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brevifolium Williamson**

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PARALYCOPODITES MOREY & MOREY, FROM THE
CARBONIFEROUS OF EURAMERICA—A REASSESSMENT
OF GENERIC AFFINITIES AND EVOLUTION OF
“LEPIDODENDRON” BREVIFOLIUM WILLIAMSON¹

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ABSTRACT

A study of the morphologies and evolutionary relationships of Upper Carboniferous coal swamp lycopods indicated that plants traditionally treated as *Lepidodendron brevifolium* were distinct from *Lepidodendron* at the generic level, and were not part of a morphological cline between *Lepidodendron* and *Lepidophloios*. The description of a new genus and species by Morey and Morey (1977), based on a specimen identical to *L. brevifolium* distal branches, results in the inclusions of *L. brevifolium* in *Paralycopodites*, in which it has nomenclatural priority over *P. minutissimus*. The small trees or shrubs had deciduous lateral branches and permanently retained leaves; in these characters, *Paralycopodites* is most similar to the compression-impression genus *Ulodendron* as delimited by Thomas. Bisporangiate *Lepidostrobus* cones are closely associated with the vegetative remains; the cones can be assigned to three stratigraphically complementary species throughout the range of *Paralycopodites*—Visean to Westphalian D (Middle Pennsylvanian). Extreme evolutionary conservatism is indicated by the low vegetative morphological variability and the great similarities in morphology of associated cones; in combination with the sudden Visean appearance of *P. brevifolius* and the lack of intermediates among major lycopod genera, this lends support to punctuated equilibria hypotheses. *Paralycopodites* was generally rare in coal swamps, possibly related to its production of megaspores lacking specialized adaptations for flotation. Its pattern of late Middle Pennsylvanian extinction parallels *Lepidodendron* and *Lepidophloios*.

PARALYCOPODITES is a genus of arborescent lycopods first described by Morey and Morey (1977) from a single specimen that lacked secondary tissues and was interpreted as herbaceous. In fact, the specimen they described is part of a deciduous lateral branch of a small tree—a type described by Williamson (1872b) as *Lepidophloios brevifolium* from the Calciferous Sandstone Series of Pettycur, Scotland. *Lepidophloios brevifolium* was subsequently treated as a species of *Lepidodendron* (Williamson, 1893; Seward, 1910; Scott, 1920; Hirmer, 1927), and *Paralycopodites minutissimus* Morey & Morey, is a synonym of *P. brevifolius* (Williamson) DiMichele comb. nov.

The purpose of this paper is to clarify the

morphological characteristics of *Paralycopodites brevifolius* as a taxon distinct from *Lepidodendron* and *Lepidophloios*, and not a morphological intermediate between them (Smith, 1962). The recognition of *Paralycopodites* as a unique genus lies in its morphology of persistent leaves, smooth-marginal siphonostele, homogeneous cortex and periderm, deciduous lateral branches, and consistent association with bisporangiate cones, rather than in the characters upon which the genus was founded (Morey and Morey, 1977). *Paralycopodites* differs from *Lepidophloios* and most species of *Lepidodendron* in having persistent, short, scalelike leaves. In external form, the leaves resemble an intermediate between leaf cushions of *Lepidodendron* and the imbricated leaf cushions of *Lepidophloios* (Smith, 1962). This superficial resemblance of leaves to leaf cushions, together with a homogeneous periderm and cortex has obscured the recognition of *Paralycopodites* as a genus quite separate from *Lepidophloios* and *Lepidodendron* and some specimens of *Paralycopodites* were included among the syntypes of *Lepidophloios kansanus* (Felix) Eggert (Felix, 1952; DiMichele, 1979a). Among compression-impression form genera, *Ulodendron* Lindley and Hutton, sen-

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su Thomas (1967), is most similar in external form. *Paralycopodites* trees were relatively small, with a columnar trunk that rarely branched isotomously, and deciduous lateral branch systems. This general habit was recognized from the bimodal size distribution of stems and from anatomical differences between columnar trunk specimens with small ulodendroid-branch traces and abundant small stems with little or no secondary tissues.

MATERIALS—Permineralized specimens from western Europe were examined from the Holden, Hemingway and Williamson Collections, British Museum (N.H.), London, England, Calciferous Sandstone Series of Pettycur, Fifeshire, Scotland; Felix Collection, Museum für Paläontologie, Humboldt-Universität zu Berlin, DDR—Katharina Seam, Westphalian A-B boundary of Langendreer, North Rhine—Westphalia, West Germany.

Specimens were examined from Middle Pennsylvanian coal balls from the following American coals: Copland (Taylor) coal, below Magoffin Member, Breathitt Formation, Pottsville Series—No. 5344, 5409, 5418, 5419, 5494, 7801, 10154, 13604, Lewis Creek, Leslie County, KY, Hyden Quad; No. 2189, 2190, 2199, 2211, 2232, 2287, 10037, 10136, 10172, Shack Branch, 3 miles southwest of Hyden, Leslie County, KY. Secor Coal Member, Boggy Formation—No. 22931, 22933, 23264, 23272, 23275, Westhoff Bros. Mine, Pittsburg Co., OK (SW, SE, SE, T3N, R17E). Mineral or Fleming Coal Member, Cabannis Formation, Cherokee Group—No. 796, near Hallowell, KS (Sec. 4, T33S, R22E). Harrisburg-Springfield (No. 5) Coal Member, Carbondale Formation, Kewanee Group—No. 16038, Consolidation Coal Company, Burning Star No. 4 Mine, Perry County, IL (Sec. 3, T6S, R4W). Herrin (No. 6) Coal Member, Carbondale Formation, Kewanee Group—No. 5515, 6466, 13746, 14554, 22487, 22488, 22501, 22511, 22648, 22779, 22806 and Sahara Vertical Section 2, Sahara Coal Company No. 6 Mine, Saline County, IL, Harrisburg 7½' Quad. (Sec. 30, T9S, R5E) and Sahara Vertical Section 5, Harrisburg 7½' Quad. (SE, Sec. 24, T9S, R5E); No. 6295, 6356, 18057, 18065, Midland Electric Corporation Mine, Farmington, Knox County, IL, Canton Quad. (SW, Sec. 25, T9N, R4E); No. 9066, 9346, 10374 and Delta Vertical Section 2, AMAX Delta Mine, Williamson County, IL, Marion Quad. (Sec. 28, T9S, R4E); No. 15415, 19062, Peabody Eagle No. 2 Mine, Gallatin County, IL, Shawneetown 7½' Quad. (Sec. 9, T10S, R9E). All specimens peels and slides are housed in the Paleobotan-

ical Collections (Morrill Hall), Department of Botany, University of Illinois, Urbana, IL.

DESCRIPTION—*Emended generic diagnosis*—*Paralycopodites* Morey & Morey emend. DiMichele—Arborescent lycopod with columnar to sparsely dichotomized main trunk bearing deciduous lateral branch systems. Stem siphonostelic except for protostelic basalmost and distal parts of determinate plant body; primary xylem with smooth outer margin; pith of homogeneous parenchyma with sharp contact along regular inner margin of xylem; secondary xylem present in some parts of stem. Cortex three-zoned; outer cortex homogeneous, composed of thick-walled cells, slightly elongate vertically. Bifacial periderm with massive homogeneous phellem and thin phelloderm; leaf traces distinct in phellem. Persistent, short leaves attached to diamond-shaped to somewhat alate leaf bases; relatively shallow, adaxial ligule pit. Small (1 cm diam) bisporangiate cones, with microsporangia above megasporangia, borne at tips of distal branches. Type species: *Paralycopodites minutissimus* Morey & Morey, 1977, *Palaeontographica* 162B: 64–69.

Paralycopodites brevifolius (Williamson) DiMichele comb. nov.—*Paralycopodites* is monotypic; therefore the emended generic diagnosis also serves as specific diagnosis.

Synonymy—1) *Lepidophloios brevifolium* Williamson, 1872. *Philosophical Transactions of the Royal Society of London* 162: 283–318 [BASIONYM].—*Lepidodendron brevifolium* sensu Williamson, 1893, *Philosophical Transactions of the Royal Society of London* 184B: 1–38, et authors, non Ettingshausen, 1854.—*Lepidodendron veltheimii* (*veltheimianum*) sensu Seward, 1910, *Fossil Plants* p. 77; Scott, 1920, *Studies in Fossil Botany* p. 120; Hirmer, 1927, *Handbuch der Paläobotanik* p. 202, non Sternberg 1825. [TYPE—Williamson, 1872, syntypes as illustrated specimens; Calciferous Sandstone Series, Lower Carboniferous, Pettycur, Scotland; LECTOTYPE—designated herein, selected from original figured specimens of Williamson, 1872—(Plate XLIII, fig. 20), Specimen No. 503, Williamson Collection of Fossil Plant Slides, British Museum (N.H.), London, England.]

2) *Paralycopodites minutissimum* Morey & Morey, 1977, *Palaeontographica* 162B: 64–69. [HOLOTYPE—USNM 208540, United States National Museum, Washington, D.C.].

Paralycopodites is masculine in gender, therefore the endings of both *P. brevifolius* and

P. minutissimus have been changed from the neuter to bring them into agreement.

MORPHOLOGY AND ANATOMY—*Paralycopodites brevifolius* is presently the only vegetative species of the genus recognizable in the Carboniferous, with a range from the Viséan to the Westphalian D. There are three stratigraphically complementary species of bisporangiate *Lepidostrobus* cones associated with *Paralycopodites*. This may indicate the existence of several natural species presently inseparable on the basis of vegetative morphology. Some slight differences between Lower and Upper Carboniferous specimens have been noted regarding secondary xylem, cortical structure, ligule pit depth and leaf anatomy. Highly dichotomized deciduous lateral branch systems were borne on the main trunk of *Paralycopodites*. The trunk and deciduous lateral branches have many distinct attributes and they are described separately where necessary.

Stelar tissues—*Paralycopodites brevifolius* is siphonostelic except in the distalmost branches of lateral branch systems (Fig. 1) and presumably at the trunk base. Maximum stelar diameters in the trunk are 2.5–3.0 cm (Fig. 5), with the largest illustrated by Williamson (1872a, fig. 16). The smallest stele in a trunk is 0.9 cm diam. The largest steles of lateral branches are 0.6–0.7 cm diam, occasionally larger; such specimens are usually flattened. The transition from siphonostele to protostele occurs in steles of 150–230 μm diam from deciduous lateral branches, and some steles are $<90 \mu\text{m}$ diam. Exarch protoxylem is distributed continuously or in separate elongate

groups (2–5 cells thick) around the smooth to slightly undulate primary xylem margin.

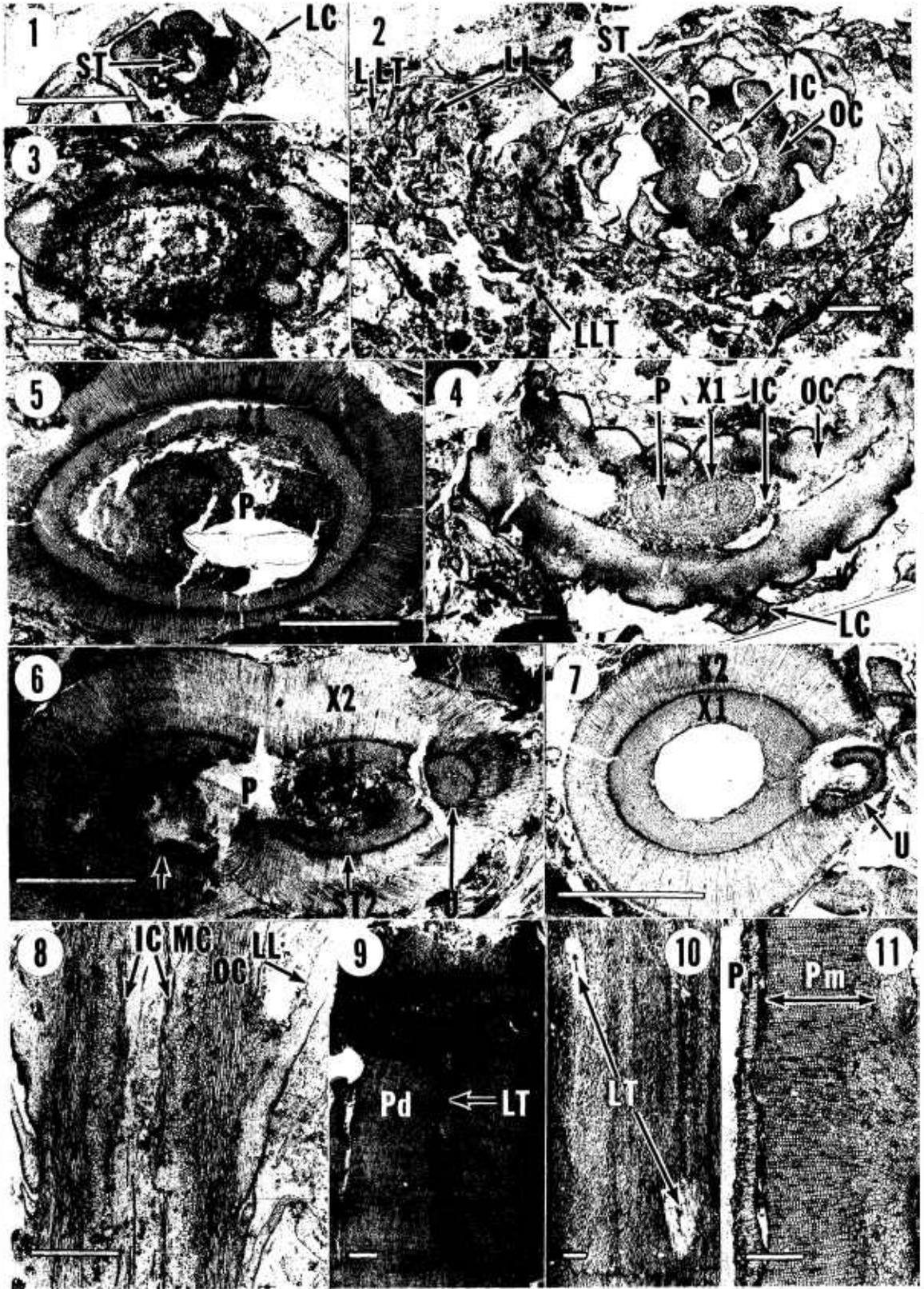
In large, woody branches of the trunk, the pith is composed of cells the same dimensions as the innermost adjacent metaxylem tracheids. Tracheids are scattered in the pith only in the vicinity of major isotomous dichotomies of the trunk (Fig. 6). The pith of lateral branch steles is a broad, sharply defined zone of parenchyma cells (Fig. 4) of which the inner two-thirds has slightly thicker walls in some specimens.

The tissue immediately outside the primary xylem is rarely preserved. It consists largely of parenchyma cells, 15 μm diam and up to 50 μm long with flat to slightly angular end walls. No sieve cells were observed.

Secondary xylem is present in all stems which have thick periderm and which are apparently part of the trunk (Fig. 5–7). Maximum wood radius observed is 2.0 cm and some branches have as little as 2–4 mm. Wood rarely occurs in lateral branches of Upper Carboniferous specimens. Some of the larger steles, 4–6 mm diam, were partially surrounded by short arcs of thin eccentric wood. Secondary xylem has been reported as a characteristic feature of small, Lower Carboniferous, *Paralycopodites brevifolius* stems (Scott, 1920; Williamson, 1895, table II). However, the original illustrations of Williamson (1872b) indicate that most small branches lacked secondary xylem, and I have not noted greater secondary xylem development in Lower Carboniferous lateral branches than in those from the Upper Carboniferous. Wood rays are narrow, generally one to two cells wide, except around leaf traces, and several to many cells high. The cells of any one ray are usually of the same

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Fig. 1–11. *Paralycopodites brevifolius*. 1. Transverse section of terminal protostelic (ST) branchlet with alate leaf bases and attached leaves (LC). Specimen 10136, slide I 14765, scale (lower left) 1 mm. 2. Transverse section of protostelic branchlet surrounded by its leaves. Leaves (LL) fusiform, becoming triangular at tip (LLT). Specimen 10172, slide I 14767, scale (lower right) 1 mm. 3. Transverse section of anisotomously dichotomized branchlet from lateral branch system. Specimen 16038, slide I 14761, scale (lower left) 1 mm. 4. Transverse section of stem from lateral branch system, lacking secondary tissues. Specimen 2199, slide I 14767, scale (lower left) 1 mm. 5. Transverse section of trunk vascular cylinder. Broad pith (P) surrounded by thick primary xylem (X1) and secondary xylem (X2). Specimen 22779, slide I 14762, scale (lower right) 1 cm. 6. Transverse section of trunk vascular cylinder near base of isotomous dichotomy; resultant steles ST1 and ST2. Right hand stele (ST2) bears a "ulodendroid" branch trace (u)—a solid tracheidal strand. Scattered tracheids occur in pith (P). Specimen 6466, slide I 14711, scale (lower left) 1 cm. 7. Transverse section of trunk vascular cylinder with medulated "ulodendroid" branch stele (u) specimen 6466, slide I 14770, scale (lower left) 1 cm. 8. Median longitudinal section of stem from deciduous lateral branch system. Cortex three zoned: inner (IC) of cylindrical cells, middle (MC) of isodiametric cells, outer (OC) of elongate cells. Leaf (LL) is attached. Specimen 10154, slide I 14763, scale (lower left) 1 mm. 9. Transverse section of homogeneous periderm (Pd) with persistent leaf trace (LT) surrounded by zone of thin-walled cells. Specimen 5409, slide I 14769, scale (lower left) 1 mm. 10. Tangential longitudinal section of periderm (Pd) with leaf traces (LT) surrounded by zones of thin-walled cells. Specimen 5409, slide I 14768, scale (lower left) 1 mm. 11. Transverse section of two zoned periderm: phellem (Pm) is much thicker than phelloderm (Pr). Specimen 6740, slide I 14773, scale (lower left) 1 mm.



shape, square to procumbent but only slightly elongate radially, and may have scalariform wall thickenings.

Cortex—Upper Carboniferous specimens of *Paralycopodites brevifolius* have a three-zoned cortex (Fig. 2, 4, 8), although neither inner nor middle cortex are usually preserved in large woody stems. The inner cortex is a narrow zone composed of cells 25–40 μm diam and up to 50 μm long, some of which have opaque contents, largely along the walls. Middle cortical cells, which are rarely preserved, are thin-walled, isodiametric, 25–80 μm diam. A sheath is apparently not formed around leaf traces in the middle cortex as is common in many other lycopod trees. The outer cortex is a relatively broad, homogeneous zone, >1.5 cm wide in some large stem specimens, and is composed of thick-walled parenchyma cells. Cell dimensions in the outer cortex vary with overall stem size, 15–100 μm diam and up to 500 μm long, with bluntly tapered ends. Outer cortical cells frequently appear to be secondarily subdivided by thin transverse walls. Toward the outer part of the cortex the cells are shorter and are nearly isodiametric in the basal part of the leaf bases.

Small stems assignable to *Paralycopodites brevifolius* from the Calciferous Sandstone Series of Pettycur have cortical zonation that is sometimes difficult to recognize. The inner cortex is a very thin, rarely preserved layer of thin-walled cells. A cavity is usually present between this zone and the homogeneous outer cortex, or between the stele and outer cortex; the cavity probably marks the site of degraded middle cortex. In slightly flattened stems, <2 mm diam, similar to that illustrated by Williamson (1872b, fig. 2), tissue zonation may be difficult to recognize due to the extreme narrowness or compression of the inner zones. This is probably the origin of reports that the cortex of Lower Carboniferous specimens is unzoned (Seward, 1910; Smith, 1962).

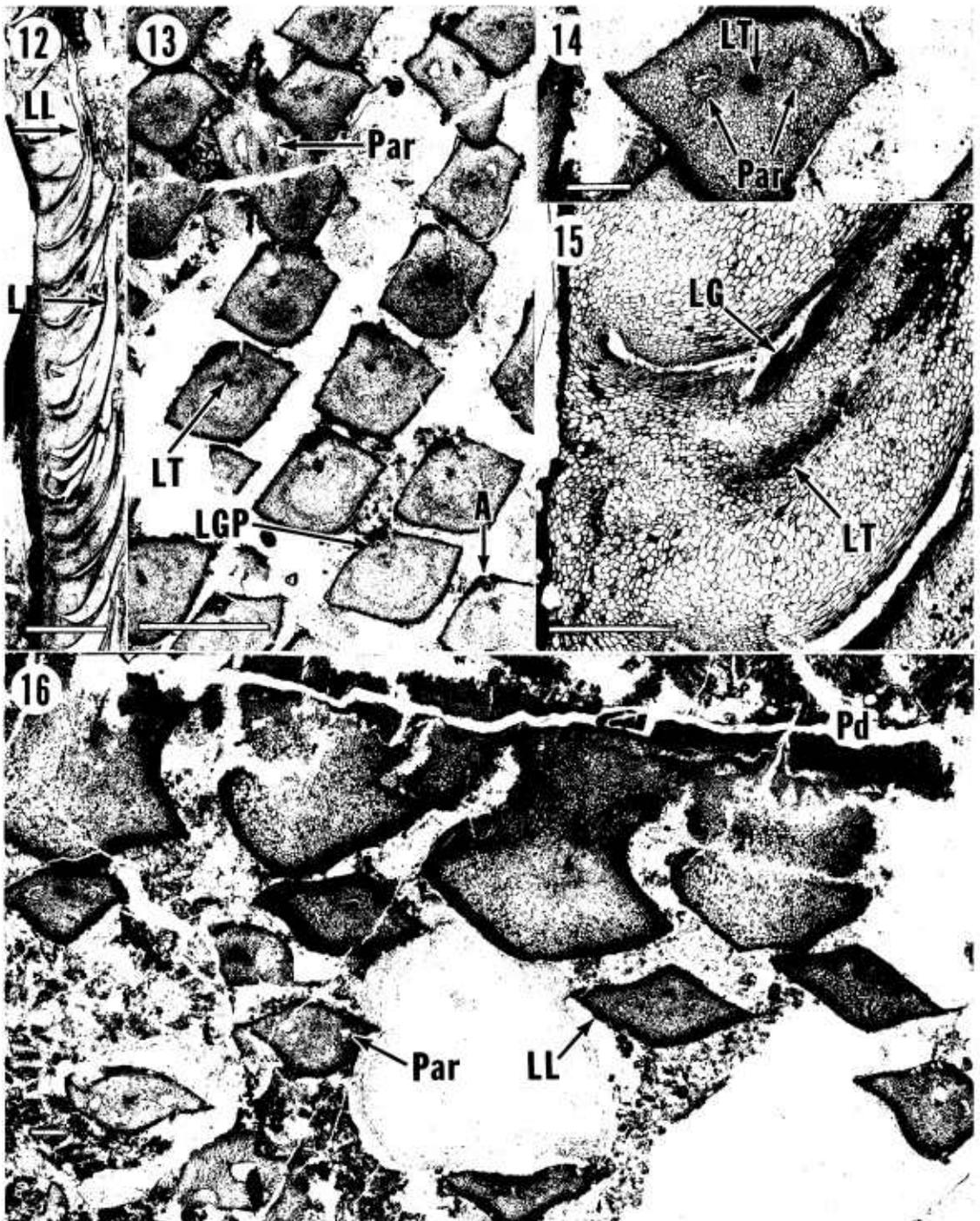
Periderm—The periderm of *Paralycopodites brevifolius* is confined usually to large diameter woody stems and is rarely present in the lateral branch systems. Periderm development began in the outer part of the outer cortex, below the leaf bases. The periderm is usually very homogeneous (Fig. 9); zonation has been recognized in only a few stems from the Sahara locality in the Herrin (No. 6) Coal Member of Illinois (Fig. 11). In most specimens a single tissue zone 2 mm to 2 cm in thickness is recognizable; it is composed of small diameter, vertically elongate cells with oval to

rectangular cross sectional outlines. There are no secretory contents, although poorly preserved material may appear to be irregularly banded by secretory cells as a result of crushing. Conspicuous leaf traces persist across the entire periderm (Fig. 9, 10), surrounded by isodiametric to slightly radially elongate cylindrical cells which may have secondary thickenings. These leaf trace zones are usually 180–400 μm diam and are identifiable in most planes of section. Leaves and/or leaf bases, often fusainized, remain attached to periderm up to 1.6 cm thick, which is often detached from the cortex.

Some well preserved specimens from the Herrin (No. 6) Coal Member of Illinois indicate that the periderm may have been two-zoned (Fig. 11). In these specimens, a thin inner zone up to 10 cells and 320 μm wide, often a mixture of secretory and nonsecretory cells, was separated frequently at irregular intervals from the main mass of homogeneous periderm. This thin inner zone may represent a phellogen that separated along the phellogen. This suggests that the largest part of the periderm was phellem and is consistent with the frequent separation of the leaf bearing periderm from the stem axis. No other specimens had any indication of a phellogen or bifacial organization of the periderm.

Leaf bases—Leaves remained permanently attached on lateral branches (Fig. 8, 12) and on some parts of the main trunk (Fig. 16) with a small amount of inter-area expansion between leaf bases. Leaf bases are rhomboidal to triangular in shape with slight lateral alations (Fig. 13, 14). The aperture of the ligule pit is located very close to the junction of stem and leaf base (Fig. 15). A keel, continuous with the abaxial side of the leaf, is present on the lower part of the leaf base. There are no plications above the pit aperture or along the keel. In tangential sections of small stems, the leaf base may appear to be vertically elongate and similar to leaf cushions of *Lepidodendron*.

The leaf bases are composed mostly of isodiametric parenchyma cells (Fig. 15). Below the epidermis is a zone of radially elongate thicker-walled cells, which is best developed below the upper epidermis and in the keel of the leaf base. Cells in the immediate vicinity of the leaf trace are radially elongate and those abaxial to the trace usually have scalariform thickenings. The leaf trace is 30–60 μm diam and is subtended by a small parichnos strand. Below the base of the ligule the parichnos strand is divided into two with one strand on each flank of the leaf trace. After the division



Figs. 12–16. *Paralycopodites brevifolius*. 12. Radial section through leaves and leaf bases showing attached leaf laminae (LL). Specimen 10136, slide I 14766, scale (bottom) 0.5 cm. 13. Oblique tangential section through leaf bases (section is most proximal to stem at base). Leaf bases have shallow ligule pits (LGP) with narrow apertures (A); leaf traces (LT) in the upper one-half of the leaf bases are flanked by large parichnos strands (Par) distal to the ligule base. Specimen 6466, slide I 14772, scale (lower left) 0.5 cm. 14. Tangential section of alate leaf base distal to ligule, with large diameter parichnos flanking leaf trace (LT). Specimen 6466, slide I 14774, scale (lower left) 1 mm. 15. Radial section of leaf base. Ligule (LG) is exerted from ligule pit above leaf trace (LT). Specimen 6466, slide I 14766, scale (lower left) 1 mm. 16. Transverse section of portion of trunk with periderm (Pd) and attached leaves (LL). Parichnos (Par) are visible in some of the leaf lamina sections. Felix Collection No. 85, scale (lower left) 1 mm.

of each parichnos strand increases, up to 700 μm (Fig. 14). Ligule pits are generally 300–800 μm deep, although Smith (1962, fig. 17) has illustrated a ligule pit 7.0 mm deep from a Lower Carboniferous specimen. The ligule pits are lined by small tabular cells continuous with the epidermis of the leaf base. Small, ovoid ligules occasionally have secretory-like contents in the upper one-half. In some specimens ligules are exerted from the ligule pits (Fig. 15) for as much as one-half of their length; this is the only occurrence of ligule exertion in the arborescent lycopods, as far as I am aware.

Leaves—The leaves of *Paralycopodites brevifolius* were described from Lower Carboniferous specimens by Graham (1935) as Type A (*Lepidodendron veltheimianum*). Leaves of Upper Carboniferous specimens have essentially the same structure and were illustrated by Morey and Morey (1977) and by Felix (1886, Plate II, fig. 3; as leaves of *Lepidodendron selaginoides*). The leaves are almost triangular in cross-sectional outline at the base and become distinctly triangular at the tip (Fig. 2, 16). The vascular bundle of the leaf is 20–50 μm diam and is surrounded by thin-walled cells and then by a narrow ring of transfusion tracheids. In the base of the leaf, large parichnos strands flank the small vascular bundle (Fig. 14, 16), but these become progressively less distinct distally and eventually cannot be recognized. A hypodermis of thick-walled elongate cells is irregularly developed, most conspicuously at the upper and lower angles of the leaf. Upper Carboniferous leaves of *Paralycopodites* differ from Type A of Graham (1935) in the distribution of the hypodermis. The hypodermis is best developed above two abaxial stomatal bands in Lower Carboniferous specimens and is more diffuse in the Upper Carboniferous leaves.

Branching—*Paralycopodites brevifolius* stem specimens are divided into a group with thick secondary tissues, rare isotomous dichotomies, and frequent anisotomous dichotomies in which small lateral steles are produced (Fig. 5–7), and a group with little or no wood and periderm and frequent anisotomous dichotomies (Fig. 1–4). The assortment of stems into two distinct groups is apparently the result of the plant's habit in which deciduous lateral branches were borne on a columnar main trunk which rarely branched isotomously. Small lateral steles of large woody specimens (Fig. 6, 7) probably represent the vascular traces to deciduous lateral branch sys-

tems. Stems of the deciduous branch systems, without secondary growth, are the most abundant shoots encountered.

Isotomously dichotomized specimens from the main stem (Fig. 6) are rare. Williamson (1872b, fig. 20) figured one specimen and a second has been found in the Herrin (No. 6) Coal Member; both have stelar diameters of about 1.0 cm. Lateral branch traces from anisotomous dichotomies appear frequently in stem segments of the trunk (Fig. 6, 7). The branch traces are initially nearly solid tracheidal strands that leave only a depression in the primary xylem of the main stele; there is no branch gap (Fig. 6, 7). In the middle cortex of the main stem the branch traces are 3.5–6.0 mm diam, have a broad pith and lack wood. There is good agreement between the size of lateral branch traces in trunk specimens and stelar dimensions of the largest woodless branches, which apparently were from the base of deciduous lateral branch systems. A branching specimen of this type from the Lower Carboniferous was figured by Scott (1920, fig. 61).

Lateral branches, with maximum stelar diameters of 6–7 mm, are frequently anisotomously branched. Branching results in stelar size diminishment, which is consistent with determinate growth in lycopod trees. Bending of both branches following dichotomy occurs only in small distal branchlets. In the lower or proximal portions of the lateral branch systems, a pseudo-monopodial main stem is developed with smaller side branches produced by anisotomous dichotomy. This pattern is maintained in all branch orders up to the most distal divisions which have more equal dichotomies (Fig. 3).

Cones—*Paralycopodites brevifolius* is consistently associated with small bisporangiate cones that probably were borne at the tips of lateral branches. No organic attachment of cones to *Paralycopodites* has been established. The associated cones are megasporangiate below, with 15–30 megaspores per sporangium, and microsporangiate above, 1–2 cm diam and up to 12 cm long. The association of bisporangiate cones with *Paralycopodites* was first noted by Williamson (1872b, 1893), and the cones subsequently have been described as: *Lepidostrobus scottii* Jongmans (1930) from the Lower Carboniferous, *L. diversus* Felix (1954) from the Middle Pennsylvanian, and *L. schopfii* Brack (1970) from the Copland (Taylor) coal of the lower Middle Pennsylvanian. The cones are similar and their structure is well known. Gordon (1910), Brack (1970), Brack-Hanes (1978), and Galtier (1970)

have described female gametophytes with archegonia from the cones.

DISCUSSION—*Paralycopodites brevifolius* was originally described as a species of *Lepidophloios* by Williamson (1872b), but many subsequent investigators identified *Paralycopodites brevifolius* with *Lepidodendron veltheimii* (*veltheimianum*) (Seward, 1910; Scott, 1920; Hirmer, 1927). They essentially followed the identification of Dawson (note to Williamson, 1872b, p. 310). The accuracy of this identification was doubted (Watson, 1907; Jongmans, 1930), but the tentative inclusion of this distinct type of plant in *Lepidodendron* reinforced the idea that it was an intermediate between *Lepidodendron* and *Lepidophloios* (Smith, 1962). The subsequent description of *Paralycopodites* by Morey and Morey (1977), without recognition of its affinities with *Lepidodendron brevifolium* of previous authors, was largely a result of the habit of the plant. Isolated deciduous lateral branches usually lack secondary tissues and thus appear superficially different from the woody trunk specimens with thick periderm.

Paralycopodites appears to be most similar in external form to *Ulodendron* Lindley and Hutton, sensu Thomas. Thomas (1967) considered that some species of *Ulodendron* (an often misused generic name) formed a natural genus—as opposed to a form genus for compressions of lycopod stems with vertical rows of oval scars. *Ulodendron*, as defined by Thomas (1967), has persistent leaves, shallow ligule pits and somewhat rhomboidal to alate leaf bases as in *Paralycopodites*. *Ulodendron* differs in the presence of inter-areas with potential for greater expansion between leaf bases than in *Paralycopodites*. Both genera produced deciduous lateral branches, but the anatomy of *Ulodendron* is not known. It seems likely that we are dealing with the same kinds of plants preserved differently, but we cannot yet establish that to a point of synonymy.

The segregation of *Paralycopodites* from *Lepidodendron* is one of several steps needed to clarify natural morphological limits to the genera of Paleozoic lycopods. *Paralycopodites* is distinct from *Lepidodendron* and *Lepidophloios* and is the only arborescent lycopod of coal swamps consistently associated with small, bisporangiate cones. *Paralycopodites* can be recognized on the basis of a suite of distinctive morphological characteristics. The stems have a well-developed siphonostele, very similar in gross form to that of *Lepidophloios*, but without a corona or any form of marginal modification of the primary xylem.

The periderm is unique among arborescent lycopods in three characteristics: 1) its homogeneity and total lack of any specialized or secretory cells, 2) the presence of persistent leaf traces surrounded by a zone of specialized cells, and 3) the possibly massive phellem and thin phellogen. The cortex is also distinctive in the thin middle cortex without ensheathed leaf traces and the massive outer cortex without sclerotic or secretory cells. The outer cortex of *Lepidophloios* stems is also massive but the cortical cells are isodiametric rather than vertically elongate. The persistent nature of the leaves in *Paralycopodites* is a unique feature among the arborescent lycopods, particularly in combination with the narrow shallow ligule pits of the alate leaf bases. Other lycopods, including some species of *Lepidodendron*, produced deciduous lateral branches; however, *Paralycopodites* is the only form to have a massive branch trace without an associated gap.

Paralycopodites brevifolius is suspected to be the parent plant of bisporangiate cones of the *Lepidostrobus*-type with many megaspores per sporangium. There is considerable evidence that some species of *Lepidodendron* produced monosporangiate cones of the *Achlamydocarpon*-type, with one functional megaspore per sporangium (Leisman and Rivers, 1974; DiMichele, 1979b). With the known types of cones for other arborescent lycopod genera, such as *Mazocarpon* from *Sigillaria* (Benson, 1918; Schopf, 1941), and *Lepidocarpon-Lepidostrobus oldhamius* from *Lepidophloios* (Schopf, 1941; Felix, 1954; Balbach, 1967; Phillips, 1979), it appears that genera based on vegetative remains are becoming sorted out into assemblages with comparably distinct types of cones. However, it is not inferred that all bisporangiate *Lepidostrobus* cones are likely to belong to *Paralycopodites*.

Stratigraphic range and evolution—*Paralycopodites brevifolius* is the only species of the genus presently recognizable on the basis of vegetative morphology. It extends stratigraphically from the Visean, in the Lower Carboniferous, to the end of the Westphalian D (Middle Pennsylvanian), in the Upper Carboniferous. Such a long stratigraphic range for a single species may be a result of extreme morphological conservatism. However, three species of morphologically similar bisporangiate cones have been recognized in association with *P. brevifolius*: *Lepidostrobus scottii* (Jongmans, 1930) from the Lower Carboniferous, *L. schopfi* (Brack, 1970) from the lower Middle Pennsylvanian of the United States,

and *L. diversus* (Felix, 1954) from the Middle Pennsylvanian of the United States. While there are only minor differences among these cones and no morphological trends are apparent, each type appears to be a distinct species. If the cones indicate the existence of several distinct species, and do belong to *Paralycopodites*, then the genus is still quite conservative morphologically, particularly in the Upper Carboniferous where two species of *Lepidostrobus* cones are associated with the same basic vegetative form.

There are no intermediates between *Paralycopodites* and the other genera of heterosporous, ligulate lycopods that also first appear in the Lower Carboniferous, *Lepidodendron*, *Lepidophloios* and possibly *Sigillaria*. The long stratigraphic range with little morphological variability is a pattern found in other genera of Carboniferous arborescent lycopods but *Paralycopodites* is an extreme example. Evolutionary-stratigraphic patterns of this nature have been recognized for many years and have consistently been regarded as due to an incomplete fossil record in which evolutionary intermediates were not preserved. These patterns have led to assertions of the punctuated equilibria hypothesis (Eldredge and Gould, 1972; Gould and Eldredge, 1977), as an alternative to phyletic gradualism which is built upon the tenets of population biology. Punctuated equilibria has found support in studies of animal evolution (Stanley, 1978; Fagerstrom, 1978), although the mechanisms are somewhat speculative at present. It appears that the origin of many major lycopod genera, which later dominated much of the Carboniferous, occurred rapidly during the Visean. This was followed by a long period of ecological adjustment, probably with gradualistic morphological changes in some taxa, which led to an array of species. In the lycopods these processes are all within very definable generic limits. The appearance and subsequent evolution of *Paralycopodites* lend support to the hypothesis of punctuated equilibria.

Paleoecology—*Paralycopodites* occurs in the following Pennsylvanian age coals: Katharina Seam of West Germany, Copland (Taylor) coal of eastern Kentucky, Secor Coal Member of Oklahoma, Harrisburg-Springfield (No. 5) and Herrin (No. 6) Coal Members of the Illinois basin. In the Katharina Seam and Copland coal, *P. brevifolius* may have been the most abundant lycopod in the swamp with smaller amounts of *Lepidophloios* and *Lepidodendron vasculare*. Flores (1978) has characterized the Copland (Taylor) coal as a lower deltaic plain deposit. The Katharina Seam was

deposited in a paralic foredeep that was apparently subject to relatively rapid and somewhat irregular subsidence as indicated by the abundance of vitrain and clastic partings (Bless, 1969; Mackowsky, 1968; Teichmüller, 1952). The Secor Coal is confined to the Arkoma Basin of southern Oklahoma and is part of a dominantly clastic interval, subject to more rapid subsidence than in adjoining shelf areas (Branson, 1962). The environment of deposition has not been investigated in detail but, floristically, the coal is more like the Katharina and Copland Coals than coals of the Carbondale Formation. The Harrisburg-Springfield (No. 5) and Herrin (No. 6) Coal Members were deposited on broad deltaic platforms either as low-lying coastal or upper deltaic plain swamps (Wanless, Baroffio and Trescott, 1969). *Paralycopodites* was not a common component of the vegetation that characterized these extensive swamps, which were dominated by other lycopods, such as *Lepidophloios* and contained much smaller numbers of ferns, pteridosperms and sphenopsids (Phillips, Kunz and Mickish, 1977). Analyses of vertical profiles of coal balls from the Herrin (No. 6) Coal Member, according to the techniques of Phillips et al. (1977), indicate that *Paralycopodites brevifolius* was confined to one or few zones of the peat profiles. Within these zones ferns and pteridosperms were often quite abundant and the major lycopods, *Lepidophloios* and *Lepidodendron scleroticum*, were usually rare.

Cordaites are rare in the Harrisburg-Springfield (No. 5) and Herrin (No. 6) Coal Members and are common in the Katharina Seam, Copland (Taylor) coal and Secor Coal, but their spatial relationships to *Paralycopodites* are not known. In the absence of coalball vertical profiles from the Katharina Seam and Copland (Taylor) coal, it is difficult to assess community relationships of plants in those swamps. *Paralycopodites* is not known from *Lepidodendron*-dominated swamps, such as coals of the Indiana Staunton Formation, the Colchester (No. 2) and Summum (No. 4) Coal Members of Illinois, in all of which cordaites are subdominant.

The pattern of occurrences of *Paralycopodites* suggests a few aspects of its requirements for growth and reproduction. As in *Sigillaria*, which was also relatively rare in Middle Pennsylvanian coal swamps, *Paralycopodites* was free-sporing and produced even more megaspores per sporangium. Such megaspores were not adapted for flotation as were the megasporophyll units of *Lepidocarpon* or *Achlamydocarpon*, the disseminules of the most common swamp lycopods (Phillips, 1979). The

production of abundant cones at the tips of deciduous lateral branches may have resulted in nearly sustained reproduction upon reaching sexual maturity. However, the abundance of *Paralycopodites* in only a few coals and its restricted occurrence in others is not consistent with its large reproductive output. It may have been adapted to relatively rapid changes in depositional environment, particularly irregular exposure of the substratum. In such cases the inferred continuous cone production would have allowed relatively rapid occupation of exposed areas of peat surface by *Paralycopodites* sporelings. Such areas may have been less accessible to *Lepidophloios* (*Lepidocarpon*) or *Lepidodendron* (*Achlamydocarpon*) which were more dependent on water for dispersal. The lower deltaic plain setting of the Copland (Taylor) coal (Flores, 1978) and the irregular conditions of swamp development in the Rhur apparently provided such a locally variable setting in which *Paralycopodites* could reach its maximum abundance.

This does not, of course, adequately explain the known distribution of *Paralycopodites* in relation to other lycopods. Other swamps, possibly of lower deltaic plain origin, as in the Indiana Staunton Formation (=upper Spoon Formation of Illinois), were dominated by *Lepidodendron vasculare*. There is no evidence of *Paralycopodites* in some coals with abundant *Lepidophloios*, such as the Baker Coal Member of Kentucky. *Paralycopodites* evidently did not survive the transition to the late Pennsylvanian in coal swamps of the mid-continent United States. This is a pattern most similar to that of *Lepidodendron* and *Lepidophloios* (Phillips, Peppers, Avcin and Laughnan, 1974), and unlike that of *Sigillaria* and *Polysporia*. Like *Paralycopodites*, *Sigillaria* and *Polysporia* produced numerous megaspores without the specialized adaptations for flotation found in *Achlamydocarpon* and *Lepidocarpon*, and were rare in Middle Pennsylvanian swamps. However, unlike *Paralycopodites*, *Sigillaria* and *Polysporia* survived into the late Pennsylvanian.

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