EVIDENCE FOR A CONDUCTING STRAND IN EARLY SILURIAN (LLANDOVERIAN) PLANTS: IMPLICATIONS FOR THE EVOLUTION OF THE LAND PLANTS

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Evidence for a conducting strand in early Silurian (Llandoverian) plants: implications for the evolution of the land plants

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Abstract.—Macerations of fragmented plant compressions of Silurian (Llandoverian) age yield sheets of organic material bearing ridges and depressions (interpreted as corresponding to surficial dimensions of cells), fragments of smooth walled tubular elements, and fragments of tubular elements with differentially thickened walls ("banded tubes"). A fragment of tissue (1.2 mm long), consisting of smooth walled tubes (17 ± 6.9 μm in diameter), surrounding 2–3 larger (18.8 ± 2.1 μm in diameter) banded tubes, was isolated from an irregularly shaped, relatively large (1 × 3 mm) compression. Comparisons between (1) fragments of tubular cell types, not organized into strands, isolated from 122 compressions, and (2) dispersed tubular cell types previously reported from the Massanutten Formation and other Silurian formations (Tuscarora and Clinton), reveal no significant morphologic differences. Comparisons between the organization of smooth-walled and banded tubular cell types found in the tissue strand and the organization of cell types in nematophytic plants (*Nematothallus, Nematoplexus, Prototaxites*) indicate a similarity in construction (tubular) but a lack of correspondence in organization. The strand of tissue is interpreted as representing part of the internal anatomy of a nonvascular land plant of unknown taxonomic affinity. On the basis of analogy with present-day embryophytes, the strand of tubular cell types is inferred to have functioned as a conductive tissue. The significance of "banded tubes" in Silurian strata is discussed, and it is concluded that, until more is known about the anatomy, morphology, and biochemistry of the parent plant(s), the habitat and systematic affinity of these organisms are conjectural.

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Introduction

Previous studies of Llandoverian and Wenlockian compression fossils from North America have recognized three categories of microfossils: (1) tubular elements of variable length having smooth and banded (=differentially thickened) walls, (2) membranous sheets of organic material bearing irregularly shaped depressions, and (3) alete and trilete spores, and tetrads (Gray and Boucot 1977; Pratt et al. 1978; Strother and Traverse 1979). Llandoverian microfossils from the Massanutten Formation of Virginia are thought to be the fragmented remains of a nonvascular macrophyte of unknown taxonomic affinity based on an inferred fluvial depositional environment, the presence of spores, and chemical composition (Pratt et al. 1978; Niklas and Pratt 1980). Owing to poor preservation, the general morphology and internal organization of these plants were previously unknown. However, Pratt et al. (1978) have speculated that the smooth and banded tubes represent fragments of tubular-filamentous tissue (nematophytic),

analogous in function to supportive or conducting plant cell types.

This paper describes additional plant compressions collected from the localities previously reported by Pratt et al. (1978) in the lower Massanutten Sandstone, Virginia. Among the various cell and tissue fragments recovered from 122 plant fragments, a single strand of tissue was isolated consisting of smooth-walled tubular elements surrounding a small number of banded tubular cell types. This fragment of tissue, interpreted to be part of the internal anatomy of an as yet unspecified macrophyte, is the largest fragment thus far reported for the Massanutten localities, and provides evidence for a discrete organization of smooth and banded tubes. In addition to the new morphologic information, stable isotope (δC^{13}) analyses of duplicate fossils are presented. In conjunction with previously reported organic chemical profiles, these data provide some insight into the biochemical composition of the Massanutten plant remains. The additional morphologic and bio-

chemical data presented here and elsewhere (cf. Niklas 1982) are relevant to the biologic interpretation of the Massanutten fossils and provide a context for evaluating current concepts on the first occurrence of the land plants and the subsequent appearance of tracheophytes (Banks 1975; Gray and Boucot 1977, 1979).

Materials and Methods

Samples of fossiliferous siltstone were collected from horizons designated by Pratt et al. (1978) as 8–9 in the lower Massanutten Sandstone along route 678 at the gap of Passage Creek, 6 km southeast of Strasburg, Virginia. The age of the Massanutten compression fossils is reported as most probably Llandoverian A or B (Pratt et al. 1978).

Two shale partings, each consisting of part and counterpart, measuring 16 × 8 cm and 17 × 9 cm were examined, and revealed 122 compression fossils on their bedding surface (roughly 281 cm²). The maximum lateral dimension of each compression was measured with a Helios microcaliper (Modern Tools Corp., Woodside, N.Y.) and a histogram of size classes constructed. Additional shale partings with compressions were reserved for stable isotope analyses. Specimens were photographed with reflected light, and representative specimens were removed from the larger partings for SEM by means of a dental drill cutting rotor. Macerations of compressions, grouped according to size class (0.26–0.50, 0.51–0.75, . . ., 2.51–2.75 mm, cf. Fig. 1), were obtained by constructing paraffin wells around specimens and treating them with HF acid for 30 min to 48 h. Macerations were neutralized with washings of distilled water, and organic debris removed by pipette for light and scanning microscopy.

Stable isotope (δC^{13}) analyses of compression fossils were performed by Krueger Enterprises, Inc., Geochron Laboratories Division (24 Blackstone Street, Cambridge, Mass.), and are based on samples designated CR-16669 and CR-16670 by that facility.

Statistical comparisons among the morphologic features of tubular cell types are based on standard 2-sample t-test, corrected by a Bonferroni inequality to df 0.05/N (where N = the number of comparisons and df = degrees of freedom) (cf. Snedecor and Cochran 1980).
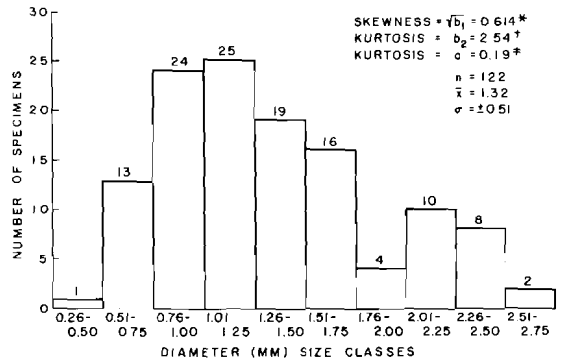

FIGURE 1.   Frequency vs. size class distribution histogram of 122 plant compressions measured on bedding surfaces of siltstone from the lower Massanutten Sandstone, Virginia. Based on N = 122, the mean diameter ($\bar{x}$) equals 1.32 ± 0.51. * = Analyses for skewness, based on $\sqrt{b_1}$, were computed and compared to one-tail 5% and 1% significance levels, since $N \simeq 150$. Two methods to compute Kurtosis (†, ‡) were used: = value for a normal distribution is b_2 = 3.0, α = value for a normal distribution, a = 0.80 (cf. Snedecor and Cochran 1980).

Collection numbers designating slides, SEM stubs, and duplicate material in the Paleobotanical Collections (Plant Science Building) at Cornell are: compression fossils No. 1203–1204; Slide No. 23-210; SEM stub No. 1–16.

Results

The compressions are circular, elliptical-bifurcate, to irregular in shape (Figs. 2–7). The histogram of compression size classes, based on the maximum dimension of 122 specimens, is skewed ($\sqrt{b_1}$ = 0.614), leptokurtic (a = 0.19), and has a mean of 1.32 ± 0.51 mm (Fig. 1). Scanning electron microscopy (SEM) of compressions, mechanically removed from siltstone parting, shows surficial depressions and ridges continuous over the surface of the fossils examined (5 in number) (Figs. 8–10). Dimensions of randomly sampled depressions are 6.7 ± 1.6 μm by 8.2 ± 2.1 μm (N = 100) and are irregular to elliptical in shape. Surfaces of in situ compressions are sometimes perforated, with holes corresponding in dimensions to surficial depressions (6.8 ± 1.8 μm by 7.9 ± 20 μm, N = 28) (Fig. 10). Cellulose acetate peels of 5 fragments having an elliptical to bifurcate outline resulted in the removal of organic material having no demonstrable organization (Figs. 11–12).

Maceration of 117 compressions produced 50
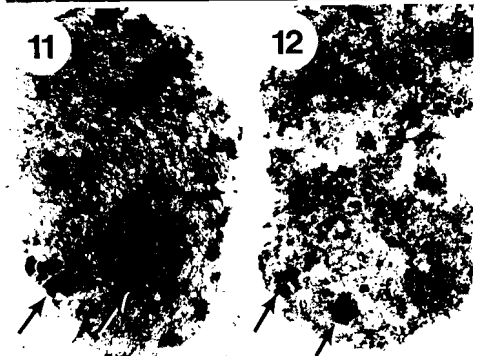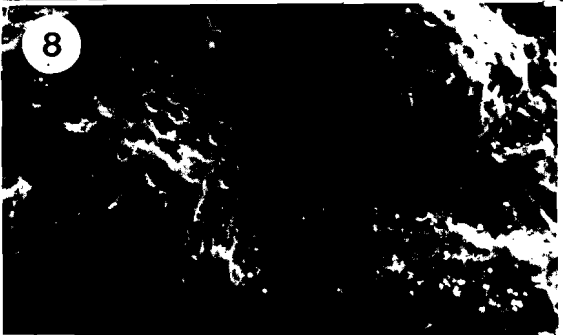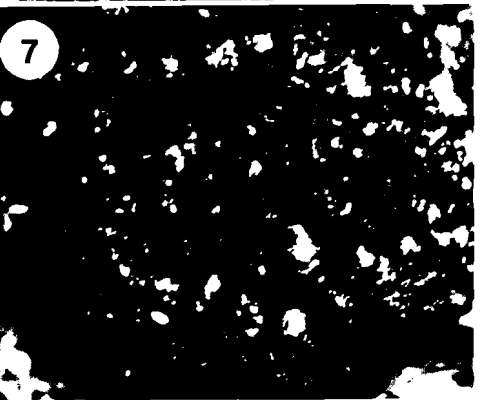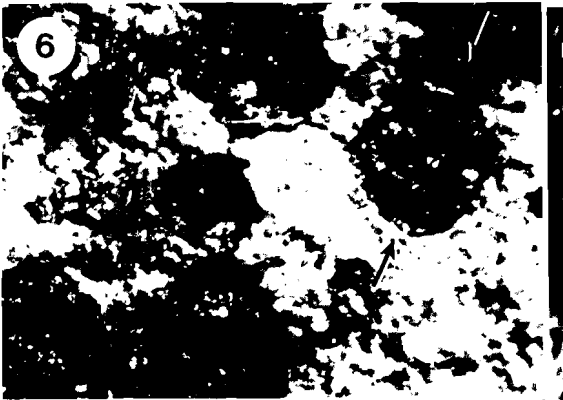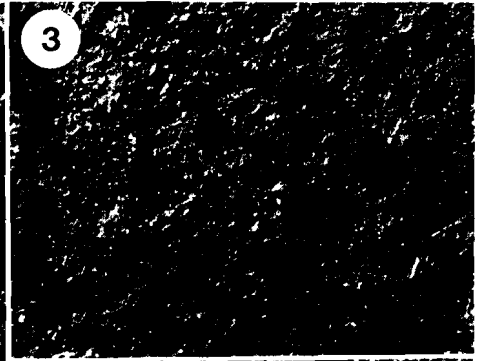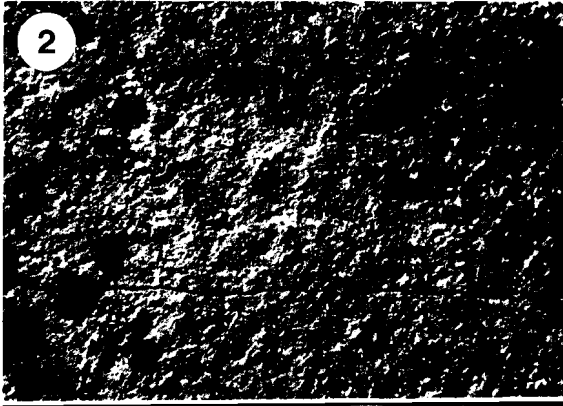
sheets of irregularly shaped organic material bearing an opaque reticulum of ridges surrounding translucent areas measuring 6.5 ± 1.3 μm by 7.9 ± 2.1 μm ($N = 50$) (Figs. 13–14). These dimensions correspond to those observed for surficial depressions on specimens examined under SEM (Figs. 8–10). In addition, three types of tubular cells were observed in these macerations: (1) smooth-walled, tubular elements, 15–31 μm in diameter (18 ± 3.6 μm, $N = 100$) (Figs. 15–19); (2) smooth, thick-walled tubules 11–35 μm in diameter (19 ± 4.3 μm, $N = 56$) with pronounced fibrillar or frayed ends (Fig. 20); and (3) tubular elements with differentially thickened walls, 13–35 μm in diameter (23 ± 3.6 μm, $N = 20$) (Fig. 21). These categories of "tubes" ranged in length from 26–53 μm (34 ± 6.6), 26–110 μm (56 ± 10) and 15–50 μm (32 ± 7.9), respectively. However, all three types of tubular elements were fragmented and had broken ends. Statistical analyses of "lengths" of tubes indicate that banded tubes break into longer fragments than either of the two smooth-walled tubes. Smooth-walled and frayed-ended tubular elements were occasionally found to be longitudinally aligned (Figs. 19–20). However, fragments of tubular elements of different cell wall constructions were not found in parallel alignment to one another. Tubular cell types were found only in compressions 2.4 mm or greater in diameter (=maximum lateral dimension).

Maceration of a relatively large compression (1 mm wide, 3 mm long) yielded a single strand of tissue (1.2 mm long; 88–100 μm in diameter) (Fig. 22). Both ends of the strand were broken transversely, and roughly one-fifth of the strand's length was occluded by a mass lacking any demonstrable cellular structure (Fig. 22). The strand was composed of an indeterminate number of longitudinally aligned, externally smooth-walled tubes (17 ± 6.9 μm in diameter, $N = 28$), that surrounded 2–3 banded tubes (18.8 ± 2.1 μm in diameter) (Figs. 23–25). Examination of the exposed, internal surface of the banded tubes revealed ridges or corrugations 1.7 μm apart (Fig. 25).

Stable isotope (δC^{13}) analyses of the compressions described here and of the material previously described by Pratt et al. (1978) yield comparable values (-25.6 ± 0, $N = 2$; -26.2 ± 0.15, $N = 2$, respectively) (Table 1).

Discussion

The most significant finding from the reexamination of Llandoverian plant remains, previously described by Pratt et al. (1978), is a single fragment of tissue consisting of a cylindrical strand of smooth-walled tubular cell types surrounding 2–3 tubes with differentially thickened cell walls (="banded" tubes). This specimen is the largest intact tissue fragment (showing a discrete biological organization) of a Lower Silurian macrophyte of presumed terrestrial habit. Aside from showing the anatomical relationship betweeen smooth-walled and banded tubes in a Silurian plant, the tissue fragment has a general morphologic correspondence with the strands of conducting cell types in present-day embryophytes. The implication that smooth and banded tubes found in some Silurian plants may have functioned as conducting elements in a terrestrial macrophyte is consistent with the fluvial depositional environment in which these fossils were buried (cf. Pratt et al. 1978), and the isolation from similar fossils of organic chemical constituents of a lignin-like nature (Niklas and Pratt 1980; Niklas 1982). Similarly,

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FIGURES 2–12. Representative compression fossils from horizon 8–9, Massanutten Formation, Virginia. Figs. 2–3, Compressions on surfaces of bedding plane (specimen No. 1203). 2.5×. Fig. 4, Compressions as viewed along broken surface, normal to bedding plane (No. 1204). 2.0×. Fig. 5, Compression (between arrows) from which strand of tissue (Figs. 22–25) was isolated (No. 1203). 3.0×. Fig. 6, Enlargement of Fig. 5, showing compression fossils and specimen from which strand was isolated (between arrows) (No. 1203). 10.4×. Fig. 7, Surface of compression with surficial irregularities (No. 1204). 33×. Figs. 8–10, Scanning electron micrographs of compression fossils (Fig. 7) cut from larger block of matrix (No. 1204). 280×. Fig. 8, Surficial depressions contiguous over larger lobelike irregularities (SEM stub No. 10A). 280×. Fig. 9, Surficial reticulum of depressions and ridges showing some evidence of a pattern (SEM stub No. 10A). 280×. Fig. 10, Perforations through surfaces of compression (SEM stub No. 14). 578×. Figs. 11–12, Cellulose acetate peels of compression fossils with opaque organic material (arrows) interspersed with less opaque material (slides No. 129–130). 22×.
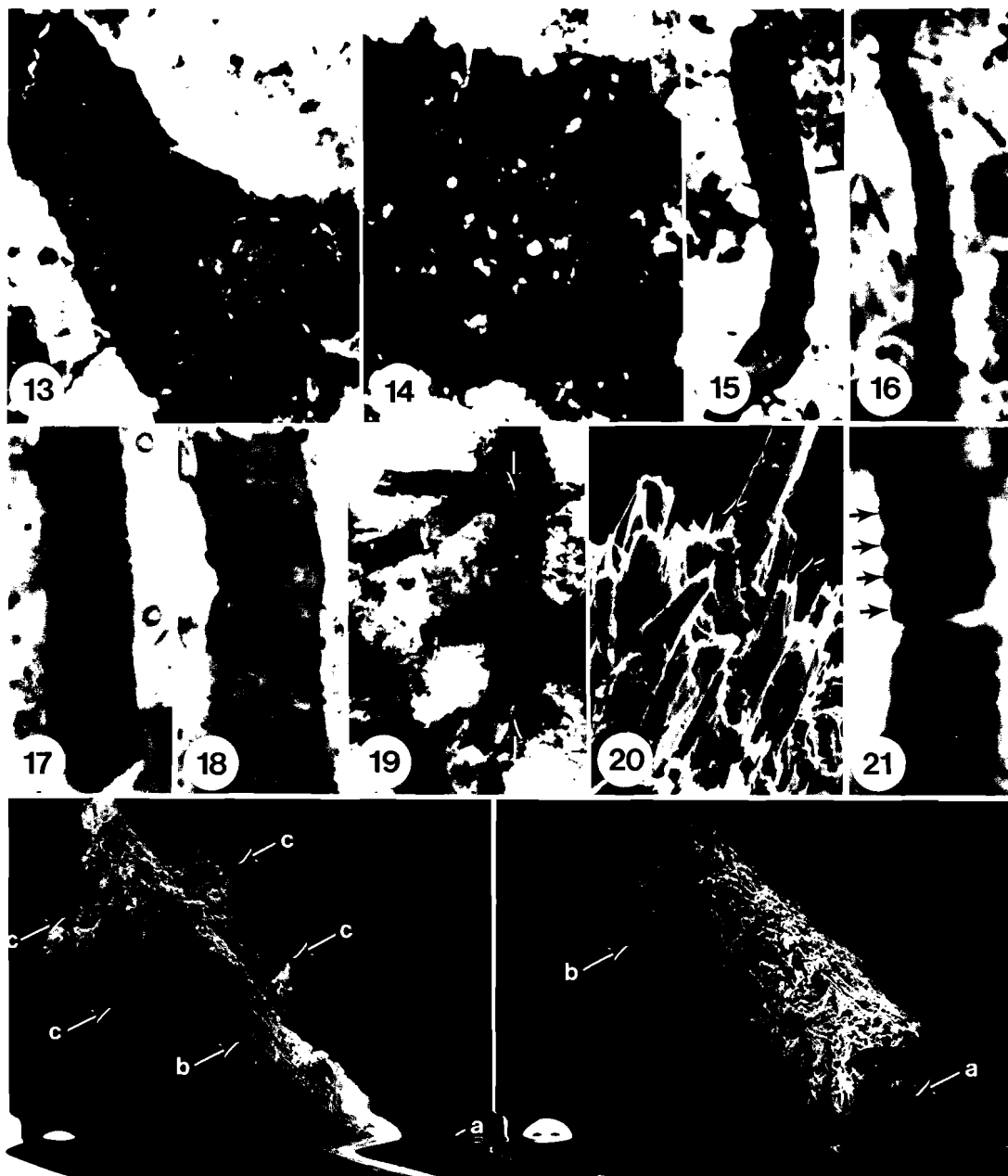
the δC^{13} values reported for dupliate samples of compression material are consistent with a terrestrial origin of the Massanutten plant remains (Table 1).

The additional information uncovered for Llandoverian plants has a bearing on two general issues. The first is the controversy revolving around the evolutionary significance of "tracheid-like" (Gray and Boucot 1977, p. 164) cell types among the remains of some Lower Silurian plants, which has resulted in a polarized interpretation. Gray and Boucot (1977 and literature cited therein) have argued that banded tubes represent evidence for the existence of "a terrestrial flora . . . well prior to [*sic*] the appearance of vascular plant megafossils" (Gray and Boucot 1977, p. 145). By contrast, others have argued that a number of plant and animal groups may have evolved "banded" tubes, and as such these cell types provide at best ambiguous information on habitat or on taxonomic affinity or anatomy (Eisenack 1972; Banks 1975; Schopf 1978). The second issue concerns the more general question of the evolutionary appearance of biochemical and structural features that permitted the survival of plants in a terrestrial habitat (Niklas 1976; Raven 1977; Lowry et al. 1980; Niklas et al. 1980; Stebbins and Hill 1980). The paleobotanical literature argues that the early land plant flora evolved from multicellular aquatic green algae that acquired features permitting survival on land (Bower 1908; Niklas 1976; Raven 1977). By contrast, Stebbins and Hill (1980) have proposed that plants evolved into terrestrial habitats as unicellular, undifferentiated forms living in the soil.

Assessed on the basis of the present and pre-

TABLE 1. Stable isotope ratio analyses.

Sample	Description	δC^{13a}	
Massanutten A	Organic matter in shale	−25.6	
		−25.6	
		−25.6	0.00[b]
Massanutten B	Organic matter in shale	−26.4	
		−26.1	
		−26.2	0.15[b]

[a] $\delta C^{13}_{sample}\%o = \left[\frac{C^{13}_{sample}}{C^{13}_{standard}} - 1 \right] \times 1000,$

where $C^{13}_{standard} = 0.011237$. ($C^{13}/C^{12}$ standard is PDB).

[b] Pairwise comparison between A and B indicates $t_{AB}^2 = 2.81$ with $t_{0.05}^2 = 4.30$.

vious studies on Llandoverian fossils, the following sections address the various issues of taxonomic affinity, habitat, function, and evolutionary patterns raised in the literature.

Taxonomic affinity.—The fragmented nature of most Lower Silurian plant remains provides few morphologic features whereby comparisons can be drawn with better-known Paleozoic taxa. Among the only consistently available features of Llandoverian and Wenlockian microfossils are the surficial dimensions of cells associated with membranous sheets ("cuticle-like" material of Gray and Boucot [1977], p. 161) and the diameters of tubular cell types (Tables 2–3). Statistical comparisons among the cellular dimensions of the Llandoverian material and various better-known thallophytes reveal no significant differences (Table 4). Thus quantitative comparisons among cell fragments for purposes of assessing systematic affinities become a futile exercise, and emphasis must be placed on qualitative differences.

Although smooth and banded tubes have been frequently reported as components of Lower Si-

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FIGURES 13–25. Fragments of tissue and tubular elements isolated from macerations of Llandoverian plant compressions from the Massanutten Formation in Virginia. Figs. 13–14, Membranous sheets of organic material bearing elliptical to irregular depressions (cf. Figs. 8–10). Fig. 13 (slide No. 210). 344×. Fig. 14 (slide No. 53). 350×. Figs. 15–18, Fragments of smooth-walled tubes isolated from macerations. Fig. 15 (slide No. 93). 580×. Fig. 16 (slide No. 55). 580×. Fig. 17 (slide No. 113). 435×. Fig. 18 (slide No. 110). 435×. Fig. 19, Two partially aligned (between arrows) smooth-walled tubes (slide No. 207). 580×. Fig. 20, Scanning electron micrograph of parallel aligned tubes with frayed or "fibrillar" broken ends (arrows) and striations/fractures along external surfaces (SEM stub No. 11). 745×. Fig. 21, Tubular cell type with differentially thickened cell walls (arrows); compare with Fig. 25 (slide No. 103). 832×. Figs. 22–25, Scanning electron micrographs of a strand of tissue isolated from a single compression (cf. Figs. 5–6) (SEM stub No. 11). Fig. 22, Banded tubes (*a*) surrounded by smooth-walled tubes (*b*), and amorphous organic material (*c*) occluding surface of tissue strand. 110×. Fig. 23, Enlargement of broken end of strand (cf. Fig. 22*a*) showing internal banded tubes (*a*) and external smooth-walled tubes (*b*). 432×. Fig. 24, Enlargement of region (cf. Fig. 23*b*) showing rounded ends of smooth-walled tubes (arrows). 1.15k×. Fig. 25, Enlargement of fractured end of strand (Figs. 22–23*a*) showing large tube with differentially thickened (banded) wall (arrow) and surrounding smaller-diameter banded tubes. 1.9k×.

TABLE 2. Comparisons among cellular outlines of Paleozoic plants. Dimensions and standard errors based on 100 cells.

Material/taxon	Age	Position or orientation of cell on thallus	Shape	Dimensions (μm)	Source
A. Massanutten specimens					
1. *Nematothallus*	Llandoverian	—	ellipsoid	6.8 ± 1.4 × 8.0 ± 1.9	—
	L. Devonian	Unknown	ellipsoid	9.5 ± 0.58 × 11 ± 0.71	—
2. *Spongiophyton*	Middle Devonian (Givetian)	Inner surface of "cuticle"	elongated to rectangular	24 ± 1.5 × 39 ± 3.8	Chaloner et al. 1974
Protosalvinia	Upper Devonian (Famennian)	Outer surface of thallus with a size change gradient along the major axis.			Niklas and Phillips 1976
3. *P. arnoldii*		Apex	irregular	14 ± 0.73	
		Distal	polyhedra	23 ± 1.7	
		Proximal	polyhedra	34 ± 2.2	
4. *P. ravenna*		Apex	irregular	20 ± 2.3	
		Distal	polyhedra	23 ± 1.9	
		Proximal	rectangular	37 ± 2.3	
5. *P. furcata*		Adaxial "grooves"	polyhedra	22 ± 2.3	
		Proximal	rectangular	38 ± 2.0	

lurian microfossil assemblages, information regarding the anatomic relationships between these two cell types is lacking (Pratt et al. 1978; Strother and Traverse 1979). Smooth-walled tubes have been reported to be crudely aligned but not attached to one another (Pratt et al. 1978, p. 131), while banded tubes have been found aggregated into compact clusters of four across and at least two deep (Pratt et al. 1978, p. 127). No previous study has reported the organic attachment of dispersed, smooth, and banded tubular cell types. The present report confirms the occasional longitudinal alignment of smooth-walled tubes and of tubes with frayed, fibrillar ends. In addition, a single strand of tissue recovered from macerations of 122 plant fragments shows the parallel alignment of smooth and banded tubular elements. This anatomical configuration is not the result of consolidation during or after deposition. The basic tubular construction of the strand has an analogue with the tissue organization seen in other Silurian and Devonian plant fossils, that have been described as "nematophytes." The nematophytes are an artificial group of problematic taxa consisting of *Nematothallus, Nematoplexus,* and *Prototaxites.* The organization of these plants may be grouped into two categories: (1) thin-walled, banded tubes intertwining with smooth-walled, smaller tubular cell types (*Nematothallus* and *Nematoplexus*); and (2) thin-walled, branched, and septate tubes intertwined among thicker-walled, large, and unbranched tubular elements (*Prototaxites*). Owing to the presence of tubular cell types with differentially thickened walls, previous studies of Llandoverian and Wenlockian microfossil assemblages have emphasized *Nematothallus* and *Nematoplexus* in drawing morphologic analogues (Pratt et al. 1978; Strother and Traverse 1979).

The fragment of tissue isolated from the Massanutten material has a clearly defined arrangement of aligned, smooth-walled tubes (17 ± 6.9 μm in diameter) surrounding a much smaller number of banded tubes (18.8 ± 2.1 μm in diameter). This organization is unlike either of the two categories of nematophytic organization. In *Nematothallus* there is no evidence for the discrete parallel alignment of banded (10–50 μm in diameter) and smooth tubes (2.5 μm in di-

TABLE 3. Comparisons among tubular elements of nonvascular fossil plants.

Nonvascular plants	Diameter (μm)				Distance between bands (μm)	
	Smooth	N	Banded	N		N
Massanutten	18 ± 3.6	20	22 ± 3.6	20	1.6 ± 2.8	40
Tuscarora[a]	8–12	—	—	—	—	—
Clinton[a]	10	—	30	—	—	—
Prototaxites:						
Large, unbranching tubes	32 ± 6.2	10	—	—	—	—
Thick, branching tubes	7 ± 2.3	10	—	—	—	—
Nematothallus	2.5	—	10(24)50	5	4 ± 0.9	4
Nematoplexus	7–10	—	2(18)28	?	—	—

[a] Reported by Strother and Traverse (1979).

ameter). *Nematoplexus* has thickened tubes (2–28 μm in diameter) occurring individually or grouped into irregular "branch-knots" (Lyon 1962). Similarly, although the larger tubular cell types (19–50 μm in diameter) in *Prototaxites* are oriented parallel to the main axis of specimens, this taxon lacks tubes with banded cell walls (Arnold 1952, 1954). However, the thick-walled, profusely branched tubes (5–10 μm in diameter) in *Prototaxites* do form a "sheath" around the larger tubes. It might be speculated that the strand of tissue described here is a smaller fragment of a sheath; however, the presence of banded tubes and the lack of branched, thick-walled tubes in our specimen would argue against an affinity with *Prototaxites*. Similarly, it might be argued that banded tubes occur during the juvenile phase in the development of *Prototaxites*. This appears unlikely, since from a functional perspective banded tubes would be more efficacious in plants of larger size.

The organization of smooth and banded tubes in the strand also parallels that seen in the conducting tissues of bryophytes (leptoids-hydroids) and vascular plants (phloem-xylem). The central strand or hydrom seen in some moss gametophytes, as well as in sporophyte setae consists of numerous smooth-walled leptoids, surrounding hydroids that are larger in diameter. According to Hébant (1977, pp. 53–54), hydroids are elongated and possess inclined terminal walls, which are usually thin due to partial hydrolysis. Hydroids lack a living protoplasm at maturity and lack differentially thickened lateral walls, pits, or any ornamentation (Table 5). Pratt et al. (1978) have described what appear to be tapered end walls in their banded tubes, and even though these microfossils were frag-

mented, they are clearly elongate. Leptoids are elongated, possess thickened lateral walls, and usually have enlarged tibia-like end walls (Hébant 1977, figs. 142, 283; 286). Although not described by Pratt et al. (1978), the smooth-walled tubes seen in our material have tapered, hemispherical end walls, quite unlike the tibia-like endings of leptoids (Fig. 24). It is evident, therefore, that the strand of tissue and isolated tubes reported here as well as elsewhere (Pratt et al. 1978; Strother and Traverse 1979) have morphologic features unlike the conducting cell types of extant bryophytes (Table 5).

Comparisons have been made between the structure of banded tubular cell types found in Lower Silurian strata and cell types found in tracheophytes. This comparison represents a central theme in controversies over the first appearance of the land plants and of tracheophytes (Banks 1975; Gray and Boucot 1977; Schopf 1977; Pratt et al. 1978; Strother and Traverse 1979; Niklas and Pratt 1980). Two factors mitigate the usefulness of drawing comparisons

TABLE 4. Comparisons (2-sample *t*-test) among the surficial cellular dimensions of various Paleozoic plants (cf. Table 2). For all entries 100 cells were sampled ($N = 100$, $3.291 < t_{0.05/15}^{148} < 3.373$). Double entries x (x) refer to comparisons between the small and large cellular dimensions for each pair.

	A	1	2	3[a]	4[a]	5
A	—					
1	17.8 (14.8)	—				
2	82.7 (75.6)	89.1 (74.9)	—			
3[a]	45.5 (29.5)	48.2 (29.5)	58.9 (67.1)	—		
4[a]	49.1 (40.2)	44.2 (37.4)	14.5 (45.0)	24.8	—	
5[a]	56.6 (46.9)	52.6 (45.7)	7.28 (40.5)	33.1	6.15	—

[a] *Protosalvinia* dimensions are for the smallest cells toward the base of the thallus.

TABLE 5.   Comparisons among Silurian banded tubes, moss hydroids, and tracheids.

	Hydroids	Banded tubes	Tracheids
1. Shape	Elongated	Elongated	Elongated
2. Protoplasm	Protoplasm absent at maturity[a]	Unknown	Protoplasm absent at maturity[a]
3. End walls	Thin, hydrolyzed, oblique	Tapering to oblique	Hydrolyzed, oblique
4. Lateral wall ornamentations and pits	Completely lacking	Spiral, annular thickenings lacking pits	spiral, annular, to scalariform, variety of pits
5. Secondary wall	Absent	Lateral wall thickenings appear to be internal	Present
6. Movement of water	Preferentially through end walls	Unknown	Preferentially through lateral and end wall pits
7. Biochemistry of walls	Polyphenols	Polyphenols (lignin-like moiety)	Lignin

[a] Hébant (1973) has demonstrated that, during degeneration of the hydroid protoplasm, acid phosphatase activity reaches a peak. This parallels the physiology of tracheid protoplasm decomposition.

between our Silurian banded tubes and tracheids. The first is the occurrence of banded tubes in plants that are clearly not vascular (nematophytes), suggesting that banded or differentially thickened cells may have evolved in a number of potentially unrelated plant groups. The second factor is the variability in the morphology of tracheids seen in modern-day tracheophytes (Bierhorst 1960). Tracheids conduct water and are found in some gametophytes and most sporophytes of vascular plants. They are elongated, nonliving at maturity, have tapering imperforate ends, and possess a variety of pits and differentially thickened cell walls that are lignified. Thus three criteria define a tracheid—function, structure, and biochemistry (Table 5). When collectively present these three criteria provide an unambiguous identification of a tracheid and hence of a vascular plant. However, Bierhorst (1960) lists exceptions to every component in the definition of a tracheid. Some tracheids may be functional and mature but lack a secondary wall with thickenings. Similarly, lignification may be an incidental, secondary modification of a tracheid cell wall. Even within an anatomic context, a "deviate" tracheid may fail to be recognized.

Based on these two mitigating factors (parallel or convergent evolution, and the often ambiguous characteristics of tracheids in modern-day plants), and despite the similarities between banded tubes and tracheids, we agree with those who argue that banded tube cell types do not provide prima facie evidence for vascular plants.

Habitat-function.—Although often related, habitat and taxonomic affinity are independent issues. A "land plant" must be considered as a grade level of structural and biochemical organization rather than as a clade of organisms. However, some authors (Gray and Boucot 1977, pp. 145–146; Taylor 1982, p. 156) conclude that the land plants are those autotrophs that customarily live on land and that have relations that "are *primarily to other plants living on land*" (Gray and Boucot 1977, p. 145; original italics). From the context, it appears that a clade perspective is taken, one that delimits "land plant" at the level of embryophytes, and excludes terrestrial green algae. Thus, the land plants are apparently defined as monophyletic. Such a definition delimits the land plants on the basis of a reproductive cycle (diplobiontic) and the presence of a structural set of characters (e.g., archegonium). This definition is weak since it restricts from consideration the significance of terrestrially adapted nonembryophyte ancestors, and it requires knowledge of life-history details that are unlikely to be recovered from the fossil record. The definition of land plant given by Gray and Boucot is acceptable when dealing with extant organisms, for which cladistic relationships may reasonably be deduced. However, the fact that a plant exploited a land habitat in the past provides no information about

its relationship with modern embryophytes or algae. The term "land plant" is by necessity circular in reasoning ("a land plant is one that lives on land") and if it is to have any meaning it must define an ecologic or niche concept—a grade. It is evident, therefore, that the question of habitat and the establishment of a land plant flora can be divorced from the issue of taxonomic affinity.

The similarity of banded tubes to tracheids has lead some to argue that there is a functional correspondence between the two (Gray and Boucot 1977). Since tracheids conduct water, a functional analogy with banded tubes would lead one to infer that Silurian plants with banded ("tracheid-like") tubes were terrestrial. Therefore, to infer (not prove) a terrestrial habitat for plants containing banded tubes, it is necessary to clearly define and prove the *function* of such tubular elements. On the basis of the morphology of extant plants, elongated, differentially thickened cells have evolved for basically two functions: (1) to resist the implosive stresses induced by the rapid internal flow of a fluid (tracheids); and (2) to resist the explosive stresses incurred by the compression of internal fluids (elators). It should be noted that not all water-conducting cell types possess thickenings (hydroids); however, this is a trivial point when dealing with Silurian tube cell types that have banding. The elator analogy would appear inappropriate to the function of the banded cell types, on the basis of the latter's length (even in the fragmented condition) and their ensheathment by smooth-walled tubular cell types. Elators and individual components of pseudoelators seen in anthoceropsids are relatively short (50–80 μm; cf. Smith 1955; Parihar 1962; Watson 1971), and if broken into fragments would reveal end walls at a higher frequency than those reported for fragments of Silurian banded tubes. However, the elator analogy cannot be ruled out, since modern examples may be unrepresentative of past morphologic diversity. However, the strand of aligned smooth and banded cell types has the general configuration of a conducting tissue. In both bryophytes and tracheophytes, water-conducting cell types are surrounded by cell-sap-conducting elements. The central location of differentially thickened cell types in the Llandoverian tissue fragment is

consistent, therefore, with cells adapted to water transport, while surrounding smooth-walled tubes may have served as analogues to phloem or leptoid cell types.

Even if the conducting function of tissues composed of banded and smooth cell types is accepted (but as yet unproven), a terrestrial habitat is not an a priori conclusion. Indeterminate growth resulting in an elongate growth habit places demands on metabolite transport even in aquatic environments. Large marine macrophytes such as *Macrocystis, Nereocystis,* and *Laminaria* have medullary cells (e.g., "trumpet cells"), albeit unbanded, that are modified for conducting metabolites (Ziegler and Ruck 1967; Parker 1971a,b; Schmitz and Srivastava 1974, 1975; Nicholson 1976). Similarly, reports of lignin-like moieties in the organic remains of Llandoverian plant fossils are not prima facie evidence of a terrestrial habitat (*contra* Gray and Boucot 1977), since a number of marine algae are known to synthesize and excrete plant phenolics that could given similar profiles when fossilized (Yentsch and Reichert 1962; Craigie and McLachlan 1964; Sieburth and Jensen 1969). Finally, Gray and Boucot (1977) have argued that tracheid-like tubes, functioning as water-conducting elements, may even be expected in an emergent aquatic (p. 164). Since these authors make a distinction between a "land plant" and an "emergent aquatic" we can conclude that, even if a conducting function was proven for "banded" tubes, the question of habitat still remains open to these authors.

Pratt et al. (1978) point out that the strongest evidence for the terrestrial origin of the Massanutten plant remains comes from their occurence in sediments of fluvial origin. Their interpretation of the depositional environment associated with these fossils is consistent with the stable isotope (δC^{13}) analyses reported here (Table 1, Fig. 26). Nier and Gulbrandsen (1939) first observed that carbon present in biological systems had a lower ^{13}C value than that found in atmospheric CO_2 or carbonate minerals. Park and Epstein (1960) found that ribulose diphosphatase fixes $^{12}CO_2$ 1.017 times faster than $^{13}CO_2$. Solution of CO_2 in water results in a preferential concentration of ^{13}C, so land plants are expected to contain less ^{13}C relative to marine plants and more of the isotopically lighter
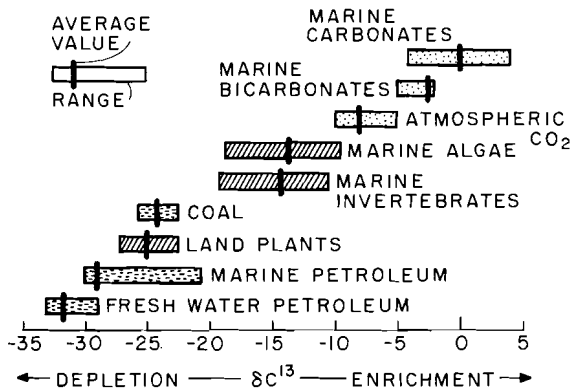
FIGURE 26. Range and average values (see upper left insert) of δC^{13}-values for various organic and inorganic sources. Analyses of Massanutten plant compressions indicate a δC^{13}-value of -25.6 ± 0 and -26.2 ± 0.15 (cf. Table 1). Although these values are consistent with a terrestrial interpretation (land plant $\delta C^{13} = -25$; coal $\delta C^{13} = -24$), methanogenic bacterial decomposition of brackish or even marine plant material can deplete δC^{13}-values.

$^{12}CO_2$ found in the atmosphere. Marine algae typically yield δC^{13} values ranging from -19 to -11, whereas land plants yield values ranging from -27 to -23. (Coal samples derived from vascular plant tissues have values of -26 to -24.) Within the context of freshwater organisms, δC^{13} values are less clear-cut, since carbonate sources in these waters may be derived in part from formerly marine carbonate-bearing sediments typically yielding -5 to $+4$ δC^{13} values. However, the fact that Silurian material is ^{13}C deficient strongly favors a terrestrial origin, since sediment sources of carbonates bias in the opposite (less negative) direction.

Evolutionary implications.—Various authors have speculated on the sequence of events leading to the appearance of the first land plants (Niklas 1976; Raven 1977; Niklas et al. 1980; Stebbins and Hill 1980). A common theme to many of these scenarios has been the physiologic and morphologic constraints attending the transition from an aquatic to terrestrial habitat. In an aquatic environment, surface area to volume ratios can be large to facilitate light gathering, gas exchange, and detoxification. Although these same functions are necessary for survival on land, the need to prevent excessive water loss restricts the plant body's surface area to volume ratio. A common solution to many life forms on land was the evolution of a cuticle. However,

all known "cuticles" that are impermeable to water are also highly impermeable to gases (such as oxygen and carbon dioxide) and to potentially toxic secondary metabolites. To accommodate gas exchange, plants have increased their surface area-to-volume ratios by means of pores opening into internal chambers, thereby permitting gas exchange and limiting water loss (by means of boundary larger effects or regulating pore diameter). The evolution of an endohydric water and mineral transport system (e.g., hydroids-leptoids, xylem-phloem) is generally considered to have evolved after plants established a tenuous, terrestrial existence. It would be reasonable to conclude, therefore, that plants possessing cuticles and conducting cell types would have evolutionarily preceded the first appearance of the vascular plants, perhaps even the first embryophytes. This conjecture would appear to be verified by the isolation of "cuticle-like" and "tracheid-like" tissue fragments from Lower Silurian strata. However, the identification of "cuticles" and "tracheids" requires a morphological and anatomical context in which to verify function. It is through function that habitat is inferred. Until we know the morphology, anatomy, and reproductive biology of the parent organism(s) that gave rise to the tissue fragments described here, speculations on the first appearance of a land plant flora will remain as ambiguous in result as they are ambitious in goal.

Acknowledgment

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