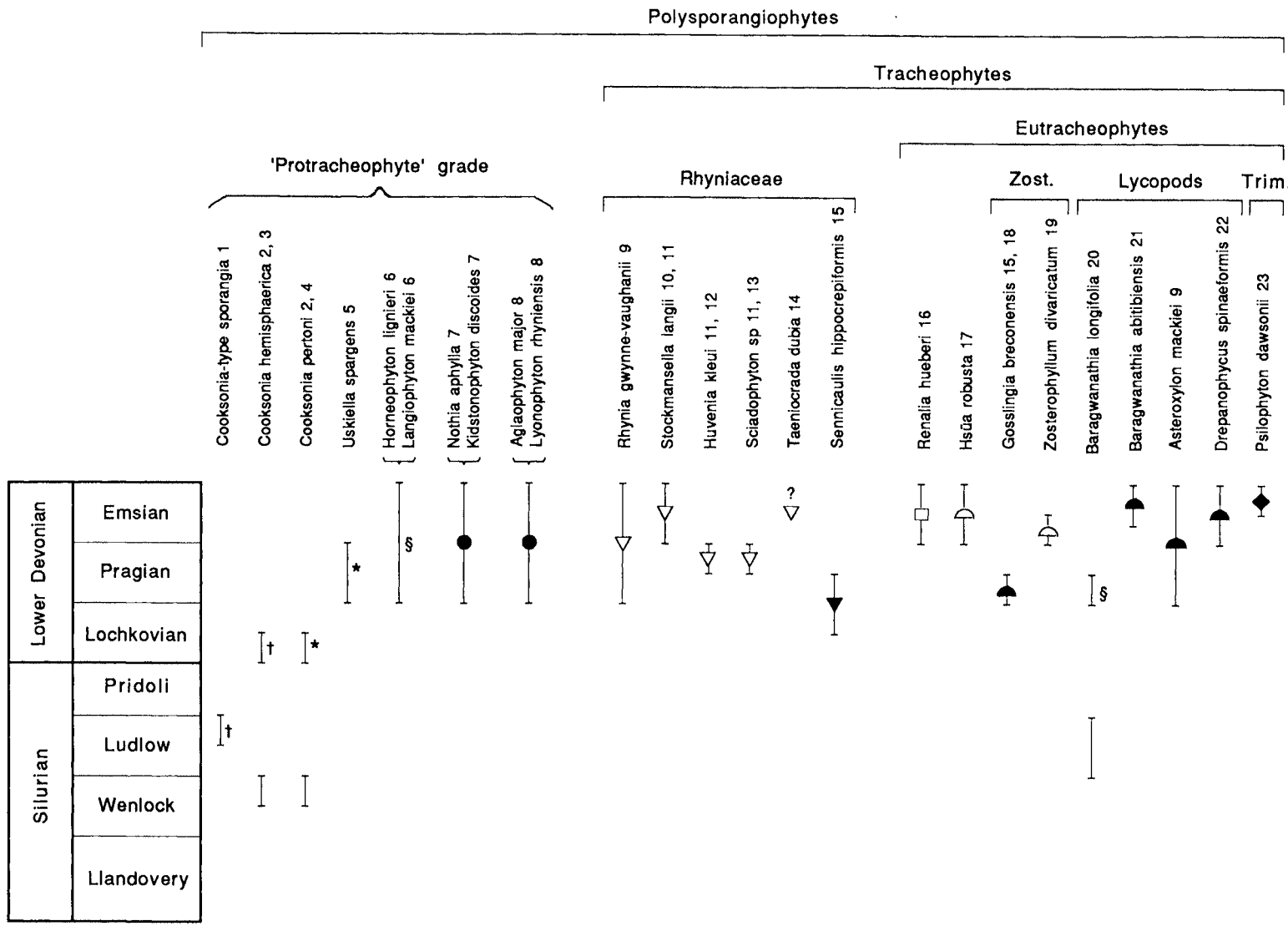
FIG. 24.—Earliest occurrences of water-conducting cells in selected early land plant taxa. Supra-generic groups based on fig. 26. The bar associated with each symbol is a measure of the accuracy of the age determination as estimated by the original authors or updated where more precise information is now available. ○ = unornamented; ▽ = S-type; △ = G-type; □ = possible scalariform pits; ◇ = bordered pits with strands of secondary wall material across pit apertures. Black symbol indicates well-documented cell type; open symbol indicates strong evidence for cell type; no symbol indicates water-conducting cells unknown. † = ornamented cells of unknown wall structure found in associated sterile axes, possibly from the named plant. * = cortical tissues (sterome) preserved, yet no evidence of ornamented water-conducting cells. § = ornamented cells of unknown wall structure. ? = stratigraphic range unknown. Trim. = trimerophytes, Zost. = zosterophylls. References: 1, EDWARDS and DAVIES 1976. 2, EDWARDS et al. 1983. 3, LANG 1937; EDWARDS and FANNING 1985. 4, EDWARDS et al. 1986. 5, SHUTE and EDWARDS 1989. 6, REMY and HASS 1991*c*. 7, EL-SAADAWY and LACEY 1979*a*; REMY and HASS 1991*b*. 8, EDWARDS 1986; REMY and HASS 1991*a*. 9, This paper. 10, FAIRON-DEMARET 1985, 1986. 11, KENRICK et al. 1991*b*. 12, HASS and REMY 1991. 13, REMY et al. 1980. 14, HUEBER 1982. 15, KENRICK et al. 1991*a*. 16. GENSEL 1976. 17, LI 1982, personal communication. 18, KENRICK and EDWARDS 1988. 19, GENSEL 1982. 20, LANG and COOKSON 1935; TIMS and CHAMBERS 1984. 21, HUEBER 1983. 22, HARTMAN 1981; RAYNER 1984. 23, HARTMAN and BANKS 1980. Time scale modified from HARLAND et al. (1982).


Polysporangiophytes
Tracheophytes
Eutracheophytes
'Protracheophyte' grade
Rhyniaceae
Zost.
Lycopods
Trim.
Cooksonia-type sporangia 1
Cooksonia hemisphaerica 2, 3
Cooksonia pertoni 2, 4
Uskiella spargens 5
Horneophyton lignieri 6
Langiophyton mackiei 6
Nothia aphylla 7
Kidstonophyton discoides 7
Aglaophyton major 8
Lyonophyton rhyniensis 8
Rhynia gwynne-vaughanii 9
Stockmansella langii 10, 11
Huvenia kleui 11, 12
Sciadophyton sp 11, 13
Taeniocrada dubia 14
Sennicaulis hippocrepiformis 15
Renalia hueberi 16
Hsüa robusta 17
Gosslingia breconensis 15, 18
Zosterophyllum divaricatum 19
Baragwanathia longifolia 20
Baragwanathia abitibiensis 21
Asteroxylon mackiei 9
Drepanophycus spinaeformis 22
Psilophyton dawsonii 23
Lower Devonian
Emsian
Pragian
Lochkovian
Silurian
Pridoli
Ludlow
Wenlock
Llandovery

calities in northern Europe and North America. However, it is clear that metaxylem composed of entirely annular- or helical-thickened cells occurs significantly earlier than metaxylem composed of pitted cells that are first recorded in the Emsian (figs. 24, 25). Pitted tracheids occur across a broad range of taxa by the Middle and Upper Devonian including representatives of the two major clades of vascular plants (see below) implying that the pitted cell evolved at least twice: once in the lycophyte clade from a G-type cell precursor and once in the nonlycophyte ('pteridophyte'-'progymnosperm'-seed plant) clade.

Of the four types of water-conducting cell currently recognized among early Devonian fossil plants, the unornamented cells are similar to the hydroids of mosses (EDWARDS 1986), whereas the G-type and scalariform pitted cells are most comparable to the protoxylem and metaxylem tracheids, respectively, of extant 'pteridophytes'. S-type cells, however, have not been recognized in any extant plant. Their known taxonomic distribution includes the type species of BANK's subdivision Rhyniophytina (*R. gwynne-vaughanii*), several other taxa formerly grouped in *Taeniocrada,* and the gametophyte *Sciadophyton* sp.

The relationships of these taxa are poorly understood, and *Taeniocrada* is especially problematic because it contains many poorly defined species probably of diverse relationships (FAIRON-DEMARET 1985; TAYLOR 1986; HASS and REMY 1991). Recent reinvestigations of two *Taeniocrada* species have led to the segregation of two new genera, *Stockmansella* Fairon-Demaret and *Huvenia* Hass and Remy. In an analysis of morphological features including the attachment, shape, and dehiscence of the sporangium, as well as the pattern of overtopping and adventitious branch production, HASS and REMY (1991) concluded that *Stockmansella, Huvenia,* and *Rhynia* are all closely related, and they circumscribed the family Rhyniaceae to include these three genera. The recognition that all these taxa also possess S-type conducting cells provides further support for their family concept.

The genus *Sciadophyton* contains large branched morphologically complex compression fossils that are interpreted as gametophytes (REMY et al. 1980), and recent descriptions of well-preserved gametangiophores from the Rhynie Chert (REMY and REMY 1980; REMY 1982; REMY and HASS 1991*a*, 1991*b*, 1991*c*), lend strong support to this contention. The discovery of S-type cells in *Sciadophyton* sp. (KENRICK et al. 1991*b*), found in association with the *Huvenia* plant, further suggests that the Rhyniaceae had gametophytes of the *Sciadophyton* type and that they differed from extant 'pteridophytes' in having a life cycle with a more or less isomorphic alternation of generations. A similar life cycle has been proposed for some of the silicified plants from the Rhynie Chert: *A. major* (gametophyte = *L. rhyniensis*), *N. aphylla* (gametophyte = *K. discoides*) and *H. lignieri* (gametophyte = *Langiophyton mackiei*) (REMY and HASS 1991*a*, 1991*b*, 1991*c*).

PHYLOGENETIC HYPOTHESES

A comprehensive cladistic evaluation of relationships among extant and fossil 'bryophytes' and 'pteridophytes' has never been attempted, but, based on preliminary analyses (MISHLER and CHURCHILL 1984, 1985; CRANE 1989, 1990), it is possible to develop a rudimentary phylogenetic framework to focus discussion of the relationships of the relevant extant and fossil taxa (fig. 26).

There is good evidence that the embryophytes are a monophyletic group readily distinguished from closely related charophyte green algae such as *Coleochaetae* (GRAHAM 1984, 1985; MISHLER and CHURCHILL 1984, 1985; GRAHAM and REPAVICH 1989; table 2, App. 1). Among 'bryophytes' there also seems to be explicit or implicit agreement that the liverworts, hornworts, and mosses are natural groups, each of which may be defined unequivocally by several characters (MISHLER and CHURCHILL 1984, 1985). Recent cladistic discussions interpret the 'bryophytes' as a basal grade of embryophytes (MISHLER and CHURCHILL 1984, 1985; BREMER 1985; BREMER et al. 1987; CRANE 1989, 1990) and consistently indicate that mosses and hornworts are more closely related to the tracheophytes than are the liverworts, based on the joint possession of stomata and the ability to distinguish metabolically the L and D isomers of methionine (fig. 26). Within this group (informally termed here "stomatophytes") MISHLER and CHURCHILL (1984, 1985) place mosses as sister group to tracheophytes based on five synapomorphies. In our view, four of these characters, although potentially useful, still have inherent difficulties, and the fifth (presence of perine [character 9, Appendix]) requires further investigation. Two other characters, however, do support the moss-trachophyte clade and exclude the hornworts (radial [axial] symmetry in the gametophyte [character 10, Appendix], and terminal aggregations of gametangia [character 11, Appendix]).

Within the moss-trachophyte group we recognize a large clade comprising all extant 'pteridophytes' and seed plants plus early fossil land plants such as *Cooksonia, Aglaophyton,* and *Rhynia.* This group (informally termed "polysporangiophytes") is defined by the presence of a branched sporophyte bearing many sporangia, and this feature unequivocally distinguishes these plants from 'bryophytes' (fig. 26). Other potential

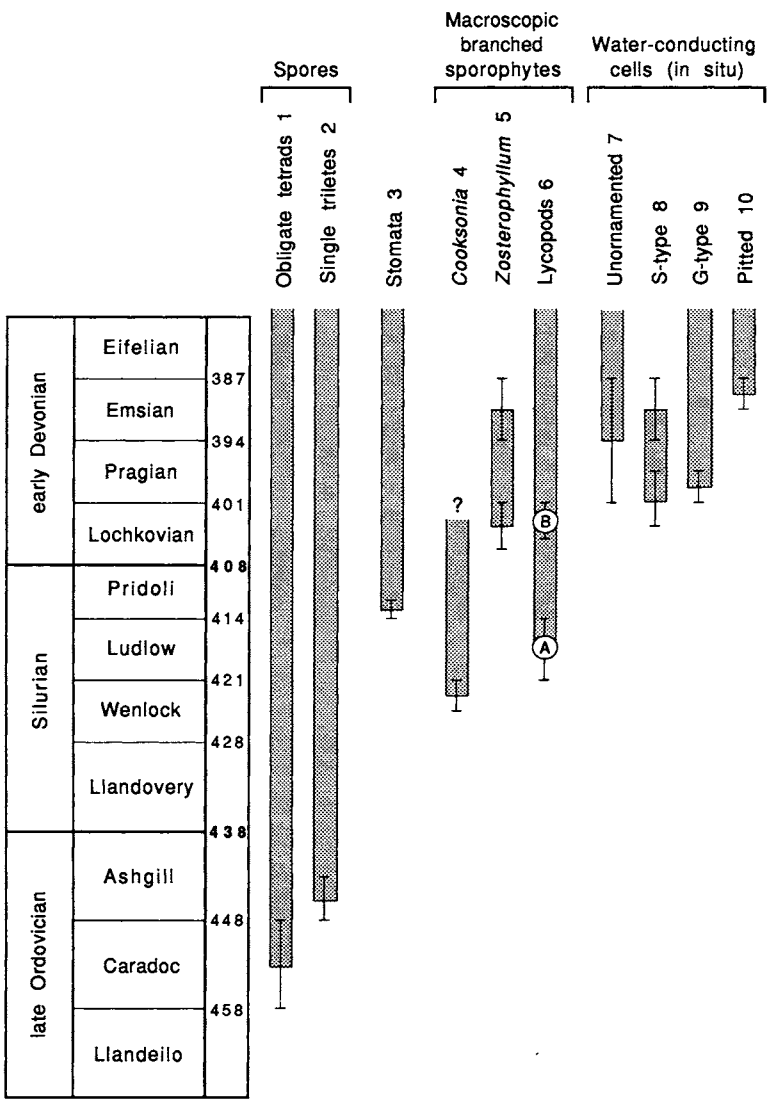


FIG. 25.—Appearance of selected land plant characters in the fossil record. Data presented are based almost entirely on northern European and North American localities because of a lack of information from elsewhere. Two exceptions are the data on obligate tetrads, some of which come from North Africa, and the lycopod compressions, where *B* indicates first occurrence in northern Europe, and *A* first occurrence in Australia. The error bars indicate the accuracy of the age as estimated by the original authors. ? indicates upper limit uncertain. References: 1, GRAY et al. 1982; see also GRAY 1985; RICHARDSON 1985; RICHARDSON and MCGREGOR 1986; NØHR-HANSEN and KOPPELHUS 1988. 2, NØHR-HANSEN and KOPPELHUS 1988; see also GRAY 1985; RICHARDSON 1985. 3, JERAM et al. 1990. 4, EDWARDS et al. 1983. 5, HUEBER and BANKS 1979; GENSEL 1982; EDWARDS and FANNING 1985. 6, (*A*) TIMS and CHAMBERS 1984; (*B*) SCHWEITZER 1983. 7, EDWARDS 1986. 8, KENRICK et al. 1991*a*, 1991*b*. 9, KENRICK and EDWARDS 1988; KENRICK et al. 1991*a*, 1991*b*. 10, HARTMAN and BANKS 1980. Time scale modified after HARLAND et al. (1982).

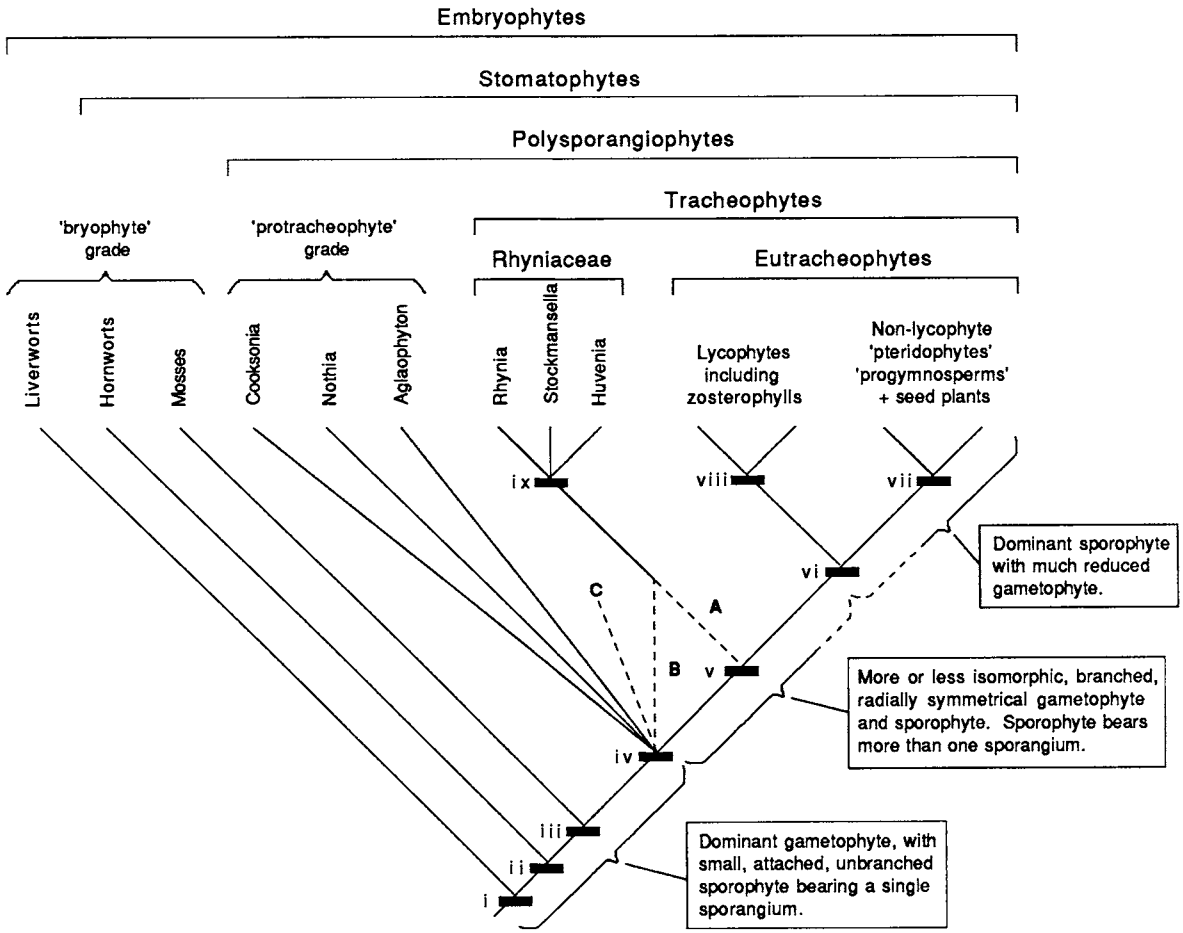


FIG. 26.—Hypotheses of embryophyte phylogeny with implications for the evolution of the 'pteridophyte' life cycle. Because of the possibility that the genus *Cooksonia* contains species of diverse relationships (EDWARDS and EDWARDS 1986) the analysis here is based on well-preserved material of *C. pertoni* described by EDWARDS et al. (1986). Cladograms generated from data in table 2. Hypothesis A: Our preferred hypothesis, Rhyniaceae (*sensu* HASS and REMY 1991) sister group to eutracheophytes, which together form the monophyletic group tracheophytes. S-type and G-type water-conducting cells homologous (strict consensus of 26 trees, shortest tree = 27 steps, number of characters = 24, consistency index of individual trees = 0.926, excluding uninformative characters consistency index = 0.882). Hypothesis B: Rhyniaceae part of an unresolved 'protracheophyte' grade. S-type and G-type water-conducting cells are not homologous. G-type cell is a synapomorphy of eutracheophytes, S-type cell is a synapomorphy of Rhyniaceae (strict consensus of 28 trees, shortest tree = 26 steps, number of characters = 23, consistency index of individual trees = 0.923, excluding uninformative characters consistency index = 0.875). Hypothesis C: 'Protracheophytes', Rhyniaceae, and the two major clades of vascular plants (lycophytes and nonlycophytes) form a polychotomy within polysporangiophytes (i.e., lycophyte and nonlycophyte clades inserted at *C*). This implies an independent origin of the tracheid in the lycophyte and nonlycophyte ('trimerophyte'-'progymnosperm'-seed plant) clades with both derived independently to the S-type cells. Independent reduction of the gametophyte generation in lycophytes and nonlycophytes is also implicit in this interpretation (strict consensus of 130 trees, shortest tree = 27 steps, number of characters = 24, consistency index of individual trees = 0.926, excluding uniformative characters consistency index = 0.867). Under hypothesis A above, potential synapomorphies include: (*i*) Embryophytes: antheridia; archegonia; cuticle; bicentriolar centrosomes; lamellae of MLS 40°–45°; preprophase band microtubules (characters 1–6, table 2; Appendix). (*ii*) Stomatophytes: stomata in sporophyte generation; ability to distinguish D-methionine (characters 7, 8, table 2; Appendix). (*iii*) Moss-polysporangiophyte clade: perine; axial gametophyte; terminal gametangia (characters 9–11, table 2; Appendix). (*iv*) Polysporangiophytes: branched sporophyte with more than one sporangium; independent sporophyte; more or less isomorphic alternation of generations (characters 12–14, table 2; Appendix). (*v*) Tracheophytes: helical or annular ornamented water-conducting cells; decay-resistant inner wall layer in water-conducting cells (characters 22, 23, hypothesis A, table 2; Appendix). (*vi*) Eutracheophytes: G-type water-conducting cells (character 24, hypothesis A, table 2; Appendix). (*vii*) Nonlycophyte clade: pitted water-conducting cell, longitudinal dehiscence of sporangium; sporangia arranged in terminal clusters (characters 15, 16, table 2; Appendix). (*viii*) Lycophyte clade: reniform sporangia; sporangia lateral on short nonvascular stalks (characters 17, 18, table 2; Appendix). (*ix*) Rhyniaceae: abscission or isolation layer at base of sporangium; "*Rhynia*"-type adventitious branching; sporangium sessile on "pad of tissue" attached directly to main axis or terminal on short subordinate branch (characters 19–21, table 2; Appendix).

TABLE 2

CHARACTERS INCLUDED IN ANALYSIS OF RELATIONSHIP BETWEEN MAJOR CLADES OF EXTANT 'BRYOPHYTES' AND VASCULAR PLANTS WITH SELECTED FOSSIL TAXA

Character/taxon	*Col.*	L	H	M	*Cook.*	*Not. (Kid.)*	*Agl. (Lyo.)*	*Rhy.*	*Sto.*	*Huv. (Sci.)*	Lyc.	Non lyc.	References
1. Antheridia	0	1	1	1	?	1	1	?	?	?	1	1	*a, b, c, d*
2. Archegonia	0	1	1	1	?	?	?	?	?	?	1	1	*a, b, c, d*
3. Cuticle	0	1	1	1	1	1	1	1	1	?	1	1	*a, b, c, d*
4. Bicentriolar centrosomes	0	1	1	1	?	?	?	?	?	?	1	?	*e*
5. Lamellae of MLS 40°–45°	0	1	1	1	?	?	?	?	?	?	1	?	*e, f*
6. Preprophase band of microtubules	0	1	1	1	?	?	?	?	?	?	1	1	*g*
7. Distinguish D-methionine	?	0	1	1	?	?	?	?	?	?	1	1	*h*
8. Stomata in sporophyte	0	0	1	1	1	1	1	1	1	?	1	1	*a, b, c, d*
9. Perine layer on spores	0	0	0	1	?	?	?	?	?	?	1	1	*m*
10. Radial, axial gametophyte	0	0	0	1	?	1	1	?	?	1	1	1	*d, n*
11. Terminal sex organs	0	0	0	1	?	1	1	?	?	1	1	0	*a, b, d*
12. More than one sporangium	0	0	0	0	1	1	1	1	1	1	1	1	*a, b, c, d*
13. Alternation of generations	0	0	0	0	?	1	1	?	?	1	2	2	*a, b, c, d*
14. Independent sporophyte	0	0	0	0	?	?	1	1	1	1	1	1	*a, b, c, d*
15. Longitudinal dehiscence	0	0	0	0	0	0	0	0	0	0	0	1	*a, b, c, d, i*
16. Sporangia in terminal clusters	0	0	0	0	0	0	0	0	0	0	0	1	*a, b, c, d, i*
17. Reniform sporangia	0	0	0	0	0	1	0	0	0	0	1	0	*a, b, c, d*
18. Sporangia lateral on short nonvascular stalks	0	0	0	0	0	0	0	0	0	0	1	0	*a, b, c, d*
19. Abscission or isolation layer at base of sporangium	0	0	0	0	0	0	0	1	1	1	0	0	*j*
20. '*Rhynia*'-type adventitious branching	0	0	0	0	0	0	0	1	?	1	0	0	*j*
21. Sporangium attached to "pad of tissue"	0	0	0	0	0	0	0	1	1	1	0	0	*j*
Hypothesis A:													
22. Helical/annular water-conducting cells	0	0	0	0	0	0	0	1	1	1	1	1	*a, d, k*
23. Decay-resistant inner layer in water-conducting cells	0	0	0	0	?	?	?	1	1	1	1	1	*a, d, k*
24. G-type water-conducting cells	0	0	0	0	0	0	0	0	0	0	1	1	*k*
Hypothesis B:													
22. G-type water-conducting cells	0	0	0	0	0	0	0	0	0	0	1	1	*k*
23. S-type water-conducting cells	0	0	0	0	0	0	0	1	1	1	0	0	*k*
Hypothesis C:													
22. G-type water-conducting cells	0	0	0	0	0	0	0	0	0	0	1	0	*k*
23. S-type water-conducting cells	0	0	0	0	0	0	0	1	1	1	0	0	*k*
24. *Psilophyton*-type pitted water-conducting cells	0	0	0	0	0	0	0	0	0	0	0	1	*l*

NOTE.—Three alternative character codings for features of the water-conducting cells are presented as hypotheses A, B, and C (see text for details). Details of characters and character coding are given in the Appendix. Abbreviations: *Coleochaete* (*Col.*), liverworts (L), hornworts (H), mosses (M), *Cooksonia pertoni* (*Cook.*), *Nothia* (*Not.*), *Kidstonophyton* (*Kid.*), *Aglaophyton* (*Agl.*), *Rhynia* (*Rhy.*), *Stockmansella* (*Sto.*), *Huvenia* (*Huv.*), *Sciadophyton* (*Sci.*), lycophyte clade (Lyc.), nonlycophyte clade ('trimerophyte'-'progymnosperm'-seed plant clade, including sphenopsids and ferns) (Nonlyc.). References: *a,* vascular plants: BIERHORST 1971; GIFFORD and FOSTER 1989. *b,* liverworts, hornworts, mosses: SCHUSTER 1966, 1984*a*, 1984*b*, 1984*c*; RENZAGLIA 1978; CRANDALL-STOTLER 1984; RENZAGLIA and DUCKETT 1988. *c, Coleochaete*: STEWART and MATTOX, 1975; GRAHAM 1984; MATTOX and STEWART 1984. *d, Cooksonia*: EDWARDS et al. 1986. *Nothia* (*Kidstonophyton*): EL-SAADAWY and LACEY 1979*a*; REMY and HASS 1991*b*. *Aglaophyton* (*Lyonophyton*): EDWARDS 1986; REMY and HASS 1991*a*. *Rhynia*: EDWARDS 1980. *Stockmansella*: FAIRON-DEMARET 1985, 1986. *Huvenia* (*Sciadophyton*): REMY et al. 1980; HASS and REMY 1991; KENRICK et al. 1991*b*; SCHULTKA 1991. *e,* GRAHAM and REPAVICH 1989. *f,* SLUIMAN 1985. *g,* BROWN and LEMMON 1990*a*. *h,* MARKHAM and PORTER 1978; POKORNY 1974. *i, Psilophyton dawsonii*: BANKS et al. 1975. *Archaeopteris*: PHILLIPS et al. 1972. *j, Rhynia*: EDWARDS 1980. *Stockmansella*: FAIRON-DEMARET 1985, 1986. *Huvenia* (*Sciadophyton*): HASS and REMY 1991; SCHULTKA 1991. *k,* KENRICK and EDWARDS 1988; KENRICK et al. 1991*a*, 1991*b*; this paper. *l, Psilophyton dawsonii*: HARTMAN and BANKS 1980. *m,* GENSEL and WHITE 1983; BROWN and LEMMON 1990*b*; GRAHAM 1990; LUGARDON 1990. *n,* MISHLER and CHURCHILL 1984, 1985.

synapomorphies of this clade include an independent, free living sporophyte and a more or less isomorphic alternation of generations that has been lost in extant members. A subset of polysporangiophytes (informally termed "eutracheophytes") can be recognized by the presence of "true" tracheids, defined as G-type cells, and probable derivative pitted forms. All extant polysporangiophytes are also eutracheophytes, but the fossil record documents an intermediate grade of organization that includes plants with branched sporophytes and nonornamented (*Nothia, Aglaophyton,* and perhaps some *Cooksonia* species) or S-type (Rhyniaceae *sensu* HASS and REMY 1991) water-conducting cells. The most parsimonious explanation for the absence of true tracheids in these plants is that the branched sporophyte evolved prior to the G-type or S-type conducting cells. This interpretation is also consistent with the stratigraphic appearance of branched sporophytes before unequivocal ornamented water-conducting cells in the fossil record (fig. 25).

Within this framework further resolution of the phylogenetic position of the Rhyniaceae (fig. 26) depends on the precise homologies between the structural features of S-type and G-type cells. There are four distinctive attributes of the S-type cell: (1) the microporate inner wall layer, (2) the spongy wall structure, (3) the helical thickening, and (4) the resistant nature of the inner wall. Because the microporate layer may be an unspecialized feature retained from the 'bryophyte' grade (see above), and because the spongy wall structure appears to be unique to the S-type cell, neither feature contributes to resolving the relationships of the Rhyniaceae. However, if the developmental controls governing the deposition of the internal helical thickenings and the decay-resistant inner wall layer in S- and G-type cells are homologous, then the S-type cell could be interpreted as an early form of tracheid. This would also imply that the fine pattern of indentations (figs. 16, 18) on the secondary wall of G-type cells may be homologous to the micropores in the S-type cell. Possession of these features would thus define a clade (tracheophytes) consisting of Rhyniaceae plus eutracheophytes (*A* in fig. 26) and would be consistent with the widespread interpretation that *R. gwynne-vaughanii* is properly regarded as a vascular plant (BANKS 1975; GENSEL and ANDREWS 1984; EDWARDS and EDWARDS 1986; CHALONER 1988; TAYLOR 1988). Plants such as *Aglaophyton, Nothia,* and perhaps *Cooksonia* (especially *C. pertoni* [EDWARDS et al. 1986]) would then constitute a 'protracheophyte' grade (nontracheophyte polysporangiophytes).

Notwithstanding the simplicity of our preferred scheme outlined above several alternative hypotheses for the evolution of water-conducting cells and early land plant phylogeny are also possible. First, the possibility that the absence of differentially thickened water-conducting elements in *Aglaophyton, Nothia,* and certain *Cooksonia* species results from phylogenetic loss needs to be considered (see YOUNG [1981]; DONOGHUE and DOYLE [1989] for discussion of the analogous situation with respect to vesselless angiosperms). Second, the helical thickenings and resistant inner wall layers of S-type and G-type cells may be fundamentally different (not homologous) and therefore would not help to resolve the position of the Rhyniaceae (which would "collapse" into the unresolved 'protracheophyte' grade; *B* in fig. 26). A third alternative is that *Aglaophyton, Rhynia,* and similar plants should be placed between the traditionally recognized lycophyte and nonlycophyte lines of land plant evolution, perhaps with *Nothia* closely related to the former and Rhyniaceae and *Aglaophyton* more closely related to the latter (*C* in fig. 26; see also CRANE [1989, 1990]; also implicit in SELDEN and EDWARDS [1989]). Under this interpretation the tracheid evolved independently in the lycophyte and nonlycophyte clades. Whether this interpretation (*C*) should be favored over *A* and *B* depends on the characters that support a close relationship for *Nothia* and *Aglaophyton* to lycophytes and nonlycophytes respectively.

EARLY EVOLUTION OF THE EMBRYOPHYTE LIFE CYCLE

All of the alternatives for the position of the Rhyniaceae outlined above have similar implications for the evolution of the life cycle in land plants (fig. 26). Whereas the haplontic life cycles of *Coleochaete* and other charophyte algae imply that the initial phases of embryophyte evolution involved the interpolation and elaboration of the diploid sporophyte generation (MISHLER and CHURCHILL 1984; GRAHAM 1985) all three of the hypotheses also suggest that the 'bryophyte'-polysporangiophyte transition involved not only proliferation and branching of the sporophyte but also further differentiation of the gametophyte beyond the condition in any extant 'bryophyte'. Evidence from the Rhynie Chert and the Lower Devonian of Germany indicates that the gametophytes of plants such as *Aglaophyton, Huvenia, Nothia,* and, by implication, *Cooksonia, Rhynia,* and *Stockmansella* were relatively large branched structures, some of which had S-type water-conducting cells, cuticle, and stomata (REMY and HASS 1991*a*, 1991*b*, 1991*c*; KENRICK et al. 1991*b*; REMY et al. 1991). Such a virtually isomorphic alternation of generations may even have persisted in certain early eutracheophytes (e.g., *Zosterophyllum* [SCHWEITZER 1983]). From these observations it is clear that the gametophytes of all extant 'pteridophytes' are highly reduced compared to those of some of the earliest polysporangiophytes

and that any consideration of the ecology of early terrestrial vegetation must take into account the existence of plant life cycles that are no longer present among living taxa.

Acknowledgments

PAUL KENRICK would like to express his thanks to Dr. DIANNE EDWARDS for her help and encouragement during the earlier part of this study. We thank Dr. DONALD EGGERT for the loan of specimens of *Asteroxylon,* Dr. MARGARET THAYER for assistance with light microscopy, CLARA RICHARDSON for drawing the reconstructions, and Dr. W. A. DIMICHELE, Dr. P. G. GENSEL, and Dr. B. D. MISHLER for their constructive reviews of the manuscript. This work was partially supported by the Richardson Fund of the Department of Geology, Field Museum of Natural History, and was greatly facilitated by recent improvements in the equipment for scanning electron microscopy at the Field Museum of Natural History, which were partially supported by NSF DIR 88-11296.

Appendix

Characters are coded 0, 1, or 2, and a ? indicates missing data. Explanations of the character coding are given below, with values in parentheses.

1, 2. *Antheridia and archegonia.* These conservative structures are treated as homologous (1) in all land plants and are relatively derived compared to the oogonia and 'antheridia' (0) of *Coleochaete.* Exceptional preservation in some fossil taxa (REMY and HASS 1991*a,* 1991*b,* 1991*c*) allows the structure of archegonia and antheridia to be observed and the homology of these features to be tested further. Antheridia and archegonia are coded as separate characters because there is no a priori reason why their occurrence should be directly correlated. However, the presence of a multicellular embryo in land plants is not treated as a separate character because, by standard definitions, an embryo must develop within an archegonium.

3. *Cuticle.* Cuticle occurs in bryophytes (HÉBANT 1977) and all vascular plants and is treated as homologous (1). Cuticles are often preserved in the fossil record.

4. *Bicentriolar centrosomes.* Centriolar development in the spermatid mother cells of land plants with biflagellate sperm (i.e., liverworts, hornworts, mosses, Lycopodiaceae, and Selaginellaceae) occurs by midpoint separation of a coaxial bicentriolar centrosome (1). In contrast, orthogonal centriolar replication (0), a process in which a new centriole arises from the side of a parental centriole at its base, is common among protists, and occurs in *Chara, Nitella,* and *Coleochaete* (GRAHAM and REPAVICH 1989). This feature cannot be observed in the fossil record.

5. *Lamellae of multilayered structure (MLS) 40°–45°.* One of the major differences between the MLS in the sperm of charophycean algae and embryophytes is the angle made between the long axis of the S_1 microtubules and that of the underlying S_2 lamellae. This angle is 40°–45° in embryophytes (1) and 90° in charophycean algae (0) (SLUIMAN 1985; GRAHAM and REPAVICH 1989). This feature cannot be observed in the fossil record.

6. *Preprophase band of microtubules (PPBs).* These are a transitory cytoskeletal array marking the site where the new cell plate will join the parental walls of mitotically dividing cells. The PPB is a characteristic feature of the cell cycle in higher plants and occurs in the three major clades of bryophytes (1). PPBs are absent (0) in the algae including *Coleochaete* and *Chara* (BROWN and LEMMON 1990*a*). This feature cannot be observed in the fossil record.

7. *Distinguish D-methionine.* The ability to distinguish metabolically between the L and D isomers of the amino acid methionine (POKORNY 1974) is interpreted as a synapomorphy (1) of the hornworts, mosses, and vascular plants (MISHLER and CHURCHILL 1984). However, some mosses fail to distinguish, and this is interpreted as a reversal. Liverworts and algae are unable to distinguish the two isomers (0). This feature cannot be observed in the fossil record.

8. *Stomata in sporophyte.* Stomata occur (1) in the sporophytes of most hornworts, mosses, and vascular plants (BIERHORST 1971; RENZAGLIA 1978; SCHUSTER 1984*c*); they are absent (0) from the sporophytes of liverworts (SCHUSTER 1966). Stomata are often clearly seen in fossil plant cuticles, being present in sporophytes and in certain morphologically complex fossil gametophytes (REMY and HASS 1991*a,* 1991*b,* 1991*c*). Mucilage cavities (RENZAGLIA 1978) interpreted as homologous to stomata (SCHUSTER 1984*c*) are found in hornwort gametophytes and require further investigation.

9. *Perine layer on spores.* The perine is the normal outer wall layer of the spores of homosporous ferns and lycopods and is found also in the microspores of the Isoetaceae and Selaginellaceae (LUGARDON 1990). A distinct perine layer is present in mosses but is absent from liverworts, hornworts, and *Coleochaetae* (BROWN and LEMMON 1990*b*; GRAHAM 1990). While it seems fairly clear that the perine of pteridophytes is derived from tapetal material, little is known about the origin of perine in mosses although it is thought to be of extrasporal origin (BROWN and LEMMON 1990*b*; LUGARDON 1990). We treat the perine of mosses and pteridophytes as homologous; however, a more precise definition of how perine deposition is qualitatively different from the deposition of other tapetally derived wall material is desirable. A TEM study of the spores of the fossil *Psilophyton* failed to show a distinctive perine layer but concluded that the remains of an outer ornamented layer could represent a partially developed or very primitive type of perispore (GENSEL and WHITE 1983).

10. *Radial (axial) symmetry in gametophyte.* Some species of *Coleochaete,* all hornworts, and the relatively basal liverwort taxa Sphaerocarpales, Marchantiales, and Monocleales are characterized by bilateral, thalloid gametophytes. In contrast, the mature gametophytes of all mosses are radial and axial (MISHLER and CHURCHILL 1984, 1985). Radial (axial) gametophytes are found in the majority of primitive extant vascular plants including *Lycopodium,* Ophioglossaceae, Psilotaceae, Stromatopteridaceae, and various Schizaea-

ceae (BIERHORST 1971, p. 78); the situation in Equisetaceae is equivocal. Evidence from the fossil record suggests that plants at the rhyniophyte grade had gametophytes that were radial and axial and, therefore, were most comparable to the gametophytes of mosses and primitive extant vascular plants (REMY and HASS 1991*a*, 1991*b*, 1991*c*; KENRICK et al. 1991*b*; REMY et al. 1991). We treat radial (axial) symmetry in the gametophyte as basic in extant lycophytes and nonlycophytes (e.g., ferns) and thus as a synapomorphy of the moss-tracheophyte clade. We follow MISHLER and CHURCHILL (1984) in interpreting the radially symmetrical gametophytes of more derived liverworts (e.g., Jungermanniales) as nonhomologous.

11. *Position of gametangia.* In the liverworts, with the exception of the derived Jungermanniales, the gametangia are typically aggregated on the gametophyte, but they are not restricted to specialized zones and are usually scattered over the thallus surface (MISHLER and CHURCHILL 1985; SCHUSTER 1984*a*, p. 763). In the hornworts, gametangia are formed over the entire thallus surface or scattered along the thalloid midline (RENZAGLIA 1978; SCHUSTER 1984*a*). In the relatively basal mosses (e.g., *Sphagnum, Andreaea,* and Polytrichales), gametangia are typically terminal on main axes or lateral branches. In pteridophytes with axial gametophytes such as Ophioglossaceae, Psilotaceae, and Stromatopteridaceae the gametangia are distributed more or less uniformly over the surface or in zones but are not confined to the apex (BIERHORST 1971). Among primitive members of the Lycopodiaceae the gametophyte grows apically and the apex finally expands due to the formation of a ring meristem (BIERHORST 1971). Gametangia are produced on the expanded apical surface and are derived from the ring meristem. Evidence from the fossil record also shows that gametangia were terminal on an expanded apex in plants of the rhyniophyte grade (REMY and HASS 1991*a*, 1991*b*, 1991*c*; REMY et al. 1991). We treat the terminal position of gametangia as a potential synapomorphy for the moss-tracheophyte clade that has been lost in primitive extant ferns. The expanded apical gametangiophore produced from a ring meristem in gametophytes of primitive extant members of the Lycopodiaceae may be homologous to the cup-shaped gametangiophores seen in fossil members of the rhyniophyte grade.

12. *More than one sporangium.* All liverworts, hornworts, and mosses have only one sporangium per sporophyte (0), and *Coleochaete,* in which no sporophyte is elaborated, is scored similarly. All extant vascular plants and many fossil taxa usually interpreted as vascular have more than one sporangium per sporophyte (1). This feature often is easily observed in the fossil record.

13. *Alternation of generations.* Alternation of generations is treated as an unordered multistate character: *Coleochaete* and all liverworts, hornworts, and mosses have a clear, heteromorphic alternation of generations in which the gametophyte is elaborated relative to the sporophyte (0); extant vascular plants have a heteromorphic alternation of generations in which the sporophyte is elaborated relative to the gametophyte (2); there is good evidence that some fossil taxa have a more or less isomorphic alternation of generations (1) in which both phases of the life cycle appear to be more or less equally elaborated (REMY and REMY 1980; REMY et al. 1980; REMY 1982; HASS and REMY 1991; KENRICK et al. 1991*b*; REMY and HASS 1991*a*, 1991*b*, 1991*c*).

14. *Independent sporophyte.* Sporophytes of 'bryophytes' undergo their entire development in intimate association with the parent gametophyte (0). The zygote of *Coleochaete* may also be retained and nourished by the gametophyte (GRAHAM 1985; DELWICHE et al. 1989) (0). The sporophytes of extant vascular plants are larger, independent, free living organisms (1). In the fossil taxa, prostrate rhizoid-bearing axes have been described from *Rhynia gwynne-vaughanii* and *Aglaophyton major* (EDWARDS 1986) providing direct evidence that these sporophytes were free living (1). *Stockmansella* and *Huvenia* are scored as free living (1) on the basis of their overall similarity in habit and size to *Rhynia.* There is no direct evidence that *Nothia* and *Cooksonia* were free living sporophytes, and because of their small size it is conceivable that these sporophytes were dependent on a gametophyte as in extant bryophytes. This character is scored as unknown (?) for these taxa.

15. *Longitudinal dehiscence.* Here we treat this feature as a simple binary character, but dehiscence features are frequently clearly seen in fossil taxa and may provide additional useful characters with further study. Markedly elongate sporangia that clearly dehisce along one, straight, longitudinal line from the apex to the base of the sporangium and splitting into one (e.g., *Psilophyton dawsonii* [BANKS et al. 1975]) or two (e.g., *Archaeopteris* [PHILLIPS et al. 1972]) valves are treated as a synapomorphy for the nonlycophyte clade (1). Sporangial dehiscence in the Rhyniaceae, where it has been clearly shown, involves splitting of the sporangium along several incomplete lines such that the valves remain intact at the apex (FAIRON-DEMARET 1985; HASS and REMY 1991). Similarly, dehiscence in hornworts and some mosses involves one to several longitudinal splits, but the valves remain attached at the apex. Dehiscence of the characteristic reniform or globose sporangia of the lycophyte clade also produces two distinct valves and, although scored (0) here, may prove to be homologous with the longitudinal dehiscence in the nonlycophyte clade.

16. *Sporangia in terminal clusters.* The proliferation of isotomous branching in proximity to sporangia, resulting in often dense terminal clusters of sporangia (e.g., *P. dawsonii* [BANKS et al. 1975]), is treated as a synapomorphy for the nonlycophyte clade (1). The general condition (0) is nonclustered, isolated sporangia.

17. *Reniform sporangia.* Reniform to elliptical sporangia with well-defined dehiscence into two valves are treated as a synapomorphy for the lycophyte clade (1); globose to elongate sporangia are treated as plesiomorphic. The occurrence of reniform sporangia in *Nothia aphylla* conflicts with the presence of nonornamented water-conducting cells in this taxon. Two interpretations are possible: first, ornamented water-conducting tissue may have been lost in *Nothia*; second, reniform sporangia may have evolved independently twice. Our treatment of *Cooksonia* as plesiomorphic (0) in this respect is consistent with the original concept of the genus based on *C. pertoni* and *C. hemisphaerica* (LANG 1937). Other fossils with apparent reniform sporangia that have been assigned to *Cooksonia* may belong to taxa such as *Renalia.*

18. *Sporangia lateral on short, nonvascular stalks.*

The loss of vascular (water-conducting) tissue in the sporangial stalk is treated as synapomorphy for the lycophyte clade (1).

19. *Abscission or isolation layer at base of sporangium.* This feature is treated as a synapomorphy of the Rhyniaceae (1) and has been reported in *R. gwynne-vaughanii* (EDWARDS 1980), *Stockmansella langii* (FAIRON-DEMARET 1985), and *Huvenia kleui* (HASS and REMY 1991).

20. *"Rhynia" type adventitious branching.* Adventitious aerial branches are treated as a synapomorphy of the Rhyniaceae (1). This branching is common in *R. gwynne-vaughanii* (EDWARDS 1980) and *H. kleui* (HASS and REMY 1991) but has not been reported for *S. langii* (FAIRON-DEMARET 1985).

21. *Sporangium attached to "pad of tissue."* This feature is treated as a synapomorphy of the Rhyniaceae (1). Sporangia are attached directly to a conspicuous pad of tissue in *R. gwynne-vaughanii* (EDWARDS 1980), *H. kleui* (HASS and REMY 1991), and *S. langii* (FAIRON-DEMARET 1985).

HYPOTHESIS A

Rhyniaceae (*sensu* HASS and REMY 1991) sister group to eutracheophytes which together form the monophyletic group tracheophytes. S-type and G-type water-conducting cells homologous.

22. *Helical/annular water-conducting cells.* The cellular processes underlying the deposition of differential thickenings are treated as homologous (1).

23. *Decay-resistant inner layer in water-conducting cells.* The decay-resistant inner wall layer found in S-type cells (KENRICK et al. 1991*a*), G-type cells (KENRICK and EDWARDS 1988), and early pitted tracheids (e.g., *P. dawsonii* [HARTMAN and BANKS 1980]) is treated as homologous. This layer, however, could potentially be a synapomorphy at a broader level in non-ornamented water-conducting cells.

24. *G-type water-conducting cells.* This distinctive cell type is treated as a synapomorphy for the lycophyte and nonlycophyte clades. Note that while it is common to many fossils in the lycophyte clade it has not been shown in fossils assignable to the nonlycophyte clade. The scoring of nonlycophytes as possessing this feature is based on tentative comparisons with protoxylem in extant Equisetaceae and Ophioglossaceae and implies that the pitted xylem cells of fossil plants such as *Psilopohyton* represent a secondary modification of G-type cells.

HYPOTHESIS B

Rhyniaceae part of an unresolved 'protracheophyte' grade. S-type and G-type water-conducting cells are not homologous. G-type cell is a synapomorphy of eutracheophytes, S-type cell is a synapomorphy of Rhyniaceae.

22. *G-type water-conducting cells.* This distinctive cell type is treated as a synapomorphy for the lycophyte and nonlycophyte clades. The differential wall thickening and the deposition of decay-resistant material are not homologous with that in the S-type cell. Note that while it is common to many fossils in the lycophyte clade, the G-type cell has not been shown in fossils assignable to the nonlycophyte clade. The scoring of nonlycophytes as possessing this feature is based on tentative comparisons with protoxylem in extant Equisetaceae and Ophioglossaceae and implies that the pitted xylem cells of fossil plants such as *Psilophyton* represent a secondary modification of G-type cells.

23. *S-type water-conducting cells.* This distinctive cell type is treated as a synapomorphy for the Rhyniaceae. Under this interpretation the differential wall thickening and the deposition of decay-resistant material are not homologous with that in the G-type cell.

HYPOTHESIS C

Rhyniaceae, lycophytes, and nonlycophytes "collapse" to become part of a major basal polychotomy within polysporangiophytes. S-type and G-type water-conducting cells are not homologous, and neither is homologous to the tracheids of the nonlycophyte clade. Elements of the 'protracheophyte' grade and Rhyniaceae could potentially form basal grades of organization in either of the two major clades of vascular plants (lycophytes and nonlycophytes). This implies that water-conducting cells of the Rhyniaceae, lycophytes, and nonlycophytes ('trimerophyte'-'progymnosperm'-seed plant) clades all evolved independently.

22. *G-type water-conducting cells.* The G-type cell is treated as a synapomorphy for the lycophyte clade. Under this interpretation the differential wall thickening and the deposition of decay-resistant material are not homologous with that in the S-type cell.

23. *S-type water-conducting cells.* This distinctive cell type is treated as a synapomorphy for the Rhyniaceae. Under this interpretation the differential wall thickening and the deposition of decay-resistant material are not homologous with that in the G-type cell.

24. *Psilophyton-type pitted water-conducting cells.* The pitted cell in the nonlycophyte clade, the earliest known type described in detail by HARTMAN and BANKS (1980), is not homologous with the S-type and G-type cells and is treated as a synapomorphy of this group, notwithstanding the occurrence of potential G-type cells in extant Equisetaceae and Ophioglossaceae as well as the presence of pitted cells in certain (presumably derived) Middle Devonian lycopods (e.g., *Leclercqia*).

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