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A Late Devonian isoetalean lycopsid, *Otzinachsonia beerboweri*, gen. et sp. nov., from north-central Pennsylvania, USA[1]

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Compressions and impressions of an isoetalean lycopsid, comprising lower portions of stems, lobed bases, attached rootlets, and rounded rootlet scars, discovered in Late Devonian (Famennian) rocks of Clinton County, north-central Pennsylvania, Appalachian Basin, USA, are here described as *Otzinachsonia beerboweri*, gen. et sp. nov. These specimens demonstrate unequivocally the existence of the isoetalean lobe-and-furrow rhizomorphic growth pattern as early as the Late Devonian. They were found in an *Archaeopteris*- and *Rhacophyton*-dominated flora at Red Hill, an outcrop of the Duncannon Member of the Catskill Formation. The fossils were found in a dark-gray to greenish-gray lenticular siltstone layer that has an average thickness of 1.0 m. This deposit is interpreted as a floodplain pond. The low-energy nature of the deposit and the fine preservation of the intact rootlets of the specimens imply little or no transport. The plants were probably growing along the edge of the floodplain pond with their lower portions submerged for at least part of the year.

Key words: Catskill Formation; cormose; Devonian; Famennian; isoetalean; lycopsid; Paleozoic; Plantae.

The Lycophytina diverged from all other vascular plants early in the geologic history of land plants, perhaps no later than the Late Silurian. According to Kenrick and Crane (1997), they comprise a monophyletic subdivision consisting of the zosterophylls and their descendents, the lycopsids and barinophytes. Because of their early evolutionary divergence, the Lycophytina exhibit a distinctive growth architecture among plants. The earliest lycopsids maintained their attachment to the substrate through rhizomes and adventitious roots. Extant lycopsids in the orders Lycopodiales and Selaginellales do the same. In one lineage of lycopsids, however, a developmental switch occurred during the Devonian that co-opted the development of part of the shoot into an underground structure with attached stigmarian rootlets known as a rhizomorph (Rothwell and Erwin, 1985). Rhizomorphs have the function of anchoring the plants in the substrate and absorbing water and nutrients, but developmentally they follow similar pathways as stems and leaves and are composed of similar tissues (Stubblefield and Rothwell, 1981; Karrfalt, 1984a; Rothwell and Erwin, 1985; but see Paolillo, 1982). Lycopsid rhizomorphs are, in effect, serial homologues of shoots (Gensel et al., 2001). The only surviving lycopsids that have a version of this rhizomorphic structure are in the genus *Isoetes* (order Isoetales). Rhizomorphs have ranged in shape from cormose, bilaterally symmetric isoetalean bases to dichotomously branched, radially symmetric stigmarian complexes. Rhizomorphic lycopsids all belong to the same clade (Rothwell and Erwin, 1985; Pigg, 1992; Stewart and Rothwell, 1993).

The lycopsid specimens described in this paper include rhizomorphs with a lobed-and-furrowed morphology and attached rootlets. They are Late Devonian in age, and are among the earliest well-preserved compressions of cormose rhizomorphic structures on record. Most of the other lycopsids from the Devonian that have preserved rhizomorphic bases appear to be also cormose, but most of the details of their morphology, such as rootlet patterns, are ambiguous due to incomplete preservation. These include Middle Devonian *Eospermatopteris* (Goldring, 1924; Pigg, 1992; Algeo and Scheckler, 1998; some specimens of which may be cladoxylaleans, Driese et al., 1997), *Lepidosigillaria* (White, 1907; Grierson and Banks, 1963), Late Devonian *Cyclostigma* (Johnson, 1913; Schweitzer, 1969; Chaloner, 1984), and *Clevelandodendron* (Chitaley and Pigg, 1996). Despite the incomplete preservation, the rooting organs of these genera are well enough known to compare with the specimens described here. This comparison demonstrates that the material from Red Hill described in this paper represents a new taxon.

MATERIALS AND METHODS

The specimens of the new lycopsid consist of five plant fossil compressions and two counterpart impressions found at Red Hill, Clinton County, Pennsylvania. Specimens ANSP 4512, ANSP 4514, ANSP 4515, ANSP 4516, and ANSP 4518 consist of the basal organs and proximal portions of cormose lycopsid axes. ANSP 4512 and ANSP 4518 occur together on one slab. Four additional lycopsid specimens from Red Hill that are mentioned in this paper are two axis fragments of cf. *Lepidodendropsis*, ANSP 4523 and ANSP 4524, and two branched lycopsid axes, ANSP 4522 and ANSP 4537. All the specimens are preserved in a dark-gray siltstone. They are in the collection of the Academy of Natural Sciences in Philadelphia (ANSP). Other lycopsid material from Red Hill, consisting of axis fragments, was examined in the field.

Specimens were examined using standard light microscopy and photography with a minimum of preparation necessary.

RESULTS

Systematics—*Division*—Tracheophyta.

Subdivision—Lycophytina.

Class—Lycopsida.

Order—Isoetales.

Genus—*Otzinachsonia* Cressler et Pfefferkorn gen. nov. (Figs. 1–5, 7–10).

Species—*Otzinachsonia beerboweri* Cressler et Pfefferkorn gen. et sp. nov. (Figs. 1–5, 7–10).

Combined form generic and specific diagnosis—*Otzinachsonia beerboweri* gen et. sp. nov. Lycopsid with axial elongation and a four-lobed cormose base. Rootlets and round rootlet scars arranged in orthostichies on the basal portion of the stem. Small rootlet scars are concentrated on the lobes; large rootlet scars are concentrated in the furrows. A transition zone between the rhizomorph, i.e., the basal part of the stem, and the distal part of the stem lacks evident scars. Distal portions of stems have spirally arranged elliptical leaf scars without leaf cushions that occur in parastichies. Tops of basal leaf scars intercept the middle of short transverse ridges. Stem diameter can reach 10 cm.

Holotype—ANSP 4512 (Figs. 2, 3, 5, 10), which is stored in the paleobotanical collections of the Academy of Natural Sciences in Philadelphia.

Paratypes—Specimens ANSP 4515 (Fig. 7), ANSP 4514 (Fig. 8), ANSP 4516, and ANSP 4518 (Fig. 1), which are also stored in the paleobotanical collections of the Academy of Natural Sciences, Philadelphia.

Type locality—Red Hill, located 2 km (1.2 miles) west of the village of Hyner on PA Route 120, Clinton County, Pennsylvania, USA.

Age and stratigraphy—The plant-bearing beds of the Red Hill outcrop occur within the biozone Fa2c (Vco palynomorph zone) (Traverse, 2003) of the Famennian, Late Devonian. Lithostratigraphically the bed belongs to the Duncannon Member of the Catskill Formation.

Etymology—Otzinachson is an indigenous name for the West Branch of the Susquehanna River, which currently flows next to the Red Hill fossil locality. The specific name honors James Richard (Dick) Beerbower, whose investigations into the development of early terrestrial ecosystems and the force of his ideas have been an inspiration to the authors, as well as many others.

Morphology of specimens—The specimens of *Otzinachsonia beerboweri* described here consist of the flared basal portions of lycopsid stems with round rootlet scars and some attached rootlets (Figs. 1, 2, 7, 9, 10). All the stems have the same general appearance while width and preserved length vary (Table 1). The maximum width of the measurable basal portions of the specimens ranges from the largest at 10.3 cm

(ANSP 4512) to the smallest, which is 3.5 cm wide (ANSP 4516). While all the specimens exhibit the flared bottom portion of a lycopsid base, some of them have preserved distal portions of the stem that have sides that are roughly parallel to each other. When the taper of the stem was measurable, the size was recorded (Table 1). These data are used to estimate the height of the individual plant. Assuming a constant tapering rate throughout the upper part of the axis in the individual represented by counterpart specimen ANSP 4512, a height of 120 cm is suggested for the intact plant.

The flared base of *Otzinachsonia beerboweri* has four lobes, which are either clearly recognizable on these specimens or are inferred from the proportions of visible lobes and furrows compared to the overall stem size (Table 2). The lobes are raised areas along the basal portions of the stems. The flared base of ANSP 4514 (Fig. 8) has four distinct lobes that protrude freely from the bottom of the main stem for a length of 3.0 cm.

Three of the five specimens have rootlets that are preserved as flattened bands, as typical in rhizomorphic lycopsids. Most of the rootlets are carbonized compressions that are uniformly compacted across their widths, but one is three-dimensionally preserved. Dark-gray siltstone sediment infilling is visible between outer and inner concentric carbonized layers and suggests that the rootlets were hollow in the living plant. Rootlets protrude in a dense compacted mass from the bottom of two rhizomorph specimens (Figs. 2, 7, 10). Rootlets are attached to the lower halves of the lobes only. In specimen ANSP 4512 rootlets appear to be most densely concentrated in the areas just below the lobes rather than in the furrows. Rootlets are between 4 mm and 5 mm wide. The maximum discernible length of a single rootlet, although incomplete, is 5.5 cm on ANSP 4512 (Fig. 10).

Rootlet scars are circular and flat on the surface of the rhizomorphs and occur in a range of sizes depending on the size of the rhizomorph and their location on it. ANSP 4515 (Fig. 7) has small rootlet scars, between 1 and 2 mm in diameter, that are concentrated on the lobes, while large rootlet scars, about 8 mm in diameter, are concentrated on the furrows. ANSP 4516 has rootlet scars that are approximately 1 mm in diameter on the lobes and 3 mm in diameter in the furrows. The base of ANSP 4518 (Fig. 1) appears to have been damaged during both the time of burial and extraction from the outcrop. Detached and possibly turned ninety degrees (Fig. 1) from the proximal end of the fractured stem is an inner cast of the stem base (shown in detail in Fig. 9). The stem base has rounded rootlet scars and several attached rootlets. The visible rootlet scars are arranged in orthostichies that increase in size from the outer rows to the inner two rows, assuming that the orientation in Fig. 9 is correct. Round rootlet scars are between 1 and 3 mm in diameter and attached rootlets are 3 mm wide.

Leaf scar morphology and pattern can be observed on most of the specimens (Table 2). The helically arranged leaf attachment scars are slightly elliptical to circular (Fig. 3). These structures are interpreted as leaf attachment scars and not leaf traces on a decorticated stem because of the preservation of rootlets on the lower end of the axis in specimens such as ANSP 4512 where all these features are evident. Leaf scars are slightly raised on the surface of the axis. Some of them have a discernible structure consisting of paired reniform prominences with the concave sides facing each other and with their ends touching at the top and the bottom (Fig. 5). The
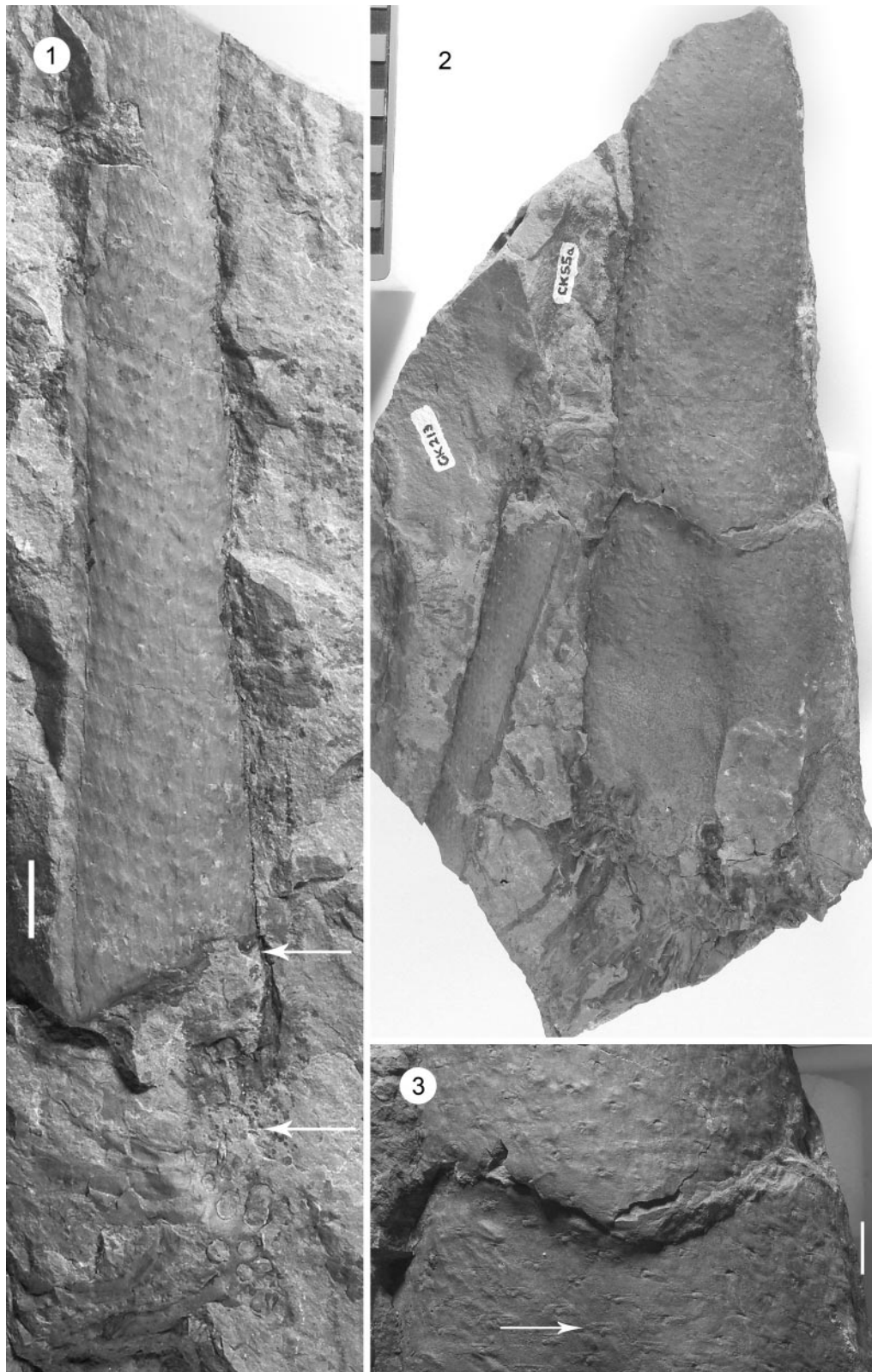
Figs. 1–3.   Holotype and paratype specimens of *Otzinachsonia beerboweri*, ANSP 4518 and ANSP 4512. **1.** Rooting organ and stem ANSP 4518. Arrows indicate missing area of preservation between rooting organ and stem. Vertical line = 1 cm. **2.** Fossil slab with rooting organs and stems of the two specimens. The smaller specimen ANSP 4518 is on the left and specimen ANSP 4512 is on the right. Scale bar at top left is in cm. **3.** Detail of leaf scars and associated transverse ridges on lower portion of ANSP 4512. Arrow points to one of the many transverse ridges visible in the image. Vertical line = 1 cm.
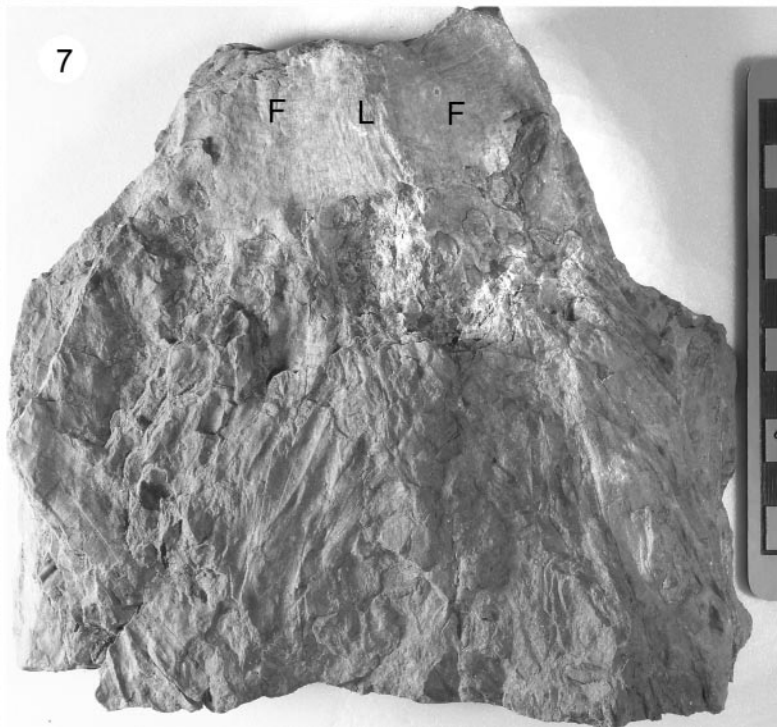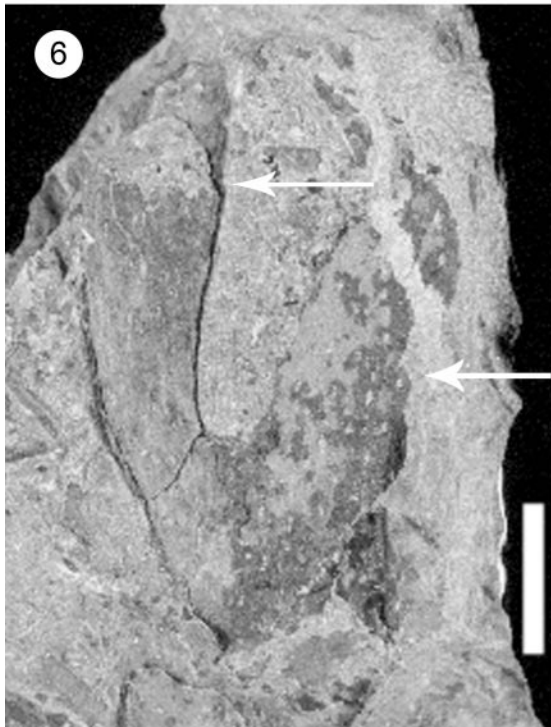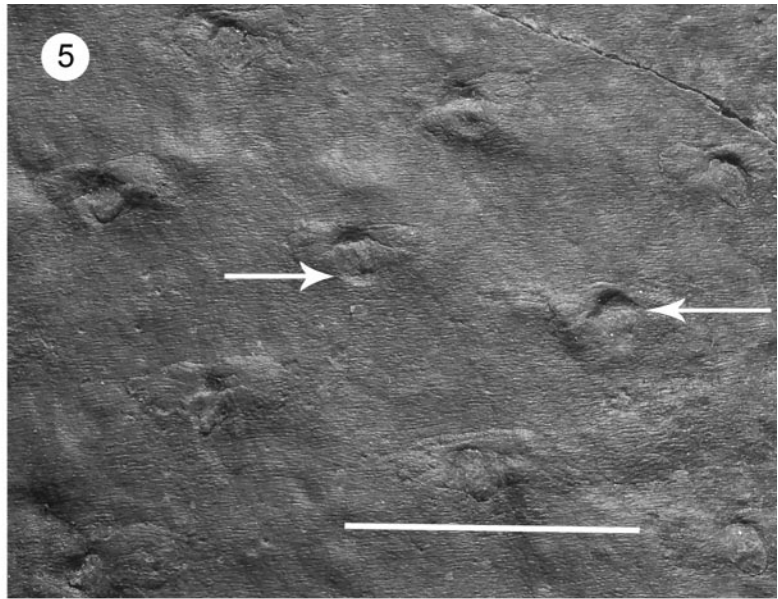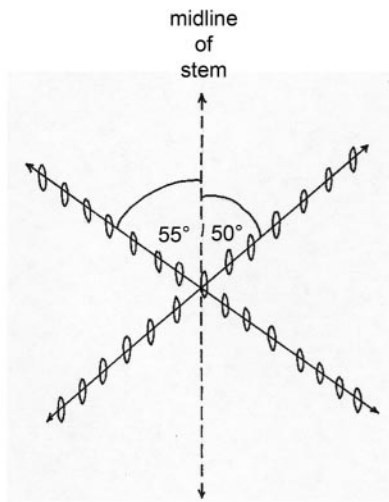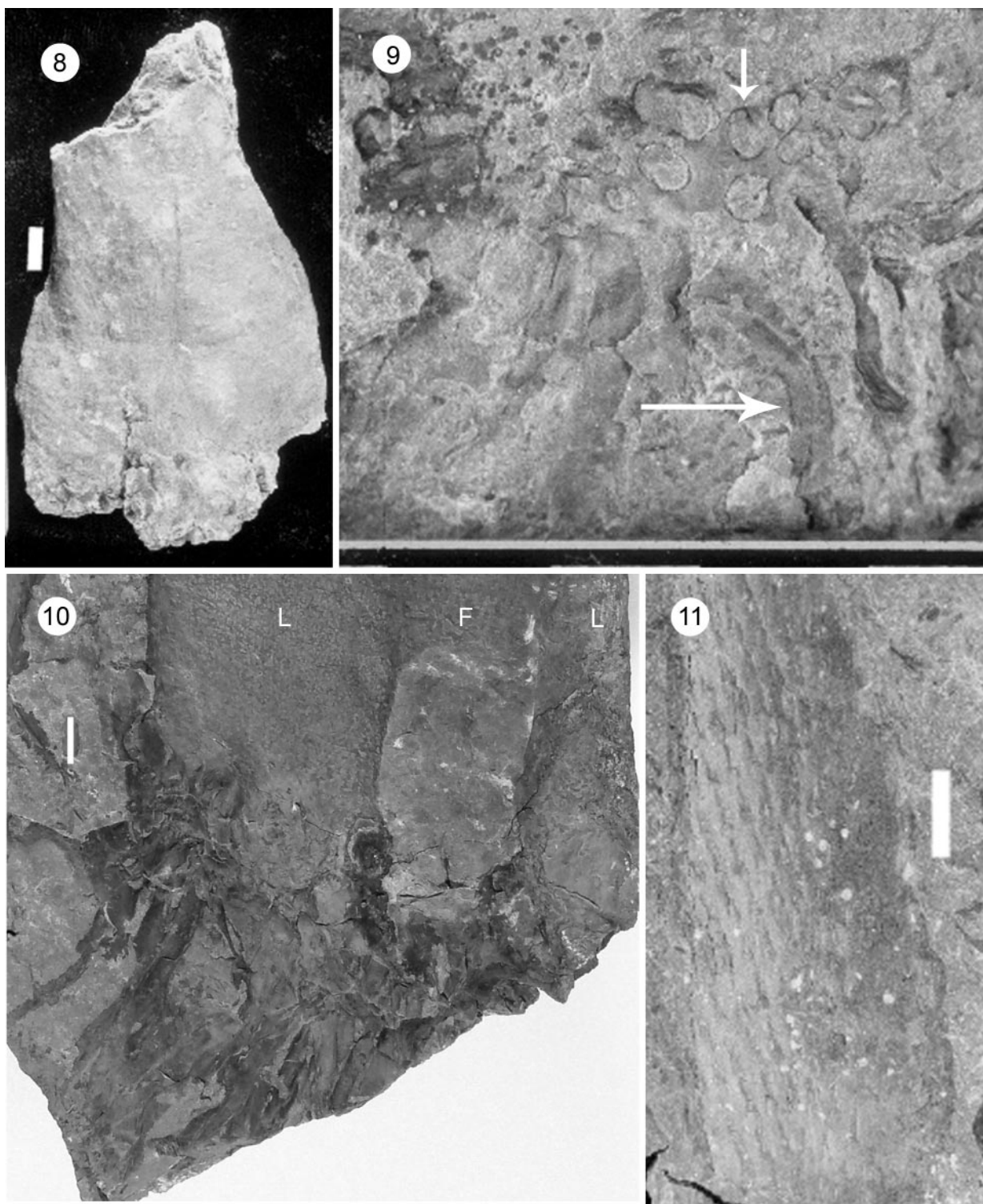
Figs. 4–7. Details of *Otzinachsonia beerboweri* holotype specimen ANSP 4512 and other lycopsids from Red Hill. **4.** Measurement method of parastichy angles using ANSP 4512 as an example. **5.** Detail of triangular leaf scar (right arrow) and possible parichnos (left arrow) on lower portion of stem of ANSP 4512. Horizontal line = 1 cm. **6.** Branched lycopsid stem fragment found at Red Hill, ANSP 4522. Taxon is indeterminate from decorticated specimen. Arrows indicate branches. Vertical line = 1 cm. **7.** Rooting organ with numerous attached rootlets, ANSP 4515. Scale bar at right is in cm. F = furrow, L = lobe.

triangular cavity between the curved prominences is interpreted as the leaf-trace scar. Possible evidence of parichnos (strands of air-filled parenchyma) is apparent in the form of small dimples below those leaf scars that are well preserved. The apices of the triangular leaf scars point towards the distal end of the axis (up). They are apparently the actual points of leaf attachment and later abscission. Prominent cortical contributions to the leaf scars, such as leaf cushions, are absent in these plants. On the specimens that have both leaf scars and rootlet scars, there is a zone devoid of scars of any kind along

an intervening portion of the stem. The lowest portion of the stem that bears elliptical leaf scars has narrow transverse ridges associated with them (Figs. 3, 5). The transverse ridges are 1 mm wide at their midpoints where they intercept the upper end of each leaf scar. The transverse ridges range from 7 to 9 mm long and taper to a point at both ends. Leaf scars on the rest of the distal axis are not associated with transverse ridges. These features are visible on specimens ANSP 4512 and ANSP 4514. Ridges become faint after the initial few centimeters of proximal leaf scars and then disappear altogether

Figs. 8–11. Fossil lycopsids of Red Hill. **8.** *Otzinachsonia beerboweri* rooting organ with conspicuous lobes but no attached rootlets, ANSP 4514. Vertical line = 1 cm. **9.** Detail of rootlet scars (upper arrow) and rootlets (lower arrow) of *Otzinachsonia beerboweri* specimen ANSP 4518. Scale bar in cm. **10.** Detail of lobed base of *Otzinachsonia beerboweri* specimen ANSP 4512, including attached rootlets. F = furrow, L = lobe. **11.** Specimen of cf. *Lepidodendropsis*, ANSP 4523, found at Red Hill. Vertical line = 1 cm.

TABLE 1. Measurements of stems and cormose bases of *Otzinachsonia beerboweri* specimens.

Specimen no.	Total length (cm)	Length of base (cm)	Max. width base (cm)	Max. width stem (cm)	Min. width stem (cm)	Taper of stem mm/cm	Estimated height (cm)
4512	31.5	13	10.3	7.2	6.6	0.6	120
4514	13.8	9.7	8.1	5.0	5.0		
4515	3.3	(partial)	9.0	—	—		
4516	4.0	4.4	3.5	2.5	2.5		
4518	13.5	3.2	(partial)	2.5	1.9	0.3	83

over a very short additional length of the axis. Ridges may have resulted from surface stretching due to internal thickening in the flared lower portion of the stem.

The angles that the leaf scar parastichies form with the longitudinal axis of the stem vary along the length of the stem. At a point 12 cm from the base of specimen ANSP 4512, the parastichies form angles of 55° and 50° to the longitudinal axis (Fig. 4), whereas at a point 18 cm from the base of the stem, the parastichies form two angles of 50°. Another specimen (ANSP 4514; Fig. 8) has helically arranged leaf scars in parastichies that form angles of 46° and 58° to the midline of the axis at a point 8.2 cm from the bottom of the stem. Leaf scars on the small axis ANSP 4518 (Fig. 1) are 2 mm apart along the parastichies. Parastichies make variable angles to the midline along the length of the small axis. At a point 1.5 cm from the fractured proximal end of the stem, parastichies form angles of 60° and 32° to the midline. At a point 7 cm from the fractured proximal end of the stem, parastichies form angles of 47° and 30° to the midline.

Other lycopsid fragments from Red Hill—Numerous other lycopsid fragments have been found within the dark-gray siltstone layer at Red Hill. They consist entirely of decorticated axis fragments that range in width from 0.8 to 10 cm. The surface textures of the specimens vary, conforming to different levels of decortication of lycopsid axes with spiral leaf trace patterns (S. Scheckler, Virginia Polytechnic Institute and State University, personal communication). Two stem fragments have leaf traces arranged in pseudowhorls that are suggestive of decorticated specimens of *Lepidodendropsis* (Fig. 11), indicating that another genus of lycopsid is present at the Red Hill locality.

Of the hundreds of lycopsid stem fragments examined from Red Hill so far, only two fragments exhibit branching. ANSP 4522 (Fig. 6) is a compression of a 4-cm-long stem fragment with a smaller branch that emerges from a main axis.

DISCUSSION

The new species *Otzinachsonia beerboweri* Cressler & Pfefferkorn is a four-lobed cormose lycopsid with axial elongation and a spiral pattern of elliptical leaf scars without leaf cushions. The uppermost part of the plant is unknown, but the rooting organ and proximal leaf scar characteristics are sufficiently different from other described lycopsids to justify the establishment of a new taxon.

All of the specimens are interpreted as having a four-lobed rhizomorph. For all of the specimens, except ANSP 4518, the four lobes can be directly observed or can be inferred from the proportions of the lobes that are free from the matrix compared to the overall dimensions of the stem. ANSP 4518 does not have any visible lobes, but consists of an inner cast with rootlet scars arranged in orthostichies of increasing rootlet scar diameter in two directions (Fig. 9). This pattern of rootlet scars is similar to the three-dimensionally preserved specimens ANSP 4516 and ANSP 4515, where the small rootlet scars are concentrated on the lobes, and the large rootlet scars are concentrated on the furrows. If, during its life, specimen ANSP 4518 had the same correspondence of small and large rootlet scars to lobes and furrows, then the dimensions of its rootlet-scar pattern supports an interpretation as four-lobed. Despite the fact that all the *Otzinachsonia* specimens found to date have been interpreted as having four lobes, the species may have had greater morphological variability. There are numerous instances of isoetalean species having a succession of lobe numbers during their ontogeny (Karrfalt, 1984b).

These lobe-and-furrow patterns of rootlets and rootlet scars are entirely consistent with the pattern of development described for *Isoetes* (Karrfalt and Eggert, 1977), and already inferred for several extinct taxa (Jennings et al., 1983). Rootlets are initiated along the rootlet primary meristem, which usually runs parallel to the furrows. Perhaps the smaller rootlet scars are traces of the more constricted distal ends of rootlets that have emerged through the thicker and expanding cortex

TABLE 2. Features of cormose bases, lobes, and leaf scars of *Otzinachsonia beerboweri* specimens.

Specimen no.	No. of lobes	Rootlets	Rootlet scars	Leaf scar shape	Leaf scar size (mm)	Lobe length (cm)	Lobe-furrow distance (crest to trough, cm)
4512	4 (inferred)	present	few	elliptical	1 × 2 2 × 2	9.5	3
4514	4	absent	indistinct	elliptical	1 × 2	9.0	1.5
4515	4 (inferred)	present	large in furrows, small on lobes	na	na	undetermined	3
4516	4 (inferred)	absent	large in furrows, small on lobes	na	na	undetermined	1.3
4518	indeterminate	few	orthostichies of small and large scars	elliptical	1 × 1.5	undetermined	undetermined

Note: na = not available.

tissues of the lobes, and the larger rootlet scars are traces of rootlets at their thicker proximal ends where they emerge from the meristem tissue. This interpretation is problematic with respect to ANSP 4518, in which the small and large rootlet scars are all on the same plane of fracture through the inner cast of the rooting organ.

Alternatively, the smaller rootlet scars might reflect younger, smaller rootlets of uniform diameter, and the larger rootlet scars might reflect older, larger rootlets of uniform diameter. If the smaller rootlets are most recently derived from the meristem tissue, then the meristem must be surrounded by lobe tissue in this species, rather than running parallel to the furrows. Another option is the possibility that the small rootlets emerged from the plant when it was small, and the larger rootlets emerged during a later ontogenetic stage when the whole plant and its rhizomorph were larger. These hypotheses are unfortunately impossible to test with the currently available material.

The morphology and dimensions of the rootlets and rootlet scars are consistent among all the specimens assigned to *O. beerboweri*. They are uniformly flattened, as would be expected of isoetalean or stigmarian rootlet compressions.

Leaf scars on the outer surfaces of the specimens cover large portions of the aerial stem. They reflect the surface pattern of the plant, and not an inner layer exposed by decortication. Decorticated stems would not retain attached rootlets and, therefore, *Otzinachsonia* had no leaf cushions. The origin of the transverse ridge above each leaf scar in the most proximal portion of the stems is possibly due to stretching during lateral thickening of the stem.

There are two size classes of *Otzinachsonia* specimens. ANSP 4516 and ANSP 4518 are small and slender, (2.5–3.5 cm maximum diameter), and the other three specimens are larger (8.0–10.3 cm maximum diameter). Despite the differences in size, their proportions are very similar. This implies secondary growth of both the aerial stem and the cormose base during ontogeny. *Otzinachsonia* was thus probably growing in multiage stands on the Late Devonian landscape.

Most of the other lycopsid stem fragments that have been found at Red Hill are decorticated and cannot be assigned to any taxon. Two specimens were found that have scars arranged in pseudowhorls (Fig. 11). On that basis, they can be compared to the genus *Lepidodendropsis*. None of the stems with rooting organs, however, have a *Lepidodendropsis*-like arrangement of traces. The numerous decorticated axis fragments found at Red Hill are allochthonous, in contrast to the autochthonous-parautochthonous *Otzinachsonia* specimens, which were mostly found with large attached rootlet masses.

Only two branched lycopsid stem fragments have been found so far out of hundreds of specimens at Red Hill. Whether they came from the same species of lycopsid as the rhizomorphic structures described here is impossible to know. *Otzinachsonia* could have been either monopodial with a terminal cone or axial sporophylls similar to *Clevelandodendron* and other post-Devonian taxa, or it could have had forked branches like many other lycopsids. Thus far, no lycopsid fertile structures have been found at Red Hill. A rich palynoflora has been described from Red Hill (Traverse, 2003), which includes *Auroraspora macra* Sullivan, a spore species that is synonymous with the possible tree lycopsid spore *Auroraspora asperella* (Kedo) Van der Zwan (Streel and Scheckler, 1990). Because of the fragmentary nature of the material, a whole-plant reconstruction of *O. beerboweri* is not possible at this time.

Comparison to other lycopsids—The only criteria available for comparing the Late Devonian *O. beerboweri* with other lycopsids are its cormose rhizomorphic structures, its leaf-scar pattern, and its overall proportions.

The earliest rhizomorphic lycopsids are Middle Devonian in age. This lineage is one of the first to produce trees, along with the progymnosperms and the cladoxylaleans. The cormose bases of the Middle Devonian genera *Lepidosigillaria* are incompletely known (White, 1907; Kräusel and Weyland, 1949; Grierson and Banks, 1963), while those of *Eospermatopteris* (Goldring, 1924) consist of large rounded casts more than 40 cm in diameter. They are quite similar to each other, which has prompted conjecture that at least some *Eospermatopteris* stumps are indeed those of lycopsids (Pigg, 1992; Algeo and Scheckler, 1998). The latter had previously been considered a progymnosperm (Stewart and Rothwell, 1993), and some specimens are now considered to be cladoxylaleans (Driese et al., 1997). The cormose bases of neither *Lepidosigillaria* nor *Eospermatopteris* show any evidence for lobes. The surface texture of *Lepidosigillaria* is quite distinct, consisting of both lepidodendroid leaf cushions and sigillarioid ribs (White, 1907). The surface texture of *Eospermatopteris* also contrasts with that described for *Otzinachsonia*. Specimens of *Eospermatopteris* are described as variously having shallow ridges and furrows, having deeper irregular furrows and wrinkles, or being just roughened (Goldring, 1924). This description does not conform to the lycopsid pattern of spirally arranged leaf traces, but three of Goldring's specimens were impressions that did have large, spirally arranged scars (Goldring, 1926). They were assigned to a new Middle Devonian arborescent lycopsid species by Grierson and Banks (1963) called *Amphidoxodendron dichotomum* based on other specimens also found in New York. This species has large leaf scars hexagonal in outline and surrounded by furrows. Basally it has strong longitudinal ridges. If *Amphidoxodendron* does indeed have affinities with specimens similar to *Eospermatopteris*, its rooting organ may also have been similar. Another Middle Devonian taxon with possible isoetalean affinities is *Longostachys latisporophyllus* of China (Cai and Chen, 1996; Pigg, 2001). It exhibits bipolar growth with branching aboveground and belowground structures, but lacks the rootlets and rootlet scars of well-characterized rhizomorphic lycopsids. *Otzinachsonia* does not resemble any of these Middle Devonian taxa.

Otzinachsonia does not closely resemble any of its Late Devonian contemporaries, either. The cormose bases of the Late Devonian species, *Cyclostigma kiltorkense* (Johnson, 1913; Chaloner, 1984) and *Clevelandodendron ohioensis* (Chitaley and Pigg, 1996), are incompletely preserved, but they nonetheless can be contrasted with *Otzinachsonia*. *Cyclostigma* may have had a bilobed base, but Pigg (1992) reports that the evidence for that is ambiguous. Lobed bases of *Cyclostigma* are known from Kiltorcan and Bear Island, however, and are on repository at the Swedish Museum of Natural History, Stockholm, and the Museum of Natural History, London (S. Scheckler, Virginia Polytechnic Institute and State University, personal communication). There is no evidence for leaf cushions in *Cyclostigma*. The surface texture is characterized by spirally arranged circular leaf scars. Stem fragments with similar circular scars have been found at Red Hill. However, these represent a decortification level of an unidentified lycopsid in which the leaf traces pass through the cortex perpendicular to the longitudinal axis of the stem. Without specimens that show the true exterior and various decortication levels, determining

whether *Otzinachsonia* has a cyclostigma-like decortification level is not possible. However, its outermost surface is unlike *Cyclostigma*.

Clevelandodendron is a slender, unbranched Late Devonian plant 2 cm wide with thick appendages on its base that narrow distally (Chitaley and Pigg, 1996). No pattern of rootlet scars or lobes are exhibited, possibly because of its mode of preservation. *Clevelandodendron* has spirally arranged elongate leaf scars that are not unlike those of *Otzinachsonia* specimen ANSP 4518. The 2-cm-wide specimen of *Clevelandodendron* is a mature plant terminated by a fertile bisporangiate strobilus. It was in all likelihood a plant with determinate growth and did not get any larger than 2 cm in thickness. The largest specimens of *Otzinachsonia* are five times larger.

Protostigmaria eggertiana is an Early Mississippian cormose structure from the Price Formation of Virginia that is believed to be the basal organ of the arborescent lycopsid *Lepidodendropsis* (Jennings, 1975; Jennings et al., 1983). *Protostigmaria* has up to 13 lobes that bear numerous rootlets. Fragments of stem comparable to *Lepidodendropsis*, found at Red Hill, are not associated with any rooting organs. The four-lobed structure of *Otzinachsonia* and its spiral arrangement of widely spaced leaf scars with no leaf cushions and high parastichy angles is quite different from *Protostigmaria/Lepidodendropsis*.

The full range of rhizomorphic forms appears to have become established by the Early Mississippian, or in European stratigraphic terms, the Tournaisian. The upper Tournaisian Oxroad Bay flora of Scotland includes stigmarian rhizomorphs and the compact anchoring structures attached to *Oxroadia gracilis* (Bateman and Rothwell, 1990; Bateman, 1992).

By the Late Mississippian (Visean), lycopsids with stigmarian bases are well established (Jennings, 1975). Pennsylvanian lycopsid floras are dominated by lepidodendraleans and sigillarians that all had stigmarian bases. Cormose lycopsids were only a minor part of Pennsylvanian lowland floras (but see DiMichele et al., 1979). These floras include well-described cormose taxa such as *Paurodendron fraiponti* (Fry, 1954; Phillips and Leisman, 1966; Rothwell and Erwin, 1985), *Cormophyton mazonensis* (Pigg and Taylor, 1985), and *Chaloneria* species (Pigg and Rothwell, 1979; Pigg and Rothwell, 1983). *Paurodendron* is a diminutive form, and *Cormophyton* is closely related to *Chaloneria* but has been found compressed in Mazon Creek nodules. Two species of *Chaloneria* are known anatomically from Upper Pennsylvanian coal balls. They are reconstructed as heterosperous monopodial plants of similar dimensions as *Otzinachsonia*, but with irregular helically arranged leaf scars and a rounded base (Pigg and Rothwell, 1983). The stigmarian taxa declined dramatically by the end of the Pennsylvanian of Euramerica, but persisted in wetlands of the Cathaysian floral realm, i.e., the continents off the northeastern part of Pangea that are now assembled as China (DiMichele et al., 2001).

By the Triassic, all of the stigmarian taxa appear to have become extinct. The first appearance of isoetalean lycopsids with total axial reduction is recorded in the Triassic. Some of these fossils have been given the name of the extant genus *Isoetes* (Bock, 1962). The axis-forming isoetalean lineage was still represented in the Triassic by species of the genus *Pleuromeia* (Mägdefrau, 1931; Retallack, 1975) and *Cylomeia* (White, 1981). *Pleuromeia sternbergii* was an unbranched plant 5–10 cm wide bearing four shortened lobes on a rhizomorph with stigmarian rootlet scars and attached rootlets

(Mägdefrau, 1931). This description is very close to that of *Otzinachsonia*, but the stratigraphic distance between the two is at least 120 million years, demonstrating the evolutionary conservatism of the isoetalean lineage.

The youngest known members of the isoetalean lineage that had axial elongation are *Nathorstiana* (Richter, 1909; Mägdefrau, 1932; Karrfalt, 1984b) and *Nathorstiella* (Glaessner and Rao, 1955) from the Early Cretaceous. Abundant well-preserved specimens of *Nathorstiana* have provided an understanding of isoetalean development and phylogeny in a rhizomorphic form. *Nathorstiana* has isoetalean-like orthostichies as an adult plant with four or more lobes, but the immature stages exhibit an abbreviated stigmarian-style growth pattern (Karrfalt, 1984b; Rothwell and Erwin, 1985).

Bateman (1994) cites this ontogenetic sequence of *Nathorstiana* as evidence that the bilaterally symmetric, isoetalean rhizomorphic lycopsid taxa are evolutionarily derived from radially symmetric, stigmarian rhizomorphic taxa, based on principles established by von Baer. Furthermore, radially symmetric rhizomorphs with spiral rhizotaxy are morphologically more similar to the embryologic stems from which they were presumably derived than are bilaterally symmetric rhizomorphs. Bateman's scenario, although sequentially similar, is not to be confused with the classic lycopsid "reduction series" of earlier workers. Potonié (1894), Mägdefrau (1956), and others had proposed a lycopsid "reduction series" in which the cormose and uniaxial isoetalean growth form had been evolutionarily derived from arborescent *Sigillaria* of the Carboniferous, which had branching stigmarian rooting systems. By way of the unbranched Mesozoic forms *Pleuromeia, Nathorstiana*, and *Nathorstianella*, the endpoint of this hypothetical linear series is the extant *Isoetes*, which has a small, cormose rooting base, no axial development, and no sterile microphylls, i.e., it is a cone with rootlets. Mägdefrau was the first to acknowledge that this hypothesis was undoubtedly an oversimplification (Mägdefrau, 1956, p. 211). An alternative view has also been presented, that the lepidodendraleans and isoetaleans had separate origins in the Paleozoic (Jennings, 1975; Stubblefield and Rothwell, 1981). In more recent years, a reevaluation of previously known forms and new descriptions of previously unknown forms have presented us with a complexity of rhizomorphic lycopsids that have been ascribed to one monophyletic "plexus" (Rothwell and Erwin, 1985; Pigg, 1992; DiMichele and Bateman, 1996b).

Environment of deposition and growth—The layer of dark-gray siltstone in which the Red Hill lycopsid specimens were found has been interpreted as an oxbow lake (Cressler, 2001), but is probably more accurately characterized as a floodplain pond that resulted from scouring during an avulsion event (Slingerland and Smith, 2004). The layer is exposed along a roadcut for 167 m and with an average thickness of 1 m. In addition to the lycopsids, there are abundant other plant fossils in the layer, which consist mainly of *Archaeopteris* branches and foliage, *Rhacophyton* axes, and lesser amounts of *Gillespiea* and gymnosperm material (Cressler, in press). The vertebrate remains in this deposit consist of disarticulated sarcopterygian and arthrodire placoderm remains and small, articulated palaeoniscoid fish.

The floodplain pond was a site of quiet deposition. Silting probably occurred during periodic flooding from a nearby active channel. The well-preserved condition of the attached rootlets and the nature of the deposit implies little or no trans-

port of the lycopsids with preserved bases. The lack of aerial parts and detached leaves, however, is puzzling. The specimens of decorticated stems, including the ones that are potentially assignable to *Lepidodendropsis*, are likely to have been transported from farther away on the floodplain. This suggests the possibility of niche partitioning among the lycopsids in this landscape. The specimens of *Otzinachsonia* with preserved rootlet-bearing bases most likely were growing on or near the edge of the pond. They may even have been growing with their bases submerged in the water of the pond. The flared bases would have given support under these conditions, analogous to the forms seen in the extant trees *Nyssa* and *Taxodium*. If this interpretation of its growth environment is correct, then *O. beerboweri* is among the earliest known swamp plants.

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