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# THE ARCHITECTURE OF *PSEUDOSPOROCHNUS NODOSUS* LECLERCQ ET BANKS: A MIDDLE DEVONIAN CLADOXYLOPSID FROM BELGIUM

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New observations on trunks of *Pseudosporochnus nodosus* Leclercq et Banks (Cladoxylopsida) from the Middle Devonian (upper Eifelian) of Goé, Belgium, show for the first time the presence of significant contiguous scars on their surfaces. The morphology of these scars corresponds to the morphology of the bases of first-order, digitately divided branches characteristic of the genus. We therefore reconstruct *Pseudosporochnus* with a sturdy trunk bearing densely and acutely inserted lateral branches capable of abscission at their base. We reject previous interpretations of *Pseudosporochnus* that do not include lateral branching of the trunk. In proposing an architectural model for *Pseudosporochnus*, we believe it to apply to other mainly Middle Devonian plants that we place in Pseudosporochnales, *Calamophyton* Kräusel et Weyland, *Lorophyton* Fairon-Demaret et Li, and *Wattieza* Stockmans. The largest trunks bearing branch scars that we can now positively identify as *Pseudosporochnus* from Goé have a diameter of 13 cm and indicate a moderately sized tree.

*Keywords:* Devonian, Cladoxylopsida, *Pseudosporochnus*, architecture, Belgium.

## Introduction

The Middle Devonian flora encompasses the transition between the small, largely herbaceous vegetation of the Lower Devonian and the *Archaeopteris* forests of the Upper Devonian. The reconstruction of *Pseudosporochnus nodosus* from Belgium created by Leclercq and Banks (1962) is one of the most striking illustrations produced of any Middle Devonian plant. *Pseudosporochnus* is one of the largest plants known from this time, and so its reconstruction is frequently seen in both systematic texts and in discussions of concepts relating to developments in terrestrial ecology and even atmospheric change. We have spent a number of years studying this and other closely related plants and, on the basis of considerable new evidence, offer a new reconstruction of *Pseudosporochnus* to replace the famous but flawed Leclercq and Banks drawing.

*Pseudosporochnus nodosus* falls within the Devonian plants assigned to Cladoxylopsida. These are united by possession of a complex primary vascular system consisting of many radially aligned and variously interconnected plates of xylem. These plants have been the subject of many confused accounts during the past 120 years, and we are in the process of clarifying morphological concepts of the Devonian members of the group. We currently recognize only one order of plants among the Middle Devonian members, the Pseudosporochnales. Within this order, we recognize only the genera *Calamophyton* Kräusel et Weyland (*sensu* Fairon-Demaret and Berry 2000), *Pseudosporochnus* Krejči (Berry and Fairon-Demaret 1997), *Lorophyton* Fairon-Demaret et Li (1993), and *Wattieza* Stockmans (Berry 2000). These genera can be most readily distinguished morphologically by the various patterns of branching within the sterile and fertile appendages that are found attached laterally, without obvious geometrical regularity, to the branches (fig. 6 in Berry 2000).

Recently, we published our analysis (Berry and Fairon-Demaret 1997) of details of morphology and variability of the branches and appendages ("lateral branching systems" of Berry and Fairon-Demaret 1997) of *P. nodosus* based on large collections from Goé, Belgium, made by Suzanne Leclercq, using both previously illustrated and unpublished material. We gave a history of studies and opinions on this plant that it is not necessary to repeat here. Neither will we discuss further the morphology of the appendages nor their arrangement on the branches. Instead, we review the history of the whole-plant concept of the genus *Pseudosporochnus*.

Stur (1881) considered the plant an alga and named it *Sporochnus krejcii* based on fossils from Bohemia. Potonié and Bernard (1904), on finding vascular tissues, changed the name to *Pseudosporochnus* and described the digitately divided axes of specimens of *Pseudosporochnus krejcii* as "trunks" and the axes distal to the division as "branches." The bases of the trunks were enlarged "like a cone that has been flattened" (Potonié and Bernard 1904, p. 25) with the exception of one extremely large example (fig. 81 in Potonié and Bernard 1904), where the base was described as "more or less in the form of a bulb" (p. 25).

Hirmer (1927) reproduced a selection of the drawings of Potonié and Bernard (1904) and provided a line drawing (fig. 175 in Hirmer 1927) of the above-mentioned biggest trunk with a bulbous base.

Zimmermann (1930) reconstructed *P. krejcii* as a small tree ca. 2 m high (fig. 1*a*). The stout trunk had a bulbous base, more inflated on the left side (as in fig. 81 in Potonié and Bernard 1904), to which a tuft of short, undivided small roots had been added. At the top, five branches, unequal in size,

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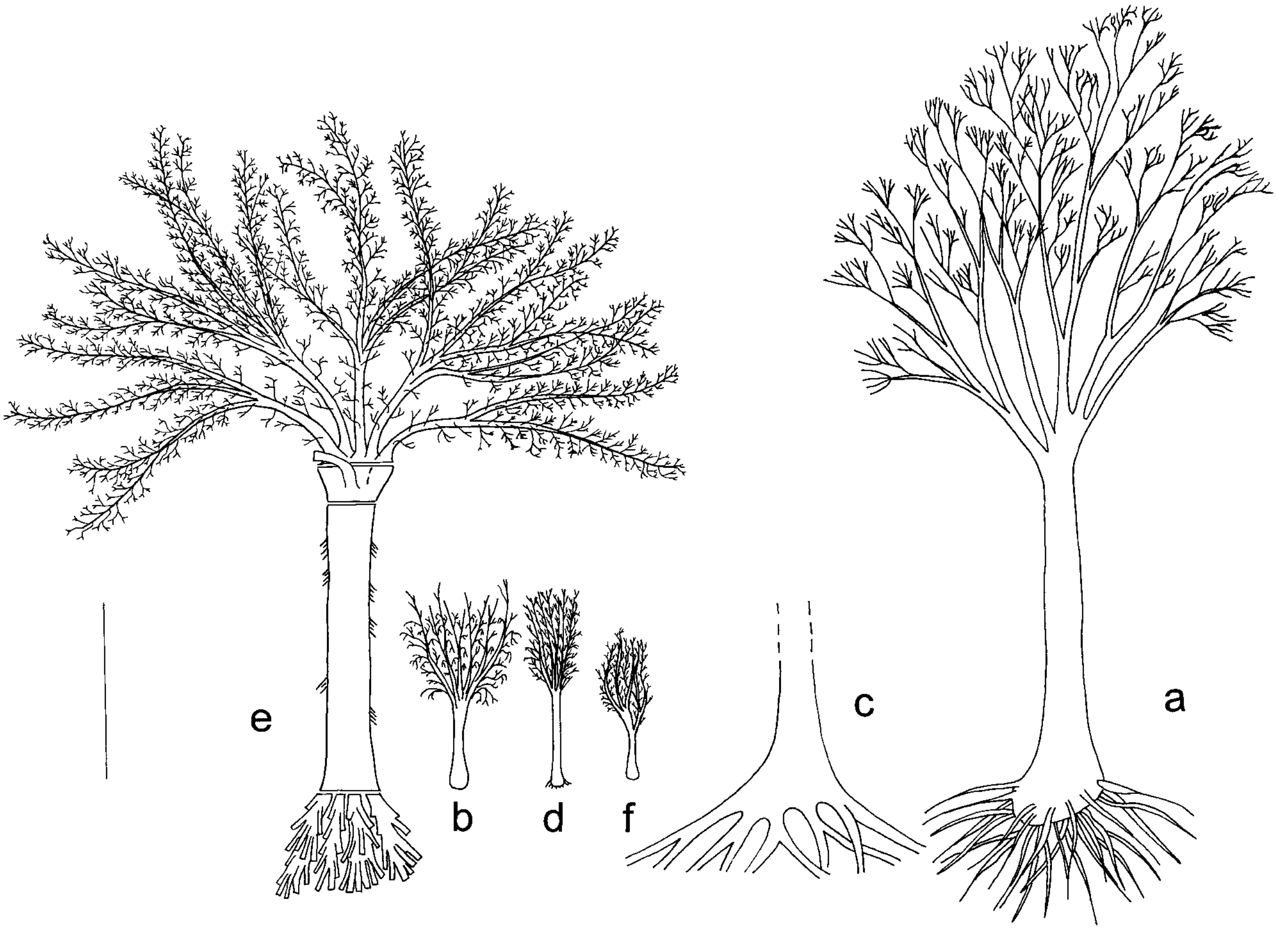

**Fig. 1** Previous reconstructions of *Pseudosporochnus* from Europe proposed between 1930 and 1968. *a*, *Pseudosporochnus krejcii* redrawn from Zimmerman (1930). *b*, *Pseudosporochnus krejcii* redrawn from Kräusel and Weyland (1933). *c*, Base of trunk of Zimmerman's second reconstruction (1949) demonstrating branching rooting system; remainder of plant similar to *a*. *d*, *Pseudosporochnus krejcii* redrawn from Nemejc (1963). *e*, *Pseudosporochnus nodosus* redrawn from Leclercq and Banks (1962). *f*, *Pseudosporochnus verticillatus* redrawn from Obrhel (1968). Approximately to scale (scale bar = 50 cm) with the exception of *d*, for which no scale was originally given.

arose at slightly different levels from what may be regarded as a series of staggered, unequal bifurcations (most similar to the ramification of the branches of *Calamophyton*, with which much early *Pseudosporochnus* material was confused). Each of these branches was further divided once or twice. Naked in their proximal half, they bore typical *Pseudosporochnus* appendages forming an elegant, loose, but apparently two-dimensional, crown.

Høeg (1931) found a large stem in the Middle Devonian of Norway that he considered to have the shape of *Pseudosporochnus*, that is, a short stout "trunk," 14 cm wide and 65 cm long, which terminated abruptly in a tuft of broken branches.

Seward (1931) illustrated *Pseudosporochnus* in his diorama of Devonian plant reconstructions with a slightly bulbous base and digitately divided stem, where the divisions occurred at slightly different levels as on Zimmermann's drawing (1930).

Kräusel and Weyland (1933) gave a new reconstruction of *P. krejcii* from Bohemia (fig. 1*b*) on the basis of new material and that previously reported by Potonié and Bernard (1904). Their reconstruction was of a short trunk, ca. 25 cm in length, that abruptly divided into a crown of five to six branches. Each of these branches was further dichotomously divided and bore laterally typical *Pseudosporochnus* appendages. It was similar to, though smaller than, Zimmermann's reconstruction, but no roots were shown.

Zimmermann (1949, 1959) reproduced his 1930 reconstruction but changed, without explanation, the tuft of roots into a sturdy divided anchoring system (fig. 1*c*).

Němejc (1963) illustrated his personal interpretation of the habit of *P. krejcii* (fig. 1*d*). Although based on Kräusel and Weyland's (1933) material, the small tree he proposed had a look different from the previous reconstruction. The six or seven branches at the top of the "trunk" did not spread; rather, they were shown close set, standing more or less parallel to one another, and densely covered by appendages, giving a bushy, long, and narrow crown. The slightly bulbous base bore a tuft of narrow roots.

Leclercq and Banks (1962) offered their famous reconstruction based on a new species, *P. nodosus*, from Goé, Belgium (fig. 1*e*). The reconstruction shows a stout, parallel-sided trunk with lateral, downward-pointing tufts of small aerial rootlets. The trunk divided abruptly into a crown of eight or nine digitately and dichotomously divided branches to which were attached typical appendages. At the base of the trunk were stout roots with short, distally directed rootlets. To demonstrate their uncertainty in the reconstruction, the roots and crown were drawn separated from the trunk by carefully placed white lines. The reconstruction has much in common with Kräusel and Weyland (1933), although with an extra level of branching added, and must have been as heavily influenced by their work as was Leclercq's reconstruction of the life habit of "*Hyenia*" (Fairon-Demaret and Berry 2000).

Obrhel (1968) gave a reconstruction of *Pseudosporochnus verticillatus* (Krejči) Obrhel (the name he considered correct for the Bohemian *Pseudosporochnus*). This had much in common with Kräusel and Weyland's (1933) reconstruction except that the division of the main trunk did not occur at a well-defined crown but, rather, in two places toward the top of the trunk (fig. 1*f*). This pattern is actually more typical of *Calamophyton* branches (e.g., Leclercq and Andrews 1960). Obrhel stated that the Leclercq and Banks's (1962) reconstruction of *Pseudosporochnus* showed the same general bauplan, even if dealing with a different species, but he cast doubt on the connection between trunk and branches of *P. nodosus*. He also criticized the system of sturdy roots that he claimed was similar to Zimmermann's unsubstantiated drawing (1949).

## Material and Methods

All the specimens considered here were collected by Suzanne Leclercq during the early 1950s from the Brandt North Quarry at Goé, Vesdre Synclinorium (Province of Liège, Belgium). Details of the lithology of this famous locality are to be found in Leclercq and Banks (1962). Seven plant-bearing beds were identified, each subdivided into thinner layers along flat bedding planes, exhibiting a variety of facies and states of preservation of the plant remains. *Pseudosporochnus* fragments are most numerous, distributed throughout the fossiliferous horizons, and are dominant in several thin layers of beds III, IV, and VI. In her field notebook, Suzanne Leclercq described these layers as "*Pseudosporochnus* cemetery." Berry and Fairon-Demaret (1997) provided an up-to-date review of biostratigraphical studies indicating a late Eifelian age for the locality.

The principal technique used to reinterpret the material was photography and observation using low-angle incident illumination, often from a single light source. This allowed observation of additional topographic detail not visible in the illustrations of Leclercq and Banks (1962).

## Determination of Potential Trunk Material

One of the most difficult problems working with the cladoxylopsid material from Goé is the fact that two genera are present, *Pseudosporochnus* and *Calamophyton* (Leclercq and Andrews 1960). At the level of the branches, there is little problem in distinguishing the two. *Calamophyton* has simple, short sterile appendages showing only dichotomous divisions and characteristic recurved sporangiophores. Appendages of *Pseudosporochnus* have a central axis on which bifurcating sterile and fertile units are borne (fig. 6 in Berry 2000). Branches of *Calamophyton* divide at a number of levels to yield up to 10 or more daughter axes. Those of *Pseudosporochnus* divide at more or less one level to yield up to five daughter axes. *Calamophyton* branch compressions also commonly have a number of transverse fractures (probably relating to some taphonomic process; Leclercq and Andrews 1960; Mustafa 1978) that are absent in *Pseudosporochnus*. Finally, while both species have a pattern of small, coaly bumps, or punctuations, on the branch surface, derived from small, often transversely elongate "nests of sclereids" in the cortex (Leclercq and Banks 1962; Stein and Hueber 1989), in *Pseudosporochnus*, it is considerably more conspicuous. In practice, with some reservation, occurrence of numerous, well-defined nests is a useful character to distinguish *Pseudosporochnus* from *Calamophyton*, at least at Goé.

Not all of the above points are relevant to larger trunks, although the presence of a strong pattern of sclereid nests can sometimes be suggestive for assignment to *Pseudosporochnus*. Our experience with the two genera leads us to a further important distinction; whereas *Pseudosporochnus* branches are very commonly preserved with an enlarged basal area suggestive of abscission from the trunk surface (see specimens 1 and 2 in "Description of *Pseudosporochnus* Trunks"), those of *Calamophyton* are found abruptly broken with no obvious basal features marking attachment to a larger organ. We associate these two types of basal preservation of branches with two types of probable trunk material found at Goé.

The first type of trunk has scars on the surface; these scars are well matched to the basal features of *Pseudosporochnus* branches. Such trunks have only small outward-pointing projections of tissues around the scars. We believe this type of trunk material to belong to *Pseudosporochnus* based on this information and the presence of well-defined sclereid nests.

The second type of trunk has longer branch bases attached, sometimes several centimeters long, and all are broken off at the same level (see, e.g., fig. 2). Such specimens were interpreted by Leclercq and Banks (1962) as possible root material of *Pseudosporochnus*, although they had no actual evidence for attachment. This type may well represent the trunks of *Calamophyton*, the abruptly broken bases of the branches having been attached preabscission directly to the ends of the cleanly fractured projecting laterals. We strongly suspect that such trunk material, with uniformly fractured lateral branches, would break down, when naturally macerated, to show attached branch bases preserved only as parallel, coalified, xylem strands. Because of their uniform length, these take on the aspect of parallel-veined leaves, thus producing the falsely leafy appearance of the plants commonly determined as *Duisbergia* Kräusel et Weyland (Kräusel and Weyland 1929; Schweitzer 1966; Mustafa 1978) at other localities in Germany. The occurrence of *Calamophyon* branches at all sites where *Duisbergia* has been studied is supporting evidence for this hypothesis, which will be elaborated elsewhere.

**Fig. 2** Unidentified ?cladoxylopsid trunk (possibly *Calamophyton*) from the upper Eifelian of Goé, Belgium. Ulg 1424 (4961/168A in Leclercq collection), previously illustrated inverted by Leclercq and Banks (1962, pl. 4, fig. 18) as *Pseudosporochnus nodosus* "root-like organ." Scale bar = 10 mm.

## Description of *Pseudosporochnus* Trunks

### *Specimen 1: Figures 3, 4*a*, 4*b*, 5*a* (Ulg 1426; 4969/654 in Leclercq Collection; Illustrated in Leclercq and Banks 1962, Pl. 4, Fig. 20)*

An axis ca. 20 cm in length, 58 mm in width, and terminated at both ends by fractures of the rock (figs. 3, 5). The proximal half and the most distal part are preserved as an impression (external mold) with fragmentary patches of coal remaining in places. Part of the distal portion of the trunk is represented by a fine sandstone internal cast compressed to ca. 5 mm thick (fig. 5*a*, marked by black lines beside trunk). Identification of this specimen as *Pseudosporochnus nodosus* is on the basis of well-defined, ca. 1-mm-sized nests of sclereids in the cortex represented both by coaly nodules on the surface of the internal cast and by depressions into the matrix on the surface of the impression, as well as the nature of apparent abscission of branches as discussed above.

The surface of the proximal impression, more or less featureless in uniform lighting (fig. 3*a*; similar to the illustration of Leclercq and Banks), is best observed with low-angle incident light aimed from the top left (fig. 3*b*). In this latter view, a hexagonal pattern of lines can be made out, each hexagon tangentially elongate, ca. 25 mm in tangential width and 16 mm longitudinally. The hexagonal lines are raised on the impression. The hexagons are arranged in vertical (longitudinal) ranks on the stem surface. However, hexagons in longitudinal rows (files) are not contiguous but separated above and below by an intervening row of hexagons that are offset. Therefore, the distance between the base of one hexagon and the hexagon longitudinally above it in the same file is ca. 26 mm.

When the same area of trunk is observed illuminated from bottom right (fig. 4*a*), the pattern of hexagons can still be made out. A feature that becomes more distinct is the presence of a transverse crescentic depression, 10–13 mm wide or more, which occupies the area below the upper margin of each hexagon (fig. 4*a*, arrows; fig. 5*a*).

On the surface of the distal, internal cast of the trunk, raised areas are observed that increase in relief distally and terminate in a crescentic ridge best viewed when illuminated from below (compare fig. 5*a* with fig. 4*a*, top). Inserted in the same offset manner as the proximal hexagons, the distance between longitudinally superposed crescentic ridges is ca. 23 mm. On the proximal slope of one of these features, longitudinal carbonized lines are visible (fig. 3*b*, arrow), spaced 1–2 mm apart. Similar longitudinal lines are observed on other parts of the stem surface, too, including on the proximal impression region (fig. 4*b*, large arrow; fig. 5*a*).

Along the margins of the trunk, best observed in uniform illumination, a characteristic profile is present (e.g., figs. 3*a*, 5*a*, left margin, distal), where deltoid areas project outward from the stem surface by ca. 6 mm. The upper (distal) margin of each deltoid area is just slightly below the perpendicular to the stem surface. The lower (proximal) and longer margin of the structure falls at an acute angle toward the top of the next deltoid region directly below. The longitudinal distance between the outer corners of successive deltoid regions is ca. 23 mm. On the right-hand margin of the trunk (figs. 3*a*, 5*a*), the deltoid regions are not preserved in a single plane, but the different structures lie at different levels within the matrix and a more complex arrangement is seen, most probably caused by the overlap of originally tangentially, as well as vertically, adjacent deltoid features. On the left-hand margin, narrow carbonized strips are visible emerging from the proximal slope of the deltoid regions (figs. 3*a*, 4*b*, 5*a*, small arrowheads).

### *Specimen 2: Figure 6*b* (Ulg 1422; 4954/173 in Leclercq Collection; Illustrated in Leclercq and Banks 1962, Pl. 3, Fig. 16)*

The identification of this badly worn specimen is partially based on the presence of nests of sclereids ca. 1 mm wide,

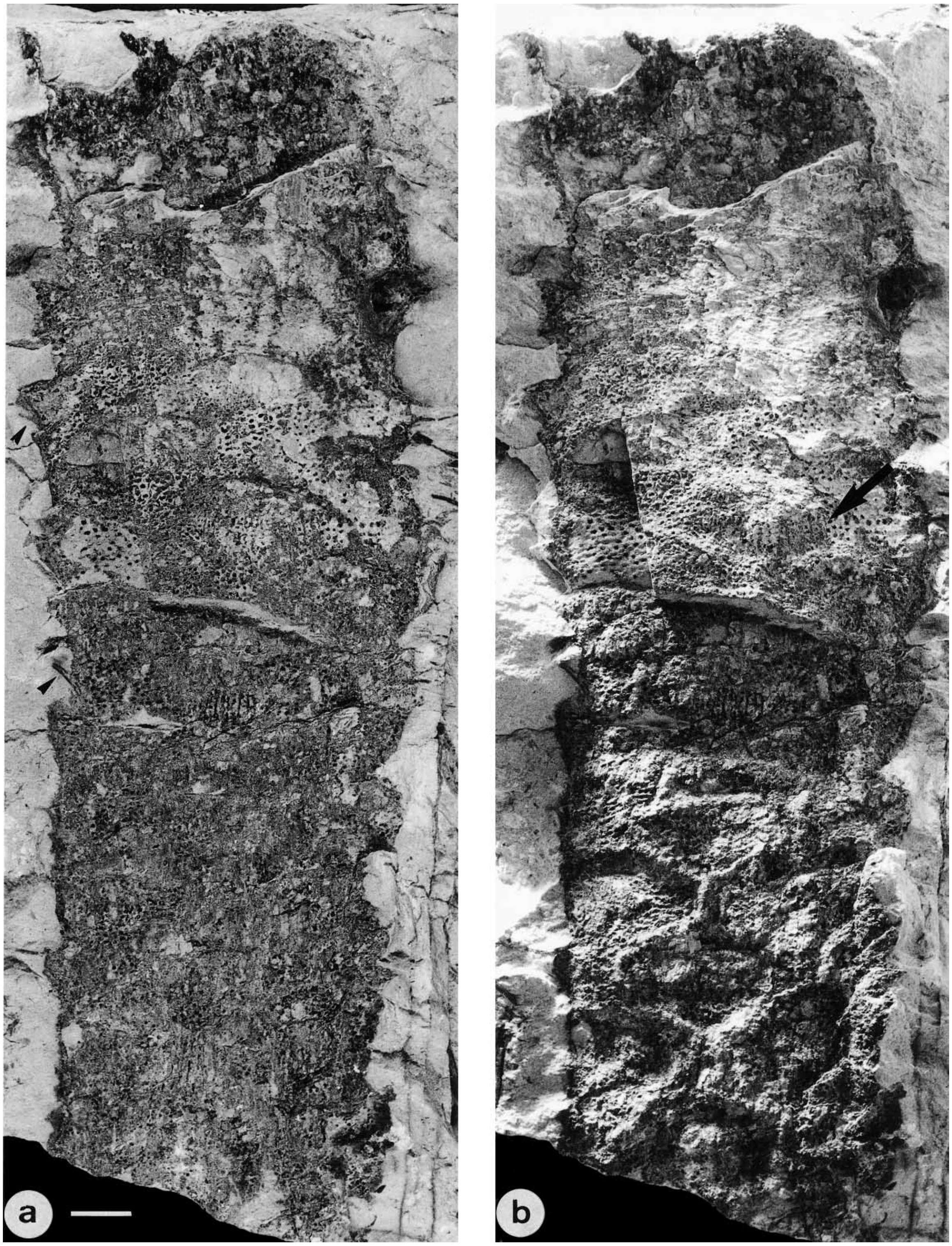

**Fig. 3** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. Ulg 1426 (4969/654 in Leclercq collection), previously illustrated by Leclercq and Banks (1962, pl. 4, fig. 20). Trunk specimen 1 in text. For interpretation see fig. 5. *a*, Trunk photographed in uniform (bidirectional) illumination, emphasizing the deltoid lateral projections (e.g., left margin mid-upper) and carbonized xylem strands emerging from some of them (small arrowheads). *b*, Trunk photographed in unilateral illumination from top, emphasizing the hexagonal branch scar pattern on impression (lower). Arrow indicates longitudinal carbonaceous strands. See also fig. 4 and line-drawing interpretation in fig. 5. Scale bar = 10 mm.

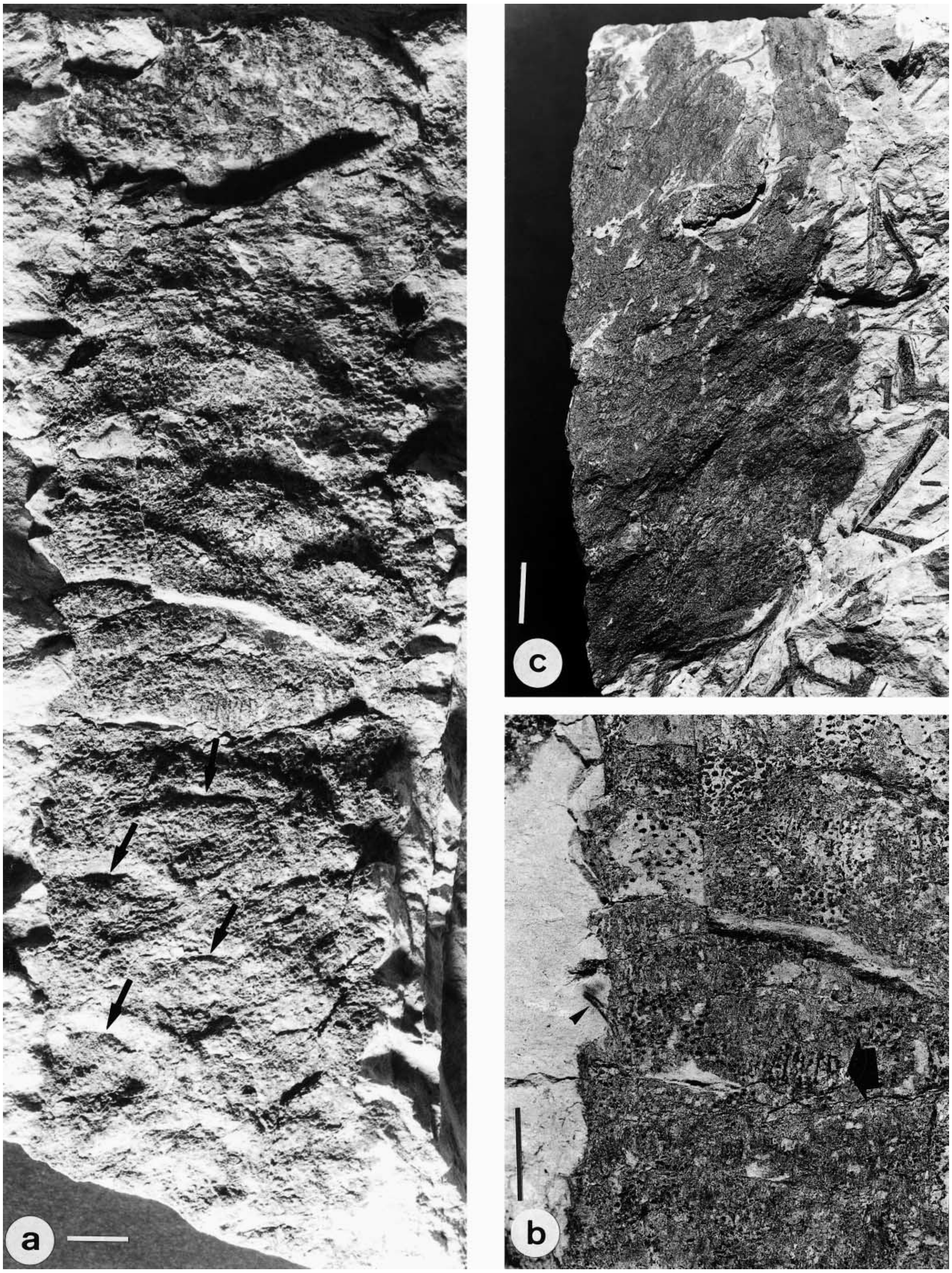

**Fig. 4** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. *a*, *b*, Ulg 1426 (as in fig. 3). *a*, Unilateral illumination from below, emphasizing the ramplike structures with crescentic upper margins preserved on the internal stem cast (upper) and crescentic depressions within upper part of branch scars on the impression (below, arrows). See also fig. 3 and line-drawing interpretation in fig. 5. *b*, Close-up of margin showing carbonaceous xylem strands emerging from branch scars (left, small arrowhead) and parallel lines of carbon within branch scar impression (large arrow, center). Scale bars = 10 mm. *c*, Ulg 1421. Lateral first-order branch attached to trunk; former "crown" specimen of Leclercq and Banks. Orientation of trunk cannot be established. Scale bar = 10 mm.

locally visible as black coal specks on the stem surface or as their impression in the matrix. This trunk fragment is ca. 12 cm long and 40 mm wide. The matrix has split very irregularly, exposing different levels through the thin compression, in places, with only an impression remaining. Several slightly prominent or depressed areas, somewhat circular in outline and ca. 12–15 mm wide, are visible (fig. 6*b*, arrows) enhanced by low-angled incident illumination. Two of these occur side by side near the middle of the specimen, and a third is located distal to, but between, them. Below their upper margin a crescentic depression, 10–12 mm wide, is obvious. We believe these areas represent the same trunk features as in specimen 1 but in a slightly different taphonomic state, with no sediment infill of the stem to allow preservation of a more three-dimensional representation.

### *Specimen 3: Figure 7*a *(Ulg 1423; 1423/5051/57B in Leclercq Collection; Illustrated in Leclercq and Banks 1962, Pl. 3, Fig. 17)*

This specimen is poorly preserved on the left-hand margin, although some deltoid regions may be recognized protruding beyond the stem surface. On the right-hand margin, small tufts of carbonized strands are observed, some 10 mm long and 30 mm between tufts (fig. 7*a*; "*ap*" on pl. 3, fig. 17 in Leclercq and Banks 1962). Narrow longitudinal carbonized strands, 0.9–1.2 mm in width, are visible on much of the surface (as illustrated by Leclercq and Banks, marked "*x.st*").

### *Specimen 4: Figures 6*a*, 7*b *(Ulg 1686; 282/1686ABCD in Leclercq Collection)*

This specimen has not previously been illustrated nor has it previously been positively identified with *P. nodosus*. It has a length of 42 cm, and its maximum preserved diameter is at least 13 cm. Only one margin is preserved on both part and counterpart, and so the true diameter has not been established. We identify it with *P. nodosus* on the basis of the presence of both deltoid structures on the stem compression margins (fig. 6*a*) and sclereid nests visible in the less carbonized areas along the left-hand margin.

Prominent deltoid areas on the left-hand margin stand out by up to 10 mm and are inserted at a regular distance of 35–40 mm (fig. 6*a*, wide arrows). These structures are believed equivalent to those at the margins on specimen 1, although the upper margin of each deltoid area in this case is a little above the perpendicular to the stem surface. Between each of these prominent features, a smaller, more rounded deltoid area can be picked out (fig. 6*a*, narrow arrowheads). In the basal region of the trunk, there are prominent, longitudinal carbonized stripes preserved within the mass of carbon and minerals that make up the trunk compression, ca. 2 mm apart (fig. 6*a*, lower; fig. 7*b*). Similar strands can be detected elsewhere on the surface. At the base of the specimen, they converge toward crescentic depressions, which, although not prominent, are still discernible (figs. 6*a*, 7*b*, arrows). However, the rest of the compression is strongly slickensided, and the coal has developed a cleavage that superficially gives the appearance of a fabric to the trunk that is slightly oblique to its length.

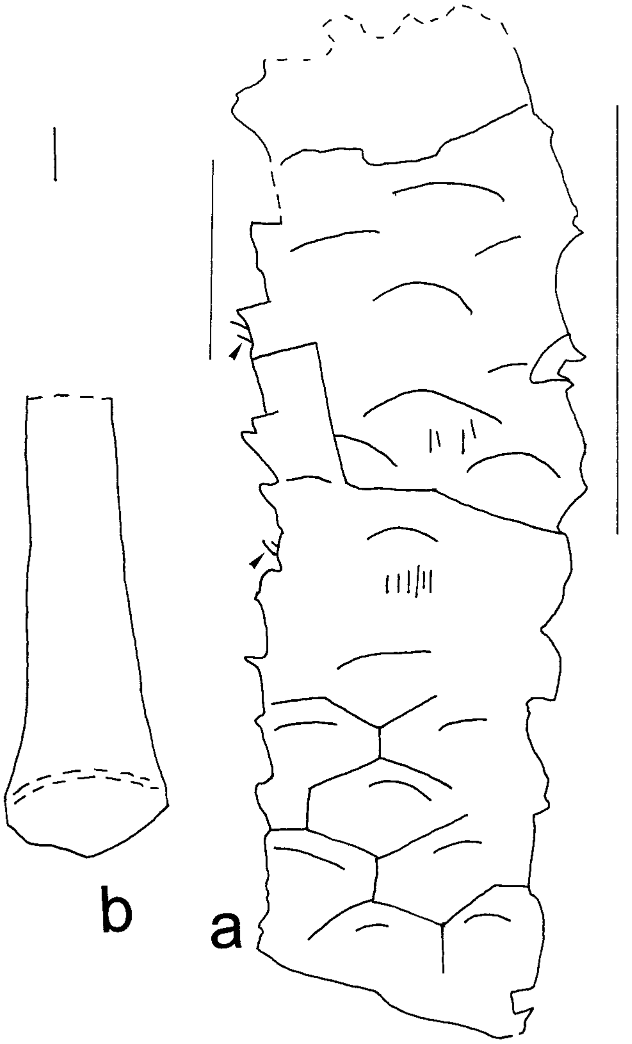

**Fig. 5** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. Ulg 1426. *a*, Line-drawing composite interpretation of information from figs. 3 and 4*a*. Black lines beside trunk indicate area that is an internal cast of the stem; all other areas are impressions. Crescentic lines on internal cast indicate ridges. Crescentic lines on impression indicate depressions. Longitudinal short lines represent carbonized xylem tissue. Arrowheads indicate carbonized xylem strands emerging from deltoid regions on margin of stem. For idealized diagram of the stem in these preservation states, see fig. 8. *b*, Base of first-order branch (dashed lines) showing characteristic crescentic depression (as in fig. 6*c*). Scale bar = 10 mm.

## Description of First-Order Branch

### *Figures 5*b*, 6*c*, Specimen Ulg 1420 (4956/462 in Leclercq Collection; Illustrated in Leclercq and Banks 1962, Pl. 2, Fig. 13)*

The surface of this first-order branch is covered with coal specks representing nests of sclereids. It has a diameter of 18 mm 10 cm from the base and 23 mm 5 cm from the base. The basal region is a maximum of 35 mm wide. Low-angle illumination (from the top) reveals the presence of a crescentic depression some 7 mm centrally above the widest part of the

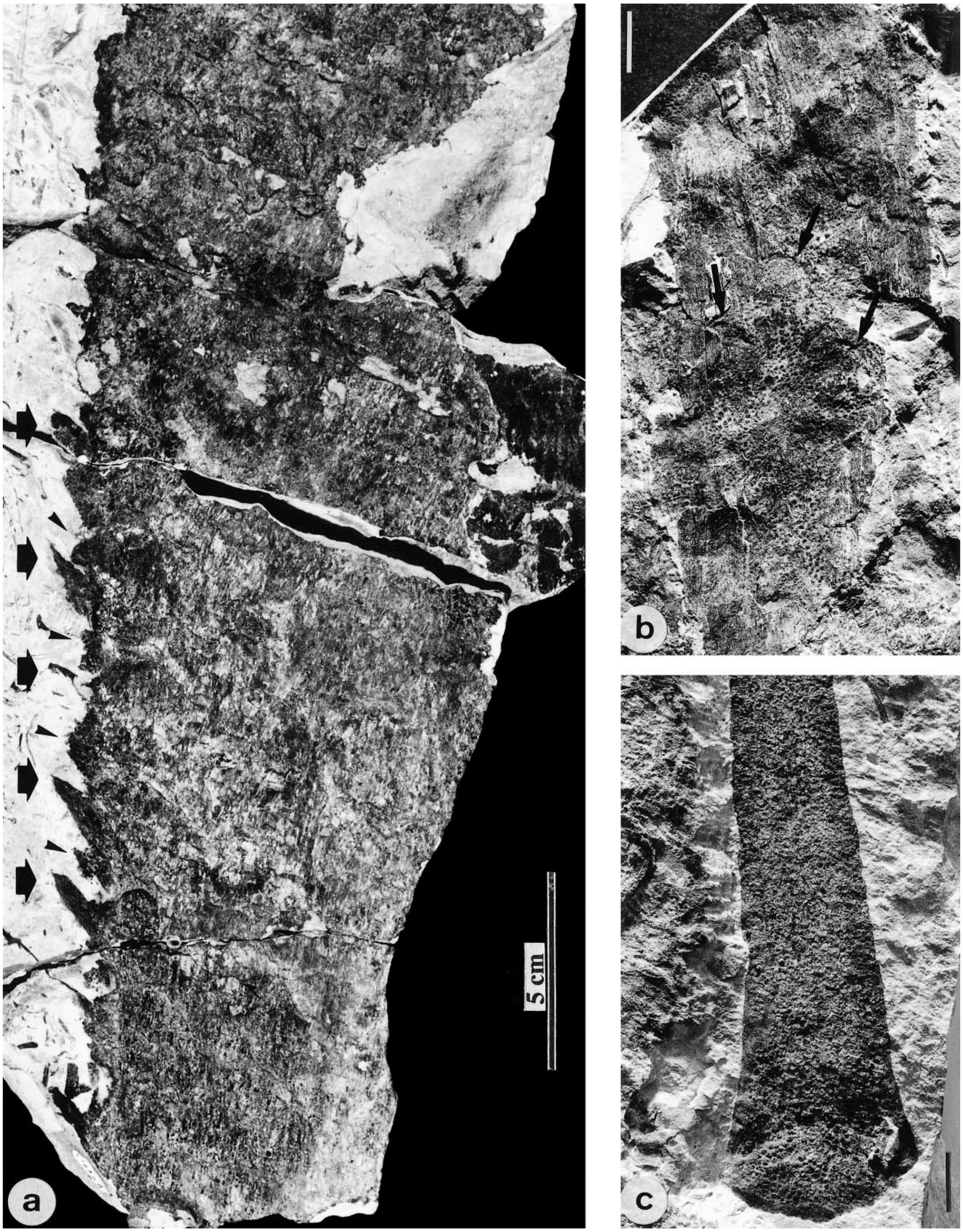

**Fig. 6** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. *a*, Ulg 1686; 282/1686ABCD in Leclercq collection. Largest trunk material demonstrating prominent "deltoid regions" on left margin (large arrows and smaller arrowheads). *b*, Ulg 1422; 4954/173 in Leclercq collection; trunk impression/compression showing depressions marking branch scars (arrows). *c*, Ulg 1420; 4956/462 in Leclercq collection, first-order branch, unilateral illumination from top showing crescentic depression delimiting branch base (cf. fig. 5*b*). Scale bars = 50 mm (*a*), 10 mm (*b*, *c*).

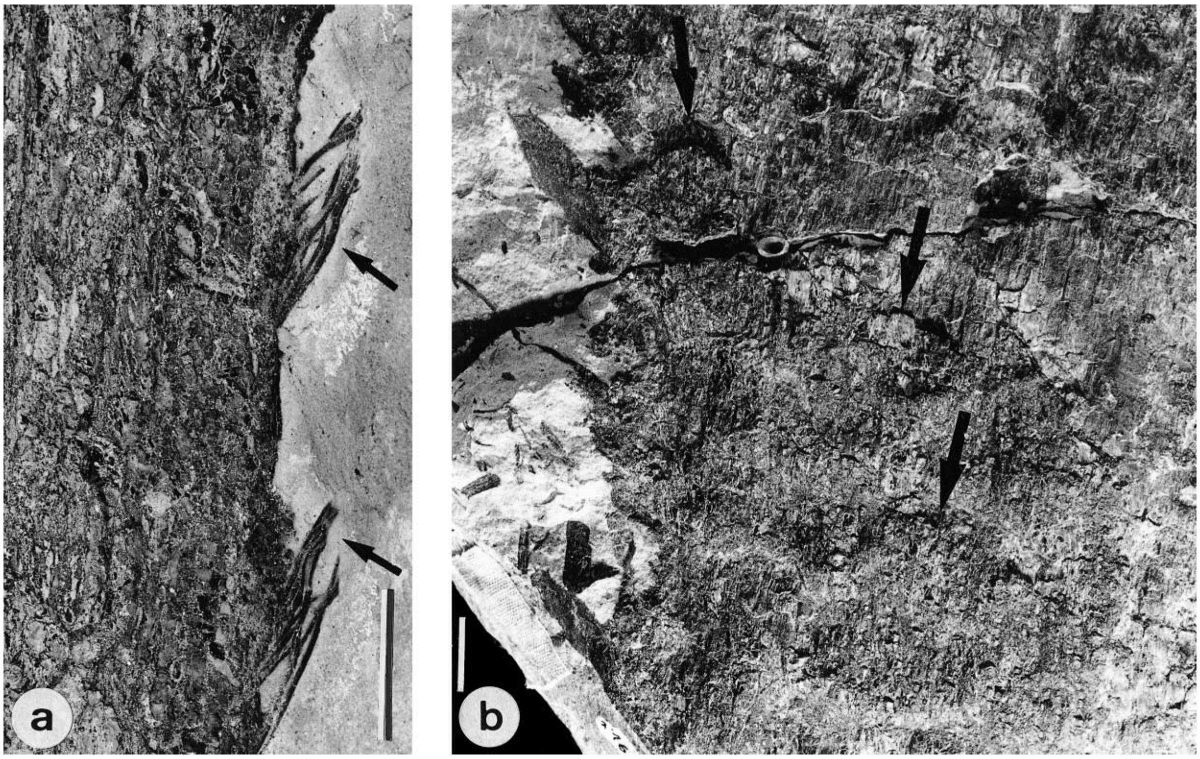

**Fig. 7** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. *a*, Ulg 1423; 5051/57 in Leclercq collection; close-up of proximal right margin of trunk showing carbonized xylem strands formerly entering first-order branch at margin (arrows) and longitudinal carbonized strands on stem compression (left). *b*, Enlargement of fig. 6*a*; trunk showing longitudinal carbonized strands on stem impression and pattern of crescentic depressions marking branch scars (arrows). Scale bars = 10 mm.

base (fig. 5*b*, dashed line; fig. 6*c*). This crescentic depression intersects the lateral margins of the base 4 mm above the widest point, delimiting two short medial lateral margins that slightly converge distally. The lateral margins of the axis immediately above the intersection of the crescentic depression are very slightly concave distally toward the almost parallel-sided main length of the branch (figs. 5*b*, 6*c*). The extreme basal margin of the branch compression consists of two angled, very slightly convex facets that meet centrally at a slightly rounded point.

## Interpretation of New Evidence

Our new information demonstrates structures never before observed on *Pseudosporochnus* and demands reconsideration of the architecture of the plant. The most critical and interesting new evidence relates to the connection between trunk and first-order branch.

### First-Order Branches

First-order branches of *Pseudosporochnus* are typically enlarged at the base. We concur with Potonié and Bernard's (1904) original description of the base of most of their material resembling a flattened cone. However, we notice at the base of the first-order branch illustrated here that there is a distinctive well-delimited area, with a crescentic top, two short lateral margins, and two slightly concave margins at the base. This morphological character has been observed by us in a number of specimens of *Pseudosporochnus* from Goé. In addition, this is a feature of basally complete first-order branches of the pseudosporochnalean cladoxylopsid *Wattieza* from Venezuela (Berry 2000). We believe that the evidence suggests that the base of the first-order branch approximates to the shape of a slightly flared and transversely flattened cone that connects to the trunk at an oblique angle. Experimental cutting of a paper cone to intersect a larger cylindrical trunk at an angle of ca. 45° yielded a basal morphology that when compressed (flattened) consisted of a markedly crescentic upper (adaxial) margin and two basal (abaxial) margins (or facets) that were only slightly convex, agreeing very well with the basal morphology observed in the compression fossil. The completeness of the base of these branches, including the almost conical base, apparently with a cortical layer and characteristic sclereid nests, suggests to us the very strong probability of abscission of first-order branches in *Pseudosporochnus* and *Wattieza* at the base. The one and only specimen of *Pseudosporochnus nodosus* that shows a single branch actually attached to trunk material, the "crown" specimen of Leclercq and Banks (1962, pl. 3, figs. 14–15; our fig. 4*c*), demonstrates clearly the enlarged base of the branch but is not informative as to the relative angle of the trunk.

### Trunk/Branch Scars

Our most informative trunk specimen (specimen 1) demonstrates a regular pattern of surface structures that are approximately hexagonal and tangentially elongate. The raised lines delimiting these structures on the impression represent either a sunken line on the living stem surface or a line where the stem surface was preferentially compressed during compaction (Berry and Edwards 1995). When these structures are preserved as an internal cast, they are upraised areas increasing in height distally and terminating in a crescentic top (fig. 8*a*). When these structures are preserved as impressions, the proximal and lateral margins are markedly hexagonal ridges, whereas the distal margin is a crescentic depression marking the top of the lateral branch (adaxial surface) plunging into the matrix (fig. 8*b*). The base of the first-order branches therefore has proximal (abaxial) and lateral margins morphologically similar to those of the trunk surface hexagons and an upper margin that is similar to the crescentic depression/ridge observed toward the top of the trunk hexagons in their various states of preservation (fig. 8*c*, shaded). Our interpretation of the relationships of these various features and preservation states is illustrated in figure 8.

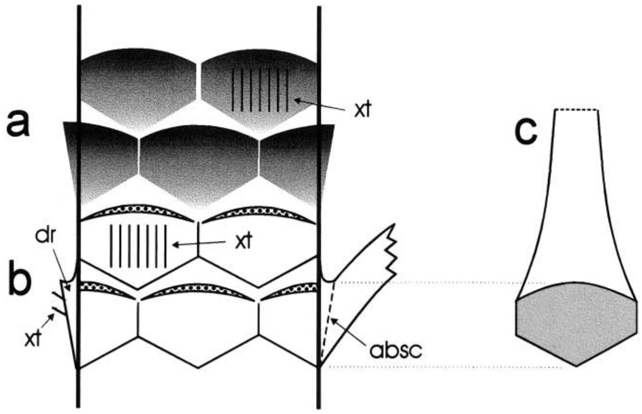

**Fig. 8** *Pseudosporochnus nodosus* Leclercq et Banks from the upper Eifelian of Goé, Belgium. Idealized interpretation of observed stem and branch preservation. *a*, Trunk internal cast. Branch scars infilled with sediment, represented by a protruding structure increasing in height distally and with a crescentic top. Surface of the branch scar may retain some carbonized remains of xylem supply to branch (*xt*). *b*, Trunk impression. Branch scars delimited by tangentially elongate, approximately hexagonal lower and medial margins preserved as ridges of sediment (see fig. 3*b*, lower). Adaxial surface of branch/branch scar going down into matrix below impression, represented by crescentic depression (stippled). Branches abscise along line of weakness (*absc*) to leave a branch scar represented by a deltoid region (*dr*) when compressed at stem margin. Branch vascular traces (*xt*) represented by parallel bands of carbonized xylem when observed in center of branch scar impressions and by narrow strands when observed emerging from branch scars (*dr*) at margins. *c*, Branch base, adaxial view. Area formerly attached to trunk is shaded (see fig. 6*c*).

### *Trunk/Branch Connection*

The basal features of the first-order branch compression can be directly compared to the features preserved on the surface of the trunk fossil (fig. 5). The slightly convex margins of the extreme base of our branch are equivalent to the lower (abaxial) margins of the hexagonal structures viewed on the trunk surface impression (fig. 5*a*, lower). The crescentic depression that delimits the top (adaxial) margin of the basal branch structure is equivalent to the crescentic features seen both at the top of the trunk compression when viewed on the internal cast (a ridge; fig. 5*a*, upper) and on the trunk surface impression (a groove/depression; fig. 5*a*, lower). The two medial lateral margins of the branch bases/hexagons appear to represent the position where two laterally adjacent branch bases contact. An idealized reconstruction of these relationships is given in figure 8.

The trunk material that we illustrate is interpreted to show morphological features from which the branches have been shed (i.e., branch scars). The uniform and consistent preservation of the branch scars in each different orientation (e.g., on the impression or internal cast surface or at the margin of the compression) strongly suggest that branches were abscised in some predetermined way along a path of programmed weakness (fig. 8*b*, *absc*). The products of this abscission were a cleanly separated, somewhat oblique/conical base on the first-order branch and a strongly three-dimensional scar on the trunk surface. These are viewed as hexagonal structures on the impression, a series of raised crescentic-topped ramps on the internal cast, and as deltoid structures at the trunk margin (fig. 8*b*, *dr*). From the long, lower face of the latter sometimes emerge carbonized strands (fig. 3*a*, arrowheads; fig. 5*a*, arrow; figs. 7*a*, 8*b*, *xt*). Where branch scars are seen on the trunk in face view, some demonstrate strands of carbonaceous xylem tissue running parallel and longitudinally across them (fig. 3*b*, large arrow; fig. 4*b*, arrow; fig. 8, *xt*). Leclercq and Banks (1962) interpreted carbonized strands emerging from their trunk material as proximally pointing aerial rootlets (Leclercq and Banks 1962, pl. 3, fig. 17, *ap*). However, similar carbonized strands of xylem tissue can also be seen emerging from the bases of first-order branches where they have been naturally macerated (Leclercq and Banks 1962, pl. 1, fig. 3; pl. 2, fig. 7). We therefore interpret the carbonized strands emerging from the trunk as distally directed remnants of the vascular supply (xylem strands) previously connected to the branches. Analogous strands of xylem can be seen with the same appearance (but a different pattern) protruding from leaf scars in living tree ferns (Cyatheaceae) where the petioles have abscised.

Larger trunk specimens up to at least 13 cm in diameter have margins demonstrating similar deltoid structures (specimens 3 and 4) to those on smaller specimens. We now associate them with the other trunk material on the basis of the lateral appearance of the three-dimensional branch scars and the presence of crescentic depressions on the trunk surfaces, as well as the presence of pronounced sclereid nests.

## New Reconstruction

Our new reconstruction of *Pseudosporochnus nodosus* (fig. 9) has been drawn to take into account the observations we have made in terms of the basic architecture of the plant. We have incorporated only information from a restricted selection of the above-described specimens most critical to the understanding of the basic architecture of *Pseudosporochnus*. It does not, for example, include the largest specimens. Our reconstruction therefore must be considered a conservative state-

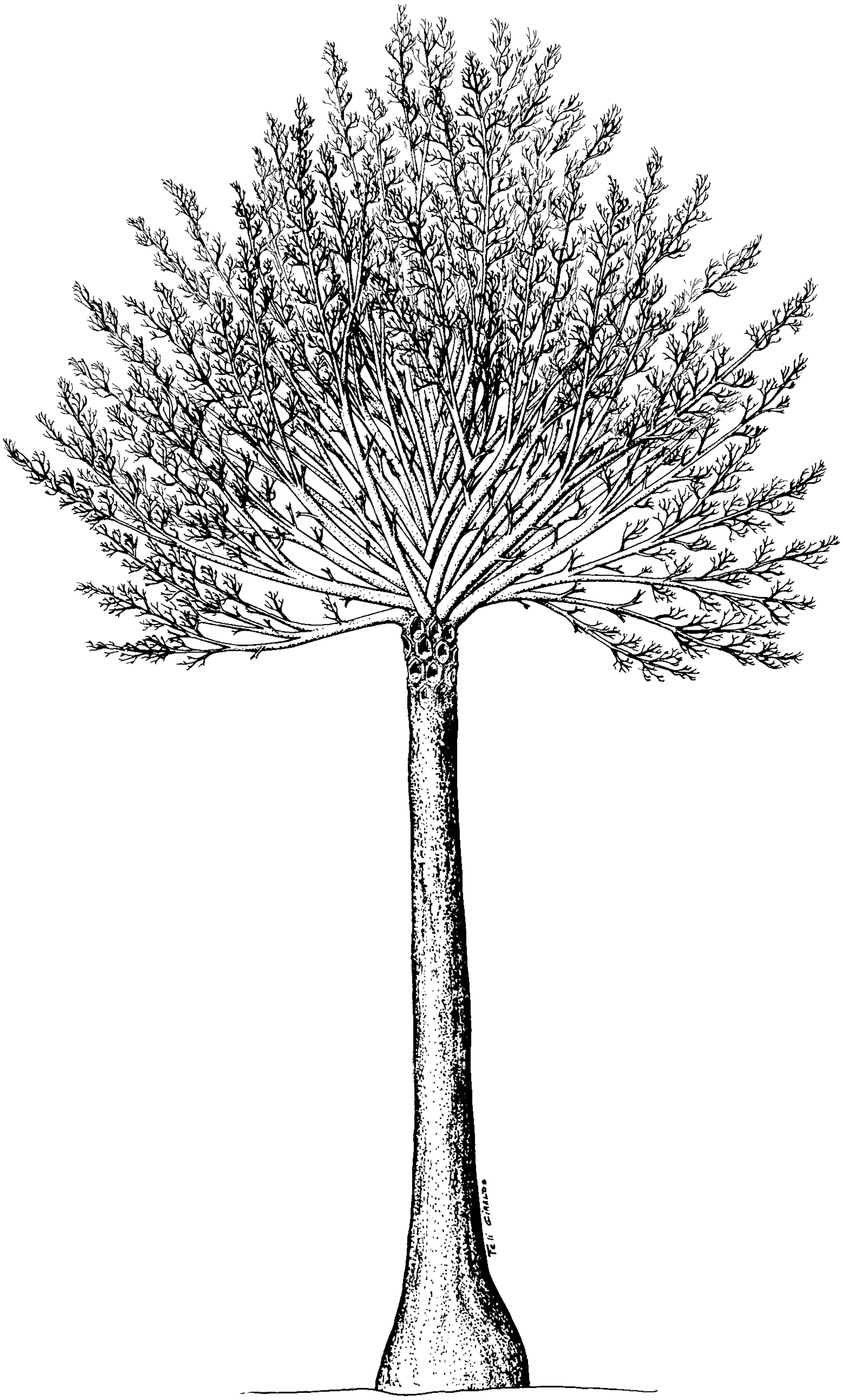

**Fig. 9** New reconstruction of *Pseudosporochnus nodosus* Leclercq et Banks based on the details of this study. Overall height ca. 2.5 m. Our confidence of each part of the reconstruction as discussed in the text.

ment of our understanding of pseudosporochnalean plants pending further investigation.

Our reconstruction is based mostly on trunk specimen 1. In this specimen, ca. 6 cm in diameter, branch scars show that probably five branches were inserted in one turn of the axis, with the next row offset by half a position. The pattern described is unlikely to be the only one found on stems of pseudosporochnalean plants; we know of other examples (to be described elsewhere) in which the branch scars are in more or less vertical ranks with no offset. Currently, we are unable to say whether the patterns are whorled, helical, or both. Ontogenetic and other growth factors probably controlled the exact spacing and arrangement of the branch insertions. The appearance would nevertheless be that of a bushy plant with densely inserted branches.

We have no direct evidence for the apical region of *Pseudosporochnus*. We therefore base it on the juvenile specimen of *Lorophyton goense* Fairon-Demaret and Li (1993) from a nearby locality. This remarkable specimen, a "whole" plant with roots and branches, with a stem width of 15 mm and length of 20 cm, has an apex, where branches are inserted acutely and crowded together, and lower branches, which are less acutely inserted and spaced further apart. This probably reflects the ontogeny of the stem.

We have a high degree of confidence in our reconstruction of the upper part of *Pseudosporochnus* below the apex, especially the lateral insertion of the first-order branches, because we now have first-hand evidence for this. For the lower part of the trunk, we use the largest specimen attributed to *Pseudosporochnus* (*krejcii*) *verticillatus* by Potonié and Bernard (1904, fig. 81). This specimen, which cannot presently be located in the Museum für Naturkunde in Berlin, and which may have been lost or destroyed, in reality has no features that allow it to be definitively attributed to a particular genus. It had a truncated top that was ca. 5 cm in diameter (conveniently similar to our most informative specimen 1) with a small number of branch bases arranged around it. The trunk tapered acropetally from a lower diameter of ca. 10 cm over a distance of some 1.5 m. The basal region was a genuinely swollen, bulbous base (not to be confused with the conical bases of first-order branches) with a maximum diameter of 20 cm. From the Goé specimens of *Pseudosporochnus*, no direct information about the base of the plant or of the rooting organs has been obtained. However, occurrence of a swollen, bulbous base is likely because such an enlarged base seems to be a characteristic of Middle Devonian arborescent cladoxylalean plants. In addition to *P. verticillatus* (Potonié and Bernard 1904), it occurs in *Calamophyton* (Schweitzer 1973), *Lorophyton* (Fairon-Demaret and Li 1993), in which the bulbous base is present but not very pronounced most probably because of the small stature of the juvenile specimen illustrated, and *Duisbergia* (Kräusel and Weyland 1938; Mustafa 1978). Our confidence in this lower part of our reconstruction of *P. nodosus* is moderate and the best we can manage at present. Details of the ramification of the branches and appendages of *P. nodosus* are as discussed in Berry and Fairon-Demaret (1997), in which we have a high degree of confidence.

Our reconstruction therefore shows a small tree ca. 2.5–3 m in total height, with a trunk diameter just above the swollen base of ca. 10 cm and with densely crowded branches in the upper part. We have drawn the lower part of the trunk with a light bark texture representing continued growth in stem diameter and thus destruction of the branch scars that would still be visible for a while after the branches were lost. This appears to be the case in the "trunk" specimen of *Pseudosporochnus krejcii* (Potonié and Bernard 1904). However, the issue of "secondary" growth of cladoxylopsid axes is a controversial matter that will be briefly discussed in "Speculations on the Ontogeny and Growth of Pseudosporochnalean Plants."

In the text above, we have expressed our relative confidences in the various architectural elements of the plant, and we believe that we now understand the overall body plan of the plant. However, we are not at all confident that the relative proportions of some parts of the plant are secure—for example, the relative lengths of trunk bearing living branches to that from which the branches have been abscised. Therefore, while we are convinced that our reconstruction shows a more realistic aspect to the life appearance of *Pseudosporochnus* than any previously published, we are also sure that it will eventually be improved once new evidence comes to light.

The restoration must also be considered conservative because we do not include the largest trunk elements that we have now positively identified with *Pseudosporochnus*; in addition, there is even larger trunk material from Goé that has yet to be associated with any of the known Goé plants, of which *Pseudosporochnus* is by far the largest. We are in the process of making further studies of Middle Devonian cladoxylopsid material from other sources, with the goal of establishing a convincing ontogenetic trajectory for this type of plant.

## Comparisons to Previous Reconstructions and Interpretations of Devonian Cladoxylopsids

Kräusel and Weyland (1933) considered the first-order branch of *Pseudosporochnus* and its associated appendages to represent the whole plant (fig. 1*b*). Other reconstructions by Němejc (1963) and Obrhel (1968) followed this example (fig. 1*d*, 1*f*). Zimmerman (1930, 1949, 1959) may have confused a potentially genuine cladoxylopsid trunk specimen illustrated by Potonié and Bernard (1904) with digitately divided first-order branches and therefore produced a larger reconstruction demonstrating the same basic architecture as the previously mentioned authors (fig. 1*a*, 1*c*).

Leclercq and Banks (1962) were the first authors to recognize the presence of a trunk to which were attached first-order branches that were digitately divided at some distance from their base (fig. 1*e*). However, they placed a lot of emphasis on a single confusing specimen that was interpreted to represent a crown of branch bases situated terminally on the trunk (fig. 4*c*). Using other specimens previously illustrated by Leclercq and Banks, we were able to observe structures interpreted by us as branch base scars directly on the surfaces of trunk material, and so our branches are inserted laterally. In addition, we reject Leclercq and Banks' interpretation for some axes showing laterally attached "rootlets" to be roots of *Pseudosporochnus*. We have no direct evidence of the roots of *Pseudosporochnus*. They are likely to have been similar to the roots of *Lorophyton* and *Calamophyton*; yet, because they are largely underground, we omit them from our drawing.

Schweitzer (1973) produced a reconstruction of *Calamophyton* Kräusel et Weyland. This featured a sturdy central trunk to which were attached lateral, profusely divided branches. His reconstruction was based on material that included a significant number of trunks of different sizes, some showing roots and/or the bases of lateral branches. The plant was illustrated reaching a height of over 2 m. This reconstruction has the same overall architecture as our *Pseudosporochnus*, but there are some fundamental differences. First, Schweitzer's reconstruction shows a very low density of lateral branches, which is at variance with the density of branch insertion shown in his illustrated trunk fossils. Second, the lax apex of the plant terminates in a digitate/dichotomous branch system similar to the lateral branches, for which no firm evidence is provided. Schweitzer suggested for *Calamophyton* that the branches become more numerous and sturdy toward the apex. Following our model, we would expect the apex to be surrounded by densely inserted, newly produced branches. However, we would expect the zone of maturity of lateral branches in a moderately developed tree to bear larger branches than those carried on the lower parts of the trunk earlier in its life history.

*Lorophyton* Fairon-Demaret and Li (1993) is represented by a unique, small juvenile specimen that includes trunk, roots, and sterile lateral branches as well as several specimens of fertile and sterile branches of larger individuals. The specimens were found on ca. 12 small slabs from a very localized lens of sediment. The 20-cm-long trunk specimen has very short remains of lateral branches basally, but in the upper half, demonstrates the attachment of undivided lateral branches that become more acutely and densely inserted toward the apex. This architecture, as will be discussed in "Speculations on the Ontogeny and Growth of Pseudosporochnalean Plants," is very similar to our reconstruction of *Pseudosporochnus* and to the descriptions and illustrations (but not reconstruction) of *Calamophyton* (Schweitzer 1973).

Soria et al. (2001) recently made an analysis of a 42-cm-long cladoxylopsid axis from the Upper Devonian (Lower Famennian) of Morocco that they named *Pietzschia levis*. This was interpreted as a stem fragment. The specimen exhibits fundamental differences from the Middle Devonian trunks that we are considering here. First, the bases of the lateral branches, which are preserved anatomically, are very wide tangentially but narrow in the radial sense and are curved around the stem surface as a large ensheathing structure. In the case of the Moroccan specimen, the morphology of the complete lateral branches is unknown but is interpreted as being a bilaterally symmetric branch/frond. The bases of branches in pseudosporochnalean cladoxylopsids are considerably thicker than those of *Pietzschia* and do not show noticeable bilateral symmetry away from the base. We are aware of Upper Devonian cladoxylopsid branch material from China, currently being studied by C. M. Berry and Li Cheng-Sen, that is both anatomically and morphologically preserved and that has bilateral symmetry, regular branching, and a tangentially wide but radially narrow (ensheathing) base that is extremely obvious in compression. If *Pseudosporochnus* and other related plants shared this character, then we believe that it would, without question, have been observed in the compression material. *Pietzschia* is a plant with cladoxylalean anatomy that falls well outside the emerging concept of the mainly Middle Devonian order Pseudosporochnales.

All of the above-mentioned plants have concerned individuals of an essentially freestanding habit. Lemoigne and Iurina (1983) studied anatomically preserved material of the cladoxylopsid *Xenocladia medullosina* Arnold from the Middle Devonian of Kazakhstan and suggested a lianoid habit based on the presence of a dissected vascular architecture that is typical of such plants. Although we lack strong morphological evidence to support such an hypothesis, it is interesting to note in this context that Snigirevsky (1992) has since reported cladoxylopsid material found attached to the surface of *Callixylon* wood, the trunk material of the progymnosperm tree *Archaeopteris*.

## Speculations on the Ontogeny and Growth of Pseudosporochnalean Plants

A primary endeavor when reconstructing a fossil as a living plant is to understand how it grows to a mature size. This is of particular importance in Middle Devonian Cladoxylopsida, which may have been the first truly large plants to dominate terrestrial ecosystems and indeed to form "forests." The main stem, or trunk, of pseudosporochnalean plants was most probably supplied by more or less radially arranged plates of xylem enclosed by an outer layer of cortex with nests of sclereids. According to this arrangement of xylem, *Pseudosporochnus* would have had a stem with a very high density-specific stiffness (Niklas 1994, 1999), and the tree could have reached a considerable height (3 m or more). With regard to Pseudosporochnales, assuming there was no massive development of aerial rootlets to reinforce the trunk, the crucial question is whether the trunks could enlarge significantly in girth by a process of secondary expansion of stem tissues to support an elongating trunk. To some authors, the answer is clearly in the negative (Soria et al. 2001, p. 924).

There are two lines of evidence that may be used to investigate this. First, anatomical evidence can be used directly to investigate secondary growth and growth potential in pseudosporochnalean trunk material. Second, studies of compression material can be used to investigate potential ontogenetic trajectories within fossil assemblages.

As far as anatomical evidence is concerned, no comprehensive studies of confirmed pseudosporochnalean trunk material are known to us. Soria et al. (2001, p. 924) stated that "potential for secondary lateral expansion is reduced in cladoxylopsids, especially in early members that lack secondary tissues." However, most detailed studies of pseudosporochnalean anatomy relate to first- and second-order branches. These branches certainly lack significant amounts of secondary tissues (Leclercq and Banks 1962; Leclercq and Lele 1968; Stein and Hueber 1989) that could be construed to demonstrate real secondary expansion, although some may contain small amounts of radially aligned "secondary" xylem around the primary xylem core. In our model of *Pseudosporochnus* architecture, we recognize branches as ephemeral organs that abscised. Each branch, highly "determinate" in nature, would have grown to fulfill its photosynthetic and/or reproductive potential at an appropriate stage of maturity of the trunk before being discarded. Therefore, we would not necessarily expect such structures to demonstrate either significant potential for, nor evidence of, extensive secondary growth. In a small (less than 5 cm diameter) specimen of *Duisbergia mirabilis* Kräusel et Weyland, a fossil we consider to probably represent the trunk of *Calamophyton* (as explained above), Mustafa (1978) demonstrated the presence of a considerable volume of aligned secondary xylem cells, up to 20 cells thick, arrayed around the primary xylem plates (Taf. 14 in Mustafa 1978; figs. 2–5). From our observation of the published figures, we estimate the aligned secondary xylem to have at least twice the volume of the primary xylem, largely arranged to enlarge the width of the primary xylem plates tangentially. Such tangential enlargement of the xylem plates must also have increased the circumference and therefore radius of the trunk. We have just commenced a thorough investigation of Mustafa's (1978) anatomically preserved cladoxylopsid trunks of various diameters in order to understand better their potential for secondary growth.

In terms of morphological support for the notion of growth of the plant and trunk, there are a number of lines of evidence available. For example, the whole-plant specimen of *Lorophyton* (fig. 2 in Fairon-Demaret and Li 1993), interpreted as a juvenile by its authors, has attached branches of only 4 mm in diameter, but isolated branches in the sediment are at least 6 mm in diameter. Attached branches are up to 12 cm long and undivided, whereas isolated branches may reach 30 cm length and bifurcate. None of the laterals on the whole plant are fertile, whereas isolated examples are. Appendages on the whole plant are ca. 20 mm long, whereas on isolated branches they may reach 45 mm. The lower branches appear to have been shed from the trunk, whereas the apex was still producing new laterals. The whole appearance is of a plant that would continue to grow, the isolated specimens demonstrating later growth stages. Again, it is worth mentioning that the source of material of this plant was extremely localized and the amount of material is a fraction of that available for *Calamophyton* or *Pseudosporochnus*. Soria et al. (2001, p. 924) interpreted *Lorophyton* as, instead, a smaller and developmentally simpler taxon than *Pseudosporochnus* or *Calamophyton* but did not discuss the presence of larger material in the fossil assemblage.

"Whole" *Calamophyton* trunk specimens from Lindlar (Schweitzer 1973) vary from 1.5 to 10 cm diameter just above their enlarged bases. The smallest plants are very similar in size and architecture to the juvenile specimen of *Lorophyton*, with small undivided lateral branches, whereas a larger specimen (illustrated as "*Hyenia elegans*" in Schweitzer 1972; see discussion in Fairon-Demaret and Berry 2000) of ca. 25-mm-trunk diameter has diminutive, yet digitately divided, branches. Unconnected digitate branches of *Calamophyton* from the same locality reach a diameter of up to 30 mm, are twice the diameter of the trunks of the smallest whole-plant specimens, and can only have been attached in growth to the largest trunks known from Lindlar (or, indeed, even larger ones).

In *Pseudosporochnus nodosus* from Goé, we now recognize trunks, showing branch scars, of 6 cm up to at least 13 cm diameter. These appear to be in a similar state of maturity; that is, both show trunk surfaces from which branches had been abscised not very long before burial and preservation of the specimens.

Among *Lorophyton*, *Pseudosporochnus*, and *Calamophyton*, such huge variation in the width of the trunk and an increase in complexity of branching with increased diameter of both the branch and the trunk on which it was borne can be explained in several ways. First, there is the possibility that the assemblages each represent the presence of several species of gradational size. Second, there is the possibility of huge intraspecific variation within the populations of these plants at the same locality, perhaps controlled by extremely local environmental conditions. Last, we might consider the facts to demonstrate that the fossils represented in each assemblage show a variety of ontogenetic stages in growth of a single species with steadily increasing girth and developmental potential until a terminal, determinate stage is reached. To us, the most parsimonious explanation is the last.

Although we have not presented conclusive evidence to demonstrate that significant secondary growth occurred in Middle Devonian pseudosporochnalean cladoxylopsid trunks, we believe that the morphological evidence is strong enough to suggest that it did occur, and what little can be gleaned from the literature on the subject is certainly not contradictory. It cannot be discounted on the basis of the anatomy of branches that, we suggest, served a completely different and ephemeral function within the plant. We are currently undertaking anatomical studies of Middle Devonian anatomically preserved pseudosporochnalean trunk material in order to see whether it supports or refutes our hypothesis.

The growth pattern that we propose for members of Pseudosporochnales allows for shedding a substantial number and volume of lateral branches during the lifetime of the plant. Perhaps even several hundred branches were dropped per growing individual. This conclusion would help explain the high number of cladoxylalean branches that can be found at some sites and the low ratio of trunk-to-branch material found in most localities. This should be taken into account when quantitative analyses of Middle Devonian plant assemblages are made.

## Conclusion

*Pseudosporochnus nodosus* grew with a central trunk and with closely crowded lateral branches that were probably abscised during ontogeny. The substantial size of some of the trunks indicates that the plants had a capability to grow to a considerable height and would have shed a large number of branches in their lifetime.

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