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Author(s): Peter Giesen and Christopher M. Berry

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RECONSTRUCTION AND GROWTH OF THE EARLY TREE *CALAMOPHYTON* (PSEUDOSPOROCHNALES, CLADOXYLOPSIDA) BASED ON EXCEPTIONALLY COMPLETE SPECIMENS FROM LINDLAR, GERMANY (MID-DEVONIAN): ORGANIC CONNECTION OF *CALAMOPHYTON* BRANCHES AND *DUISBERGIA* TRUNKS

Peter Giesen* and Christopher M. Berry¹†

*Wettiner Strasse 55, 42287 Wuppertal, Germany; and †School of Earth and Ocean Sciences, Cardiff University,
Main Building, Park Place, Cardiff CF10 3YE, Wales, United Kingdom

Middle Devonian Pseudosporochnales (Cladoxylopsida) are among the earliest tree-sized plants in the fossil record. We describe here new and spectacular complete specimens of *Calamophyton primaevum* Kräusel et Weyland from Lindlar (Eifelian, early Mid-Devonian), Germany. These demonstrate for the first time roots, trunk bases, trunks, trunk apices, and crowns of attached digitate branches in organic connection for multiple specimens of one taxon of pseudosporochnaleans from the same horizon. Completely preserved trunks are between 0.8 and 2.0 m long. Middle portions of the trunks demonstrate that the branches were abscised a short distance from the trunk surface, leaving branch bases of consistent length superficially similar to leaves. Such trunks and “leaves” were previously named *Duisbergia mirabilis* Kräusel et Weyland. Trunk diameter decreases distally in the lower half of the trunk but usually increases distally below the top. Some trunks may have divided dichotomously. The trunk apex is domed and takes up the entire width of the top of the trunk, up to 100 mm in diameter. Overall, the new evidence is not consistent with existing models of pseudosporochnalean growth. The suite of specimens suggests that the upward-growing primary body of the trunk increased in diameter, reaching a mature diameter ~1–2 m from the ground. Lower parts of the plant are therefore likely to have increased in diameter by a process of secondary growth.

Keywords: Devonian, fossil, Pseudosporochnales, forests.

Introduction and Background

Members of Pseudosporochnales (Cladoxylopsida) are central to current discussions of the origin of forest ecosystems in the Mid- and Late Devonian epochs. Genera of Pseudosporochnales are established on the basis of branch and appendage morphology (Berry 2000). Reconstructions of *Pseudosporochnus nodosus* Leclercq et Banks (late Eifelian) and an unidentified species of *Wattieza* Stockmans (Givetian to Frasnian), based on increasingly complete specimens (Berry and Fairon-Demaret 2002; Stein et al. 2007) as well as a juvenile specimen of *Lorophyton goense* Fairon-Demaret et Li (1993), have led to an accurate understanding of the whole-plant morphology of individuals. These have a vertical trunk with an enlarged, upward-tapering base and densely inserted digitate lateral branches, forming a crown, that were abscised as the plant grew taller. However questions remain about the morphology of the trunk apex, the ontogeny of Pseudosporochnales, and the whole-plant morphology of the earliest currently recognized member of the group, *Calamophyton primaevum* Kräusel et Weyland (Eifelian-Givetian).

On the basis of specimens he collected from Lindlar, Germany (Middle Eifelian), in the 1960s, Schweitzer (1973, 2009)

provided a whole-plant reconstruction of *C. primaevum*. He recognized *C. primaevum* branches on the basis of complex digitate ramification and characteristic complex fertile appendages. He did not, however, convincingly demonstrate the connection between such branches and a trunk. Schweitzer's reconstruction of *C. primaevum* contradicts current reconstructions of Pseudosporochnales because of (1) lax insertion of the lateral branches and (2) the termination of the trunk in a digitate apex that appears determinate. *Duisbergia mirabilis* Kräusel et Weyland (1929) was based on material from Germany. The principal fragments may have come from only one plant collected at the Kirberg locality (Middle Givetian), the width of the stem of which was only partially preserved. Attached on one side of the stem were a number of broadening, flat, striated structures interpreted as “leaves.” Carbonaceous strands in the trunk suggested a polystelic vasculature. Kräusel and Weyland also illustrated what were interpreted as large sporangia between the “leaves,” in a specimen from Gräfrath (Upper Eifelian). In 1934, the same authors illustrated broad bases of new specimens from the Kronprinzenallee locality, although the key trunk and base specimens were only temporarily exposed and therefore only briefly examined by one of the authors (Kräusel and Weyland 1934). Nonetheless, they were supposed to have demonstrated the presence of attached “leaves” toward the top of the trunk. On this basis, they provided a reconstruction showing an enlarged, upward-tapering

¹ Author for correspondence; e-mail: berrycm@cf.ac.uk.

base up to ~24 cm wide and a “leafy” stem up to ~2 m long (see fig. 1a). A second reconstruction had a once-divided trunk. In 1938, they illustrated a long *Duisbergia* stem with “leaves” on both sides that appeared to radiate from a narrow central axis (Kräusel and Weyland 1938). This specimen and its counterpart have recently been located in the museum of the Town Hall “Bergischer Löwe” in Bergisch Gladbach. Preparation of the counterpart shows that the main axis was much broader (3 cm; see fig. 2b) than suggested by the original illustrations. This specimen demonstrates the “leafy” appearance characterizing *D. mirabilis*, as understood by Kräusel and Weyland.

Schweitzer (1966) illustrated *D. mirabilis* from Lindlar, including trunks with short “leaves” and the impressions of bases of “leaves” arranged in longitudinal rows. He also illustrated large, upward-tapering trunk bases up to 30 cm in diameter with suggestions of a complex vascular system. However, there were no specimens showing connection between the trunk bases and the main “leafy” trunks and no distal parts of the trunks. His new reconstruction of *Duisbergia* was not dissimilar from that of Kräusel and Weyland, but it suggested very dense insertion of “leaves” in longitudinal rows on the distal part of an otherwise naked, narrowing trunk. The “leaves” got shorter toward the top of the trunk. He provisionally placed *Duisbergia* in Lycopsidea.

Mustafa (1976, 1978b) described new specimens of *D. mirabilis*, principally from the Köster Quarry (Upper Eifelian) near Hagen-Ambrock, that included both “leafy” trunks and permineralizations. Rare specimens (e.g., CP 719; palaeobotany collection, Münster University) display both “leafy” morphology and permineralized trunk tissues. Mustafa (1978b) recognized that the trunk contained anatomy typical of cladoxyloids.

In this article, we present new, spectacular, almost complete specimens of *Duisbergia* from Lindlar that show in connection the trunk base, the trunk, the trunk apex, and digitate *Calamophyton* lateral branches in vertical ranks distally that, in abscising, left leaf-like stubs on the trunk. This allows a new understanding of the morphology of possibly the earliest tree form (fig. 1b, 1c). Furthermore, the unique nature of the assemblage of whole-plant fossils and the unexpected morphology of the trunk allow consideration of issues related to the growth and ontogeny of pseudosporochnalean cladoxyloids, especially in comparisons to models of the growth of the Late Devonian cladoxyloid *Pietzschia* Gothan (Meyer-Berthaud et al. 2010).

Material and Methods

Plant fossils have been reported from the quarry operated by Otto Schiffarth Steinbruch in Lindlar, Rhineland, for almost 50 years (Schweitzer 1966, 1972, 1973, 1974, 2009). The sandstones extracted are from the Mühlenberg beds. Almost all of the material described by Schweitzer was obtained in the early 1960s from a small sandstone lens, 3 m × 4 m × 0.6 m, ~1 m below a prominent mudstone layer (fig. 2 of Schweitzer 1966). Quarrying operations removed the bedrock to form a vertical face, extending for ~10 m above and 50 m below the fossiliferous horizon, thus effectively ending fossil discoveries at the site.

The main source of new material is a large block from a

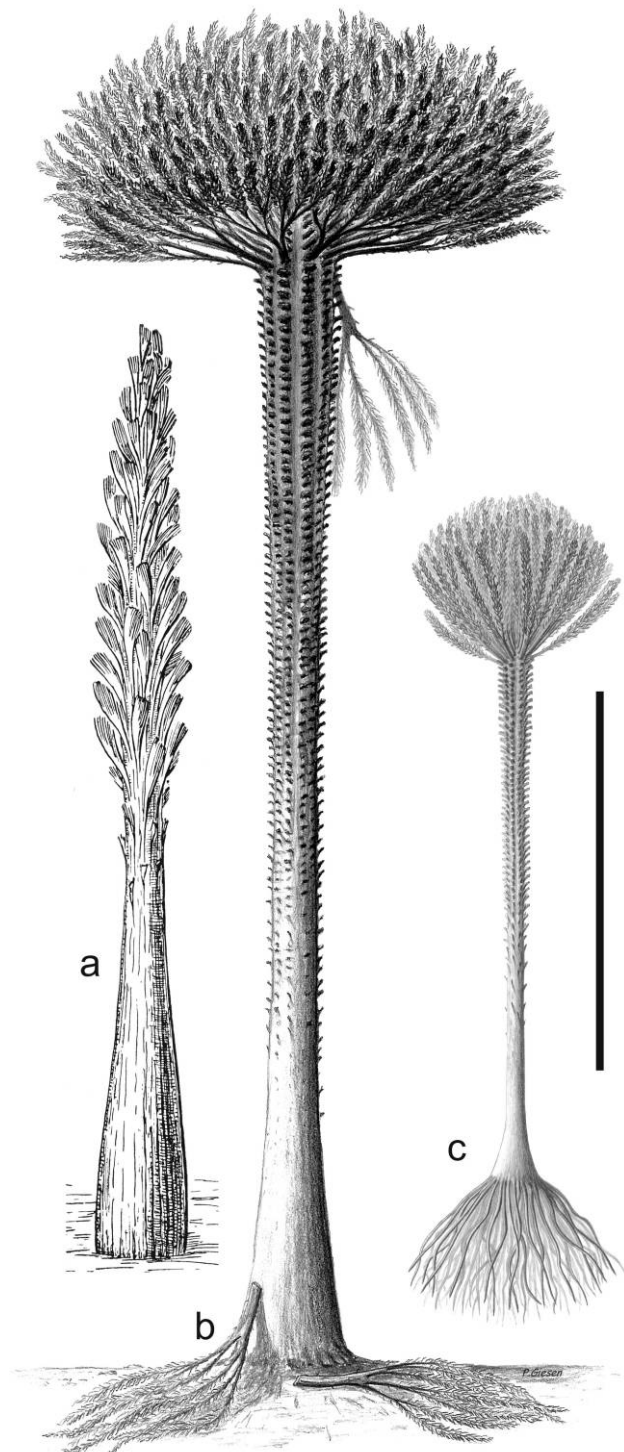


Fig. 1 a, Reconstruction of *Duisbergia mirabilis* by Kräusel and Weyland (1934). b, c, New reconstructions of large and juvenile specimens based on trunks A (b; fig. 5) and 5 (c; fig. 7d). Scale bar = 0.5 m.

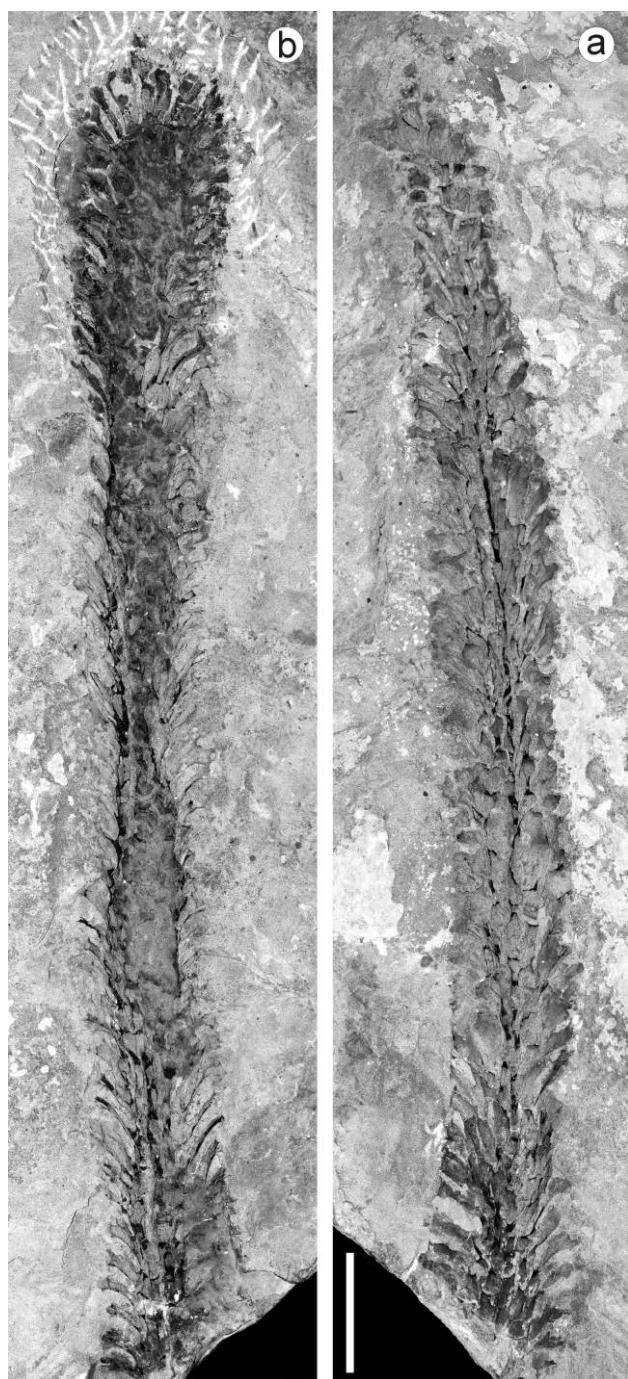


Fig. 2 *Duisbergia mirabilis* Kräusel et Weyland; unnumbered specimen, Bergisch Gladbach Museum fossil collection. *a*, Part, suggesting a narrow stem with long leaves; cf. figs. 1–3 of Kräusel and Weyland (1938). *b*, Counterpart, degaged to demonstrate full width of trunk. Scale bar = 50 mm.

new working ledge high on the west side of the quarry at the same horizon as Schweitzer's lens, ~1 m below the mudstone bed (fig. 3*a*, arrow). The sandstone block measures 2.45 m × 0.6 m × 0.3 m. In 2008, Peter Giesen discovered a fragmentary *Duisbergia* trunk bearing *Calamophyton* branches on the sur-

face of the block (fig. 11*a*). Extraction (fig. 3*a*) was initially prevented by the hardness of the massive sandstone unit, but a large rootball (figs. 4, 5; stump C, fig. 6*b*) broke free. Splitting the sandstone finally revealed the presence of complete plants within (fig. 4). Recovery of the entire block was achieved in April 2009 with the use of a diamond rock saw and assistance by students from Bonn University led by Dr. Georg Heumann and Rolf Goßmann.

The block appears to be the edge of a channel-like fill or elongate submarine scour (fig. 3*a*) within generally cross-bedded sandstones. The sandstones at this level are gray-green to yellow, with much iron staining. On the east side and beneath, the block was easily separated from a natural scoured surface. However, on the west side (fig. 3*a*, left), the block had to be cut free of the rest of the “channel” fill, which was less fossiliferous and more sandy. There are plant fossils all through the block, but the most prominent are two complete plants that are preserved from the roots up to their apices and branches, aligned with the apices pointing north. These occurred just on top of a level several centimeters thick that contains the molds of numerous large crinoid ossicles and dark mudstone clasts. Crinoid ossicles are also present in lesser concentrations through much of the block. The juxtaposition of excellently preserved terrestrial plant fossils and marine bioclasts indicates deposition close to the marine/terrestrial interface, and the tight packing of the plant fossils within the “channel” suggests a catastrophic depositional event.

Approximately 30 m south, in the highwall of the quarry, several small trunks were preserved in an oblique, almost upright, orientation in the massive sandstone bed between the scoured surface and the overlying mudstone unit, with their bases (including roots) at differing levels and lacking any paleosol (see fig. 3*b*). These are not in life position but were probably deposited during a single sedimentation event. Similar material was collected laterally in the same horizon.

Further research in a neighboring quarry (Bergische Grauwacke Steinbruch [BGS]) in spring 2010 led to the discovery of the same horizon ~300 m west of the Schiffarth site, which yielded further, almost completely preserved fossil plants. The fossiliferous lenses in the Schiffarth quarry are therefore not just local phenomena. The sedimentological features associated with the widespread horizon—e.g., eroded base, angular mud clasts, marine bioclasts up to 10 cm in diameter, graded bedding, and many complete land plants—strongly suggest a deposit laid down during and immediately after a single high-energy terrestrial/coastal flooding event. Although most of the sandstones quarried in the Lindlar area are shallow marine storm sediments (H. Bahlburg, Münster University, personal communication), the features observed within the fossiliferous layer are unique in the exposed Mühlenberg beds. A tsunami origin cannot be discounted.

The plant fossils have little sand within them, unlike some other cladoxylpsid trunk material (e.g., Goé, Gilboa). Rather, the trunks are preserved as compressions or with a thin layer of highly degraded limonite infill, with some carbonaceous preservation of the longitudinal xylem strands. Branches are usually found as compressions.

Schweitzer's original specimens are problematic to locate because repositories were rarely stated in his publications. Much of his collection is now housed in the Swedish Museum

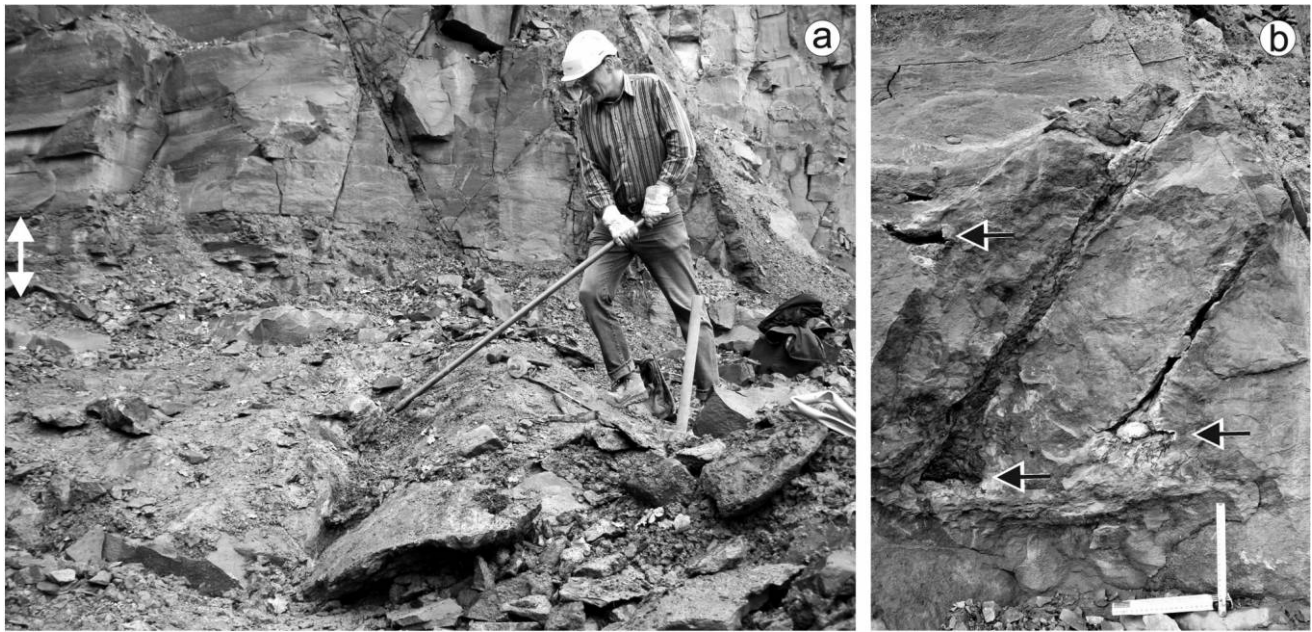


Fig. 3 *a*, P. Giesen trying to remove the large fossiliferous sandstone block at Schiffarth Quarry, Lindlar. The crowbar rests on the right-hand side of the scoured surface, visible in profile in the center foreground, in which the fossiliferous block is sitting. Arrow shows extent of the overlying mudstone layer. *b*, Three *Calamophyton* trunks in situ in the highwall at the Schiffarth Quarry, Lindlar. Bedding is horizontal, and the trunks are oblique to bedding. Arrows indicates bases. The middle trunk is GQ1, and the trunk on the right is GQ2. Vertical scale = 0.22 m.

of Natural History in Stockholm. Other material is in the Goldfuss Museum, Bonn University, and the Ruhr Museum, Essen (fossils from the now closed Fuhlrott Museum, Wuppertal). Some of this material, figured and unfigured, has been used in this research. Finally, from the Schiffarth Quarry, Lindlar, we studied collections made in the 1960s by Friedrich Rochow, also now in the Ruhr Museum, that are presumed to come from the same level as Schweitzer's material. All new material described in this work is in the Goldfuss Museum of the Steinmann Institute for Geology, Palaeontology and Mineralogy, Bonn University, prefix PG MD. The age of the Lindlar deposit is regarded as Mid-Eifelian on the basis of palynology and lithostratigraphic correlation (Riegel 1968; Streele et al. 1987; Fairon-Demaret and Berry 2000).

Taxonomy and Circumscription of Taxa

Pseudosporochnalean cladoxyloids are best recognized at the generic level by the morphology of the sterile and fertile appendages that are carried on the branches (Berry 2000). *Calamophyton primaevum* Kräusel et Weyland in Weyland (1925), from Kirberg, is the most completely understood and perhaps the only species currently recognized within the genus (see history and discussion in Fairon-Demaret and Berry 2000); the fertile appendage bears three pairs of elongate sporangia on short, recurved stalks on each of two daughter axes distal to a bifurcation of the terete proximal axis (Leclercq and Andrews 1960; Bonamo and Banks 1966; Leclercq 1969). In this article, on the basis of material from Lindlar, *C. primaevum* branches are demonstrated to be attached to the distal end of *Duisbergia mirabilis* trunks. Abscission of most of the

branches left short branch bases attached to the trunk, which in certain conditions of preservation look like leaves. The type localities for *C. primaevum* and *D. mirabilis* are the Middle Givetian quarry at Kirberg, and therefore it seems very likely that the two plant fossil species, as originally defined (Weyland 1925; Kräusel and Weyland 1929), came from the same plant taxon. However, we cannot be sure that no other cladoxylopid plants had trunks with abscising branches giving the form of *D. mirabilis*. In light of current changes in the International Code of Nomenclature concerning fossil plants (Miller et al. 2011), as well as the considerable age difference between Kirberg and Lindlar, we do not propose a formal synonymy at this time. We add to our concept the bases, roots, trunks, and anatomy of fossils from other locations and stratigraphic levels in Germany, including Lindlar. We can call our conceptual whole-plant construct the "*Calamophyton primaevum* plant."

Duisbergia macrocaticosus Mustafa (1978a) is a single trunk specimen from Germany (Hagen-Ambrock, Upper Eifelian) that demonstrates large branch scars that are more or less flush with the surface. As proposed by Berry and Fairon-Demaret (1997, p. 368), and subsequently demonstrated (Fairon-Demaret and Berry 2000; Stein et al. 2007), *D. macrocaticosus* belongs to a cladoxylopid such as *Pseudosporochnus* or *Wattieza*, where branches are shed complete, rather than to *Calamophyton*, where abscission takes place a few centimeters above the base of the branch.

The status of the genus *Hyenia* has been questioned, because the only remaining specimen from the type collection of *Hyenia elegans* (Kräusel et Weyland 1926) was shown to have the same fertile-appendage morphology as *Calamophyton* (Fairon-Demaret and Berry 2000). Schweitzer (2009) robustly de-

fended the genus and its existence at Lindlar. He provided a reconstruction of the plant (Schweitzer 1972) with a rhizome, following Kräusel and Weyland (1932), among others. *Hyenia*, following Kräusel and Weyland and Schweitzer, also has fertile appendages with a single bifurcation and two pairs of recurved sporangia. Pending our further work on considerable new material, references to *Hyenia* at Lindlar in this article refer to the concept of *H. elegans* as defined by Schweitzer (1972, 2009).

Description

The most important new fossils are two more or less complete *Calamophyton primaevum* plants from the sandstone block in Schiffarth Quarry, A and B (figs. 4, 5), as they provide overwhelming evidence for the whole-plant reconstruction. Both show an expanded trunk base, thin, strap-like roots, and a trunk of the *Duisbergia mirabilis* type. The trunks have no laterals near the base but show increasingly well preserved branch bases distally, arranged in longitudinal ranks. Near the top of the trunk, complete branches are attached in a close crown. These branches show complex digitate branching and have dichotomous sterile appendages, together characteristic of *C. primaevum*.

Trunk A, the longest in the extracted block, is 1.46 m in length, and trunk B is 1.26 m long, excluding roots. Both trunks are 130 mm in width at the base and ~50 mm in diameter at the mid-length. A third, almost complete but smaller plant 0.8 m long, 60 mm in diameter at the base, and 20 mm in diameter mid-length was revealed crossing the sandstone block obliquely (trunk 5 in fig. 5; also fig. 7d). Two further trunks, including the longest complete trunk so far of 2 m, were found at the BGS locality.

An important new observation is the presence of the complete top of the trunk in some specimens. This is approximately hemispherical or flattened-hemispherical in shape, taking up the whole of the width of the supporting trunk. In this account, this is called the “trunk apex.” The apical meristem is presumed to form a (small) part of this structure. Details of the trunks are described in the relevant sections below, supported by details of the numerous other trunks, apices, and branches preserved or extracted in a more fragmentary state.

Base and Roots

The bases of the trunks are not generally well preserved in three dimensions, lacking a firm sandstone infill. They contrast with the roots, where sand penetration between the roots prevented significant compaction of the rootmass, which retained its shape more robustly (fig. 6a, 6b). The very lowest part of the trunk consists of an apparently flat basal disk, from which the diameter of the trunk rapidly diminishes distally over the basal few centimeters before tapering further more gradually. There is sometimes a groove in the impression of laterally compressed bases that represents this widest portion of the trunk, the boundary between the basal disk and the upright trunk (fig. 6a, arrow). The diameters of the basal disks found vary with respect to the sizes of the plants. The disk diameter of the smallest whole plant (trunk 5 in fig. 5; also fig. 7d) is 60 mm, and that of the largest base is 200 mm. In almost all

examples, the basal disk is not preserved in its natural position with respect to the trunk, having been squashed and tilted usually by up to 45° and occasionally by more. This is clearly apparent in the specimens that were observed upright in the quarry wall (fig. 3b).

Individual compressions of roots are narrow (usually 2–5 mm in width, 4–6 mm on large bases), parallel sided, and undivided, have a smooth surface, and extend for up to at least 200 mm from the point of attachment to the trunk base (figs. 5, 6c, 6e, 6f); in the field, roots of large trunk bases reached lengths of more than 300 mm. The diameter diminishes rapidly over the distalmost few millimeters, resulting in a rather blunt tip (fig. 6f). There is an indication of a darker-colored central vascular strand that takes up ~30% of the width of the root (fig. 6g). In some rare cases, roots are preserved three-dimensionally by infill of sand replacing cortex. A transverse section of one root 3.5 mm in diameter reveals basic anatomy (fig. 6b). Such roots appear cylindrical, delimited by a black carbon layer of coalified epidermal cells. Centrally, there is a compressed carbon stele that appears as a complex actinostele ~1 mm across.

Most roots emerge from the basal disk of the trunk, going downward and outward with respect to the living plant. A very small number of possible roots have been observed in positions suggesting that they emerged from the trunk surface up to 50 mm above the basal disk, therefore possibly forming some sort of loose root skirt. The best-preserved base, C (figs. 5, 6a, 6b), shows a solid, truncated, cone-like mass of almost straight roots expanding away from the basal disk. This suggests that the roots, despite their narrowness, were rather stiff and were able to retain their life position despite violent transport. We can see no evidence that the roots were transported within a ball of soil to their place of deposition, as the sediment between the roots is indistinguishable from the remainder of the matrix.

Exposed surfaces, for example, on trunk base C (fig. 6a, 6b), show high numbers of densely crowded roots emerging on the entire surface of the basal disk. A base that allows a reasonable estimation of the root number is seen in figure 6c, 6d. The diameter of the basal disk is ~8 cm, that of the roots 2–3 mm. In transverse section (fig. 6d), there are approximately five to eight attached roots per square centimeter, suggesting that the total number on this rather small base was 250–400. Large bases, e.g., of trunk C, which seem to comprise a similar density of roots, must have had well over 1000.

Trunks

There are three essentially complete trunks with trunk apices in the large sandstone block from the Schiffarth Quarry (A, B, 5; figs. 4, 5). The largest of the specimens measured “standing” obliquely in the quarry wall (GQ1; fig. 3b) had attached branches at the expanding top and, while not including the actual apex, is probably almost complete. The two largest complete specimens were measured at the BGS locality, and at least one of these may be collected at some time in the near future. Diameters measured each 10 cm distally along the trunks, starting from 0 cm at the basal disk, are shown in figure 8.

Trunks: specimens A and B (figs. 4, 5, 7f, 7g, 9, 10). These two specimens are the best preserved and show features typical



Fig. 4 *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar: split inside surface of the large sandstone block, part (a) and counterpart (b), with two complete *Calamophyton* plants and several additional partial specimens. Line drawing interpretation is in fig. 5. Scale bar = 1 m. Specimen PG MD 37 A, B.

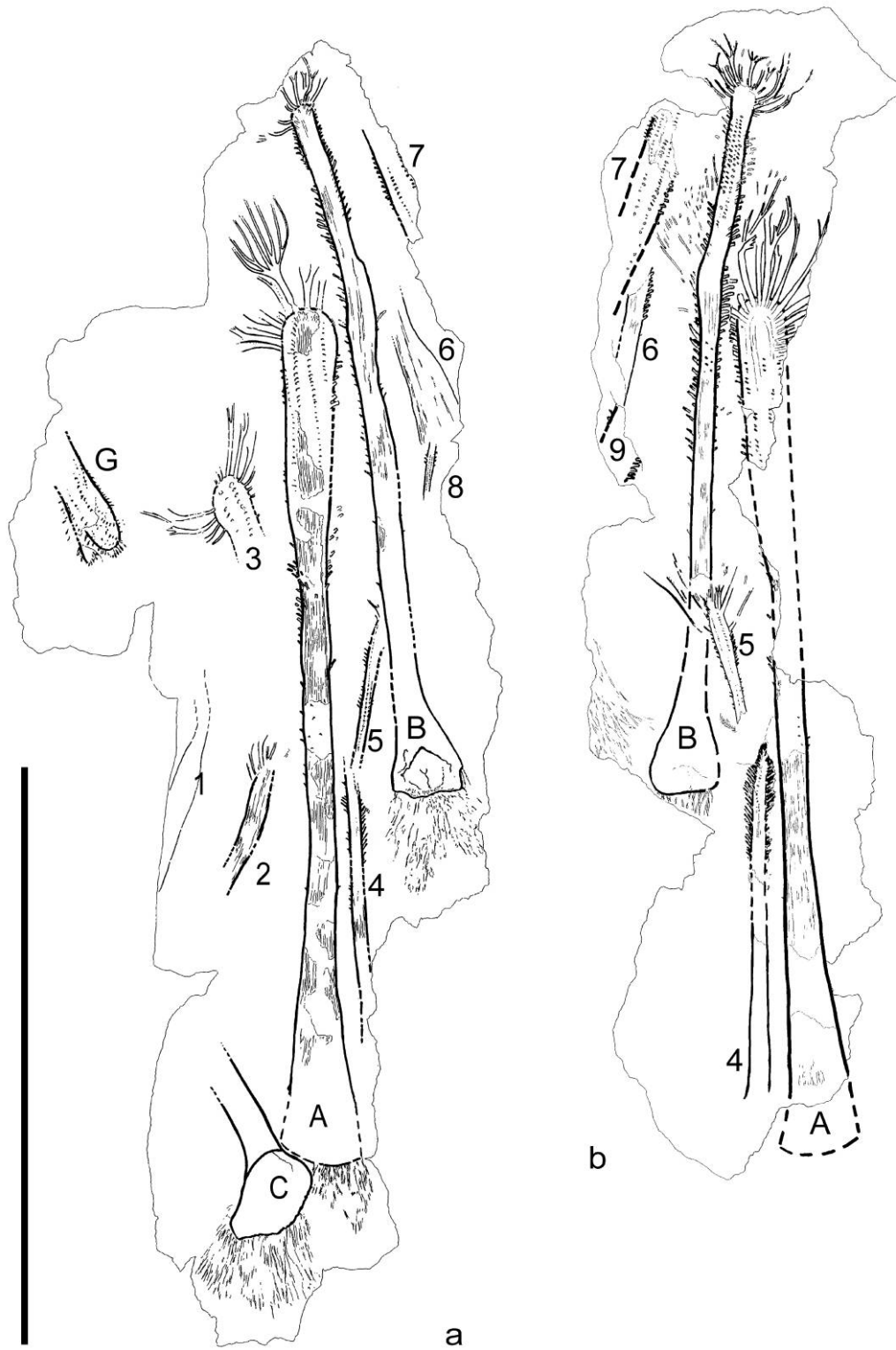


Fig. 5 Line drawing interpretation of surfaces of part (a) and counterpart (b) illustrated in fig. 4. Two complete *Calamophyton* plants, A and B, and a large, rooted base C are shown. Trunk 5 is also complete but is hidden within the surface of the slab in this view. Partial trunks 1, 2, 4, and 6–9, apex 3, and dividing apex G are also indicated. Scale bar = 1 m. Specimen PG MD 37 A, B.

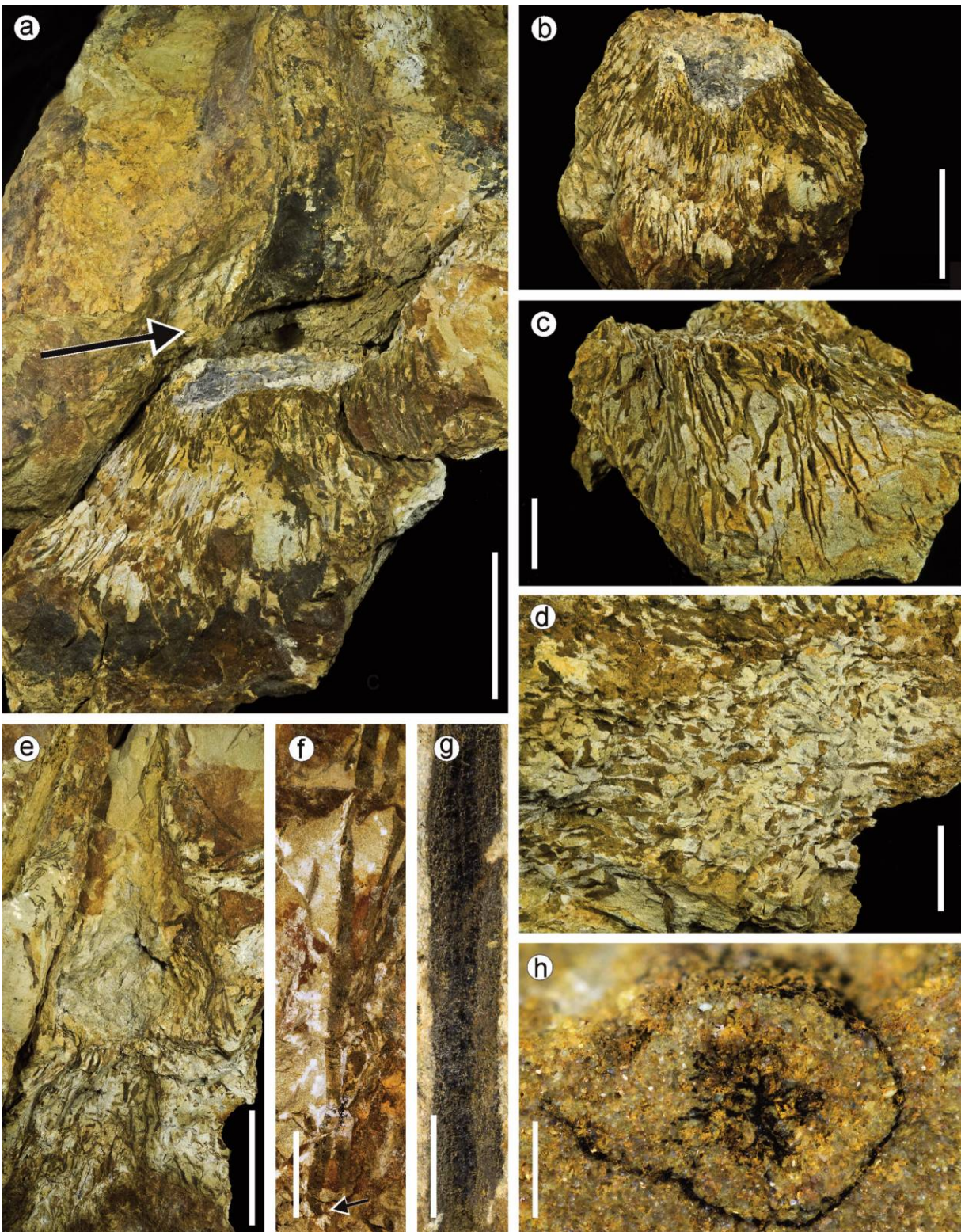


Fig. 6 Roots and bases of *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. *a, b*, Base and rootball of base C (see fig. 5*a*). Specimen PG MD 37 A. *a*, Base with rootball in place. The widest part of the base is represented by a deep groove (arrow). *b*, Rootball, which naturally separated from the main specimen, turned a little counterclockwise (when viewed from above) and top-rotated toward camera. *c, d*, Two views of a detached rootball, showing a lateral view with roots (*c*) and the top surface indicating the density of roots going down into matrix (*d*). Specimen PG MD 43 A. *e*, Base of trunk B (see fig. 5*a*), showing emerging roots. Specimen PG MD 37 A. *f*, Close-up of root in specimen

of the remainder of the material. A thick infill of powdery, degraded limonite makes up the bulk of the preservation, through which run longitudinally carbonaceous strands, best seen in trunk A (fig. 7f). These strands have a width of between 1 and 3 mm, depending on their orientation, and are separated by the same dimensions. This is a common appearance of the preservation of a cladoxypsid trunk vascular system, consistent with the pseudosporochnalean affinity now attributed to *Calamophyton*. Similar strands can be seen in patches on other specimens.

In trunk A, from the basal disk there is a distinct distal taper over the proximal 0.5 m until the sides become more or less parallel for another 0.4 m. Laterals are not visible on the base and proximal regions of the trunk. Between ~0.7 and 0.8 m from the trunk base, small branch bases become apparent sporadically. They are up to 5 mm wide and up to 10 mm in length, with an abruptly truncated tip, and are generally poorly preserved. There is little evidence that these branch bases go down into the matrix on the areas of trunk impression visible between the patches of stem limonite. Between 0.8 and 1.0 m from the trunk base, the branch bases increase in length to up to 20 mm and to 6–7 mm in apparent transverse width. Distal to 1.1 m, the attachments of branches on the trunk impression become obvious, and five longitudinal ranks of attachments are visible on the part. On the counterpart, three more ranks are visible on the trunk impression; two more, visible at the edges, appear to be oriented at an angle different from those on the part. Therefore, there are at least eight ranks of branch insertions and almost certainly 10. In this area, branch bases (false scars) exposed on the trunk impression are 6–10 mm in transverse width and 1–2 mm in longitudinal extent. The longitudinal spacing of branch attachments in individual ranks in this region is 9–10 mm. Over only the last 80 mm of the stem are complete branches attached, forming a dense crown with branch bases of up to 14 mm in transverse width.

On trunk B, much the same pattern is followed for the proximal 1 m. Branch bases are not well preserved, but longitudinal spacings of branches are ~10 mm, and there are probably also 8–10 ranks.

A clear difference between the two trunks relates to the diameter of the distal parts. Both trunks are of about equal diameter at the base, and both narrow to a ~50-mm width. However, trunk A expands in apparent width to 100 mm distally, while trunk B decreases suddenly to 35 mm in width following a kink (figs. 5, 10b, arrow). Attached branches at the apex in A are up to 14 mm in width, whereas in B they are only up to 8 mm. One possibility is that trunk B bifurcated at the kink, but multiple fractures in the rock at this point make this difficult to ascertain. In trunk A, distally there is an increase in the gap between laterally adjacent ranks of branch bases to ~20 mm (fig. 9), whereas in trunk B, the ranks of branch bases become almost contiguous (fig. 7g). For trunk A, the occurrence of 20 mm of smooth trunk between the ranks

is sufficient to accommodate a doubling of the diameter of the trunks distally without insertion of additional ranks.

Trunks: other specimens. Figure 11b shows the shape and nature of branch attachments in section when observed on trunk impressions lacking carbon. They are convex at the branch base and have a slightly concave upper (distal) margin, forming a half-moon or bean shape in transverse section.

Specimen E (fig. 11a), a distal trunk and crown with a diameter of 80 mm, illustrates the appearance of the distal trunk, with wide separation of the ranks of branch bases on a trunk impression. Branch bases are aligned in the bottom of longitudinal grooves (fig. 11a, 11d, 11e), suggesting that they formed rows slightly raised above the smooth surface between them in life. The most proximal part of the illustrated specimen is abruptly constricted because it is twisted through 90° below the slab surface.

Specimen G (figs. 5a, 11c) shows apparent bifurcation of the distal end of a trunk, with longitudinal ranks of branch bases. At the base of the specimen, ~70 mm in diameter, five ranks of branch attachments are seen in the main width of the trunk, with perhaps another five ranks crushed together hidden on the left-hand margin. A domed trunk apex 65 mm long and 70 mm wide lies over the void (fig. 11c, dark shadow, center) of another similar-sized apex going below and emerging to the right of it (fig. 11c, arrow). Branch attachments ~8 mm wide are closely spaced on the axis surface, and only short branch bases are present at the margins. So far, this is the only direct evidence of a dichotomizing *Calamophyton* trunk.

Between trunks A and B there are also smaller plants preserved, including trunks 4 and 5 (fig. 5). Trunk 5 was embedded at an oblique angle in the block, but it was possible to follow and uncover it through and on the back side of the part. To demonstrate this complete plant, photos of the five uncovered trunk sections were combined in a composite image given in figure 7d; a line drawing is provided in figure 12. The basal disk is ~60 mm wide and the attached roots at least 150 mm long. Over the proximal 100 mm the trunk narrows rapidly to ~20 mm, a width that remains stable over almost its entire length of 0.78 m. About 100 mm below the apex, it widens to ~25–30 mm. Branch bases are arranged in longitudinal rows. Trunk 4 (fig. 7e) is almost complete distally, except for the trunk apex, but the basal disk and roots are missing. The distal portion demonstrates closely inserted branch bases.

The two longest trunks come from the BGS locality. Trunk I is 2.0 m long. Preservation is poor because of fragmentation of the rock. The basal diameter is ~150 mm. The trunk width decreased rapidly to 70 mm over the proximal 0.2 m and to ~50 mm at 0.5 m from the base. The trunk widens distally from 1.5 m to the apex, where it is ~70–80 mm wide. The branch rows are clearly visible but twisted. Branches had been lost before burial. Trunk H is 1.57 m long. The base is relatively well preserved, with a basal disk ~200 mm in diameter

PG MD 37 A (in b), back side of the rootball; arrow indicates the distal tip. g, Root of base C, showing dark central strand (compressed xylem). Specimen PG MD 37 A. b, Ground surface, showing root cross section; the outer epidermis forms a circle, with sand replacing cortex and central compressed xylem suggestive of actinostele. Specimen PG MD 40 A. Scale bars = 100 mm (a, b, e), 20 mm (c, d, f), 5 mm (g), or 1 mm (h).

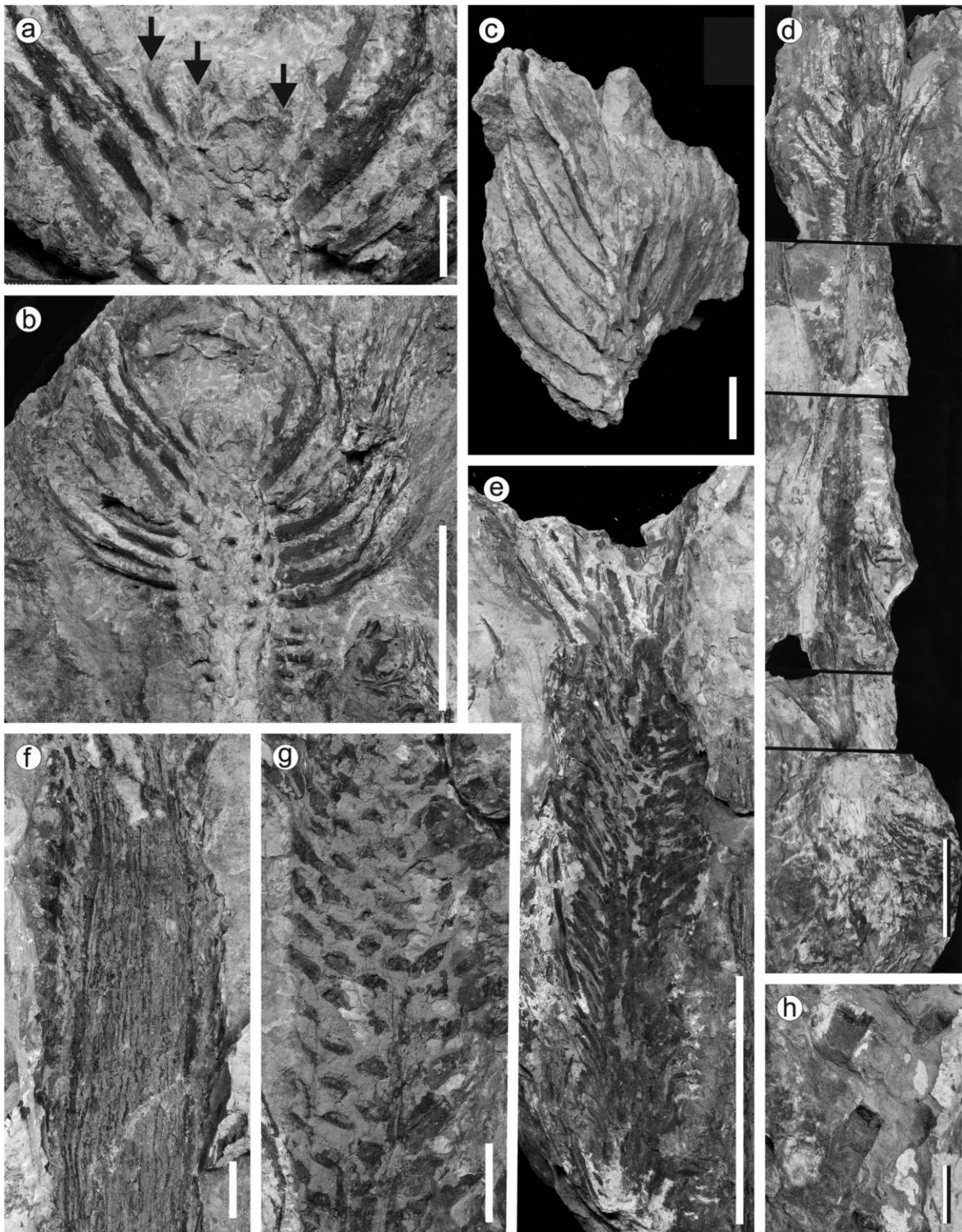


Fig. 7 Trunks and apices of *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. *a, b*, Apex of trunk D, specimen PG MD 38. Branches are recurved toward apex. Short developing branches near apex are indicated with arrows. *c*, Specimen of trunk near apex, showing view of adaxially recurved lateral branches. Specimen PG MD 42. *d*, Composite view of trunk 5, assembled from photographs of part and counterpart and reverse of slab where necessary (black lines indicate where images are joined). Roots at base. Line drawing interpretation is in fig. 12. *e*, Incomplete narrow trunk 4, showing region near the apex with attached branches at the top (see fig. 5*b*). Specimen PG MD 37 B. *f*, Compression of middle

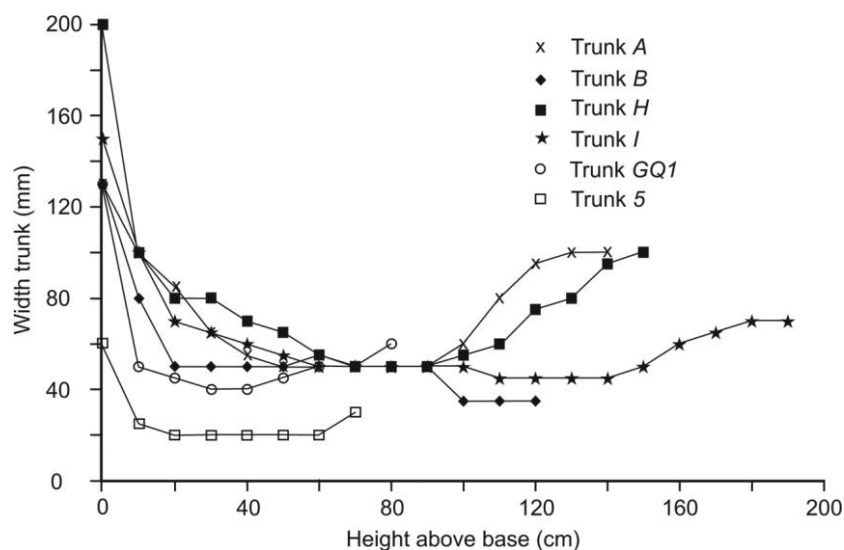


Fig. 8 Diameters of *Calamophyton primaevum* trunk compressions versus distance above base. For trunk illustrations, see fig. 15.

and ~300-mm-long roots. The diameter of the trunk decreases over the proximal 0.5–0.6 m to ~50–55 mm and widens distally to ~100 mm near the apex. Branches of the crown are lost except for a few longer branch bases. The branch rows of the distalmost 0.2 m of the trunk appear somewhat twisted.

Apices with Branches

Trunk apices are dome shaped and occupy the full width of the axis immediately beneath them. At the top of trunk A (fig. 9), the trunk apex is ~90 mm wide and ~40 mm long. On trunk B (fig. 10a), the trunk apex is 40 mm wide and 30 mm long. The branches, which are inserted close to the apex and perpendicular to the surface of the stem, are seen to bend adaxially in the majority of cases (figs. 7b, 7c, 10a), often more or less covering the apex itself (figs. 7d, 7e, 11a). In trunk A, branches are attached only for the distal 80 mm (including the trunk apex itself), in trunk B for 50 mm, and in trunk E (fig. 11a) for ~90 mm. This therefore leaves room for about four to seven actively photosynthesizing branches around the apex in each of ~10 ranks. The width of the attached branches varies between trunks, from 4 mm in specimen 4 to 8 mm in specimen B and 14 mm in specimen A.

The only specimen in which the tip of the apex is clearly visible is D (fig. 7a, 7b). The trunk is 50 mm wide and the apex 25 mm long. Digitate branches 8–10 mm wide and bending inward are attached only to the distalmost 85 mm; below that, all branches are abscised. Importantly, some of the connected branches that can be examined on the reverse of the slab carry well-preserved appendages, including some that are fertile. The latter can be positively identified to *C. primaevum* (fig. 13g, 13b). All branches appear to be fully grown except

those attached to the distalmost 10 mm of the trunk apex. There one can make out tiny, adaxially bending, undivided branchlets with blunt ends. The smallest one, attached 5 mm to the left of the apex tip, is 6–7 mm long and 1–2 mm wide. Another, 10 mm to the right of the apex tip, is somewhat larger, 12 mm long and 3 mm wide. From a ~15–20-mm distance from the apex tip, fully grown branches are attached. A schematic reconstruction of the apex of specimen D is provided in figure 14. The specimens therefore show an abrupt transition between relatively well preserved, fully grown branches and small, presumed juvenile branches.

Branches and Appendages

The branching typical of *Calamophyton*, a series of multiple and variously spaced dichotomies in three dimensions yielding a variable number of distal/terminal axes, is present in the attached lateral branches. The basal division of the branch occurs 80 mm from the trunk in specimen A, where the maximum length of the branch is 230 mm, with tips not preserved (fig. 9). On trunk B, the distances are ~60 and 110 mm, respectively (fig. 10a). On specimen D, the respective distances are 50 and 170 mm (fig. 7a, 7b). On the small trunks 4 (fig. 7e) and 5 (fig. 7d), they are 30–40 and 100–200 mm, respectively. These small branches divide to give only two or three smaller distal axes; the larger ones of trunk A give seven or eight smaller distal axes.

Isolated branches (fig. 13a–13c) have terminal axes that curve gently in toward the center line. They may demonstrate transverse cracks across the branch below the first division. The proximal ends of isolated branches are always abruptly truncated, without any sign of widening, and match the

of trunk A (figs. 4a, 5a), showing longitudinal stripes representing multiple vascular bundles. Branch bases on left margin. Specimen PG MD 37 A. g, Compression of top of trunk B (figs. 4b, 5b), showing ranks of attached branch bases. Specimen PG MD 37 B. b, Branch bases cleanly broken off at the same distance from the trunk. Specimen PG MD 41. Scale bars = 20 mm (a, c, f, g), 100 mm (b, d, e), or 10 mm (h).



Fig. 9 *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. Upper trunk and apex of trunk A (see fig. 5b). Digitate branches attached close to the domed trunk apex. Scale bar = 100 mm.

abruptly and cleanly truncated tips of the branch bases attached to trunks (fig. 7g, 7h). The branches therefore appear to abscise at a well-regulated distance from the stem (usually 10–20 mm, exceptionally 5–10 or 20–25 mm), leaving branch stubs of even length that superficially resemble leaves in some states of preservation. Very occasionally, the attached branch bases show well-preserved dimples of scleroid nests in the cortex characteristic of Pseudosporochnales (fig. 13d, 13f). Where the cortex has broken down or split away, macerated carbonized remains of the dissected vascular system are sometimes observed (fig. 13f).

Appendages are rarely well preserved because of the relative coarseness of the sandstone at Lindlar. They are small, unwebbed dichotomizing terete structures (fig. 13e), as described by Schweitzer (1973, his fig. 13a–13f). Fertile appendages, as found attached to trunk D (figs. 7b, 13g, 13h), show a basal dichotomy, paired sporangia carried terminally on small, re-

curved lateral units (fig. 13b, white arrow), and distal forked extensions of the main axes. These are consistent with the material from Lindlar described by Schweitzer (1973, his figs. 14a–14f, 14h–14m, 15c) and other material attributed to *C. primaevum*, including the type (Fairon-Demaret and Berry 2000).

Discussion

Whole-Plant Reconstruction

Compared with previous attempts to reconstruct Middle Devonian pseudosporochnalean plants, our task is quite simple, as the almost complete specimens (e.g., trunk A) allow an unprecedented framework for the visualization of individual plants. Our first reconstruction (fig. 1b) is drawn more or less from specimen A, paying attention to the number and size of the branch bases and the width of the stems in the lower part.

The main point of interpretation in the reconstruction is the width of the trunk in the distal portions beneath and in the zone of branch attachment. Here our measurements of the trunk show that it increases in diameter distally by a factor of up to 2. We have noticed some distortion in this area on several specimens and note that the main increase in the diameter of the trunk is accounted for by an increase in width of the zones between the ranks of branches. Branch diameter and width clearly increase distally.

The width of the distal trunk A is perhaps exaggerated in part by the closeness and size of the branch bases and also by the lateral forces exerted by sideways compression of the attached branches. In specimen B, the width of the trunk actually decreases, perhaps as a result of bifurcation, as discussed above. We are, however, very sure that there is a genuine increase in the width of the upper trunk distally in five of the six trunks measured. Therefore, our reconstruction shows an increase in the width of the trunk toward the top and particularly a broadening of the zones between the ranks of branches, but we have also reduced the width of this top part very slightly from the measured specimen because of the possible exaggeration of width suggested above.

The reconstruction of specimen 5 (fig. 1c), a smaller individual, is similarly based on the actual specimen. The lateral branches are smaller and simpler. The vertical ranks of branches are well established, even in such a small individual. Again, the upper trunk expands distally.

On the basis of the considerable material on hand, it is very unlikely that all trees showed a dichotomy of the trunk. Evidence for dichotomy, however, comes from two specimens described above. Trunk G (fig. 11c) shows direct evidence, whereas in trunk B (figs. 5, 10b) dichotomy has been interpreted from the sudden kink followed by an immediate reduction of width. In their first reconstruction of *Duisbergia mirabilis*, Kräusel and Weyland (1934) proposed both undivided and divided “leafy” trunks. Their divided trunk was based on an unfigured specimen that we have not located.

Size of Calamophyton Branches

The sizes of the branches attached are small, compared with those in Schweitzer’s (1973) reconstruction (his fig. 17) assembled from amalgamated isolated fragments. The new material



Fig. 10 *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. *a*, Apex and attached branches of trunk B (see fig. 5*b*). *b*, Distal parts of trunks A and B, counterpart (see fig. 5*b*). Arrow indicates abrupt narrowing and kink in trunk B. Note the change in appearance of trunks, depending on level of preservation. Specimen PG MD 37 B. Scale bars = 20 mm (*a*) or 100 mm (*b*).

suggests that the large “fronds” he postulated, terminating in more than 150 terminal axes, did not exist. There is strong evidence that the three specimens found separately and used by Schweitzer (1973, his text figs. 9–11) to reconstruct a frond are not even *Calamophyton*. The specimen illustrated by his figure 10 is housed in the Fuhlrott Museum collection. Preparation of the branches revealed fertile appendages typical for *Hyenia elegans* sensu Schweitzer (1972). An unprepared large branch with a total length of ~350 mm, found by Schweitzer at Lindlar (also in the Fuhlrott Museum), revealed no more than 13 distal axes after uncovering (fig. 13*c*).

The largest known almost complete *Calamophyton* branch is that of *Calamophyton bicephalum*, a species thought to be conspecific with *Calamophyton primaevum* (Fairon-Demaret and Berry 2000), found at Goé in Belgium and described by Leclercq and Andrews (1960). It is incomplete, with branch tips missing. The branch, 20 mm wide at the base, divides after 90 mm successively into at least 15 (in total, perhaps 20) terminal axes. The preserved length of the specimen is ~300 mm without branch tips. The total length of the branch system is estimated at 400–500 mm. This suggests that the plants so far found at Lindlar are small to medium-sized, compared with those at Goé.

Comparison with Previous Work from Lindlar

In this study, we unite parts of the material of two plant taxa previously described by Schweitzer from the Schiffarth Quarry, Lindlar. These include some of the trunk material attributed to *D. mirabilis* by Schweitzer (1966). The material we include shows branch bases and attachments arranged in vertical ranks (e.g., his pl. 21, fig. 3 and pl. 25–29, excluding fig. 3 of pl. 27). We do not include the large trunk bases he illustrated, which appear to show an oblique pattern of xylem tissues that have not been demonstrated in organic connection with the trunks and are quite unlike those we have. The second set of material was described as *C. primaevum* by Schweitzer (1973). We exclude all his trunk bases and trunks that show no sign of vertical ranks of branches or other features characteristic of our new complete specimens. However, we accept some of the vegetative and fertile branch and appendage material that is characteristic of *Calamophyton* (e.g., pl. 21, 23–25). Further analysis of the excluded material will be presented in forthcoming discussions of *H. elegans* and *Weylandia rhenana* from Lindlar.

The major difference in our approach is, therefore, that we regard the lateral organs of *D. mirabilis*, previously considered “leaves,” as being the bases of abscised lateral digitate branches of *C. primaevum*. The leaf-like appearance is due to the fraying of the internal polystelic vascular system typical of cladoxylpoids, combined with the position of abscission of the branches some distance distal to the branch base, as previously suggested by Berry and Fairon-Demaret 2002 (p. 701).

Anatomy

The best descriptions of the anatomy of *D. mirabilis*, here recognized as being the trunk of the *C. primaevum* plant, are by Mustafa (1978*b*), who described material primarily from the Köster Quarry near Hagen-Ambrock (Brandenberg beds). The trunks are from ~40 to 200 mm in diameter, and the xylem

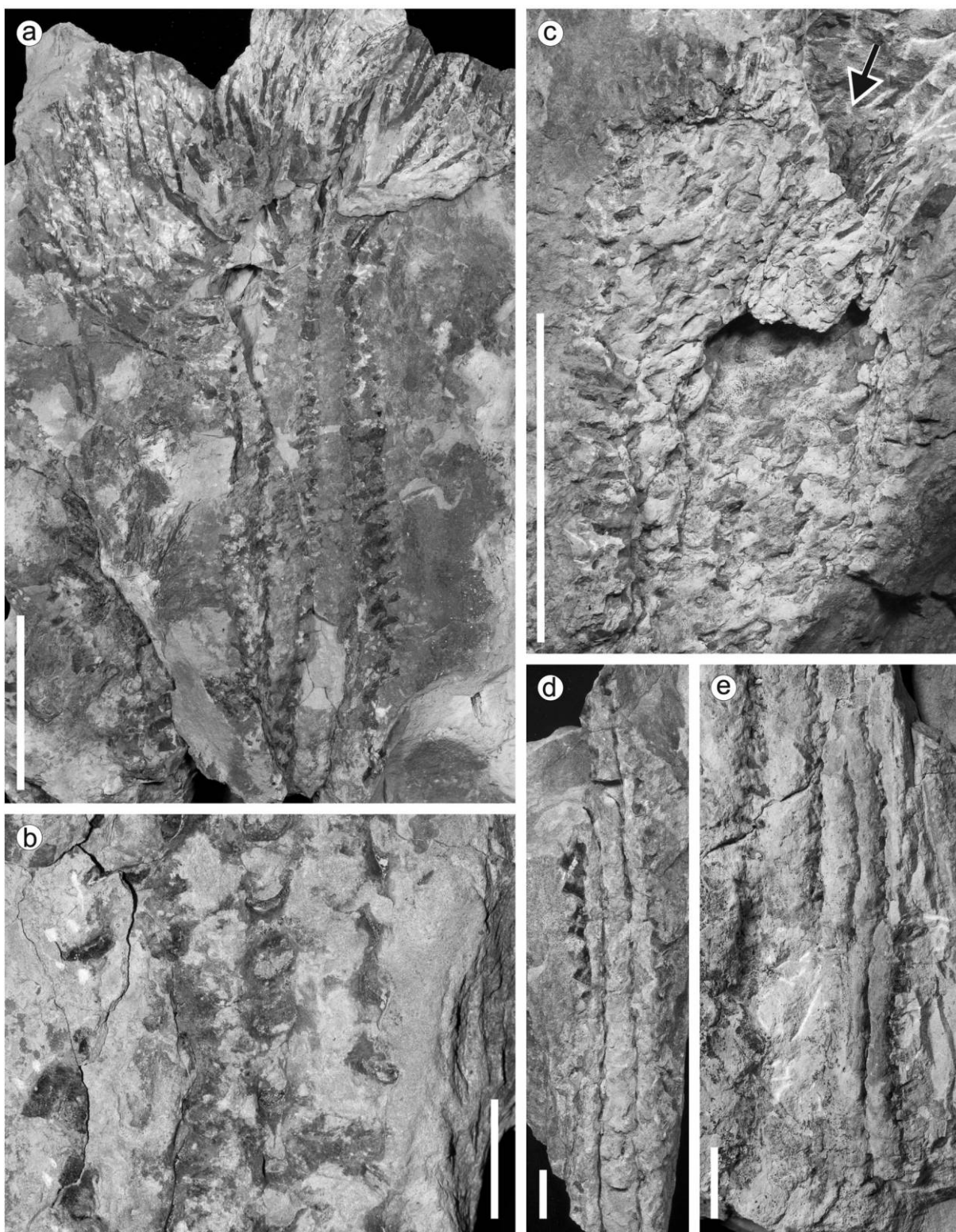


Fig. 11 Trunks and apices of *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. *a*, Apical region of wide trunk E, showing attachment of digitate branches. Note the *Duisbergia*-like trunk with widely spaced ranks of branch bases and a smooth stem surface between them. Specimen PG MD 37 B, back side. *b*, *Duisbergia*-like trunk impression surface with branch bases in profile on left. Branch bases seen in section going down into the matrix (center) have a convex-upward, bean-shaped to crescentic outline. Specimen PG MD 44. *c*, *Duisbergia*-like trunk G, showing apical division (see fig. 5*a*). Left-hand trunk visible on surface of slab; right-hand trunk goes through the void (center, shadow)

is preserved in pyrite. The vascular system consists of a ring of ~60 radially aligned xylem plates that surround a large area of pith in the center. The xylem plates have a central primary xylem area up to 0.7 mm wide and 5 mm in radial extent. This is surrounded by secondary xylem, or “aligned xylem,” radial files of xylem cells usually up to 20 and occasionally more cells deep. In the smaller trunks, the xylem plates are close together, and in the larger stems they are further apart. Anatomy of the branches of *Calamophyton* is also polystelic, but the individual xylem plates are relatively longer and more frequently interconnected (Mustafa 1978*b*).

In our study, we have noted only longitudinal carbonaceous strips on the stem compressions and partial casts, consistent with radially aligned plates of xylem. In the roots, we noted what appears to be a stellate carbonaceous strand, which is consistent with the type of strand observed in the roots of *Pietzschia levis* (Soria and Meyer-Berthaud 2004).

Ontogeny and Growth Models

The trajectory of growth and form of pseudosporochnaleans from juvenile to mature adult is a matter of debate. Considering the currently accepted bauplan of Pseudosporochnales, there are two contrasting hypothetical models of growth, by Berry and Fairon-Demaret (2002) and Meyer-Berthaud et al. (2010). The “whole-plant” fossils from Lindlar can be considered a test of these two theoretical models. Figure 15 shows outline drawings of the main specimens that have been used in this study and gives a good representation of plants of different heights and diameters, probably preserved in a catastrophic uprooting, transport, and deposition event. We interpret these as sampled from a natural population showing different ontogenetic stages of growth within an envelope of natural variation. Diameters of the specimens, including the base and at least part of the trunk apex, were recorded along the trunk (fig. 8). Below, we compare the fossils with representative growth stages predicted by the two models. As they do not show representative growth stages predicted by either of the two models, we propose a new model.

Berry and Fairon-Demaret (BFD) model (fig. 16a). Berry and Fairon-Demaret (2002) suggested that secondary growth of the trunk was made possible by the addition of “aligned xylem” around each of the individual plates that make up the complex, dissected vascular system, thereby leading to enlargement of the trunk below the apex. If secondary growth was sustained, then the trunk would take on a tapered profile.

The BFD model predicts that trunk fossils would be found that were broadly self-similar in proportions, no matter their size (fig. 16*a*). Our fossils (fig. 15) support this model, in that the complete specimens are approximately self-similar. However, the observation that the apex is most often larger than the mid-region of the trunk is unexpected and cannot be explained by this model.

Meyer-Berthaud, Soria, and Decombeix (MBSD) model (fig. 16b). Meyer-Berthaud et al. (2010) suggested a growth

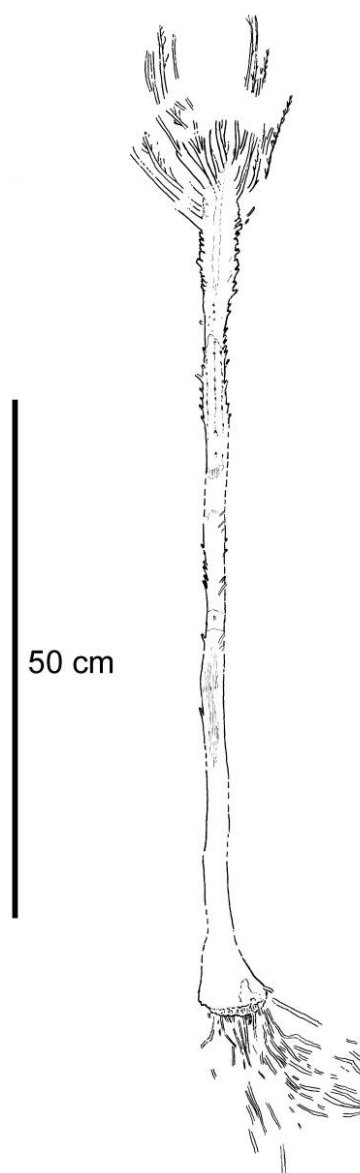


Fig. 12 *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. Line drawing interpretation of trunk 5, the smallest complete specimen (see figs. 5, 7*d*).

model for Cladoxylopsida, including Pseudosporochnales, influenced and supported by studies of the exceptionally well preserved anatomy of species of latest Devonian *Pietzschia* Gothan (a non-pseudosporochnalean genus; Soria et al. 2001; Soria and Meyer-Berthaud 2004, 2005). In the MBSD model, the size of the primary body increased dramatically in the earliest stages of growth to form a short, obconical trunk “mostly or entirely underground,” supported by “fused roots”

and is visible in the area indicated by the arrow. Specimen PG MD 37 A. *d, e*, *Duisbergia*-like trunk impressions, showing ranks of branch attachments laterally compressed to appear as grooves in stem surface. Specimen PG MD 45 (*d*) and unnumbered specimen of the Schweitzer collection in the Goldfuss Museum (*e*). Scale bars = 100 mm (*a, c*) or 20 mm (*b, d, e*),

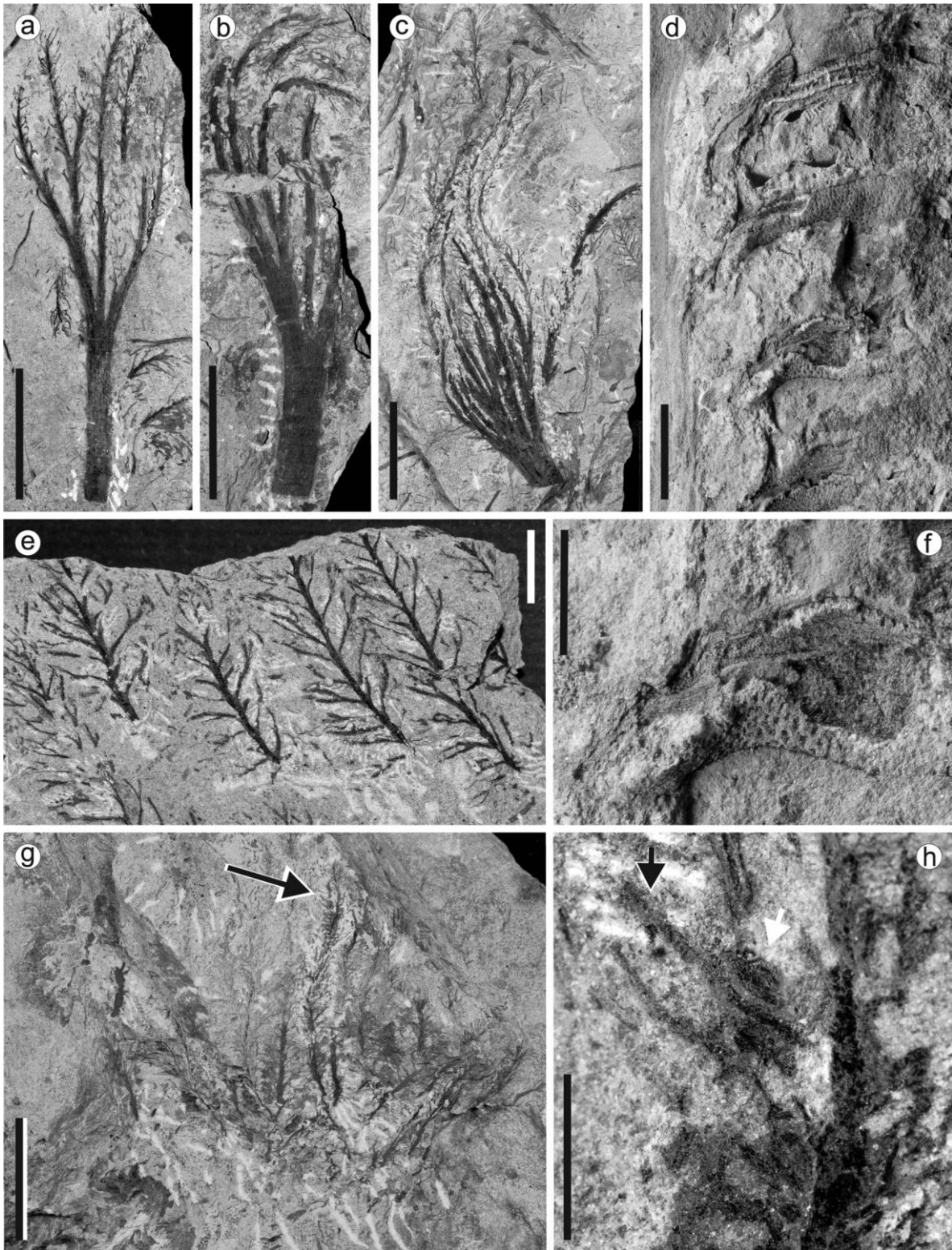


Fig. 13 Branches and appendages of *Calamophyton primaevum* from the Schiffarth Quarry, Lindlar. *a, b*, Typical appearance of digitate branches from Lindlar. Outer branches curve in toward the center line. Distal branches sometimes divided dichotomously. Note cleanly abscised branch bases. Specimens RE 551.734.300 A 1981 and RE 551.734.300 A 1982 of the Rochow collection in the Ruhr Museum. *c*, Specimen of *Calamophyton* collected by Schweitzer and prepared by P. Giesen, showing 13 terminal branches. Specimen SFM-PAL-155, former Fuhlrott

(a root mantle). The widest part of the trunk formed by primary growth at about ground level. Then, as the apex grew upward, the size of the primary body, and therefore of the trunk, either stayed the same or decreased. Meyer-Berthaud et al. (2010) allowed for no secondary increase in the diameter of the trunk, except for the lowest obconical part in Pseudosporochnales, which might then take on a “swollen” shape, with the roots becoming more separated (Meyer-Berthaud et al. 2010, their fig. 4f). In this model, addition of secondary tissue to the vascular strands in Pseudosporochnales resulted in compression of stem parenchyma rather than in an increase in trunk diameter.

The MBSD model predicts that (1) some trunks would be found that were short and broad, sometimes exceptionally so (fig. 16b, stage 1), as well as some that were long and proportionately slender (fig. 16b, stage 3), but with swollen bases; (2) juvenile specimens would display a phase of growth in which the base would be obconical, supported by fused roots (a root mantle); and (3) the trunk would be parallel sided or would taper upward. These predictions are not supported by our observations. Specifically, (1) no short, broad trunks have been found in our assemblage (nor in any other pseudosporochnalean assemblages worldwide); (2) moderately small specimens appear already to have developed a flat, enlarged base; and (3) trunks display prominent areas where the diameter increases significantly distally, as well as regions that taper or remain parallel sided. The MBSD model is therefore rejected for *Calamophyton*.

The Giesen and Berry (GB) model. The unexpected feature of the new, complete plants of probably small to middle-sized *Calamophyton* is that the minimum diameter of the trunk is not usually at the top but is in the mid-region. Our fossils do suggest that the upper trunk of *Calamophyton* is largely primary. Evidence for this includes the lateral abscising branches and also that the top of the trunk is domed rather than tapered. The trunk halfway between the apex and the basal disk is, however, one-half the diameter of each. Therefore, the trunk overall generally takes on a dumbbell shape. All conical bases of the plants appear approximately self-similar, with maximum diameter at the flat basal disk.

A relatively juvenile stage of ontogeny is likely to be represented by trunk 5, among others, in which the base of the stem is 60 mm in diameter, narrows to 20 mm at 0.2 m above the base, and widens only to 30 mm at the very top, 0.7 m above the base. It has small, relatively simple branches.

We suggest that the primary body became larger distally after initial establishment of the plant and successful growth of a viable juvenile. The width of lateral branches was measured to increase distally along stem A, suggesting increased vigor and size of the primary body. After reaching a certain level, ~100 mm diameter, the size of the trunk being produced

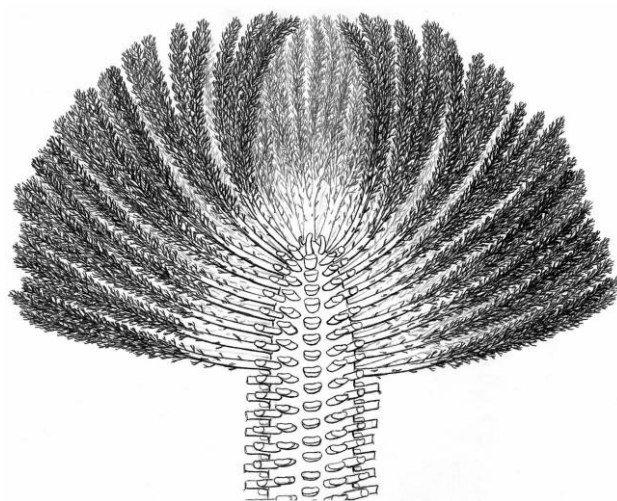


Fig. 14 Schematic reconstruction of *Calamophyton primaevum* trunk apex, reconstructed from the specimens described in this article.

at the apex appears to have remained constant during the next phase of growth.

Secondary growth is invoked to increase the diameter of the base and lower trunk while the apex is elongating the upper trunk. The base is consistently tapered upward, and the very bottom of the trunk is more or less flat in all sized specimens.

We propose a new model of growth for *Calamophyton*, the GB model (figs. 16c, 17c). Juvenile *Calamophyton* is small and slender, with a secondarily expanding base and relatively small, simple branches. As the plant becomes more established, secondary expansion of the trunk generally is accompanied by both an increase in size and vigor of primary growth at the apex and significant secondary expansion of the lower trunk and base (fig. 17c). The maximum size of the primary body is reached some distance from the ground (~1–2 m).

The only other complete single specimen of a pseudosporochnalean with both roots and branches attached is the specimen of *Lorophyton goense* Fairon-Demaret et Li (1993) from Belgium. The stem is ~0.2 m long and ~15 mm in diameter, with a slightly enlarged base. The apex is not clearly visible but is surrounded with simple branches bearing appendages. Because other larger, more complexly structured branches of the same plant were present at the type locality, Fairon-Demaret and Li considered the specimen to be a juvenile plant, as do we. It is entirely consistent with our understanding of the earliest stages of pseudosporochnalean growth. The apex does not expand upward visibly, but this may be due to the

Museum collection in the Ruhr Museum. *d, f*, Branch bases attached to trunk. Note dimples representing sclereid nests on well-preserved surface of branches. Remains of vascular bundles are visible where the branch surface has disintegrated or been removed. Unnumbered specimen of the Schweitzer collection in the Goldfuss Museum. *e*, Typical appearance of well-preserved sterile distal branches and appendages. Specimen RE 551.734.300 A 1983 of the Rochow collection in the Ruhr Museum. *g*, Fertile branches emerging from back of top of trunk D (fig. 7a, 7b). Arrow indicates appendages enlarged in *b*. Specimen PG MD 38. *h*, Enlargement of fertile appendage indicated in *g*. White arrow indicates recurved sporangia. Black arrow indicates distal extension of main axis. Specimen PG MD 38. Scale bars = 50 mm (*a–c, g*), 10 mm (*d, e*), or 5 mm (*f, h*).

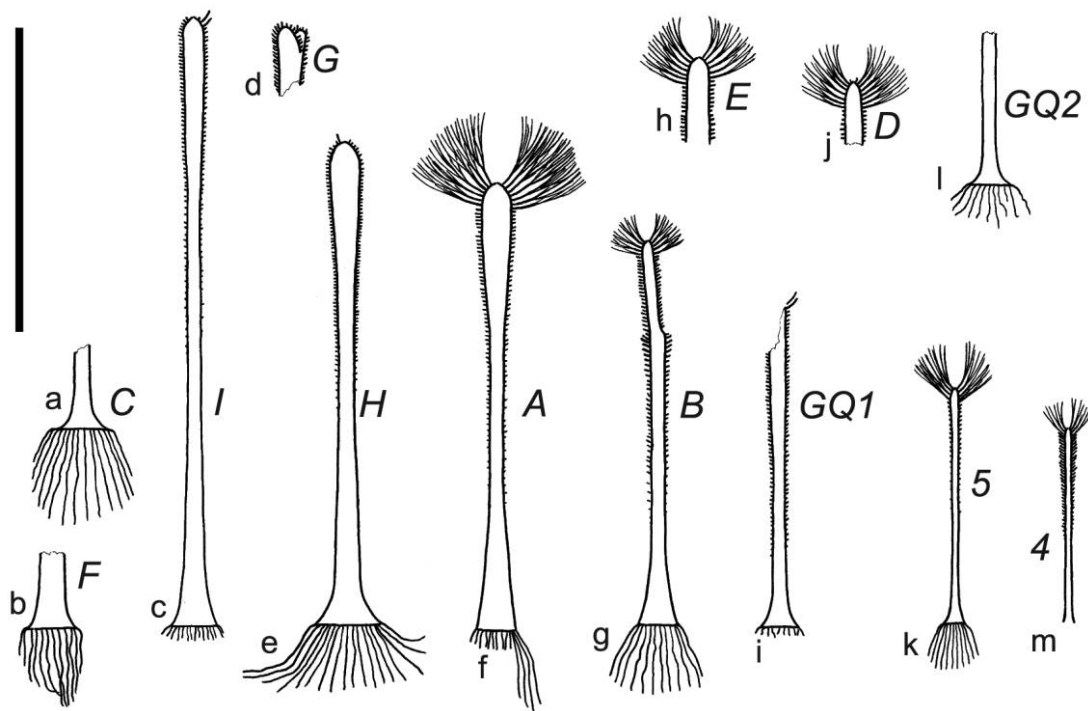


Fig. 15 Schematic outline drawings of the most important specimens of *Calamophyton primaevum* from the BGS and Schiffarth Quarries, Lindlar. *a*, Base C; see fig. 6*a*, 6*b*. *b*, Base F (drawn from photographs). *c*, Trunk I (BGS quarry; drawn from photographs). *d*, Dividing apex G (figs. 5*a*, 11*c*). *e*, Trunk H (BGS quarry; drawn from photographs). *f*, Trunk A (figs. 4, 5). *g*, Trunk B (figs. 4, 5). *h*, Apex trunk E (fig. 11*a*). *i*, Trunk GQ1 (fig. 3*b*, middle). *j*, Apex trunk D (fig. 7*a*, 7*b*). *k*, Trunk 5 (fig. 7*d*). *l*, Trunk GQ2 (fig. 3*b*, right). *m*, Trunk 4 (fig. 7*e*). Scale bar = 1 m.

extremely small size of this specimen, which is far shorter than any of our *C. primaevum* plants.

Comparison of *Calamophyton* (GB model) and *Pietzschia*. Figure 17 compares the main points of the growth model of *Pietzschia*, as presented by Meyer-Berthaud et al. (2010), and our GB model of *Calamophyton*. The main differences are (1) the length of the phase of growth where the size of the primary body expands, denoted the epidogenetic phase (*E*) by Eggert (1961); (2) consequently, the height at which the maximum diameter of the primary body is reached (D_{MP}); (3) the role of roots, fused as a mantle around the trunk base in *Pietzschia* and free in *Calamophyton*; and (4) the hypothetical occurrence of considerable secondary growth (*S*) in *Calamophyton*.

Meyer-Berthaud et al. (2010) and previous studies by those authors demonstrate that the trunks of the various *Pietzschia* species did not expand by a process of secondary growth. Apart from the lack of secondary tissues, the overall structure of the trunk is constrained by the presence of a primary cortex and abundant sclerenchymatous tissues within the outer regions of the stem, which play an important role in mechanical stability. In arguing that pseudosporochnaleans had a similar growth, Meyer-Berthaud and colleagues interpreted that in permineralized axes belonging to the genus *Xenocladia* Arnold, their proposed candidate for the anatomy of a pseudosporochnalean trunk, secondary growth of xylem plates, led not to expansion of the trunk but rather to compression of the parenchyma and pith.

If *Calamophyton* did have *Pietzschia*-style growth, then the

assemblage of the different-sized trees we have measured would have to represent the outcome of an extremely wide variation in the size of the initially formed maximum primary diameter (M_{PD}) at ground level. We do not accept this, for the reasons already stated, in that we find neither short, wide, juvenile *Calamophyton* trees nor obconical, root mantle-supported juveniles, nor indeed any other matching pseudosporochnalean material. Furthermore, we would have to accept that the primary body shrank toward the midpoint of the trunk and then increased in size once again toward the top.

Expanding the GB model. The best-preserved large pseudosporochnalean trunk compression is that attributed to *Wattieza/Eospermatopteris* from South Mountain, New York (probably earliest Frasnian in age), illustrated by Stein et al. (2007, their fig. 2*a*). It is ~6 m long and ~500 mm in diameter at the base, tapering significantly over the basal 0.6 m to ~350 mm diameter and then gently over the next 3.5 m until it reaches a more or less steady diameter of ~140 mm for the distalmost 1.5 m, until the broken top. At no point does the diameter of the trunk increase distally. We interpret this taper in the lower part as representing steady and accumulating secondary growth of the trunk in a zone spreading longitudinally upward over time from the base. By analogy with our model of *Calamophyton* growth, the maximum diameter of the primary body may have been ~140 mm, and this may have been achieved for the first time perhaps ~2 m or more from ground level.

In our model of *Calamophyton* growth (fig. 16*c*), we include

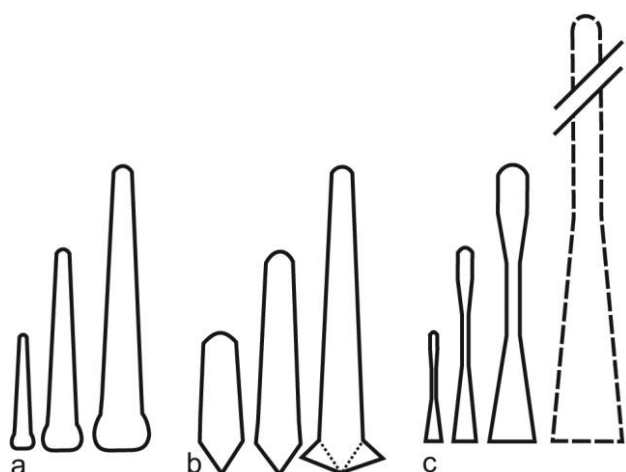


Fig. 16 Schematic models of pseudosporochnalean growth, not to scale. *a*, BFD model, based on Berry and Fairon-Demaret (2002), allowing for continuous secondary growth in all parts of the trunk. *b*, MBSD model, based on generalized model for Cladoxylopsida by Meyer-Berthaud et al. (2010), allowing secondary growth only in the lowest part of the stem (see text). *c*, GB model, based on specimens illustrated in fig. 15. Hypothetical stage 4 (dashed lines) indicates potential ultimate phase of growth in line with the architecture of *Wattieza/Eospermatopteris*.

a final hypothetical stage (dashed lines) that represents a mature trunk similar in form, but perhaps not size, to the *Wattieza/Eospermatopteris* specimen mentioned above. Here the zone of basal secondary expansion has spread beyond the lower part of the trunk (which showed upward expansion of the apex in previous stages). The large apex continues to grow upward at a steady size. We have no fossil evidence for this stage of growth at Lindlar. If the lower trunk did not continue to increase by further secondary growth, we would have to accept that our largest plants are essentially the final stage of a determinate growth pattern and that the upward expansion of the top of the trunk may relate to the onset of fertility.

The expanding apex of *Calamophyton* was not supported by an external root mantle, as in *P. levis* (Soria and Meyer-Berthaud 2004) and tree ferns, but was a freestanding trunk. The fossil evidence and our model suggest that there should have been a potential zone of biomechanical weakness during a vulnerable part of the ontogeny, where the large apex and crown of branches were supported by a relatively narrow trunk and wide base. The fact that the fossils come to us so complete after probably violent transport seems to indicate that the narrow part of the trunk was, in fact, strong and was stiff enough to support the crown. Some trees today, such as the Cuban belly palm, have a stem that increases in diameter upward at some stage of their growth.

This evidence from compression fossils must be further explored with anatomically preserved material. Little material from known ontogenetic stages of pseudosporochnalean trunks exists, including a lack of *Duisbergia* and similar trunk permineralizations that show branch traces, implying that they are secondarily modified and that all traces of branch development have disappeared in preserved examples.

Evolutionary Considerations

Calamophyton is the oldest established genus of pseudosporochnaleans (starting in the Eifelian, early Mid-Devonian). It is likely that the non-pseudosporochnalean Late Devonian *Pietzschia* body plan, based on primary growth only and featuring an important root mantle, is derived from the earlier form. This would require that the period of expansion of the apex is reduced to the first few centimeters of the trunk and more pronounced emergence of roots from the trunk surface to support and nourish this phase of growth. Therefore, the emergence of the *Pietzschia* body plan may be an example of heterochrony.

Eifelian Forests

The famous stumps of the late Givetian *Gilboa* fossil forest, in New York State, have in recent years been shown to rep-

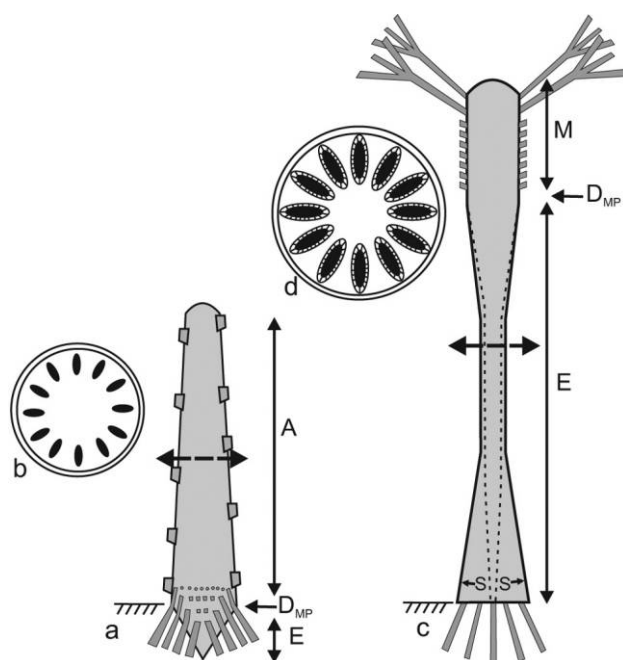


Fig. 17 Models of growth of *Pietzschia* and *Calamophyton*. *a*, *b*, Stem development in *Pietzschia*, redrawn from Meyer-Berthaud et al. 2010 (their fig. 4d, 4e). *a*, The first phase of growth is epidogenetic (*E*), rapid expansion of size of primary body. The second phase of growth is apoxogenetic (*A*), with a gradual decline in the size of the primary body. Roots form a fused supporting mantle; maximum primary diameter (D_{MP}) is at ground level. *b*, Schematic anatomy of section of *Pietzschia* trunk. Primary xylem strands (black) are separated by thick ribs of sclerenchymatous tissues and surround a wide pith. *c*, *d*, Stem development in *Calamophyton*, following the GB model proposed in this article, with a moderate-sized specimen shown. *c*, Epidogenetic (*E*) phase of growth is long and above ground, with dashed lines showing the hypothetical size of the primary body at a given height. The maximum primary diameter (D_{MP}) is at 1–2 m height. The final phase of growth is menetogenetic (*M*), with steady size of primary body; all tissues below the apex are subject to secondary modification and growth (*S*). *d*, Schematic anatomy of section of *Calamophyton/Duisbergia* trunk. Primary xylem strands (black) are surrounded by aligned (secondary) xylem and surround a pith (interpreted from Mustafa 1978b). Not to scale.



Fig. 18 Reconstruction of assemblage of *Calamophyton primaevum* trees from Lindlar, drawn by P. Giesen and based on this work.

resent the bases of large pseudosporochnalean stumps (Stein et al. 2007). Studies based on nearby localities had suggested that the Gilboa forest was monospecific (Driese et al. 1997; Mintz et al. 2010), but it is now known that the Gilboa forest was a combination of giant cladoxyloids and rhizomatous woody aneurophytalan progymnosperms, with arborescent lycopsids in the vicinity (Stein et al. 2012), growing in a coastal environment. This is the best evidence to date of the structural composition of any Devonian forest.

The combination of large cladoxyloids and aneurophytes is also found in the late Eifelian assemblages at Goé, Belgium (Berry and Fairon-Demaret 2001), where both *Calamophyton* and *Pseudosporochnus* are present. However, there is no evidence of the growth position of these plants, as no paleosol is preserved. Further work has yet to be done on *Calamophyton* trunks from Goé, particularly concerning whether they can be recognized from *Pseudosporochnus* trunks with the new

criteria that are established on the basis of the Lindlar material. Trunks regarded as *Pseudosporochnus*, which appear to have branches abscised very close to the surface, are up to 13 cm in diameter (Berry and Fairon-Demaret 2002), and the largest *Eospermatopteris*-like trunks at Goé are 19 cm in diameter. This suggests that a true forest-size vegetation was established.

At Lindlar, *Calamophyton* seems to be the predominant plant. Our reconstruction (fig. 18), drawn by Peter Giesen, shows the *Calamophyton* plants as a monospecific stand on the basis of the material we have sampled in the basal scoured “channel” and observed in the same horizon nearby. It is not intended as a reconstruction representative of the entire Lindlar ecosystem. We hope that it might give a different perspective on Lindlar, in comparison to the reconstruction proposed by Schweitzer (2009, his fig. 25), in which *Calamophyton* and *Duisbergia* plants stand isolated in a rather desolate landscape dominated by small plants. It emphasizes the relative propor-

tions of the specimens we have observed, spaced at a distance that is dictated by the length of the branches. We also emphasize the nature of the “forest floor,” which is littered with discarded branches and which must be home to many detritivorous arthropods. In this image, the sizes of the drawn plants are close to those of the observed specimens, meaning that the tallest plants are ~2–2.5 m. We have not established the maximum height of *Calamophyton*, because we are unsure about the affinity of the largest bases of trunks previously attributed to *Duisbergia*. These bases (Schweitzer 1966, text fig. 5 and pl. 21, fig. 1; Schweitzer and Giesen 2002, text fig. 4) have a complex oblique pattern of xylem plates and should not be included in *Calamophyton* as we currently understand it. We estimate (guess) that the *Calamophyton* plants might have reached a height of ~3–4 m.

Besides the monospecific *Calamophyton* assemblages, suggesting monospecific stands, significant numbers of large *Hyenina* plants and *Weylandia* (possibly another member of Cladoxylopsida) have recently been found in the same fossiliferous horizon at the neighboring BGS quarry. *Weylandia* perhaps formed local monospecific stands, too. This might have also been the case with *Hyenina*, which was the predominant plant at the Schweitzer location. The cladoxylopsids, when we include *Weylandia*, must have made up at least 90% of the Lindlar flora, as suggested by the “snapshot” preserved in the

fossiliferous flood horizon. Further work is planned on the new specimens attributed to *Weylandia* and *Hyenina*. Aneurophytes, such as *Rellimia*, are also present but are found only rarely (Schweitzer 2009). The same is the case with *Thursophyton*, *Protobarinophyton*, and the herbaceous lycopsid *Leclercqia*.

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