STEM-ROOT TRANSITION OF AN UPPER PENNSylvanian Woody Lycopsid

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ABSTRACT
Anatomically preserved specimens of a woody lycopsid showing the transition from the stem to the rooting region are described from the Upper Pennsylvanian Duquesne Coal of Ohio. Specimens have exarch protoxyles that are apparently medullated at distal levels and exhibit abundant secondary xylem. Cortical tissues accompanying the stems have periderm, and show leaf bases or cushions. Although features of the stems are compatible with those of the arborescent Lepidodendrales, the plants have a rounded cormose rooting region, rather than the much-branched and elongated stigmatic system usually associated with the order. Specimens of this type expand our knowledge of the diversity among Paleozoic lycopsids and document the occurrence of representatives with an Isoetes-like base in Pennsylvanian strata.

Stems and rooting structures of arborescent lycopsids are relatively common plant fossils in Paleozoic strata, with both permineralized and compressed (or mold-cast) remains abundantly represented. Specimens showing the attachment of the root to the stem are also known from casts of arborescent forms. The most common taxa have much-branched stigmatic systems as the rooting structures (see Frankenberg and Eggett, 1969), and photographs or reconstructions of these are commonly included in textbooks (e.g., Bierhorst, 1971; Walton, 1940). Other fairly large taxa exhibit less extended rooting systems that appear either as rounded (i.e., Lepidosigillaria, White, 1907) or lobed (i.e., Protostigmaria, Jennings, 1975) plant bases. A few anatomically preserved examples that show the stem-root transition are also known from Carboniferous deposits (i.e., Paurodendron, Phillips and Leisman, 1966; Oxroadia, Long, 1971), but these are not assignable to the Lepidodendrales. An additional anatomically preserved specimen, Nataliana sinuata Baxter (1978) has recently been described as showing the transition from the stem to the rooting structure (Baxter, 1978). This specimen will be considered further in the discussion section of the paper. Histological preservation of the stem-root transition in the Lepidodendrales is known only from a single specimen with sigillarian stem structure at one end and stigmatic anatomical features at the other. The specimen exhibits an exarch protoxyle in the stem region. The stele is reduced to a tiny rod of primary xylem toward the base, but the primary tissues are incompletely preserved at this level and the saw-cut apparently passed between the stem and root regions (Frankenberg, 1968). Additional information about the anatomy of the stem-root transition in the Lepidodendrales could possibly be forthcoming as a result of the recent discovery of Lepidocarpon embryos (Phillips, Avcin, and Schoof, 1975), but at present the internal features of this region remain poorly understood for most Paleozoic taxa.

Arborescent lycopsid remains are a prominent component of the flora at an Upper Pennsylvanian coal ball locality in eastern Ohio (Rothwell, 1976). Many specimens are assignable to the Sigillariaceae, but forms of less certain taxonomic affinities have recently also been recognized. Many of these have an exarch protosteole that is apparently medullated at the distal-most preserved levels of the stem. They also exhibit bipolar growth and abundant secondary xylem production, features that are compatible with those of lepidodendralean taxa. Several of these specimens show features of a stem at one end and evidence of the rooting system at the other, but do not exhibit elongated and dichotomously branched stigmatic structures as had first been expected. Rather, they terminate in a rounded corm-like base. Therefore, the material provides an unusual opportunity both to characterize the anatomy of the stem-root transition in an additional lycopsid, and to describe a new representative of less common growth form.

MATERIAL AND OCCURRENCE—Specimens are preserved by calcareous cellular permineralization in coal balls collected from the Upper Penn-
sylvanian, Duquesne coal (Conemaugh group). The outcrop occurs in a road cut on the south side of Ohio Route #22 (NE 1/4, SE 1/4, SE 1/4 Sec. 6 Wayne Township, Smithfield Quadrangle, Jefferson County) approximately 8 km west of Steubenville, Ohio. Sections were prepared for microscopic examination by the well-known cellulose acetate peel technique (Joy, Willis, and Lacey, 1956). Peels and slides of the material are deposited in the Paleobotanical Herbarium, Department of Botany, Ohio University. Pertinent slides bear acquisition numbers 0,580–0,750 in the above repository.

Description—Eight specimens show features of a transition from the stem to the rooting region. They are up to 22 cm long and 1.9 cm in maximum diam, and all are either partly or completely decorticated, but exhibit excellent preservation of the primary and secondary xylem that allows for characterization of several structural and developmental features. Each specimen consists of an elongated stem that grades downward into a transition region (Fig. 23). At the base of the plant root traces diverge downward and laterally (Fig. 3, 4, 6). For the purpose of description the stem is designated as the region distal to the level of the lowest leaf trace. The rooting region is recognized by the divergence of root traces, and the intermediate zone is interpreted as a transition region. The occurrence of roots only at the base of the axis and their divergence primarily away from the position of the apex of the stem (Fig. 6, 18) demonstrates that the stems were erect and that the plants exhibited bipolar growth like that of Isoetes, Paurodendron, and like numerous currently known taxa of the Lepidodendrales and Pleuromeiales. Some specimens were peeled in transverse section (Fig. 1–5), while others were oriented in a somewhat oblique longitudinal view (Fig. 6, 7). Three specimens were first examined in one view and then recut at right angles to the originally exposed surface such that they were observed in both longitudinal and transverse sections (e.g., the specimen in Fig. 6, 17–22).

Stem—The stems are represented by primary xylem that is surrounded by abundant wood (Fig. 1). Extraxylary tissues are detached from the stem region of all specimens, but closely associated lycopsid periderm and leaf bases probably represent the same taxon (Fig. 5). Numerous spirally arranged leaf traces diverge from the periphery of the primary xylem and extend through the secondary wood within broad rays (Fig. 6, 7). Traces are closely spaced at the base of some stems (Fig. 6), but more distantly disposed in others (Fig. 7). Twenty-two centimeters of stem extend from the base of the longest specimen (Fig. 1–4). As is typical of the available stems, the primary xylem is crushed (Fig. 8), but near the distal end it has a diameter of about 2.5 mm. The diameter of the primary xylem decreases proximally until at the transition region the secondary tracheids appear to radiate from a central point (Fig. 2, 15, 23). The periphery of the primary xylem is fluted somewhat like that of Sigillaria (e.g., Delevoryas, 1957) and like stems described as Lepidodendron dacyrodiiodes (Leisman, 1970), but unlike Sigillaria the outer margin of the metaxylem is relatively smooth, with numerous protoxylem strands accounting for the bulk of the ridges (Fig. 8, 11). In transverse view protoxylem strands extend outward as small points that are interspersed with more-or-less hollow areas (Fig. 11). The latter often contain remnants of poorly preserved, thin-walled cells. Protoxylem tracheids are 8–12 μm in diameter and exhibit spiral wall thickening patterns. Fimbrii have not been observed. Centripetally, the cells increase in diameter and the angular metaxylem tracheids reach a maximum diameter of 120 μm. Secondary wall thickening patterns of the scalariform and reticulate type characterize the metaxylem tracheids (Fig. 14). Fimbrii are present on many of the well preserved tracheid walls. Crushed remnants of xylem parenchyma are present at the center of the largest steles (Fig. 8), suggesting that the stems are medullated at more distal levels. Additional xylem parenchyma cells occur among the more peripheral metaxylem tracheids. The amount of xylem parenchyma decreases toward the base of the stem, where there is a tiny stele consisting almost entirely of tracheids.

Specimens exhibit a prominent secondary xylem zone that is 2.4–7 mm wide at the base of the stems, and diminishes in thickness distally. In transverse view the secondary xylem is dissected into wedges of radially aligned tracheids by broad rays that accompany the leaf traces (Fig. 1, 5). The rays increase in width toward the periphery of the wood. Narrow rays are also present within the wedges of tracheids. Longitudinally, individual secondary tracheids follow a sinuous course, undulating between broad rays of the leaf traces (Fig. 6, 7). As a result, they typically appear to be cut in transverse section whether seen in cross or longitudinal views of the stem (Fig. 1, 6). Some tracheids in this zone appear to be quite long (Fig. 13), while others are shorter and branched (Fig. 9, 12). In radial view the secondary tracheids typically appear to end at the same level (Fig. 13, at top) as is characteristic of plants with storied wood, but this appearance is probably caused primarily by the tracheids undulating around the leaf trace rays and therefore all passing out of the plane of section at the same level. The occurrence of isolated
tracheid ends such as the one at the bottom of Fig. 13 (at arrow) supports this interpretation. Individual secondary xylem tracheids are 20–90 μm in diameter and have reticulate wall thickening patterns on both radial and tangential walls (Fig. 12, 13). Fimbrials are absent from all but the best preserved tracheids.

Leaf traces typically diverge opposite protoxylem strands (Fig. 8) and follow a horizontal course through the secondary wood. In transverse view the individual traces are difficult to distinguish from a vertical column of cells that connects them to the basal margin of the foliar ray (Fig. 9), but in some instances an ovoid bundle of about six tracheids can be identified (Fig. 10). Protoxylem has not been distinguished. Cells of the connecting tissue have scalariform and reticulate wall thickening patterns like those of typical tracheids (Fig. 10), but are short, branched and highly contorted. Similar cells are also present interspersed among the elongated secondary xylem tracheids near the margin of the foliar ray (Fig. 9). The remainder of the ray area is either hollow or partially occupied by the remnants of thin-walled cells (Fig. 6, 7, 9).

**Transition region**—Between the most proximal leaf trace and the level where root traces diverge is a region 4–10 mm long (Fig. 6, 7). The xylem in this transition region is 7–14 mm in diam and has a smooth outer margin (Fig. 2, 6, 7). In transverse sections adjacent to the stem the primary xylem is apparently represented by a point at the center of the axis (Fig. 15), but as in comparable regions of *Isoetes* and *Pauroden- dron* the primary and secondary origin of the tracheids cannot be determined with certainty (Pao-lillo, 1963; Phillips and Leisman, 1966). Radial files of apparently secondary tracheids radiate from this point, and are often separated by narrow radially disposed spaces (Fig. 2, 15). The latter may represent the positions of uniseriate rays where the cells have not been preserved. In this region, and at the base of the stem a cylindrical zone of crushed tracheids often occurs near the center of the axis (Fig. 2 at arrow, 3). Toward the rooting region the widths of the rays increase and the rows of tracheids become increasingly disorganized (cf. Fig. 3, 4). The central point from which the cells radiate also diminishes in prominence, but can usually be

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Fig. 1–6. Woody lycopsid—Fig. 1–4. Slightly oblique transverse sections of a single specimen at various levels of the plant. 1. Stem stele approximately 20 cm above transition zone. 1408 L Top #9. ×4. 2. Level where the rooting region is sectioned at the far left and right and the transition region is seen at the center. Arrow indicates the position of the zone of compacted tracheids. 1408 D Top #98. ×4. 3. Level where the rooting region extends nearly to the center at the right, and some tissue of the transition region is sectioned at the left center. 1408 C Bot. #2. ×4. 4. Basal-most level where little stelar tissue remains at the left and root traces diverge from the right. 1408 C Bot. #52. ×4. 5. Transverse section of stem with extrastelar tissues preserved at the left. Note the expanded tissue that either represents a leaf cushion or leaf base. 1399 A Top #9. ×7. 6. Somewhat oblique longitudinal section of a plant base showing stem, transition and rooting regions. Extrastelar tissues are preserved at the left. 1423 E Bot. #22. ×3.5. I, leaf base or leaf cushion; r, rooting region; s, stem region; t, transition region.

Fig. 7–14. Woody lycopsid. 7. Somewhat oblique longitudinal section of plant base showing more distantly spaced leaf traces than seen in Fig. 6. 1387 C(1) Side #115. ×3.5. 8. Transverse section of stem stele at a relatively distal level. Note the crushed xylem parenchyma with black internal contents within the metaxylem zone. 1408 L Top #12. ×29. 9. Tangential section near the periphery of the secondary xylem showing a leaf trace within a broad ray. Note the contorted configurations of tracheids adjacent to the ray. 1423 E Bot. #25. ×18. 10. Cross section of a leaf trace and cells of the connective tissue. 1399 A Top #7. ×85. 11. Transverse section at the margin of the primary xylem in the stem. 1399 A Top #9. ×130. 12. Transverse section of tracheids in the central part of the transition zone. 1423 F Top #22. ×88. 13. Radial section of secondary xylem. Note the tracheid end (at arrow). 1408 J(1) Top #96. ×150. 14. Longitudinal section of the stem showing wall thickening patterns on metaxylem tracheids. 1408 J(1) Top #96. ×140. c, connective; p, protoxylem; t, leaf trace.

Fig. 15–22. Woody lycopsid. 15. Transverse section showing base of the transition zone at center and upper extent of the rooting region at left and right. 1381 Q(1) Top #2. ×8. 16. Transverse section showing the central zone of the rooting region. Note the central point from which the tissues radiate (at arrow) and the disorganized appearance of the tracheids at this level. 1423 E Side #29. ×23. 17. Transverse section of rooting zone showing the disposition of tissues at this level. Note the central zone of tracheids, the radiating files of secondary tracheids and the small files of radially aligned tracheids that diverge at wide angles (at arrow). Extrastelar tissues are preserved at the bottom. 1423 E Side #29. ×5. 18. Longitudinal view of the base of the plant showing the divergence of root traces, and the inner and middle cortical zones. 1423 E Bot. #16. ×19. 19. Longitudinal section showing the extrastelar tissues in the transition (at top) and rooting (at bottom) region. 1423 E Bot. #22. ×13. 20. Radial files of tracheids at the margin of the xylem in the rooting region that may represent a root trace. 1423 E Side #38. ×55. 21. Root trace within the tissue of the outer cortex. 1423 E Side #38. ×58. 22. Transverse section of a root trace near the periphery of the outer cortex. Cells that surround the tracheids may represent inner cortical tissue that accompanies the trace to the periphery of the plant. 1423 E Side #48. ×58. i, inner cortex; m, middle cortex; o, outer cortex; rt, root traces.
traced to near the base of the tracheidal zone (Fig. 16 at arrow).

In the transition region the axis of several specimens becomes ellipsoid in section view (Fig. 2). Cells at the ends of the ellipse have a distinctly more disorganized tracheid and ray arrangement than those in other areas (Fig. 2, 15, 23), and many of the tracheids appear to have their long axes oriented parallel to the circumference of the stele (Fig. 15). The periphery of the xylem zone also bulges outward from the ends of the ellipse (Fig. 2, 15, at right). The resulting bilateral symmetry continues to the base of the plants. In some specimens the zones are at opposite sides of the axis (Fig. 2), while in others they may be separated by as little as 140° (Fig. 15).

Rooting region — As one sections from the transition region into the base of the plant the disorganized appearing zones of xylem extend progressively toward the center of the axis, where they join and characterize the central zone of the rooting region (Fig. 2–4, 16–17). As a result, the rooting region extends further toward the stem at opposite ends of the ellipse than in other areas. The specimen in Fig. 1–4 is cut in oblique transverse view such that it is sectioned at a lower level at the right side of the figures. Therefore, one sees primarily the transition region at the left of Fig. 2–4, while a progression toward the base of the rooting region appears at the right. The peripheral stelar zone of the rooting region is characterized by radial files of secondary tracheids and by interspersed empty spaces (Fig. 3, 4, at right). Toward the base of the plant the central zone diminishes in size and the peripheral files of tracheids increase in length. Files below the bulging areas of the transition region are by far the longest (Fig. 17). In some instances small files of tracheids diverge from the larger files at wide angles (Fig. 17 at arrow).

Root traces originate from the periphery of the central zone, but are typically broken off near their points of origin (Fig. 3–4, 17–18). They are therefore extremely difficult to distinguish from the small files of secondary tracheids (Fig. 17, 20). Additional traces may originate from the large files of secondary tracheids, but their identity can usually not be determined with certainty (Fig. 20). In transverse view root traces can be identified by the appearance of the tracheids that radiate from a point (Fig. 18).

Extrastellar tissues — Although the specimens have no attached extrastellar tissues, their constant association with a single type of lycopod cortex and periderm suggests that the stele, periderm and leaf base in Fig. 5 represent the same plant. The occurrence of some steles surrounded by collapsed cylinders of periderm and leaf bases also supports this interpretation. In the stem region the extrastellar tissues are 1.8–3.8 mm thick and consist of radially aligned cells surrounded by an outer area of tissue (Fig. 5). At intervals the latter tissue expands outward as widely spaced leaf bases (Fig. 5). This tissue has two zones of radically aligned periderm cells. The inner zone is made up of straight files with broken tangential cell walls that give this zone the

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Fig. 23. Stereo-diagram of the stelar region. Upper segment represents a relatively distal level where the primary xylem zone is prominent and possibly medullated. The middle segment illustrates the basal-most level of the stem and transition region, where the primary xylem is reduced to a tiny rod. The lowest segment shows the base of the vascular system where root traces (not included) diverge at the bottom, and is cut at a level where both the transition and rooting (at left and right) regions are evident. Note the absence of leaf traces and accompanying broad rays in the transition region. ×3.
appearance of numerous closely spaced and radially disposed dark lines (Fig. 5). Toward the exterior, the second zone of periderm cells also shows broken tangential walls, but the cells lack internal contents and occur in prominently distorted files (Fig. 5). At the outer margin of the tissue is a zone of isodiametric and internally sepaate cells with relatively thin walls. Some cells of this zone are randomly disposed, while others are arranged in a more radial fashion. This latter zone varies in thickness from two or three cells, to many cells in the regions of the leaf bases (Fig. 5). Details of the cortex and leaf bases are currently under investigation as part of a study to characterize the above ground parts of this plant, and will be addressed more thoroughly in a subsequent paper.

In the rooting region the extrastellar tissues are typically absent, but in one specimen they are more completely preserved than are comparable tissues of the stems (Fig. 6 at left, 17, 19). Cells are apparently of both primary and secondary origins, and are generally the same in both transition and rooting regions. The latter tissues consist of several zones, and are roughly similar to, although simpler than, those of stigmarian rooting systems (Eggert, 1972; Frankenberg and Eggert, 1969). Adjacent to the xylem of the rooting region is a narrow zone of compact parenchyma with a clearly delimited outer margin (Fig. 18). In the transition region this tissue appears as black fragments of incompletely preserved cells (Fig. 19). At the base of the plant, cells of this type surround the root traces up to the point where they are broken off (Fig. 18). This tissue is similar to the inner cortex of Stigmaria ficoides (Frankenberg and Eggert, 1969).

Outside the parenchyma zone is an empty space that conforms to the middle cortex of stigmalian axes (Fig. 17–19). Root traces are not continuous across this space, but are present within the more peripheral tissues. The peripheral, or outer cortex, is 2.8–4 mm thick and grades from extremely delicate and poorly preserved remnants of cells to well preserved, isodiametric parenchyma with yellow or amber contents (Fig. 19). Cells at the outermost part of the zone are somewhat larger and often show interior septation. Toward the center of the zone the cells in some areas grade to rows of radially aligned cells with similar internal contents (Fig. 19). The latter cells appear to be of secondary origin, and probably represent a periderm that is similar to that in the rhizomorph of Paurodendron (Phillips and Leisman, 1966).

Monarch vascular bundles, apparently representing traces to the roots, traverse the outer cortical zone of the rooting region. The traces are wedge shaped, and consist primarily of radially aligned rows of tracheids with reticulate thickening patterns on all walls (Fig. 21). At the outer margin of this zone the traces are surrounded by approximately two layers of relatively large and thin-walled cells with no internal contents (Fig. 22). The latter cells may be comparable to the inner cortical-type cells that accompany stigmalian lateral appendages from their divergence from the stele to the periphery of the axes (Eggert, 1972; Frankenberg and Eggert, 1969). The root traces of our specimens are all broken off at the outer margin of the cortex, but no abscission zone like that of Stigmaria has been observed.

Discussion—Bipolar growth leading to the production of an upright stem and downward growing rooting system is characteristic of most major spermatophyte taxa, but is extremely rare for the pteridophytes. With the exception of Isoetes, Stylistes (Karrfalt and Eggert, 1977) and possibly some species of Selaginella, the extant pteridophytes all have unidirectional growth and adventitious rooting systems. Among extinct lycopod taxa bipolar growth was apparently much more widespread, with representatives preserved in strata that range from Devonian to Recent. However, anatomical features of the stem-root transition are rarely preserved and remain poorly known.

The specimens described above provide the first anatomical evidence for the stem-root transition in an arborescent lycopod with a cormose base. Excellent preservation of stelar and some cortical tissues in the stem, transition, and rooting regions allows for the characterization of changes that occur from level to level in the plant. The known features suggest that the specimens represent a new member of the Lepidodendrea with a basal region resembling Lepidosigillaria, Protostigmaria and Nathorstiana, as well as Isoetes. Common features of these forms include bipolar growth and upright stems that remain unbranched for at least some distance above the plant base. Nathorstiana and Isoetes stems are typically unbranched, while the attachment of Protostigmaria to a stem has yet to be reported. Additional lepidodendral features of the Ohio specimens are an exarch protostebe, apparently medullated at distal levels, and abundant secondary xylem production well above the base of the plant. As is characteristic of Carboniferous arborescent lycopsids (Eggert, 1961), the Ohio stems have primary xylem that increases in diameter and secondary xylem that decreases in thickness at successively more distal levels. Outward extensions of the cortex that represent either leaf bases or leaf cushions and radial alignment of cells in some parts of the cortical zone further suggest an alliance with the Lepidodendreae.
At the proximal end of the Ohio stems the primary xylem is reduced to a point from which the surrounding secondary tracheids radiate, and in this respect conforms to the structure described earlier for the base of a sigillarian stem (Frankenberg, 1968). Toward the base of the Ohio specimens the axis becomes ellipsoidal in section view and no traces are produced. These features and continued radial alignment of the tracheids characterize a transition to the rooting region. In the rooting region one finds a less orderly arrangement of the tracheids and the cells appear to be oriented both longitudinally and parallel to the circumference of the axis. The tracheids are also branched and highly contorted. Using the disposition of the tracheids and the divergence of root traces as criteria for recognizing the uppermost limits of the rooting region, one finds that it extends toward the stem further at two points that lie at the periphery of the stele and along the long axis of the ellipsoidal plant base. This accentuates the bilateral symmetry of the region and gives the base of the plant an apparently *Isoetes*-like configuration. In *Isoetes* transverse sections at the stem-root boundary expose the rooting region at the ends of the plane of symmetry and stem tissue at the center (Paolillo, 1963). Thus, the transition-rooting regions of the Ohio specimens have an interrelationship that is identical to that seen at the stem-root boundary in *Isoetes* (compare Fig. 2, 15 to Plate 18, Fig. A of Paolillo, 1963). Such a configuration suggests that the base of the Ohio specimens developed from a bilaterally symmetrical and possibly sunken meristem similar to that of *Isoetes,* and prompts one to speculate that Ohio specimens with well-preserved cortical tissues at the base will exhibit a basal furrow like that of *Isoetes.*

Several previously described taxa of fossil lycopsids also show anatomical features of the stem-root transition, but these are either smaller forms (i.e., *Oxroadia,* Long, 1971; *Paurodendron,* Phillips and Leisman, 1966) or are probably borne on extended and branched stigmatic systems (i.e., *Sigillaria,* Frankenberg, 1968). *Paurodendron* (Phillips and Leisman, 1966), *Oxroadia* (Long, 1971) and possibly *Calamopsis dubia* (Solms-Laubach, 1896; see Long, 1971) are small plants that branch near the ground and have solid protosteles with no secondary tissue development above the base of the stems. In *Oxroadia* the roots appear to extend from near the bases of older roots, and in this respect they may be similar to *Selaginella selaginelloides* as interpreted by Karrfalt (1977). No transition region or cormose base is produced by *Oxroadia* (Long, 1971). By contrast, *Paurodendron* does have a transition region and a cormose base like our specimens, but the features listed above suggest that it is more distantly related to the Ohio material than are members of the Lepidodendrales. The proposal that *Paurodendron*-type specimens represent stems of the Selaginellales also supports the above suggestion (Schlanker and Leisman, 1969).

In the introduction of this paper we mentioned a specimen that has recently been described as an herbaceous lycopod with a basal rhizomorph (Baxter, 1978). So unlike other known lycopsids are the features of *Nataliana sinuata* Baxter (1978) that further remarks about the specimen are in order. The small, closely spaced leaves of the specimen are spirally arranged and have a single vein. In these features *Nataliana* agrees with the structure of axes assignable to the Lycopsida, but the absence of roots or root traces from the base of the axis leaves the rooting nature of this region in doubt. Moreover, endarch primary xylem that surrounds the pith, extensive secondary xylem development and secondary tracheids with oval bordered pits on the radial walls (Baxter, 1978) are unlike comparable features of known herbaceous lycopsid stems. However, the above features are all characteristic of two major taxa of Paleozoic seed plants—the Cordaitopsida and the Coniferopsida. Cordaiales are well represented in Iowa coal balls like the one that bears *Nataliana,* but needle-like leaves of cordaitean origin are associated primarily with the fertile shoots (e.g., *Cordaianthus*). Like *Nataliana,* *Cordaianthus* secondary (fertile) shoots bear numerous closely spaced and spirally arranged leaves with a single vein. Additional similarities of the two taxa are steles with radially aligned tracheids, and steles that may form a cylinder proximally and become increasingly dissected at progressively more distal levels (Rothwell, 1977). In addition, some cordaitean axes of this type apparently have only sterile needlelike leaves, fertile scales not having been observed (Fry, 1956). In this regard it is interesting to note that specimens, apparently assignable to *Nataliana,* have been reported briefly from Iowa coal balls as cordaitean shoots of an uncertain morphological nature (Fry, 1956). The specimen figured by Fry (1956, Plate 7, Fig. 7) is approximately 3.1 cm long, as compared to 3.5 cm for the *Nataliana* specimen. Like *Nataliana* the former specimen has a narrow basal zone, apparently devoid of appendages, and a wider distal zone that bears closely spaced and spirally arranged needlelike leaves. The overall morphological similarity of *Nataliana* and the Fry specimen, and their common occurrence in coal balls from the Denominian Series of Iowa strongly suggest that they represent the same taxon. The occurrence of uniseriate rays and multisierate oval bordered pits in the secondary xylem of *Nataliana* also supports a cordaitean alliance.
An alternate interpretation of the affinities of Nataliana and the specimen figured by Fry (1956) is with the conifers. The latter group is well represented in Pennsylvanian strata by compression and impression specimens, but anatomically preserved material is extremely rare and remains have not been reported from North American coal-ball material. Nevertheless, the features of these specimens conform nicely to those of typical conifers. The absence of fertile scale-like leaves (usually termed scales in Cordaites) on the specimens in question is also compatible with the suggestion that such specimens may represent vegetative shoots of conifers. Systematic placement aside, the absence of root traces from the proximal end of Nataliana indicates that the taxon is not morphologically equivalent to known lycopsids with cormose plant bases.

As discussed above, the stem structure of the Ohio specimens conforms to that of the Leptodendrales. The age of the material (late Pennsylvanian) coincides with the known stratigraphic range of the order, but the base of the plant is obviously more like that we typically associate with the Isoetales. If one assumes that the cormose base of the Isoetales has arisen by a progressive reduction of the axially elongated and much-branched stigmarian systems that are associated with Lepidodendron, Sigillaria and similar forms, then the Ohio specimens appear to be both stratigraphically and phylogenetically out of place. If, on the other hand, one considers the presently known stratigraphic range of woody lycopsids with bipolar growth and cormose rooting structures, then it becomes apparent that representatives of this less common growth form have been present since Devonian time. These include Lepidosigillaria from Devonian strata, Protostigmaria from Mississippian deposits, the Ohio specimens from Pennsylvanian coal balls, and the taxa that are currently assigned to the Pleuromeiales and Isoetales from Mesozoic and more recent times. In this context it becomes equally plausible that either the stigmarian system gave rise to cormose forms by a reduction series such as that proposed by Potoń (1894), Mägdefrau (1931, 1932), Stewart (1947) and others, or that the cormose forms have had a parallel development with those that exhibit stigmarian systems (Jennings, 1975). In this regard, it is also possible that taxa with a cormose base gave rise to those with stigmarian systems.

Still another possibility is that the structure and development of the two types of rooting systems are relatively similar (Karrfalt, 1975), and that within some lycopsid taxa, habitat and plant habit may have had as much influence on the overall morphology of the plant base as long-term phylogenetic trends or evolutionary changes. In this regard it is interesting to note that the largest arborescent forms with stigmarian systems apparently grew in swampy environments, while those with a cormose base are typically smaller and often preserved in coarser sediments. Many of the latter may have also grown on more compacted and solid soils, or may have become buried during growth (Karrfalt, 1975). If the swampy environments had soils that were either made up of soft mud or loosely consolidated peat, then the matrix would offer less resistance for the presumably massive growing apex of Stigmaria (Karrfalt, 1975), and also provide a less rigid rooting medium. In such a situation a large and laterally extended rooting system would have been required to prevent the arborescent forms from uprooting and toppling. The tendency of stigmarian systems to grow horizontally rather than downward through the soil (Frankenberg and Eggert, 1968 and references cited therein) is consistent with this interpretation.

By contrast, smaller taxa and forms growing in firmer soils would require a less extended rooting system to keep the plant upright. This proposal is consistent with the fact that none of the lycopsids with cormose rooting systems are known to have grown to the massive size or to have branched as extensively as the largest lycopsids with stigmarian systems (e.g., Lepidodendron). One can therefore speculate that the disappearance of taxa with the largest and most highly branched rooting systems may be due as much to the loss of a suitable environment at the end of the Paleozoic as to their inability to compete successfully with representatives of other major plant taxa.

LITERATURE CITED


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