

**GROWTH HABIT OF THE LATE PALEOZOIC RHIZOMORPHIC
 TREE-LYCOPSISID FAMILY DIAPHORODENDRACEAE: PHYLOGENETIC,
 EVOLUTIONARY, AND PALEOECOLOGICAL SIGNIFICANCE¹**

WILLIAM A. DiMICHELE², SCOTT D. ELRICK³, AND RICHARD M. BATEMAN^{4,5}

²Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC20560, USA; ³Coal Section, Illinois Geological Survey, University of Illinois, 615 E Peabody, Champaign, IL61820, USA; and ⁴Jodrell Laboratory, Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3DS, UK

- *Premise of the study:* Rhizomorphic lycopsids evolved the tree habit independently of all other land plants. Newly discovered specimens allow radical revision of our understanding of the growth architectures of the extinct Paleozoic sister-genera *Synchysidendron* and *Diaphorodendron*.
- *Methods:* Detailed descriptions of six remarkable adpression specimens from the Pennsylvanian of the USA and three casts from the late Mississippian of Scotland are used to revise and reanalyze a previously published morphological cladistic matrix and to reinterpret their remarkable growth forms.
- *Key results:* Contrary to previous assertions, *Synchysidendron* resembled *Diaphorodendron* in having a distinct and relatively complex growth habit that emphasized serially homologous, closely spaced, deciduous lateral branches at the expense of reduced monocarpic crown branches. Lateral branches originated through several strongly anisotomous dichotomies before producing during extended periods large numbers of *Achlamydocarpon* strobili. The comparatively large diameter of abscission scars remaining on the main trunk and the emergence of branches above the horizontal plane suggest that the lateral branch systems were robust. Lateral branches were borne in two opposite rows on the main trunk and continued upward into an isotomously branched, determinate crown; their striking distichous arrangement caused preferred orientation of fallen trunks on bedding planes.
- *Conclusions:* This discovery identifies the plagiotropic growth habit, dominated by serial lateral branches, as ubiquitous in the Diaphorodendraceae and also as unequivocally primitive within Isoetales s.l., a conclusion supported by both the revised morphological cladistic analysis and relative first appearances of taxa in the fossil record. Previously assumed complete homology between crown branching in Lepidodendraceae and that of all earlier-divergent genera requires reassessment. Saltational phenotypic transitions via modification of key developmental switches remains the most credible explanation for architectural evolution in the group. The resulting architecture allowed Diaphorodendraceae to co-dominate disturbed, clastic, equatorial wetlands from the Asbian to the Early Permian.

Key words: arborescent lycopsids; *Diaphorodendron*; evolutionary-developmental change; growth architecture; Isoetales s.l.; lateral branching; lycophyte; pedomorphosis; Pennsylvanian; saltation; Scotland; *Synchysidendron*; USA.

The modern lycopsids are a depauperate remnant of a group that was once much more morphologically and taxonomically diverse, dominating vast portions of the Earth's terrestrial landscape during the late Paleozoic (Phillips and DiMichele, 1992; Pigg, 2001). This paper considers the most derived lycopsid clade, the Isoetales, which included large trees that originated in the late Devonian and populated extensive wetlands of the

Carboniferous and Permian. For long one of the most charismatic subjects for paleobotanical study, these trees increased in neobotanical relevance with the phylogenetic confirmation that that they represent an origin of arboreous (tree-sized) growth that is independent of the euphyllophyte lineage that encompasses all modern trees (e.g., Phillips and DiMichele, 1992; Bateman, 1994; Sanders et al., 2011). Thus, the rhizomorphic lycopsids constitute a crucial case-study in the parallel origins of such fundamental features as bipolar growth, secondary thickening, periderm formation, and the many physiological traits needed to produce and maintain a large body size.

Unsurprisingly, these independently evolved trees share a morphology that appears unintuitive to the neobotanical eye. Isoetaleans are characterized by distinctive “stigmarian” rooting organs, best termed rhizomorphs (Rothwell, 1984; Bateman et al., 1992; DiMichele and Bateman, 1996a; Pigg, 2001)—organs homologous with the lobed or cormose bases of the more typically isoetoid group(s), which also were prominent in Paleozoic landscapes (DiMichele et al., 1979; Jennings et al., 1983; Pigg and Rothwell, 1983; Bateman and DiMichele, 1991; Bateman, 1992, 1994; Chitale and Pigg, 1996; Cressler and Pfefferkorn, 2005). In addition, the strongly determinate, modular (arguably herb-like) growth of the rhizomorphic lycopsids has long made

¹Manuscript received 5 December 2012; revision accepted 11 April 2013.

John Nelson and Howard Falcon-Lang collaborated in the Illinois Basin fieldwork on which this research is partially based. With regard to the Scottish material, we thank Ian Rolfe and the late Charles Waterston for providing background information into Thomas Allan's Craighleith specimen, Norman Butcher for accompanying R.M.B. to the remains of the Craighleith exposure, and Colin Beveridge for providing the Starcross Park specimen. Jonathon Wingerath and Dan Chaney generously assisted with preparation of the Laco and Iowa specimens. National Museum of Natural History Photographic Services provided images of Specimen 2. Paula Rudall, Gar Rothwell, and an anonymous reviewer kindly critiqued the manuscript. W.A.D. and R.M.B. contributed equally to the work.

⁵Author for correspondence (e-mail: r.bateman@kew.org)

doi:10.3732/ajb.1200623

them a favored subject of ontogenetic inference among paleobotanists (e.g., Eggert, 1961; Rothwell, 1984; Bateman, 1992, 1994; Sanders et al., 2011).

Although the arborescent rhizomorphic forms constitute several genera, all are based on a unique common ground plan: (1) bipolar development, (2) determinate aerial and subterranean axes, (3) differentiation between a main aerial axis and strobilus-bearing lateral aerial axes, (4) main aerial and subterranean axes that divided in broadly isotomous fashion, the main aerial axes only dividing during the final phases of determinate growth (at least, in tree-sized species) to form a crown, (5) strobilus-bearing lateral axes generated via strongly anisotomous divisions, and (6) some or all of the lateral branches (reduced to a single branch/peduncle in *Sigillaria*) terminating in strobili. It is important to distinguish within this body-plan two distinct branching systems: the crown branches, and the lateral branches that are the focus of this paper. The lateral, strobilus-bearing axes were derived from strongly anisotomous divisions of the main stem (which might consequently be termed “pseudomonopodial”) and were caducous (deciduous), dropping from the main stems as apical growth proceeded upward. Developmental studies of these plants strongly suggest that, in some of the more derived forms, the lateral branches were reduced to peduncles only, bearing either single or paired strobili (for discussion regarding the developmental aspects of these extinct Paleozoic lepidodendrids see Bateman and DiMichele, 1991; Bateman, 1994; Wang et al., 2003; Opluštil, 2010).

In this paper, we focus on one particular genus of rhizomorphic arborescent lycopsids, *Synchysidendron* DiMichele & R.M. Bateman (1993). Improperly typified in the original detailed description (DiMichele and Bateman, 1992), the valid authority for this genus name is the 1993 publication by the same authors. The plant was initially characterized as *Lepidodendron dicentricum* (Felix) DiMichele (1979a) from petrifications—specifically, from stems permineralized in coal-balls—thereby initiating a search for the most comparable organ-species named among the archetypal “tire-track” adpression fossils (a collective term for compressions, which retain original organic material, plus impressions, which do not; Shute and Cleal, 1987). Wnuk (1985) subsequently attributed adpressions from Pennsylvania, United States to this form as *Lepidodendron bretonense* Bell. However, B. Thomas and N. Jud (personal communication, 2012) suggest that the correct name is *Lepidodendron andrewsii* Lesquereux, and that this species may be the most common adpression form of *Synchysidendron* in the Middle Pennsylvanian of Euramerica. Other species have been recognized in the Pennsylvanian of China (Cleal and Wang, 2002), where the genus persisted until near the end of the Permian (Wang and Chen, 2001).

Preamble: Correlating the recircumscribed genera across preservation states—The genera *Synchysidendron* and *Diaphorodendron* DiMichele were circumscribed primarily on the basis of character-rich anatomically preserved material, whereas the new specimens described here lack anatomical preservation; those from the United States are two-dimensional adpressions, whereas those from Scotland are three-dimensional casts. Traditionally, such specimens are taxonomically differentiated primarily according to the “topography” of their leaf cushions, a task made more difficult by the tendency of these trees to differ in degrees of decortication (e.g., Taylor et al., 2009, p. 287; Gensel and Pigg, 2010). Such typological characterization led to most specimens being ascribed to *Lepidodendron* Sternberg. This narrowly based classification raises the crucial question of

whether these adpression fossils can be ascribed to genera segregated more recently from *Lepidodendron* such as *Synchysidendron* and *Diaphorodendron* DiMichele (1985). In characterizing the anatomy of lepidodendrids from the Early and Middle Pennsylvanian of Euramerica, we (DiMichele, 1979a, 1981, 1983, 1985; Bateman and DiMichele, 1991; Bateman et al., 1992; DiMichele and Bateman, 1992, 1996a) critically re-examined the concept of *Lepidodendron* as it had come to be applied to both anatomically preserved petrification and adpression fossils. The overriding feature of importance in the traditional circumscription is the outline shape of the leaf cushion, which is required to be higher than wide relative to the long axis of the branch. Within this basic cushion shape, additional characters permitted segregation of other genera of adpression fossils, leaving *Lepidodendron* as a default should such characteristics be absent or indiscernible. Lesser features, such as dorsal and/or ventral keels and field lines, permitted delimitation of organ-species within what remained of the organ-genus *Lepidodendron*.

However, anatomical evidence began to bring this broad *Lepidodendron* construct into question. Typical “*Lepidodendron*” leaf cushions were found to be characteristic of several distinct anatomical forms, each correlated with strongly contrasting reproductive structures. Nonetheless, subtle features of the leaf cushions other than height to width ratio, such as the presence of infrafoliar parichnos, allowed true *Lepidodendron* sensu DiMichele (1983) to be distinguished from the other forms (DiMichele, 1985; DiMichele and Bateman, 1992). In this way, the linkage of anatomical features to leaf-cushion characters allowed adpression genera to be circumscribed using a larger underlying suite of characters. Finally, a morphological phylogenetic analysis of the best-known arborescent lycopsid taxa (Bateman et al., 1992), conducted following their reconstruction as conceptual whole-plants (sensu Bateman and Hilton, 2009), revealed clearly that the simple, almost ubiquitously preserved feature of a higher-than-wide leaf cushion is a plesiomorphic (primitive or ancestral) characteristic. Present in the shared ancestor of at least most of the members of the rhizomorphic lycopsid clade, this character state is therefore of limited utility for circumscribing whole-plant genera. Nonetheless, it graphically illustrates the value of reciprocal illumination between fossils preserved in contrasting states.

MATERIALS AND METHODS

Novel specimens—Reconsideration of the growth habit of *Synchysidendron* was made possible by the authors’ discovery of eight previously undescribed specimens of *Synchysidendron* and *Diaphorodendron*—six from the Pennsylvanian of the USA and two from the late Mississippian of Scotland. Five of the American specimens are from the Illinois Basin. Three were discovered in active coal mines in Illinois, two in situ in underground mines and the other in the spoil rock of a surface mine. Two additional specimens were found above a coal bed in Iowa, at the margin of the basin. The sixth specimen was collected in the late 19th century from a coal mine in the Illinois Basin and was refound in the collections of the National Museum of Natural History, Washington DC. The two Scottish specimens, both originating from the Edinburgh region, were received by R.M.B. during the brief period of his employment as resident paleobotanist at the Royal Museum of Scotland, Edinburgh. A further specimen from Scotland, described briefly and obscurely by Allan (1823) but since overlooked, is also considered here in greater detail.

Specimen 1 (Figs. 1–3), a *Synchysidendron*, was located in the American Coal Company, New Future Mine (NFM) in southern Illinois, in the Dykersburg Shale roof of the Springfield (No. 5) Coal, Carbondale Formation, which is late Desmoinesian in age, equivalent to the late Asturian or early Cantabrian in western European terminology and the late Moscovian in international terminology (Ogg et al., 2008). The fossil consisted of a large tree trunk, forked in its

upper regions, lying prostrate along the axis of a mine tunnel; the enclosing Dykersburg Shale was deposited in a tidal mudflat that formed as sea-level rose and transgressed the peat swamp during the earliest phases of an interglacial interval. The trunk was surrounded by many smaller branches, which we interpret as the remains of deciduous lateral branch systems and associated strobili. Other plants fossilized nearby were mainly stems and foliage of the medullosan pteridosperms *Neuropteris flexuosa* and *Macroneuropteris scheuchzeri*, with smaller amounts of the ground-cover plant *Sphenophyllum emarginatum*, plus calamitalean stems and associated foliage, *Annularia spinulosa*. Samples of this lycopsid specimen could not be collected for safety reasons; therefore, the material is represented only by photographs taken in the mine combined with measurements made at the time of discovery.

Specimen 2 (Figs. 4, 5) is a large trunk of *Synchysidendron* that has been divided into four sections, each embedded in a separate plaster slab 215 cm long by 41 cm wide and encased in a wooden box, that have long been housed in the National Museum of Natural History as part of the Lacoë Collection (LC). Collected prior to 1895 (the date when R. D. Lacoë donated his collection to the U. S. National Museum), the specimen was entered into the NMNH catalogue as USNM 7304 on 20 December 1899. It was collected in the vicinity of Morris, in Grundy County, Illinois, an area where the Colchester (No. 2) Coal was extensively mined underground during the late 1800s. The roof shale of this coal, the Francis Creek Shale, is the source of the classic Mazon Creek flora and fauna, and is of Middle Pennsylvanian, Desmoinesian, age.

If placed within the confines of classifications developed for the addressed preservation state, both these American specimens would be assigned to *Lepidodendron andrewsii* Lesquereux f.

Specimen 3 (Fig. 6) is a *Synchysidendron* that is believed to have originated from Craighleith Quarry, located in the northwest suburbs of Edinburgh, Scotland. It is preserved in an elongate block of well-consolidated, orange-yellow medium sandstone 46 cm long, 18 cm wide, and 14 cm in its shortest (stratigraphically vertical) dimension. The flattest surface of the block bears very distinctive bioturbation structures that are consistent with known plant-bearing horizons in the middle of the remaining exposure at the quarry, which was examined by R.M.B. and Norman Butcher and logged by the latter in May 1995. Sadly, this pit—paleobotanically most famous for having yielded a log-jam of several large casts of the arboreal pteridosperm *Pitus withami* (Witham, 1833; Long, 1979)—was largely infilled during the 20th century and now contains a supermarket.

Specimen 4 (Fig. 7a) emerged from obscurity when Ian Rolfe (personal communication, 1995) drew R.M.B.'s attention to a much earlier discovery, reputedly from the same quarry, of a lycopsid axis similar to Specimen 3 but bearing four larger leaf scars. Found by Thomas Allan, this specimen was donated to the Royal Museum of Scotland in June 1820 as a putative palm fossil (Allan, 1823). Fortunately, Allan provided an exceptional wood-cut plate of the fossil, a *Synchysidendron*, which is here treated as Specimen 4. Allan (1823) also reported the existence of a further similar specimen that bore five branch scars comparable in size to those of Specimen 3 (ca 30 mm in diameter); it was found in a quarry that penetrated the same Craighleith Sandstone but was located in the southeast suburbs of Edinburgh, near Dalkeith (Millar, 1827). All three of these Edinburgh specimens appear to be large, elongate portions of bark that are thought to have been stripped longitudinally from their parent stems and transported prior to fossilization in the Craighleith Sandstone, which is estimated to be of late Visean (putatively Asbian) age.

Specimen 5 (Fig. 7b–d) is a *Synchysidendron* trunk that was donated by Colin Beveridge to R.M.B. during his field visit to the source locality at Starlaw Park (formerly Tailend Farm) in Livingston, West Lothian, ca 20 km west of Edinburgh, in February 1996. It was severed using a portable rock saw from among a fairly well-preserved in situ forest of several rooted stumps reputedly of late Visean (Asbian; ca 340 Ma) age. The excised block is 35 cm long and consists entirely of a cylindrical pith cast composed of fairly coarse, pale yellow sandstone with some coalified organic matter preserved in the outer surface for about half of its circumference, delimiting two lateral branch scars and many poorly preserved leaf cushions.

Specimens 6 and 7 (Figs. 8, 9) are trunk segments of *Diaphorodendron* collected near Pella, southeastern Iowa. They are illustrated and discussed here for comparative purposes. Both are from a rhythmically laminated fine sandstone deposited about 1 m above the Black Oak coal. One of the oldest coals in this area of Iowa (Ravn, 1986), the Black Oak lies close above the Mississippian-Pennsylvanian unconformity surface. In this far northwestern region of the Illinois Basin, deposition on the unconformity surface was delayed until near the Atokan-Desmoinesian (approximately the Bolsavian-Asturian, middle Moscovian) boundary. The plant remains present in this deposit include some very large lycopsid trunks and sections of tree crowns that appear to have been killed catastrophically. Consequently, they have certain features, such as attached

leaves and possibly attached lateral branches, that set them apart from the other specimens reported in this study. Specimen 6 consists of two sections of the same trunk, both catalogued as USNM 528668. Specimen 7 resides in the collections of the University of Iowa and is catalogued as SUI 119929. These specimens are here designated Pella 1 and Pella 2, respectively.

Specimen 8 (Fig. 10a) is of indeterminate affinity, though its gross morphology suggests that it is assignable to Diaphorodendraceae. The specimen was a wide but rather short trunk segment preserved in rhythmically laminated siltstone to fine sandstone from above the Murphysboro Coal, of Middle Pennsylvanian, early Desmoinesian age (early Asturian, middle Moscovian). The trunk was located in the now-reclaimed Creek Paum surface mine in Jackson County, southern Illinois. Because of its size and the physical conditions under which it was found, the “specimen” could not be collected; it is therefore represented here by a photograph only.

Specimen 9 (Fig. 10b), also uncollected and so represented here only by a photograph, similarly cannot be attributed to any greater taxonomic resolution than family Diaphorodendraceae. The specimen occurred in a gray siltstone in the roof of an adit at the Millennium mine in southern Illinois, in the Dykersburg Shale roof of the Springfield Coal, Carbonade Formation, of late Desmoinesian age. Retaining some organic material, this putative partial stem exhibits a single row of 10 branch scars.

Phylogenetic reconstruction—The present analysis was based on the morphological cladistic data matrix of Bateman et al. (1992). This study scored 16 reconstructed whole-plant species of 10 genera: the large-bodied trees *Paralycopodites* Morey & Morey, *Sigillaria* Brongniart, *Diaphorodendron*, *Synchysidendron*, *Lepidodendron*, and *Lepidophloios* Sternberg, and the smaller-bodied pseudoherbs/shrubs *Oxroadia* Alvin, *Paurodendron* Fry, *Hizemodendron* R.M. Bateman & DiMichele, and *Chaloneria* Pigg & Rothwell. The conceptual whole-plant species were coded for 115 bistate characters (80 phylogenetically informative), yielding a primary matrix that contained only 5% missing values. Ten of these characters (nine parsimony-informative, though two autapomorphic at the genus level) described plant architecture.

Three of these nine informative architectural characters were recoded for *Synchysidendron* in the current study, such that they mirrored scoring of equivalent characters for *Diaphorodendron*: C3, trunk frequently dichotomous [0] vs dichotomies infrequent or absent [1]; C6, lateral branches borne on the crown [0] vs on the trunk [1]; C7, cones per lateral branch one [0] vs more than one [1]. For each of these three bistate characters, the coding for *Synchysidendron* species was revised from 0 to 1 (for details of character scoring and the original matrix see Bateman et al., 1992; Bateman, 1994). The resulting lightly revised matrix was subjected to a branch-and-bound search algorithm to obtain all most-parsimonious trees, and the preferred most-parsimonious tree was presented using both the Acctran and Deltran optimization algorithms of the program PAUP* version 4.0b10 (Swofford, 2003). To maintain consistency with previous analyses of these taxa, trees were rooted using a hypothetical ancestor that closely resembled *Oxroadia gracilis* Alvin emend. R.M. Bateman (Bateman, 1992). Statistical robustness of nodes was assessed via 1000 full heuristic bootstrap replicates.

RESULTS

Description: Specimen 1 (NFM)—The main trunk of the NFM aggregate specimen exceeded 10 m in exposed length, which included neither the base of the plant nor the tips of the crown branches (Fig. 1). The main trunk was ca 50 cm in diameter and showed little detectable taper throughout its preserved length (Fig. 1a). The primary dichotomy of the stem apex was preserved; the derivative branches measured 30 cm in diameter but tapered to 25 cm in diameter without undergoing further branching (Fig. 1b). The diameter of the unbranched stem immediately below the dichotomy could not be measured accurately because it was obscured by roof shale and a square roof bolt; we estimated it to exceed 37 cm.

Two opposite rows of “ulodendroid” branch scars extend along the entire length of the trunk (Fig. 1a) and continue throughout the preserved portions of the crown branches (Fig. 1b). Although only one row could be seen in most parts of the specimen, differential exposure of parts of the trunk was

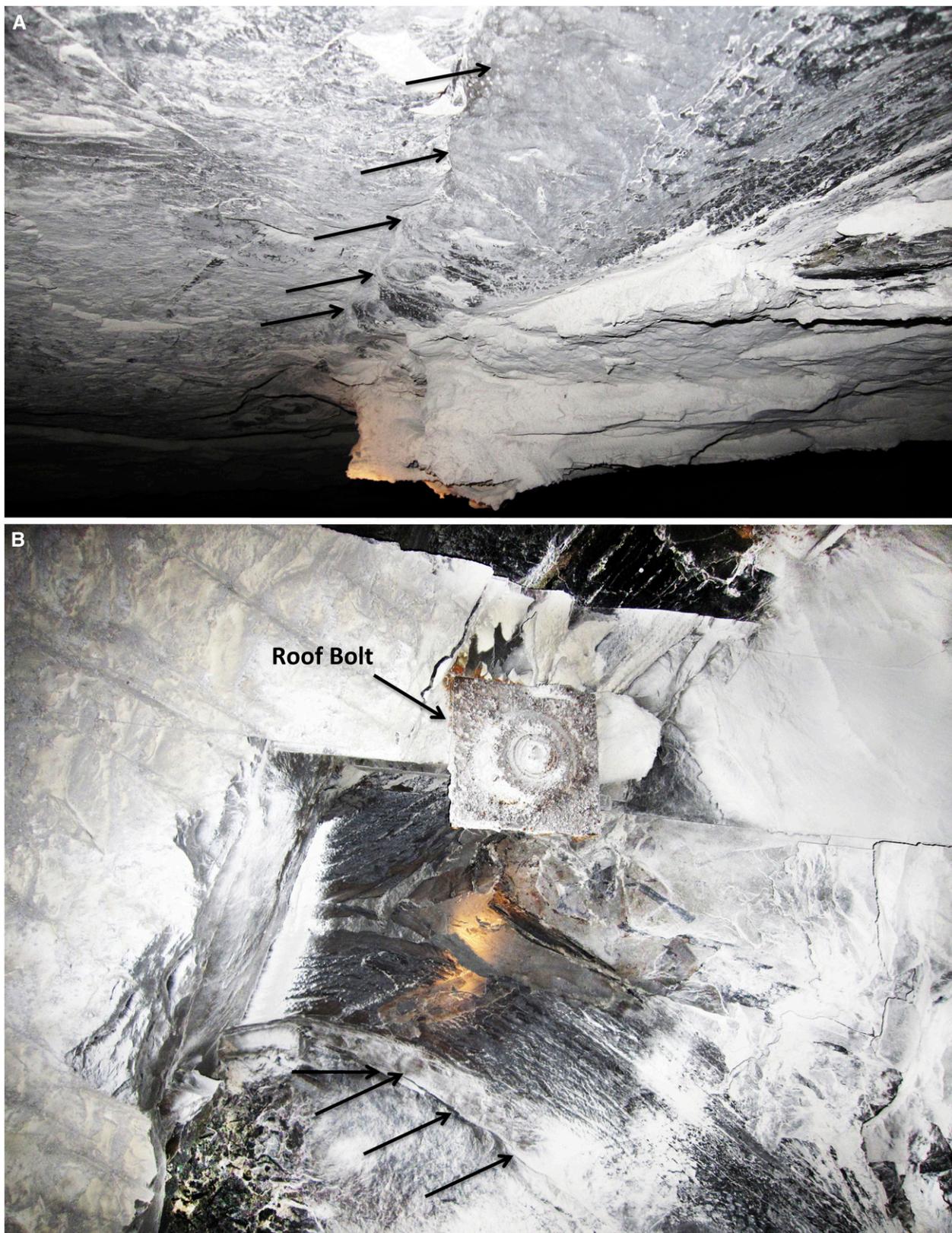


Fig. 1. Specimen 1: *Synchysidendron* from the American Coal Company, New Future Mine, photographed in situ in the roof shale of the Springfield coal, Illinois. (a) View of main trunk, looking toward the base. Arrows indicate five closely spaced lateral branch scars along the outer margin of the trunk. Scars are approximately 10 cm in diameter. (b) Main fork of the crown (to right), partially obscured by shale and a roof bolt 15 cm square. Arrows indicate three lateral branch scars.

sufficient to demonstrate that two rows were present in life. The branch scars are circular and 90–100 mm in diameter, enclosing a central, often slightly raised, annular region ca 30 mm in diameter that possibly represents the remains of the central vascular cylinder. Closely spaced lines extend radially from within this central area to the edge of the branch scar. The scars are closely juxtaposed, typically being separated by less than 20 mm and touching in some regions of the stem (Figs. 1, 2).

We interpret the many portions of much smaller branches immediately adjacent to the trunk as the remains of the lateral branch systems, though no branch bases could be identified with confidence among the litter. Branches ranged from 50 mm to less than 10 mm in diameter. The remains of these lateral branch systems divided anisotomously to various degrees (Fig. 3a, b). Most of the branches that were sufficiently well preserved to be examined in the required detail had retained their microphyllous leaves.

Both the main stems and the lateral branches have leaf cushions preserved on the outer surfaces. These cushions are consistent with those of *Lepidodendron andrewsii* and exhibit the features previously attributed to *Synchysidendron dicentricum* (Felix DiMichele & R.M. Bateman (DiMichele, 1979a; DiMichele and Bateman, 1992, 1993). All cushions are longer than wide when measured relative to the long axis of the stem, though they contrast in outline between the main stem, where cushions are only slightly longer than wide, and the lateral branches, where they are considerably longer than wide. They are also markedly smaller on observable regions of the main stem than on the lateral branches. One lateral branch ca 26 mm in diameter bore leaf cushions averaging 11.1×4.8 mm (Fig. 3a). On a region of the trunk 300 mm in diameter, located just above the initial crown dichotomy, the leaf cushions measured only 3.1×2.8 mm (Fig. 2a: scar = 90 mm). The cushions were relatively thick in the radial dimension and protuberant, as indicated by a unidirectional lateral imbrication in some specimens (Fig. 2b)—this is interpreted as reflecting lateral compression and slight displacement.

Although some features of these cushions were obscured by the attached leaves, most of the surficial characteristics diagnostic of rhizomorphic lycopsid trunks and branches could be determined (Fig. 2b). The leaf scar is present in the upper one-third of the leaf cushion. It is roughly equidimensional with a well-developed upper angle and a rounded lower angle. Cushions have an upper keel and a well-developed, though somewhat rounded, lower keel that extends from below the scar to the lower angle of the cushion; in some specimens, the lower keel has weakly developed plications. Lateral field lines extend from the leaf scar to the lateral angles of the cushion and are weakly developed. Infracoliar parichnos were not observed on any of the many leaf cushions examined, whereas in *Lepidodendron sensu stricto*, a pair of such imprints is located below the leaf scar, flanking the top of the lower keel.

Admixed with the branch debris were numerous strobili. These were all of the same type and were of the relatively smaller variety of arborescent lycopsid strobili, measuring 110–150 mm in length and 10–13 mm in width (Fig. 3c). Within each cone, sporophylls are densely packed and show clear differentiation between basal laminae, borne nearly orthogonally to the cone axis, and upswept distal laminae. Microsporangia and megasporangia could not be distinguished with certainty, and our inability to collect usable specimens precluded palynological preparation.

Description: Specimen 2 (LC)—The LC specimen consists of four segments of the trunk of a large lycopsid tree (Fig. 4). We presume that these specimens were all part of the same original

trunk, given their common geographic origin (all are derived from the same locality), their sequential numbering, comparable size, similar condition of preservation, progression of typical external form from decorticated to leaf-cushion-bearing, and general similarity in morphological characteristics. Together, the four segments constitute a preserved length of 704 cm. The maximum trunk diameter is 37.5 cm, as measured on the distalmost segment.

The trunk demonstrates two opposite rows of branch scars (Fig. 4c, d), each pair set at the same distance from the base of each segment, indicating that opposing lateral branches were produced simultaneously (assuming that the trunk elongated at the same rate across its entire diameter). Each scar is a vertically elongate ellipsoid, their diameters varying due to both preservational effects and differences in the original branch size. The scar typically consists of three zones: (1) an outer zone that bears concentric, noncontinuous lines and is often wider toward the bottom of the scar, (2) a middle zone that is marked internally by lines that radiate outward from a central annulus, and (3) a small central annular core that lacks internal features but is often raised slightly relative to the surrounding tissue. The maximum dimensions of the largest scar, measured to the outer edge of the outer zone, are 98 mm long \times 74 mm wide. The maximum dimensions measured to the outer edge of the middle zone are 70 mm long \times 58 mm wide, whereas the central annulus measures only 13 mm in diameter (Fig. 5a).

There is no evidence of tearing of the external bark beneath the scars—at least, in the area external to the central annulus, which is probably the location of the vascular cylinder—suggesting that the development of an abscission layer was complete by the time the branches were shed. The branch scars are relatively widely spaced, ranging from 80 mm to 177 mm apart within a single row. Interscar distances change systematically throughout the length of the trunk, being greater in segment 3 and in the upper half of segment 4 than in the lower half of segment 4, where there is a gradual, systematic increase in interscar distances from the base to the top of the specimen (Fig. 4c, d). No scar is observed in direct contact with another.

Leaf cushions are best preserved on segment 4. They vary slightly in size and shape throughout the specimen, ranging from 8.5 mm long \times 6 mm wide to 10 mm long \times 5 mm wide (Fig. 5b). When approaching the branch scars, the cushions become more equidimensional and can even be wider than high. Tails are evident on the best-preserved cushions. The leaf scar of the cushion is located slightly above the midpoint and is protuberant, giving the entire leaf cushion a thick and somewhat fleshy appearance, though postmortem flattening has often distorted this feature. Below the leaf scar, a distinct groove is often present, curving upward at the margins; a similar feature was described and illustrated for permineralized specimens from coal balls (under the now superseded name *Lepidodendron dicentricum* Felix) by DiMichele (1979a). Both the upper and lower keels are rounded; the upper keel commonly has a single fold or notch, possibly below the ligule pit aperture, whereas the lower keel can have between one and several such notches. Field lines running from the basal angles of the leaf scar to the margins of the cushion are weakly developed, and no infracoliar parichnos were observed.

Description: Specimen 3 (Craigeith, new)—This presumed external mold represents a strip of periderm that is 38 cm long but only 5.7 cm wide at its widest point (Fig. 6a). Largely an impression, but retaining some coalified organic matter in the leaf cushions and branch scars, this striking adpression fossil



Fig. 2. Specimen 1: Details of branch scars and leaf cushions of *Synchysidendron*. (a) Three branch scars (ca 10 cm in diameter) indicated by arrows. Relatively well-preserved middle scar shows central annulus surrounded by radiating lines in the outer zone. (b) Leaf cushions adjacent to the center branch scar in (a), illustrating the near-equidimensional shape and projection above the stem surface that is typical of some architectural regions of *Synchysidendron*. (c) Lateral branch scars on the main trunk (arrows to right of roof bolt) and on the crown branches (arrows to left of roof bolt). Roof bolt is 15 cm square (bright yellow spot is the beam from a helmet lamp).

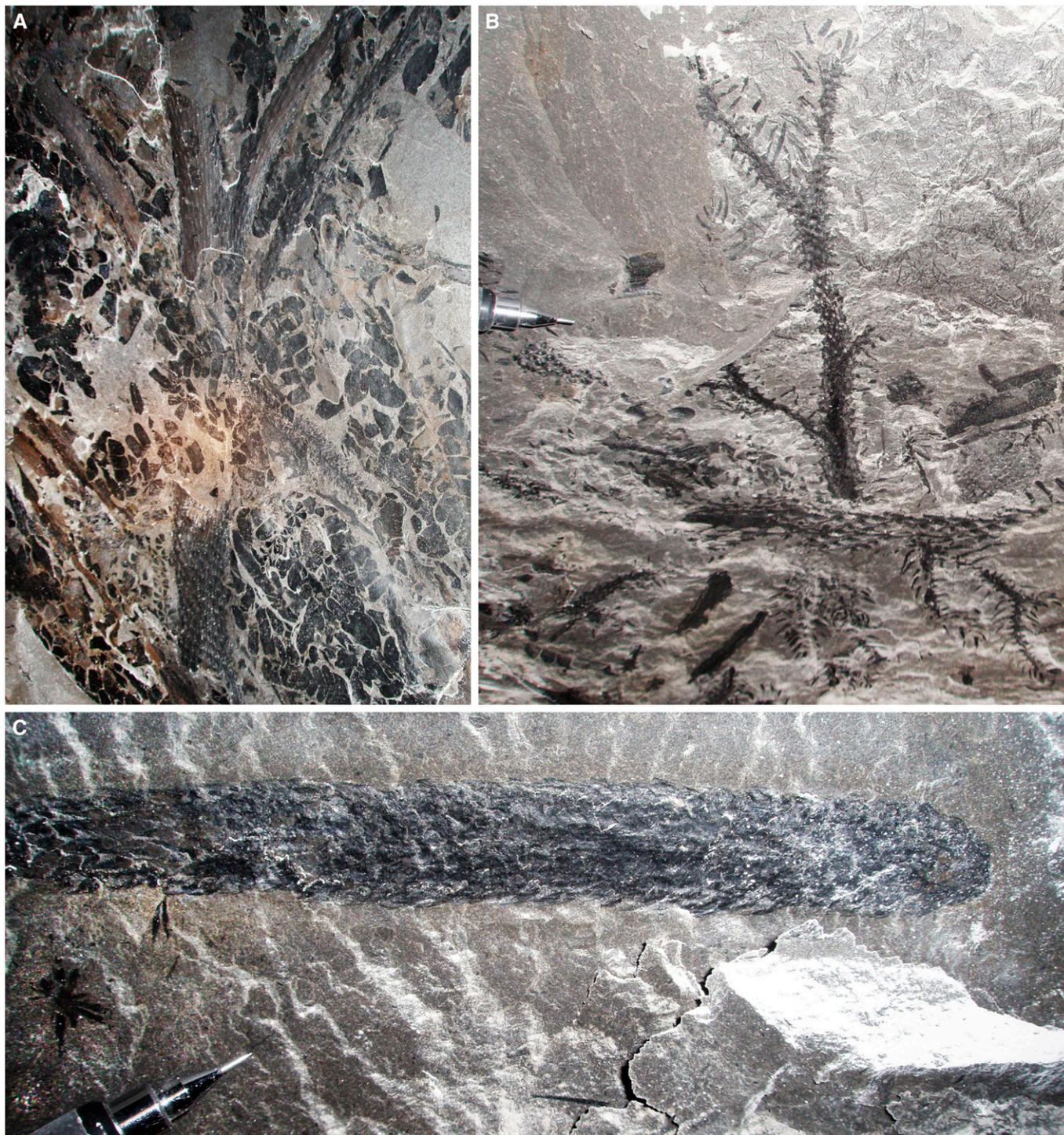


Fig. 3. Organs associated with Specimen 1: (a) Portion of a lateral branch system of *Synchysidendron* illustrating anisotomous branches. The associated pteridosperm foliage is *Neuropteris flexuosa*. Base of branch is ca 4 cm in diameter. (b) Small lateral branch fragments with anisotomous branches and attached foliage. (c) *Achlamydocarpon*-type cone showing narrow shape and attached sporophylls. Scale: pencil barrel is 9.5 mm in diameter (b, c).

preserves the original surface morphology of the stem with considerable acuity (Fig. 6b).

The eight and a half scars are presented in perfect linear alignment, showing comparatively small but nonetheless variable separation that ranges from 15 mm to as little as 1 mm. An average of 9.4 ± 4.3 mm ($n = 8$) of periderm separates the scars, and

their centroids are 46.4 ± 4.7 mm apart (range = 38–52 mm, $n = 8$). The lateral branch scars form longitudinally elongate ellipses averaging 37.2 ± 2.7 mm \times 28.4 ± 0.7 mm (ranges = 34–42 \times 27–29 mm, $n = 9$; Fig. 6b). Within each scar occurs a raised annulus, here tentatively interpreted as representing the vascular trace (Fig. 6c). The annuli circumscribe ellipses that average



Fig. 4. Specimen 2: *Synchysidendron* USNM 7304 from R.D. Lacoé collection. Segments of a single trunk from the roof shale of the Colchester coal, Illinois. The tops of the specimens are to the top of the image, and they are arranged sequentially from basalmost (a) to uppermost (d). All specimens at the same magnification; the scale is 18 inches (45.8 cm). Note that the branch scars, visible only in specimens (c) and (d), are paired and opposite. Images: National Museum of Natural History Photographic Services.

$8.1 \pm 0.7 \times 6.4 \pm 1.1$ mm (ranges $7.2\text{--}9.0 \times 4.4\text{--}6.6$ mm, $n = 7$), being one-third the diameter of the branch. Projecting from the center of each annulus is a solid vascular trace averaging $3.0 \pm 0.3 \times 2.6 \pm 0.5$ mm (ranges = $2.4\text{--}3.5 \times 2.0\text{--}3.3$ mm, $n = 7$; Fig. 6c). Morphometric samples of 10 leaf cushions from each of three areas of the specimen yielded fairly consistent

measurements of 3.9×3.4 mm, 4.0×3.1 mm, and 4.1×3.0 mm, respectively (Fig. 6d–f). Thus, the cushions are small and almost equidimensional, the transverse dimension approximating 80% of the longitudinal dimension.

Examination of the vascular traces and putative vascular cylinders projecting from the branch scars suggested that the

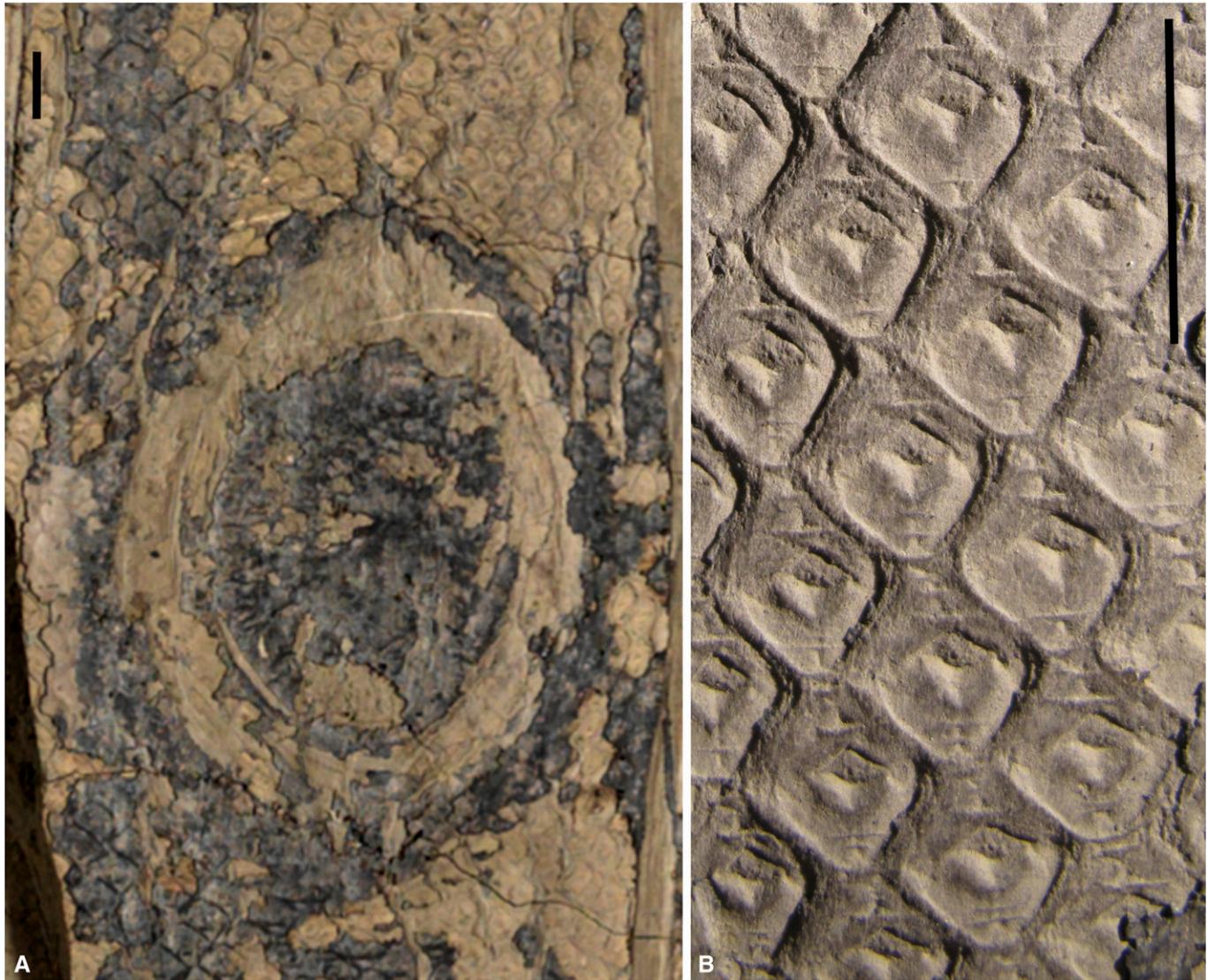


Fig. 5. Specimen 2: *Synchysidendron*. (a) Detail of branch scar showing three zones, including the central annulus surrounded by radiating lines in the central zone, but revealing no evidence of surface-tissue tearing during branch abscission. (b) Leaf cushions of a protuberant, near-equidimensional form typical *Synchysidendron*: wide, thick leaf-scar centrally located, groove beneath the leaf scar, slightly curved tails, and a notch at the top of the leaf cushion, just below the upper tail. Scale bars = 1 cm.

branches emerged from the stem at an angle midway between the vertical and the horizontal. If the branches are assumed to have been circular in transverse section, the ratio of the long and short diameters of the ellipses of the branch scars (ca 1.3) can be used to estimate the angle of emergence, which in this case proved to be about 35° above the horizontal plane. The angled divergence allows the likely apex of the stem to be identified (in this case, it is the opposite end from that bearing the partial branch scar). This suspected acropetal–basipetal polarity, when combined with patterns of apparent folding and possibly tearing of the periderm, suggests that stresses in the periderm of the scars were non-uniform. In at least five of the scars, only a single fold is present below the central vascular strand, whereas above the strand two slightly divergent folds are evident.

A larger fold running the length of the specimen lateral to the scars weakened an attempt to use the curvature of the

specimen to estimate via simple euclidean geometry the original diameter of the stem. Projecting from a chord of 56 mm and concavity of 15 mm yielded an estimated diameter of 70 mm. However, this figure should be viewed as a minimum value, as the longitudinal fold artificially increased the apparent curvature of the specimen; thus, a diameter of twice that figure cannot be ruled out.

Description: Specimen 4 (*Craigleith*, old)—Specimen 4 (Allan, 1823) resembles Specimen 3 so closely in preservation, morphology, and relative dimensions that R.M.B. initially considered the possibility that it was the counterpart to Specimen 3 (Fig. 7a). However, the branch scars are spaced proportionately a little further apart, and Allan's text provided an approximate scale which shows that Specimen 4 represents an appreciably larger stem than Specimen 3. The peridermal fragment is approximately 48 cm longitudinally by up to 21 cm transversely.



Fig. 6. Specimen 3: Recently found specimen of *Synchysidendron* from the Visean of Craighleith Quarry, Edinburgh. (a) Entire specimen showing nine closely spaced branch scars. (b) Enlarged view of scar 4, showing the arrangement of internal tissues and details of leaf cushions. (c) Further enlarged view of vascular strand in center of umbilicus of scar 4. (d) Enlarged areas of two regions of periderm showing several near-equidimensional leaf bases. (e, f) Further enlarged individual leaf bases, each showing leaf scar above lower field. Images: Richard Bateman. Scale bars: a = 50 mm; b = 10 mm; d = 5 mm; c, e, f = 2.5 mm.

The slightly elliptical branch scars are $78 \pm 3 \times 69 \pm 3$ mm ($n = 3$) in overall dimensions, and each exhibits a raised annulus and central vascular strand similar to those described in Specimen 3; in this case, their diameters are approximately 14 mm and 5 mm, respectively (i.e., twice those recorded in Specimen 3). The scars are spaced further apart (134 ± 11 mm, $n = 3$) and separated by wider expanses of periderm (56 ± 11 mm, $n = 3$). Their ellipses deviate by only 10% from a perfect circle, indicating that the branches were emitted only slightly above the horizontal plane. The leaf cushions are about half as long again longitudinally as transversely, varying from ca 7×4.5 mm to 9×6 mm. None of the available data can help to estimate the original diameter of the stem. It is possible that this is a portion of a trunk, whereas Specimen 3 represents a primary crown branch.

Description: Specimen 5 (Starlaw Park)—This internal cast is almost circular in transverse section, describing an ellipse 194×181 mm (Fig. 7b). The deeply ridged exterior of the stem strongly suggests that the leaf cushions were greatly elongated, though the cushions themselves have not been adequately preserved anywhere on the specimen. The 250 mm length of trunk reveals only two branch scars that are separated by 87 mm of periderm; thus, a distance of 143 mm separates the centers of the two longitudinally elongate scars. The putatively lower scar is 59×34 mm (Fig. 7c), and the upper scar 54×33 mm; the inner region of the lower scar can be measured at $18 \text{ mm} \times 11$ mm, and it is therefore, like Specimen 3, one-third the diameter of the entire scar. The upper scar appears to be offset clockwise by about 10 mm relative to the lower scar, rather than describing a perfect longitudinal alignment. Very localized and poorly preserved leaf bases appear strongly longitudinally elongated (Fig. 7d).

Description: Specimen 6 (Pella 1)—This specimen consists of two segments of the same trunk, preserved as impressions; thus, the observer views the outer surface from the “inside” (Fig. 8a, b). Such preservation reduces the accuracy of branch-scar measurements and prevents definite rejection of the possibility that branches remained attached at the time of burial. The comparatively narrow size of these trunk segments suggests that they are crown branches rather than parts of the main trunk, located above the first isotomous division. Internal details of the branch scars are not visible. However, there appear to have been segments of the branch still adherent, and the central vascular system and surrounding tissues (i.e., the annulus) remain visible. These features are upwardly directed, suggesting that the branches were borne above the horizontal plane.

Specimen 6a is 17 cm in diameter and 120 cm long (Fig. 8a). It bears four branch scars measuring, bottom to top: $50 \text{ mm long} \times 40 \text{ mm wide}$, $45 \text{ mm long} \times 30 \text{ mm wide}$, ca $40 \text{ mm long} \times 30 \text{ mm wide}$, ca $40 \text{ mm long} \times 30 \text{ mm wide}$. Interscar distances, bottom to top, are 170 mm, 190 mm, and 180 mm. The best-preserved leaf cushions are 11–12 mm long \times 3–3.3 mm wide (Fig. 8e); they are flattened and have oppositely curved tails. The leaf scar is placed well above the midpoint of the cushion, approximately 7 mm from the base. It is distinctively biconvex, 2 mm long \times 2 mm wide, with a ligule pit located at the top. Leaf traces and flanking foliar parichnos are obscure. The upper and lower keels are sharp and narrow. Fine plications are present on the lower keel, though often obscured by indifferent preservation. The leaf cushions are separated by stem expansion zones (interareas) 2–2.3 mm wide. Intrafoliar parichnos are absent.

Specimen 6b is 13 cm in diameter and 77 cm long (Fig. 8b). It bears three branch scars, bottom to top: $40 \text{ mm long} \times 35 \text{ mm wide}$, $45 \text{ mm long} \times 40 \text{ mm wide}$, $45 \text{ mm long} \times 30 \text{ mm wide}$. A second row of branch scars is evident on the “reverse side” of this specimen (these scars, here represented by raised areas, were originally located on the other side of the now-absent original stem, and were hollow internal areas—the converse of the well-marked scars impressed into the sediment). These “shadow scars” are located at approximately the same level on the trunk as the better-preserved scars. The centers of each pair of opposite scars are set 30–35 mm from the margin of the specimen, indicating that originally they were directly opposed. Interscar distances, bottom to top, are 205 mm and 155 mm. The leaf cushions of this specimen exhibit dimensions and a state of preservation similar to those of Specimen 6a.

Description: Specimen 7 (Pella 2)—As with Specimen 6, the trunk segment that constitutes Specimen 7 is preserved as an impression of the outer surface of one side of the trunk but is viewed from the “inside” (Fig. 8c). Lateral branches may still have been attached to this plant at the time of its death because branch scars are poorly developed. The position of lateral branches is clearly marked, but their positions show leaf cushions that unquestionably were those of the base of the lateral branch. Superimposed on these leaf cushions are masses of tissue that show vertically elongate, irregular striations and are tentatively identified as the periderm and interior tissues of the lateral branch (Fig. 9a). Branch scars are obscured by this mode of preservation, and, in fact, may not have been present at all if the lateral branches were not yet shed. The angle against which these lateral branch tissues are pressed against the scar indicates that they were borne above the horizontal plane. This specimen also suggests that, at least in *Diaphorodendron*, several generations of lateral branches were present concurrently. Although we cannot discern the extent of these branching systems at the time of tree death, the size of the scars shows that these lateral branches emerged as large-diameter axes, apparently having mirrored the trunk in being initiated by unusually broad meristems.

The diameter of this trunk segment suggests that it is either part of a main trunk or derived from the basalmost part of the crown. Surface features of the specimen, such as disruption of leaf cushion patterns and undulations of the surface, offer subtle evidence of a second row of branch scars that are located at the same vertical positions as the first. The center points of both the obvious row and the obscure row are approximately 80 mm from the stem margin, once again suggesting opposite placement of branches.

The specimen is 22.5 cm in diameter and 83 cm long. There are one partial and four complete branch scars, which measure, bottom to top: $60 \text{ mm long} \times 70 \text{ mm wide}$, $55 \text{ mm long} \times 55 \text{ mm wide}$, $70 \text{ mm long} \times 80 \text{ mm wide}$, $60 \text{ mm long} \times 60 \text{ mm wide}$. Interscar distances, bottom to top, are 120 mm, 115 mm, 100 mm, and 100 mm. Leaf cushions, where best preserved on the main trunk, are 7.5–8.5 mm long \times 2.5–3.0 mm wide (Fig. 9c). At the bases of the branches—seemingly on the lateral branches themselves—leaf cushions are smaller, principally in the vertical dimension (5–6 mm long \times 2.5–3.0 mm wide), resulting in a slight shape change. The cushions are flattened and have oppositely curved tails. The leaf scar is located near the center of the long dimension, approximately 4 mm from the base; it is distinctively biconvex, 1.0–1.2 mm long and wide, with a ligule pit located at the top. Leaf traces and flanking foliar parichnos are obscure. Features of the surrounding matrix suggest that leaves were still in



Fig. 7. (a) Specimen 4: Specimen of *Synchysidendron* from the Visean of Craigleith Quarry, Edinburgh, illustrated by Allan (1823, plate XIV). (b–d) Specimen 5: Recently found specimen of *Diaphorodendron* from the Visean of Starlaw Park, Livingston, near Edinburgh. (b) Almost entire cylindrical portion of trunk, showing two branch scars that are widely separated vertically and slightly displaced laterally (arrowed). (c) Enlarged view of lower scar, showing distinct outer cylinder and inner core. (d) Enlarged areas of region of periderm showing poorly preserved, longitudinally elongate leaf bases. Images: Richard Bateman. Scale bars: a, b = 50 mm; c = 25 mm; d = 10 mm.

attachment to the stem at its time of death and burial. The upper and lower keels are sharp and narrow. Fine plications are present on the lower keel, though as in Specimen 6, these are generally obscured by preservation. The leaf cushions are separated by interareas 1.5–2.0 mm wide. Infrafoliar parichnos are absent.

Description: Specimen 8 (Creek Paum)—This trunk impression lacks distinguishable leaf cushions but shows two rows of branch scars, each of three scars (Fig. 10a). One row appears to have been preserved as molds of the stem surface, whereas the more obscure row to the right appears to represent a sub-peridermal view, seen from the inside-out. The stem impression appears to have been distorted during preservation, resulting in a longitudinal fold and imposing on the previously opposing scars a postmortem vertical offset.

With the above caveats in mind, the identity of the specimen cannot be resolved to a taxonomic level lower than family Diaphorodendraceae. The stem is minimally 450 mm in diameter. Branch scars are ellipsoidal in shape, approximating a vertical dimension of 177 mm and a horizontal dimension of 125 mm. Each consists of two well-defined zones; a raised central annulus ca 7 mm in diameter is surrounded by a zone that is marked by radiating lines that extend to the margin of the scar. Branch-scar pairs are widely separated vertically, by 145 and 155 mm, respectively (Fig. 10a).

The margins of the scars are sharp and show no evidence of tissue damage. This suggests that the abscission layer was completely developed throughout most of the scar at the time the branch was shed, only the central annulus potentially remaining attached. The vertically elongate shape suggests that the branches were borne at an upward angle.

Description: Specimen 9 (Millennium)—This compression fossil of a putative partial stem fragment ca 490 mm and exceeding ca 180 mm in diameter (Fig. 10b). It exhibits a single linear row of 10 branch near-circular scars that average ca 66 mm in longitudinal diameter and ca 62 mm in transverse diameter, typically set ca 13 mm apart and with center points ca 55 mm from the stem margin.

As in previous specimens, the scars are demarcated by a set of three concentric rings, a narrow annulus innermost and the sharply lineated rim outermost, encompassing large numbers of radially arranged lines.

Leaf scars appear to be strongly longitudinally elongated, but were poorly preserved and so cannot be described in detail.

Phylogenetic analysis and optimization—The preferred most-parsimonious tree resulting from the revised morphological cladistic matrix is shown in Fig. 11, together with bootstrap values. Rescoring three architectural characters for *Synchysidendron* yielded the same nine most-parsimonious trees (only three differ at the genus level, specifically in the placement of the primitive isoetalean *Chaloneria*) that were obtained from the original analysis by Bateman et al. (1992) and reproduced in several subsequent studies. Also, most phylogenetic branches were of similar length and hence attracted similar levels of bootstrap support. The main exception to this generalization was the branch immediately subtending the genus *Diaphorodendron*, which halved in length and suffered a decrease in bootstrap support from 96 to 85% as a result of the loss of its previous architectural synapomorphies. In contrast, the genus *Synchysidendron* continued to attract high support of 98% and the family Diaphorodendraceae 100%. The requirement for fewer

transitions in C3 (degree of trunk dichotomy) and C6 (extensive lateral vs crown branching) across the tree yielded a consistency index (informative characters only) of 0.635 and a retention index of 0.824; both figures were reduced by 0.010 relative to the original analysis. Optimization of architectural characters on the internal nodes of the preferred most-parsimonious tree was also simplified, such that optimizations of only one architectural character (C1: nonarboreous vs arboreous) gave contrasting results between Acctran and Deltran algorithms at two important nodes. Architectural optimizations resulting from the original analysis are summarized in Fig. 12a, and those generated during the present analysis are presented in Fig. 12b.

DISCUSSION

Architectural reinterpretation of *Synchysidendron*—Reappraisal of *Synchysidendron* means that it is now inferred to have the same fundamental growth architecture as *Diaphorodendron*, revealing that the classic lepidodendrid umbrella-like crown filled with cones—often attributed to the arborescent lycopsids in toto and so appearing in innumerable arboreal reconstructions of Pennsylvanian equatorial forests—is probably evolutionarily derived and limited to the Lepidodendraceae s.s.

More specifically, given this spectrum of substantial and unusually informative new specimens, we can state with confidence that *Synchysidendron* had an above-ground growth architecture that was dominated by the production of deciduous lateral branches. Furthermore, present evidence suggests that the lateral branches were effectively confined to a single plane (vertical in life), conferring on these trees a plagiotropic growth habit and a strong bilateral symmetry when viewed in transverse section. The vertical distribution of scars indicates that the lateral branches were closely packed along the sides of the plant (Figs. 1, 2, 4–6) and emerged above the horizontal plane.

Architecture within the now fragmented lateral branch systems is notoriously difficult to reconstruct (cf. the detailed quantitative methods applied to *Oxroadia* by Bateman [1992]). In the case of *Synchysidendron*, successive divisions appear to have been variably spaced (Fig. 3) and may have been confined to a single vertical plane. Plants with this pattern of lateral branch formation are generally characterized as having a plagiotropic branching habit. Although the lateral branches had substantial diameters where they joined the trunk, dichotomies (both anisotomous and isotomous) early in branch growth apparently resulted in rapid decrease in branch diameter during determinate apoxogenetic growth (sensu Eggert, 1961) and generated surprisingly small cone-bearing arrays when mature (Fig. 3).

The axial dichotomy that initiated crown formation appears to have been oriented such that the two opposing rows of lateral branches projected outward in the same plane as that containing the axial dichotomy (Fig. 1b); consequently, the bilateral symmetry of the trunk extended upward into the crown. This growth habit is problematic from the point of view of the placement and spacing of the lateral branches. Branches borne on opposite sides of the trunk would not interfere with each other's expansion to full size, whereas lateral branches borne on the inside portions of the initial trunk dichotomy—as observed on Specimen 1 (Fig. 1b)—would likely have become seriously entangled with each other unless they were unusually small. In addition, the close placement of these branch scars, juxtaposed throughout much of the stem length in Specimens 1–3 (Figs. 1–6), suggests a dense, almost thicket-like coating of branches and associated



Fig. 8. Specimens 6 and 7: *Diaphorodendron* from the roof sandstone of the Black Oak coal, Iowa. (a, b) USNM 528668; blocks arranged in sequence, specimen from lower on trunk to left, and top of stem oriented toward the top of the image. Only one row of branch scars is visible. Note that lateral branch scars are obscured, probably due to retention of the lateral branches. (c) SUI 119929. Again, only a single row of branch scars is visible, and these are obscured by retention of lateral branches. (d) Detail of leaf cushions from SUI 119929; note the elongate aspect, large leaf scar in the upper half of the cushion, well-marked keels, and distinctive plicate interareas. (e) Detail of leaf cushion from USNM 528668; note the flat, elongate aspect, curved tails, and the distinctive shape of the *Diaphorodendron* leaf scar. Scale bars: a–c = 10 cm; d, e = 1 cm.

foliage along the side of the plant. Much would depend on the plane in which the first dichotomy of the lateral branch system took place and the angle that it subtended (cf. Bateman, 1992).

Ontogenetically, we presume that there existed a progression down the trunk of branches passing from emergent phases of development through expansion to cone formation, cone maturation, branch death, and abscission. However, in the absence of branches in attachment, we cannot even speculate on the physical distance that separated these contrasting ontogenetic

zones or the time involved in completing this developmental progression. There is no evidence of tearing at any point around any of the branch scars, suggesting that abscission was reliable and complete; no branch appears to have fallen away while still partly attached to the trunk, except perhaps by the umbilicus-like central vascular cylinder. To this observation can be added the apoxogenetic/determinate aspects of both the lateral branch systems and the tree as whole, indicated in both cases by progressive diminution of the primary body with successive branchings,



Fig. 9. Specimens 6 and 7: *Diaphorodendron* from the roof sandstone of the Black Oak coal, Iowa. (a) Specimen 7 (SUI 119929), showing details of lateral branch attachment. The remnant of the attached lateral branch can be seen addressed against the stem—viewed here from the “inside” due to the nature of preservation of this specimen. Note that the leaf cushions on the lateral branch area are much smaller than those on the main trunk. Imprints of the some of the internal tissues of the branch are preserved as the longitudinally striated mass in the center and left of the scar area. (b) Specimen 6 (NMNH 528668), showing leaf cushions that demonstrate a general *Diaphorodendron* aspect: distinctive leaf scar, well-marked upper and lower keels, curved tips of tails, and faint but well-developed plications, particularly on the lower keel. (c) Specimen 7 (SUI 119929): leaf cushions of narrow and very flat aspect with large, distinctive leaf scars, curved tails, and well-developed interarea. Scale bars: a–c = 1 cm (b, c: same magnification).



Fig. 10. Specimens 8 and 9. (a) Specimen 8: Indeterminate Diaphorodendraceae from roof sandstone of Murphysboro coal, Illinois. Note the two rows of branch scars on opposite sides of the trunk, the right-hand row distorted and partially obscured. Branch scars show a typical annulus surrounded by a distinct area of radiating striations, and average 12.5 cm in horizontal diameter. (b) Specimen 9: Indeterminate Diaphorodendraceae from roof shale of Springfield coal, Illinois; a compression fossil exhibiting a single row of 10 well-formed and closely spaced branch scars ca 6 cm in horizontal diameter. Scale: hammer head = 18 cm.

the deciduous nature of the microphyllous leaves, and the shedding or obliteration of the outer rind of leaf cushions as the plant developed (see, in particular, Specimen 2). In toto, these observations strongly indicate that lateral branches were shed from the plant during its life rather than post mortem.

Additional, though ambiguous, developmental information can be inferred from contrasts in spacing of lateral branches along the trunk. If such branches were produced with regular, metronomic timing, then any differences in spacing would most likely reflect changes in the rate of trunk elongation, perhaps reflecting external environmental conditions affecting growth rates (notably temperature and moisture availability). Thus, closer spacing of branches would indicate periods of slower growth under less favorable conditions. If, on the other hand, lateral branch initiation responded to particular environmental triggers, closely spaced branches could reflect periods particularly favorable for growth and reproduction.

Arborescent lycopsids had very limited phloem systems (Seward, 1902; Scott, 1906; Eggert and Kanemoto, 1977; DiMichele and Phillips, 1985; Phillips and DiMichele, 1992; Green, 2010), raising the vexed question of whether photosynthate was transported throughout the plant or was used only locally. Studies of symplastic water transport in some extant angiospermous trees (e.g., Sokołowska and Zagórska-Marek, 2012) leave open the possibility that the products of photosynthesis may similarly have been transported in parenchymatous

tissues, particularly given that arborescent lycopsids were remarkable in lacking secondary phloem connection between the shoot and root systems (Phillips and DiMichele, 1992).

Efficient branch-shedding also suggests that these plants could have spored continuously once the lowest lateral branches had reached maturity—a mode of reproduction strikingly different from that inferred for members of the Lepidodendraceae, which appear to have entered their reproductive phase only near the end of determinate growth when the crown matured (see, for example, the exceptional work by Opluštil, 2010). As in most rhizomorphic lycopsids, the strobili of the *Synchysidron* plant were confined to strongly anisotomous branching systems resembling that shown in Fig. 3b. In plants such as those described here that produced plagiotropic, deciduous lateral branches, the strobili were borne exclusively in the lateral branch arrays, which extended from the trunk into the crown branches. In the Sigillariaceae and Lepidodendraceae, the lateral branch systems were strongly reduced such that they generally bore only a single large cone; in the sparsely branched Sigillariaceae, these highly reduced lateral branches were borne throughout the trunk, whereas in the Lepidodendraceae they were confined to the crown branches and thus to the final phase of tree growth. We presume that the lateral branches of Diaphorodendraceae were abscised following cone maturation/spore release; shedding the branches once the associated cones were mature would facilitate the unimpeded dispersal of

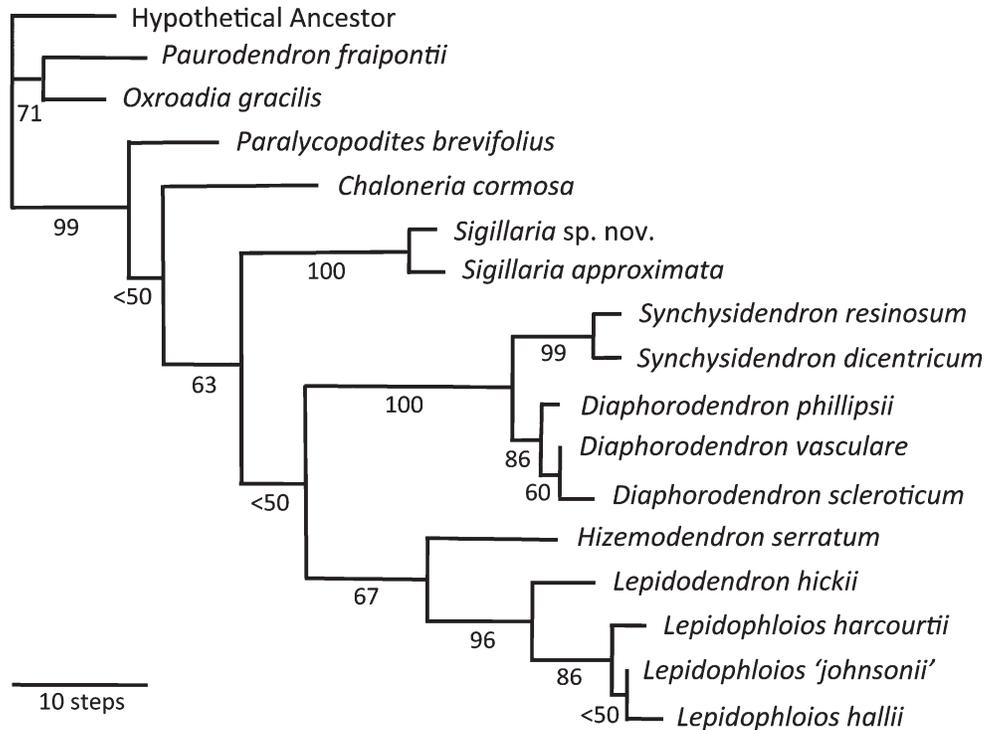


Fig. 11. Preferred most-parsimonious tree resulting from reanalysis of the morphological cladistic matrix for 16 reconstructed whole-plant species originally published by Bateman et al. (1992), illustrating the reduced length of the branch subtending *Diaphorodendron*. Numbers on branches indicate percentage bootstrap support.

microspores and especially of sporangium–megasporophyll units (*Achlamydocarpon* ‘aquacarps’ sensu Phillips, 1979) from cones produced on the branch immediately above that undergoing abscission.

Taphonomic implications—Because of the growth habit described above, it is likely that the smaller-diameter axial fragments, which are characteristic of *Synchysidendron* and *Diaphorodendron* across all preservation states (i.e., adpression, three-dimensional cast, and permineralized coal-ball petrification), are derived from the lateral branch arrays. Putative trunk specimens of these tree species are exceptionally rare in coal balls (for an example of one such specimen see DiMichele, 1981) but are more frequent in adpression floras. However, during the course of extensive surveys of coal mines, particularly underground where prostrate trunks are often well exposed, W.A.D. and S.D.E. have rarely encountered specimens clearly exhibiting opposite rows of branch scars. This phenomenon extends to the three three-dimensional casts, some still in situ, described here by R.M.B. This apparent rarity of such reports may be due to one or more of the following reasons, the first of which relates to recognition and the remaining two to taphonomy:

- (1) Paleobotanists are not looking for this feature and/or lack an adequate search image.
- (2) The lateral branch scars tend to occur most often along the margins of flattened (and sometimes partially mud-cast) tree trunks, where they are most easily overlooked by fieldworkers. Their nonrandom position may reflect the fact that some of the later-forming lateral branches remained attached to the tree and so tended to orient fallen trunks such that they settled on the substrate with a preferred orientation

(see also Wang et al., 2005). In other words, the trees may have had a strong tendency to adopt a stereotypically two-dimensional death pose.

- (3) The difficulty in recognizing lateral branch scars is compounded in trees preserved in a decorticated state (e.g., the lower portions of specimen 2: Fig. 4a, b); unfortunately, most prostrate trunks lack clear details of surface morphology. It was comparatively easy to reconstruct the basic growth habit of the laterally branched genus *Paralycopodites* from coal-ball specimens because of the relatively small size of the plant, which permitted frequent preservation of trunk fragments. In contrast, *Synchysidendron* and *Diaphorodendron* were large trees, occupying the upper size classes of known arborescent lycopsids (e.g., DiMichele and Bateman, 1992).

Specimen 1 was preserved in the roof shale of the Springfield (No. 5) coal bed. This gray shale is interpreted as a tidal deposit (Elrick and Nelson, 2010) that buried the surface of the Springfield coal very rapidly, preserving much of the final peat forest effectively in situ. Accommodation space for the sediment appears to have come from a combination of a rapidly rising sea level and compaction of the peat substrate under the weight of the incoming sediment. The study specimen appears to have been killed before completion of its natural life-span, as its leaves are still in attachment to fragments of both the lateral branch systems and the crown branches. In general, leaves are found in attachment to branches of *Synchysidendron* only infrequently, irrespective of whether they are preserved as adpressions, casts, or petrifications.

Paleoecological implications—Our discovery of Specimen 3 in Craigleith Quarry led to historical researches that now suggest

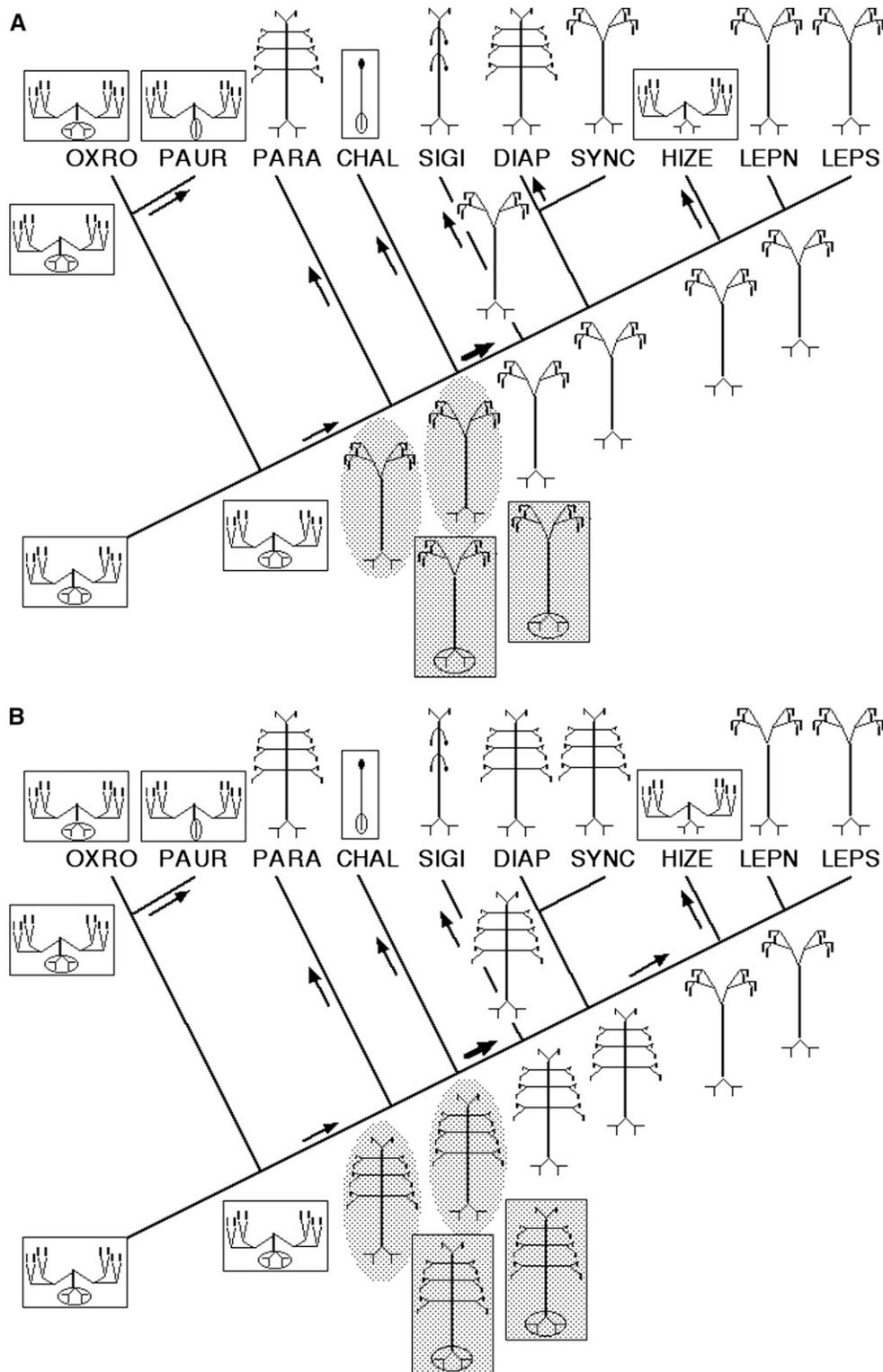


Fig. 12. Architectural characters mapped onto the preferred most-parsimonious topology to reconstruct hypothetical ancestral architectures occupying internal nodes of the cladogram, rooted using the architecture of *Oxroodia*. Homoplasy in the relevant characters results in significantly different architectures at the stippled nodes, according to whether Acctran (left) or Deltran (right) optimization is used. Internodes involving state changes in at least one architectural character are arrowed; the large arrow denotes positional differences between the two contrasting optimizations. (a) Characters as coded by Bateman et al. (1992) and presented by Bateman (1994, fig. 14). (b) Three of 10 parsimony-informative architectural characters recoded according to the present study. Genera are, from left to right: *Oxroodia*, *Paurodendron*, *Paralycopodites*, *Chaloneria*, *Sigillaria*, *Diaphorodendron*, *Synchysidendron*, *Hizemodendron*, *Lepidodendron*, *Lepidophloios*.

to us that *Synchysidendron* may have been a dominant component of the tropical vegetation that occupied the eastern portion of the Scottish Midland Valley in Asbian times. Similar strips of lycopsid bark have been reported from quarries through the Craigleith Sandstone at Craigleith (Allan, 1823; Specimen 4 in the present study: Fig. 6a), Dalkeith (Millar, 1827), and Slateford, southwest of Edinburgh (P. Cook, personal communication, 1995), while the in situ forest that yielded Specimen 5 shows that *Diaphorodendron* occurred penecontemporaneously a further ca. 20 km to the west.

The Illinois Basin specimens of both *Synchysidendron* and *Diaphorodendron* are all of late Middle Pennsylvanian age and all occur in rock layers immediately overlying coal beds, known as roof shales, that reflect several potential sedimentological origins (Gastaldo et al., 1995). The sediments that enclose Specimen 1 from siltstone above the Springfield coal, Specimens 6 and 7 from sandstones above the Black Oak coal, and Specimen 8 from sandstone above the Murphysboro coal, all bear evidence of tidal rhythmicity during deposition. In addition, there exist numerous examples of lycopsid tree stumps rooted in the very top of the Springfield and Black Oak coals, suggesting that these deposits formed as coal swamps were flooded during the transition from glacial to interglacial conditions—most likely accompanied by changes from humid to wet subhumid conditions and associated changes in sediment transport dynamics (Cecil and Dulong, 2003). The roof shale of the Colchester coal, which yielded Specimen 2, also is most likely a tidal deposit associated with the final phase of swamp drowning, as indicated by both the frequent pinstripe lamination of the rock and the presence of upright tree stumps that evidence rapid burial and high rates of sediment input. The abundant occurrence of species of Diaphorodendraceae in coal balls (e.g., Phillips and DiMichele, 1981; DiMichele and Phillips, 1988), and the common occurrence of these plants in adpression assemblages formed during the drowning phases of coal swamps, suggest strong ties to wetlands, particularly those with organic-rich substrates, throughout the history of the lineage.

The effective absence of reported juvenile plants of virtually any arborescent lycopsid remains perplexing. Phillips and DiMichele (1992) suggested that the rhizomorph and early stage trunk were established slowly, reaching nearly full girth before a period of exceptionally rapid elongation and attainment of reproductive maturity. However, this model increasingly appears more applicable to Lepidodendraceae than to Diaphorodendraceae, which exhibit several features that suggest comparatively long life-spans: the presence of an abundance of deciduous lateral branches; clear evidence of either obliteration or shedding of the outer rind of primary leaf-cushion-bearing tissues in the basal portions of the trunk; the large size of the plants, probably exceeding 30 m in height; the production of abundant lateral branches that permitted temporally extended and high-volume reproduction; and the continuance of lateral branch production into the dichotomized crown, representing the final phase of the plant's determinate ontogeny. Their fossil occurrences suggest that these plants were generally rare, but could become locally abundant in peat-substrate habitats, as known from both coal-ball and drowning-phase roof-shale floras. Thus, we assume that their biology reflects adaptation to disturbed habitats, perhaps in part as a means of evading competition with incumbents (DiMichele and Bateman, 1996b). If so, suitable sites would have appeared only intermittently and irregularly across the coal-swamp landscape.

Phylogenetic implications—As initially described (DiMichele, 1979a), *Synchysidendron* was tentatively reconstructed as having cones borne singly on peduncles produced in a well-developed terminal crown. This inference was perpetuated in subsequent formal descriptions of the genus (DiMichele and Bateman, 1992, 1996a) and in the associated morphological cladistic analysis (Bateman et al., 1992). However, the present discoveries challenge our original interpretation by demonstrating that *Synchysidendron* possessed abundant deciduous lateral branches. This finding solidifies this growth habit as ubiquitous across the Diaphorodendraceae (DiMichele and Bateman, 1992), as both *Synchysidendron* and *Diaphorodendron* are now inferred to share the same fundamental architecture.

Predictably, this relatively simple recoding of just three characters for two conceptual whole-plant species of a single genus (*Synchysidendron resinosum* DiMichele & R.M. Bateman and *S. dicentricum* (Felix) DiMichele & R.M. Bateman) had no effect on the topology of the morphological cladograms originally reported by Bateman et al. (1992) and Bateman (1994), and only slightly reduced the associated homoplasy indices. Of far greater interest are the consequences of recoding for phylogenetic branch length (and associated statistical support for particular clades: Fig. 11) and especially for optimization of architectural characters across the topology (Fig. 12).

Considering first branch length, three of the branches shown in Fig. 11 are of particular interest. Those subtending the genus *Synchysidendron* and the family Diaphorodendraceae (*Synchysidendron* plus *Diaphorodendron*) are unchanged in length and so continue to attract near-maximum bootstrap support. However, the branch subtending *Diaphorodendron* is approximately halved in length and its bootstrap value consequently reduced from 96% to (an albeit still respectable) 85%. Thus, the present revision to greater architectural homogeneity weakens—though by no means eliminates—the support for a genus-level separation of *Synchysidendron* from *Diaphorodendron*. We consider the phylogenetic distance that still separates the two genera as sufficient to justify the continued recognition of both genera. Vegetative branches of *Synchysidendron* are distinguished from those of *Diaphorodendron* by their solidly parenchymatous, deeply invaginated pith, heterogeneous rays, phelloderm of alternating bands of thin-walled and thick-walled cells, and leaf cushions retained via tangential interarea expansion, whereas its lateral branches/peduncles lack pith (cf. DiMichele and Bateman, 1992, table 2). The revised branch lengths in the phylogenetic tree play a more significant role by increasing support for Bateman's (1994) suggestion that *Diaphorodendron* may have evolutionarily preceded the more derived *Synchysidendron*.

The consequences of the revised architectural scoring are most profound for reconstruction of architectures in the internal nodes on the cladogram. In particular, the original analysis hypothesized plesiomorphy for crown branching and independent origins of lateral branching in *Paralycopodites* and *Diaphorodendron* (Fig. 12a). However, revising the architecture of *Synchysidendron* as laterally branched results in lateral branching replacing extensive crown branching as the "core" architecture across much of the cladogram, thereby restricting crown-branched trees to the highly derived Lepidodendraceae sensu Bateman et al. (1992; see also DiMichele and Bateman, 1996a, b); that is, to *Lepidodendron* plus *Lepidophloios* plus the architecturally pedomorphic genus *Hizemodendron* (Fig. 12b). This, in turn, leads us to question the homology assumed between the crown branching evident in the highly derived Pennsylvanian Lepidodendraceae and that observed in the supposedly primitive,

small-bodied, semiprostrate pseudoherbs *Oxroadia* and *Paurodendron*, which first appeared in the early Mississippian (Bateman, 1992; Bateman et al., 1992). In addition, both the original and the revised matrix suggest that, at least under Deltran optimization, an intermediate architecture may have existed that consisted of upright shrubs with compact rhizomorphs (stippled in Fig. 12).

Bateman (1994) argued against lateral branching as the primitive condition within rhizomorphic lycopsids, on the grounds of “developmental parsimony”. Specifically, the architecture dominated by lateral branches is the most complex known within the clade, consisting of a fully developed rhizomorph, stem, strong development of lateral branches on the stem, and a more modest, arguably near-vestigial crown that continues to bear lateral branches (the “ABcD1d2” modular architecture). In addition, the lateral branching of the above-ground axial system contrasts markedly with the repeatedly isotomous branching of the below-ground axial system (i.e., the rhizomorph). For these reasons, Bateman (1994) assumed that this plagiotropic architecture—roughly corresponding with Stone’s model *sensu* Halle et al. (1978)—required the most complex developmental controls.

Evidence supporting a converse view derives from first appearances in the fossil record. Specifically, strongly developed lateral branching characterizes not only the earliest-appearing tree lycopsid to be analyzed in our matrix, *Paralycopodites* (earliest Mississippian: DiMichele, 1980; see also Thomas, 1967) but also the earliest known tree lycopsid, *Leptophloeum* (late Devonian: Wang et al., 2005), and the earliest known lycopsid *per se*, the herbaceous *Asteroxylon* (early Devonian: e.g., Kidston and Lang, 1920). Moreover, the modest-sized tree *Paralycopodites*, which possesses the laterally branched tree architecture, is the first arboreal genus to diverge in our phylogeny (Fig. 12).

Evolutionary implications—We have, in the past, constructed complex evolutionary scenarios to account for the radical architectural transitions summarized in Fig. 12. Together, these scenarios addressed many of the key issues in contemporary evolutionary biology, including homology, heterochrony, allometry, heterotopy, stage insertion/deletion, and saltational evolutionary-developmental change (e.g., Bateman and DiMichele, 1991; Bateman et al., 1992; Bateman 1994). Our new insights into the architecture of *Synchysidendron*, and their profound consequences for our concepts of architectural plesiomorphy in the rhizomorphic lycopsids, encouraged us to review our broader perceptions regarding the evolutionary patterns and processes operating in the group—a group that exhibits an unusually strong modular architecture and an associated ontogeny that is far more highly canalized than that of any modern tree originating from within the euphyllphyte clade.

In many ways, the lateral branches that are the crux of this paper present the greatest challenge to homology assessment. Of the four fundamental architectural modules recognized by Bateman (1994), only the lateral branches—ephemeral determinate axial systems expressed highly iteratively—are initiated repeatedly and so show serial homology. A further complication presented by the Diaphorodendraceae-type architecture is that the lateral branches are expressed both before and, to a lesser degree, after the initial isotomy of the stem—in other words, on both the trunk and (presumably reduced in size) within the crown. These two cohorts of branches are probably best viewed as being structurally but not positionally homologous. Those presented as

dense distichous ranks along the trunk appear to have formed relatively early in the developmental history of the tree and at the expense of the development of an extensive crown (and of the more distally positioned lateral branches subtended by the crown); complete suppression of lateral branching on the trunk appears necessary to generate an extensive crown of the kind that characterizes the derived *Lepidodendron* clade. In the parlance of evolutionary-developmental change, a nonterminal stage deletion (loss of lateral branching on the trunk prior to the first isotomy) sets the stage for subsequent hypermorphosis (delayed offset of growth) of both the crown branches and associated, cone-bearing axes that are all that remains of the formerly extensive lateral branches (Bateman, 1994).

This evolutionary-developmental distinction results in profound functional divergence between the Lepidodendraceae and Diaphorodendraceae, as members of the *Lepidodendron* clade formed a canopy and reproduced only toward the end of their lifespan, a high-risk ecological strategy requiring either rapid growth or a high level of structural and physiological tolerance to various kinds of disturbances. At least some species of Diaphorodendraceae, notably the more expensively constructed *Diaphorodendron scleroticum* (cf. Phillips and DiMichele, 1992), may also have been relatively tolerant of disturbances when considered from an “economics” perspective. The lateral branches, here highly reduced to mere cone peduncles (Bateman, 1992, 1994; see also Opluštil, 2010), appear to have been confined to the dichotomized crown region. Upon abscission, these deciduous lateral branch-peduncles left a distinctive kind of branch scar typical of *Lepidophloios* and *Lepidodendron* s.s., sometimes described as “halonial” (Jonker, 1976; DiMichele, 1979b). In a pattern of growth and reproduction very different from those of either the Diaphorodendraceae or Lepidodendraceae, *Sigillaria* underwent little if any development of a dichotomized crown during the later, apoxogenetic phases of determinate growth. The much reduced, strobilus-bearing lateral branches were borne on the main trunk and possibly also in the few crown branches produced, raising the interesting question of whether the cone peduncles are highly reduced homologues of the lateral branches of *Synchysidendron* and *Diaphorodendron* (Bateman et al., 1992; Phillips and DiMichele, 1992).

In addition, our present results considerably increased the perceived phylogenetic distance separating derived crown-branched genera of Pennsylvanian Lepidodendraceae from putatively primitive crown-branched genera that occur in the Mississippian, such as *Oxroadia* and *Paurodendron* (Figs. 11, 12). The precise nature of the architectures of these two groups merits close re-examination to explore the possibility that their branches are nonhomologous. This task would be greatly enhanced if more complete reconstructions could be achieved for shrub- to tree-sized rhizomorphic lycopsids of the late Devonian and Mississippian, such as *Leptophloeum* (Wang et al., 2005) and *Valmeyerodendron* (Jennings, 1972), respectively. In either case, a combination of developmental stage deletion and various modes of paedomorphosis remain the most credible explanation for the apparently independent origins of the small-bodied, pseudo-herbaceous genera *Oxroadia*, *Paurodendron*, and *Hizemodendron* (Bateman and DiMichele, 1991; Bateman, 1992, 1994).

Finally, our previous analyses of architectural transitions among the rhizomorphic lycopsids were a major impetus to our development of a modern theory of saltational evolution, defined as “a genetic modification that is expressed as a

profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage” (Bateman, 1994; Bateman and DiMichele, 1994, 2002). The idea of a nongradualistic framework for macroevolution has since progressively accumulated adherents (e.g., Rutishauser, 1995; Carrión and Cabezudo, 2003; Vergara-Silva, 2003; Theißen, 2006, 2009; Ziermann et al., 2009; Zander 2010; Reuveni and Giuliani, 2012; Rosenblum et al., 2012), and we remain committed to its basic principles. In the case of the multiple transitions from dominant lateral branching to exclusive crown-branching that are the focus of this paper, it is extremely difficult to envisage a mechanism that would allow a transition from one architecture to the other that was gradual. Rather, the sudden suppression of a simple developmental switch that previously permitted lateral branching remains a far more credible evolutionary mechanism.

We will close this essay by balancing our speculative conclusion with a pertinent cautionary quote from Thomas Allan’s 1823 (p. 236) discussion of “the bark of a vegetable [presumed to be] connected with the Palm-tribe” that is reproduced herein as Fig. 7a: “... these unknown species of vegetables ... give us a glimpse of former periods, which sets conjecture at defiance, and smiles at the vain attempts of theory to unravel.”

LITERATURE CITED

- ALLAN, T. 1823. Description of a vegetable impression found in the quarry of Craighleith. *Transactions of the Royal Society of Edinburgh* 9: 235–238.
- BATEMAN, R. M. 1992. Morphometric reconstruction, palaeobiology and phylogeny of *Oxroadia gracilis* Alvin emend. and *O. conferta* sp. nov.: Anatomically-preserved rhizomorphic lycopsids from the Dinantian of Oxroad Bay, SE Scotland. *Palaeontographica B* 228: 29–103.
- BATEMAN, R. M. 1994. Evolutionary-developmental change in the growth architecture of fossil rhizomorphic lycopsids: Scenarios constructed on cladistic foundations. *Biological Reviews of the Cambridge Philosophical Society* 69: 527–597.
- BATEMAN, R. M., AND W. A. DiMICHELE. 1991. *Hizomodendron*, gen. nov., a pseudoherbaceous segregate of *Lepidodendron* (Pennsylvanian): Phylogenetic context for evolutionary changes in lycopsid growth architecture. *Systematic Botany* 16: 195–205.
- BATEMAN, R. M., AND W. A. DiMICHELE. 1994. Saltational evolution of form in vascular plants: A neoGoldschmidian synthesis. In D. S. Ingram and A. Hudson [eds.], *Shape and form in plants and fungi*, 63–102. Linnean Society, London, UK.
- BATEMAN, R. M., AND W. A. DiMICHELE. 2002. Generating and filtering major phenotypic novelties: neoGoldschmidian saltation revisited. In Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins [eds.], *Developmental genetics and plant evolution*, 109–159. Taylor & Francis, London, UK.
- BATEMAN, R. M., W. A. DiMICHELE, AND D. A. WILLARD. 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: An essay in paleobotanical phylogenetics. *Annals of the Missouri Botanical Garden* 79: 500–559.
- BATEMAN, R. M., AND J. HILTON. 2009. Palaeobotanical systematics for the phylogenetic age: Applying organ-species, form-species and phylogenetic species concepts in a framework of reconstructed fossil and extant whole-plants. *Taxon* 58: 1254–1280.
- CARRIÓN, J. S., AND B. CABEZUDO. 2003. Perspectivas recientes en evolución vegetal. *Annals of Biology* 25: 163–198.
- CECIL, C. B., AND F. T. DULONG. 2003. Precipitation models for sediment supply in warm climates. In C. B. Cecil and N. T. Edgar [eds.], *Climate controls on stratigraphy*, 21–27. *Society of Sedimentary Petrology SEPM Special Publication* 77.
- CHITALEY, S., AND K. B. PIGG. 1996. *Clevelandodendron ohioensis*, gen. et sp. nov., a slender upright lycopsid from the Late Devonian Cleveland Shale of Ohio. *American Journal of Botany* 83: 781–789.
- CLEAL, C. J., AND Z. WANG. 2002. A new and diverse plant fossil assemblage from the upper Westphalian Benxi Formation, Shanxi, China, and its palaeofloristic significance. *Geological Magazine* 139: 107–130.
- CRESSLER, W. L. III, AND H. W. PFEFFERKORN. 2005. A Late Devonian isoetalean lycopsid, *Otzinachsonia beerboweri*, gen. et sp. nov., from north-central Pennsylvania, USA. *American Journal of Botany* 92: 1131–1140.
- DiMICHELE, W. A. 1979a. Arborescent lycopsids of Pennsylvanian age coals: *Lepidodendron dicentricum* C. Felix. *Palaeontographica B* 171: 122–136.
- DiMICHELE, W. A. 1979b. Arborescent lycopsids of Pennsylvanian age coals: *Lepidophloios*. *Palaeontographica B* 171: 57–77.
- DiMICHELE, W. A. 1980. *Paralycopodites* Morey & Morey, from the Carboniferous of Euramerica: A reassessment of the generic affinities and evolution of “*Lepidodendron*” *brevifolium* Williamson. *American Journal of Botany* 67: 1466–1476.
- DiMICHELE, W. A. 1981. Arborescent lycopsids of Pennsylvanian age coals: *Lepidodendron*, with description of a new species. *Palaeontographica B* 175: 85–125.
- DiMICHELE, W. A. 1983. *Lepidodendron hickii* and generic delimitation in Carboniferous lepidodendrid lycopsids. *Systematic Botany* 8: 317–333.
- DiMICHELE, W. A. 1985. *Diaphorodendron* gen. nov., a segregate from *Lepidodendron* (Pennsylvanian age). *Systematic Botany* 10: 453–458.
- DiMICHELE, W. A., AND R. M. BATEMAN. 1992. Diaphorodendraceae, fam. nov. (Lycopsidea: Carboniferous): Systematics and evolutionary relationships of *Diaphorodendron* and *Synchysidendron*, gen. nov. *American Journal of Botany* 79: 605–617.
- DiMICHELE, W. A., AND R. M. BATEMAN. 1993. Validation of *Synchysidendron* gen. nov. (Fossiles). *Taxon* 42: 647–648.
- DiMICHELE, W. A., AND R. M. BATEMAN. 1996a. The rhizomorphic lycopsids: A case-study in paleobotanical classification. *Systematic Botany* 21: 535–552.
- DiMICHELE, W. A., AND R. M. BATEMAN. 1996b. Plant paleoecology and evolutionary inference: Two examples from the Paleozoic. *Review of Palaeobotany and Palynology* 90: 223–247.
- DiMICHELE, W. A., J. F. MAHAFFY, AND T. L. PHILLIPS. 1979. Lycopsids of Pennsylvanian age coals: *Polysporia*. *Canadian Journal of Botany* 57: 1740–1753.
- DiMICHELE, W. A., AND T. L. PHILLIPS. 1985. Arborescent lycopsid reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois). *Review of Palaeobotany and Palynology* 44: 1–26.
- DiMICHELE, W. A., AND T. L. PHILLIPS. 1988. Paleoecology of the Middle Pennsylvanian-age Herrin coal swamp near a contemporaneous river system, the Walshville Paleochannel. *Review of Palaeobotany and Palynology* 56: 151–176.
- EGGERT, D. A. 1961. The ontogeny of Carboniferous arborescent Lycopsidea. *Palaeontographica B* 108: 43–92.
- EGGERT, D. A., AND N. Y. KANEMOTO. 1977. Stem phloem of a Middle Pennsylvanian *Lepidodendron*. *Botanical Gazette* 138: 102–111.
- ELRICK, S. D., AND W. J. NELSON. 2010. Facies relationships of the Middle Pennsylvanian Springfield Coal and Dykersburg Shale: Constraints on sedimentation, development of coal splits and climate change during transgression. *Geological Society of America (North-Central Section) Abstracts with Programs* 42: 51.
- GASTALDO, R. A., H. W. PFEFFERKORN, AND W. A. DiMICHELE. 1995. Characteristics and classification of Carboniferous roof shale floras. In P. C. Lyons, E. D. Morey, and R. H. Wagner [eds.], *Historical perspectives of early twentieth century Carboniferous paleobotany in North America*, 341–352. Geological Society of America Memoir 185.
- GENSEL, P. G., AND K. B. PIGG. 2010. An arborescent lycopsid from the Lower Carboniferous Price Formation, southwestern Virginia, USA and the problem of species delimitation. *International Journal of Coal Geology* 83: 132–145.
- GREEN, W. 2010. The function of the aerenchyma in arborescent lycopsids: Evidence of an unfamiliar metabolic strategy. *Proceedings of the Royal Society, B, Biological Sciences* 277: 2257–2267.

- HALLÉ, F., R. A. A. OLDEMAN, AND P. B. TOMLINSON. 1978. Tropical trees and forests: An architectural analysis. Springer, Berlin, Germany.
- JENNINGS, J. R. 1972. A new lycopod genus from the Salem Limestone (Mississippian) of Illinois. *Palaeontographica, B* 137: 72–84.
- JENNINGS, J. R., E. E. KARRFALT, AND G. W. ROTHWELL. 1983. Structure and affinities of *Protostigmaria eggertiana*. *American Journal of Botany* 70: 963–974.
- JONKER, F. P. 1976. The Carboniferous “genera” *Ulodendron* and *Halonia*—An assessment. *Palaeontographica, B* 157: 97–111.
- KIDSTON, R., AND W. H. LANG. 1920. On Old Red Sandstone plants showing structure from the Rhynie Chert Bed, Aberdeenshire, 3. *Asteroxylon mackiei* Kidston & Lang. *Transactions of the Royal Society of Edinburgh* 52: 643–680.
- LONG, A. G. 1979. Observations on the Lower Carboniferous genus *Pitus* Witham. *Transactions of the Royal Society of Edinburgh B* 70: 111–127.
- MILLAR, J. 1827. *Encyclopaedia edinensis*. J. Anderson, Edinburgh, UK.
- OGG, J. G., G. OGG, AND F. M. GRADSTEIN. 2008. The concise geologic time scale. Cambridge University Press, New York, New York, USA.
- OPLUŠTIL, S. 2010. Contribution to knowledge on ontogenetic developmental stages of *Lepidodendron mannebachense* Presl, 1838. *Bulletin of Geosciences* 85: 303–316.
- PHILLIPS, T. L. 1979. Reproduction of heterosporous arborescent lycopsids in the Mississippian-Pennsylvanian of Euramerica. *Review of Palaeobotany and Palynology* 27: 239–289.
- PHILLIPS, T. L., AND W. A. DiMICHELE. 1981. Paleoeecology of Middle Pennsylvanian age coal swamps in southern Illinois—Herrin Coal Member at Sahara Mine No. 6. In K. J. Niklas [ed.], *Paleobotany, paleoeecology and evolution*, vol. 1, 231–285. Praeger, New York, New York, USA.
- PHILLIPS, T. L., AND W. A. DiMICHELE. 1992. Comparative ecology and life-history biology of arborescent lycopsids in Late Carboniferous swamps of Euramerica. *Annals of the Missouri Botanical Garden* 79: 560–588.
- PIGG, K. B. 2001. Isoetalean lycopoid evolution: From the Devonian to the Present. *American Fern Journal* 91: 99–114.
- PIGG, K. B., AND G. W. ROTHWELL. 1983. *Chaloneria* gen. nov.; heterosporous lycopoides from the Pennsylvanian of North America. *Botanical Gazette* 144: 132–147.
- RAVN, R. L. 1986. Palynostratigraphy of the Lower and Middle Pennsylvanian coals of Iowa. *Iowa Geological Survey Technical Paper* 7: 1–224.
- REUVENI, E., AND A. GIULIANI. 2012. Emergent properties of gene evolution: Species as attractors in phenotypic space. *Physica A* 391: 1172–1178.
- ROSENBLUM, E. B., B. A. J. SARVER, J. W. BROWN, S. DES ROCHES, K. M. HARDWICK, T. D. HETHER, ET AL. 2012. Goldilocks meets Santa Rosalia: An ephemeral speciation model explains patterns of diversification across time scales. *Evolutionary Biology* 39: 255–261.
- ROTHWELL, G. W. 1984. The apex of *Stigmaria* (Lycopsidea), rooting organ of the Lepidodendrales. *American Journal of Botany* 71: 1031–1034.
- RUTISHAUSER, R. 1995. Developmental patterns of leaves in Podostemaceae compared with more typical flowering plants: Saltational evolution and fuzzy morphology. *Canadian Journal of Botany* 73: 1305–1317.
- SANDERS, H., G. W. ROTHWELL, AND S. E. WYATT. 2011. Parallel evolution of auxin regulation in rooting systems. *Plant Systematics and Evolution* 291: 221–225.
- SCOTT, D. H. 1906. The structure of *Lepidodendron obovatum* Sternb. *Annals of Botany* 20: 317–319.
- SEWARD, A. C. 1902. On the so-called phloem of *Lepidodendron*. *New Phytologist* 1: 38–46.
- SHUTE, C. H., AND C. J. CLEAL. 1987. Palaeobotany in museums. *Geological Curator* 4: 553–559.
- SOKOLOWSKA, K., AND B. ZAGÓRSKA-MAREK. 2012. Symplasmic, long-distance transport in xylem and cambial regions in branches of *Acer pseudoplatanus* (Aceraceae) and *Populus tremula* × *P. tremuloides* (Salicaceae). *American Journal of Botany* 99: 1745–1755.
- SWOFFORD, D. L. 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer, Sunderland, Massachusetts, USA.
- TAYLOR, T. N., E. L. TAYLOR, AND M. KRINGS. 2009. *Paleobotany: The biology and evolution of fossil plants*, 2nd ed. Academic Press, New York, New York, USA.
- THEIßEN, G. 2006. The proper place of hopeful monsters in evolutionary biology. *Theory in Biosciences* 124: 349–369.
- THEIßEN, G. 2009. Saltational evolution: Hopeful monsters are here to stay. *Theory in Biosciences* 128: 43–51.
- THOMAS, B. A. 1967. *Ulodendron* Lindley and Hutton and its cuticle. *Annals of Botany* 31: 775–782.
- VERGARA-SILVA, F. 2003. Plants and the conceptual articulation of evolutionary developmental biology. *Biology and Philosophy* 18: 249–284.
- WANG, Q., B.-Y. GENG, AND D. L. DILCHER. 2005. New perspective on the architecture of the Late Devonian arborescent lycopoid *Leptophloeum rhombicum* (Leptophloeaceae). *American Journal of Botany* 92: 83–91.
- WANG, Q., S.-G. HAO, D.-M. WANG, Y. WANG, AND T. DENK. 2003. A Late Devonian arborescent lycopoid *Sublepidodendron songziense* Chen emend. (Sublepidodendraceae Kräusel et Weyland 1949) from China, with a revision of the genus *Sublepidodendron* (Nathorst) Hirmer 1927. *Review of Palaeobotany and Palynology* 127: 269–305.
- WANG, Z.-Q., AND A.-S. CHEN. 2001. Traces of arborescent lycopsids and dieback of the forest vegetation in relation to the terminal Permian mass extinction in North China. *Review of Palaeobotany and Palynology* 117: 217–243.
- WITHAM, H. T. M. 1833. The internal structure of fossil vegetables found in the Carboniferous and Oolitic deposits of Great Britain. A & C Black, Edinburgh, UK.
- WNUK, C. 1985. The ontogeny and paleoeecology of *Lepidodendron rimosum* and *Lepidodendron bretonense* trees from the Middle Pennsylvanian of the Bernice Basin (Sullivan County, Pennsylvania). *Palaeontographica B* 195: 153–181.
- ZANDER, R. H. 2010. Taxon mapping exemplifies punctuated equilibrium and atavistic saltation. *Plant Systematics and Evolution* 286: 69–90.
- ZIERMANN, J. G., M. RITZ, S. HAMEISTER, C. ABEL, M. H. HOFFMANN, B. NEUFFER, AND G. THEISSEN. 2009. Floral visitation and reproductive traits of *Stamenoid Petals*, a naturally occurring floral homeotic variant of *Capsella bursa-pastoris* (Brassicaceae). *Planta* 230: 1239–1249.