

***Ahnetia*, a new lignophyte stem from the Lower Carboniferous of southern Algeria.**

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14   **Abstract:** A new taxon of lignophyte is described based on a permineralized stem from the  
15   Late Tournaisian (Lower Carboniferous) of the Central Ahnet region, Algeria. It shows  
16   similarities with arborescent seed plants described in the Lower Carboniferous of Europe and  
17   North America such as *Eristophyton waltonii* Lacey and *Cauloxylon ambiguum* Cribbs.  
18   However, the primary and secondary vascular system of the stem display an original  
19   combination of characters and it is assigned to a new genus: *Ahnetia*. The preservation of  
20   extraxylary tissues (secondary phloem, periderm, cortex) allows formulating hypotheses on  
21   the stem's growth potential. The early appearance of a periderm indicates that *Ahnetia* was  
22   capable of significant secondary growth and that the specimen likely represents a young axis  
23   of a larger plant. By its Late Tournaisian age, this specimen represents the oldest known  
24   occurrence in North Africa of a lignophyte capable of significant secondary growth after the  
25   extinction of the progymnosperm *Archaeopteris*.

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27   **Key-words:** Early Carboniferous, Algeria, lignophyte, tree, anatomy

## 1. Introduction

The Early Carboniferous (Mississippian) floras of Gondwana have been traditionally reconstructed as low diversity and dominated by arborescent lycopsids (e.g., [Anderson et al., 1999](#)). While work by Ianuzzi and Pfefferkorn (2002) has provided more information on the floras of Gondwana's warm temperate belt (30°S-60°S) during the late Viséan to earliest Serpukhovian, our knowledge of the composition and distribution of Gondwana floras during the Early Mississippian (Tournaisian) remains noticeably scarce. In addition to their paucity, Gondwanan fossil plants from that period are to date mostly represented by compression-impression assemblages, which might only reflect a fraction of the total plant diversity at that time ([Scott and Galtier, 1996](#)). For example, Early Mississippian anatomically preserved plants recently described from Australia suggest the presence of more diverse floras and complex terrestrial ecosystems, at least in the north-eastern part of Gondwana ([Hueber and Galtier, 2001](#); [Galtier et al., 2007](#); [Decombeix et al., 2011b](#)).

In North Africa, the Mississippian compression-impression assemblages studied since the 1920's are typically largely dominated by arborescent lycopsids (e.g., [Lejal-Nicol, 1985](#) and [references therein](#)). Two floral stages have been recognized in the literature. The first one is a Tournaisian to early Namurian flora dominated by lycopsids with a few sphenopsids and "pteridophylls" (i.e., fern and/or seed fern foliage). These assemblages do not differ strongly from those of the Famennian, and in several cases they have been described as "Devonian-Carboniferous" floras. Within this first floral stage, [Lejal-Nicol \(1985\)](#) considers the Viséan floras to be the most diversified since they contain sphenopsids and "pteridophylls" that are seemingly absent in older (Tournaisian) deposits. It is however only during the second floral stage, after the Namurian, that the floras of the North African region apparently became more diversified, with relatively abundant sphenopsids, filicophytes, pteridosperms, "pteridophylls", and gymnosperms ([Lejal-Nicol, 1985](#)). While these compression/impression

floras are known in several regions of North Africa (Chad, Libya, Egypt, Sinai, Niger; [Lejal-Nicol, 1985 and references therein](#)), only one assemblage of anatomically preserved plants has been reported, in a Namurian volcanic sequence of the Tazekka region (Western Morocco, [Galtier et al., 1986](#)). The assemblage is dominated by the arborescent lycopsid *Lepidophloios* but also contains a fern (*Botryopteris*), and axes and seeds of lyginopteridalean seed plants. A gymnospermous trunk was also found in a nearby lava flow ([Chalot-Prat and Galtier, 1989](#)). It has a wood anatomy similar to that of *Eristophyton*, a genus also known in Mississippian localities of Western Europe ([Galtier and Meyer-Berthaud, 2006](#); [Decombeix et al., 2007](#)).

In the context of ongoing work on the diversity and biology of Mississippian lignophyte trees, we describe here an anatomically preserved woody stem of late Tournaisian age from the Ahnet Basin, in Southern Algeria ([Fig. 1](#)). This specimen shows anatomical characters comparable to that of putative arborescent seed plants that have been reported in Mississippian deposits of Europe, North America, and Australia ([Galtier and Meyer-Berthaud, 2006 and references therein](#); [Decombeix et al., 2011a](#)). The primary and secondary vascular system of the stem present an original combination of characters and it is assigned to a new genus. Although the stem is only a few centimeters in diameter, the preservation of extraxylary tissues (secondary phloem and some periderm) allows to formulate hypotheses on its growth potential and to compare it in detail to that of other Mississippian lignophytes. By its late Tournaisian age, this specimen represents the oldest known occurrence of a woody lignophyte in North Africa after the extinction of the progymnosperm *Archaeopteris*.

## 2. Material and methods

Tournaisian deposits in the Ahnet region of the Algerian Sahara consist of the succession of three formations (Fig. 2) that have been described in detail by Conrad (Conrad, 1984; Conrad et al., 1986), and more recently by Wendt and collaborators (2009):

- the Khenig Sandstones (“Grès du Khenig”), of early and middle Tournaisian age (Tn1-Tn2), which correspond to a deltaic to coastal environment. These sandstones contain in some places remains of lycopsids (trunks, *Stigmara* rooting structures, cortical molds);

- the Teguentour Mudstones (“Argiles du Teguentour”), of early Late Tournaisian age, that correspond to a transgression period;

- the Tibaradine Sandstones (“Grès de Tibaradine”), of late late Tournaisian age, representing deltaic to coastal environments.

The base of the Viséan is indicated by the Iridet Formation (“Dalle des Iridet” of Conrad), a conspicuous sequence of alternating calcareous and shale layers that corresponds to a new transgressive pulse.

The anatomically preserved stem described in this paper was collected by Jacqueline Conrad in the Tibaradine Sandstones during a geological prospection in the Central Ahnet. The named geographical feature closest to the collection site is Hassi Ti-n-Etenaï, a well that is located about 180 km south-west of Aïn Salah, in the Tamanrasset Province (N 25° 47', E 1° 32' Fig.1; Conrad, 1984). This is close to the locality 254(Ad) of Wendt et al. (2009, Fig. 2).

A drawing of a transverse section of the specimen and a picture of a general view have already been published (Galtier, 1988; Galtier and Meyer-Berthaud, 2006, “new taxon 3”), as well as a description of the secondary phloem (Decombeix et al., 2014). However, this paper is the first detailed anatomical and systematic treatment of the specimen. The stem is 6.5 cm long, with a maximum diameter of 2.7 x 3.7 cm in its distalmost and best preserved part. It is in this region of the specimen, where both pith, secondary xylem, and bark are well preserved, that thin-sections were made following the classical method (Hass and Rowe, 1999). The

other extremity of the stem is decorticated and only contains the pith and a small amount of secondary xylem. Initially three slides were made in transverse section (slide Ai01, Bi01, B<sub>1</sub>i02), two radial section (B<sub>1</sub>iL01 and B<sub>2</sub>iL01), and one in tangential section (B<sub>2</sub>Tg01). Additional wafers and thin-sections in transverse section (A<sub>2</sub>01 to A<sub>2</sub>05) were later made in one of the remaining blocks to follow the course of the primary xylem strands and leaf traces. Observation and photography were conducted with Sony XCD-U100CR digital cameras attached to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound microscope. Images were captured using Archimed software (Microvision Instruments) and plates were composed with Adobe Photoshop CS5 version 12.0 ([Adobe Systems Inc.](#)). Transformations made to the images in Photoshop include cropping, rotation, and adjustment of contrast. Cell and tissues measurements were made with ImageJ version 1.45 ([Rasband 1997–2015](#)). The specimen and corresponding slides are deposited in the AMAP Research Unit, Collections de Paléobotanique, Université de Montpellier, under the accession number UM ALG-JC874.

### 3. Description

#### *3.1. General aspect (Fig. 3; plate I)*

In transverse section, the center of the stem is composed of a large eustele with 13-15 small primary xylem strands distributed at the periphery of a parenchymatous pith containing conspicuous sclerotic nests ([Fig.3; Plate I, 1-4](#)). The ratio of the stele diameter to the total axis diameter calculated on slide UM-JC784-Ai01 is about 1: 1.7. Small simple leaf traces are emitted according to a complex spiral phyllotaxis ([Fig. 4](#)). The pith is surrounded by a 5 mm-thick ring of dense secondary xylem with not distinct growth ring. Secondary phloem, periderm, and cortex tissues are preserved in some regions ([Plate I, 1, 5](#)).

### 3.2. *Pith* (Plate I, II)

The pith is slightly elliptical in transverse section, with a maximum diameter of 2.1 cm (Plate I, 2). It is composed of parenchymatous cells and conspicuous sclerotic nests. Parenchyma cells are polygonal to rounded and isodiametric, with a diameter of 37-153  $\mu\text{m}$  in transverse section and 34-162  $\mu\text{m}$  in radial section. There is no difference in shape between the cells in the center of the pith and those in contact with the secondary xylem. On the other hand, parenchyma cells located close to the sclerotic nests are often transversely elongated around the nest, which give them a radiating aspect (Plate II, 1-5). Sclerotic nests are distributed within the pith with no obvious arrangement (Plate I, 1, 2). Their diameter varies between 0.25 and 2 mm in transverse section and 0.4 to 1.8 mm in radial section. The smallest nests are composed of only a few cells and are more abundant in the outer part of the pith. The total number of sclerotic nests visible on a single transverse section is variable: more than 60 can be observed on slide Ai01 and only about 20 on slide Bi01. This does not seem to correspond to a trend along the stem, since many nests are present at both ends of the specimen. No particular arrangement of the nests has been detected, even if a small sclerotic nest is frequently present very close to the location of the smallest immersed primary xylem strands (e.g., Plate II, 1). The shape of the nests is variable; some have a rounded outline while other are elongated either in the transverse or tangential plane (Plate I, 1-4). Some appear to be dividing. The cells that form the nests are polygonal in all views and of a size comparable to that of the parenchymatous cells. Some cells have a small rounded lumen while other seems to be entirely lignified.

### 3.3. *Primary xylem and leaf trace emission* (Fig 4, 5; Plates I- III)

At first view the distribution of the primary xylem strands around the periphery of the pith appears irregular. However, the observation of successive transverse sections show that there

are about 13 primary xylem strands located about 5-6 mm from one another (Fig 4, 5). The apparent irregularity is due to the frequent divisions of the strands linked to leaf trace production (Fig.5). The primary xylem strands are always in a peri-medullar position, i.e. separated from the secondary xylem by some parenchyma cells, with the exception of departing leaf traces (Fig.4, 5; Plate II, 1-5). The most sunken strands are located 300-500  $\mu\text{m}$  from the first secondary xylem cells. All strands are very small, with a diameter in transverse section of 77 to 183  $\mu\text{m}$  (Plate II, 1-5). They occur either isolated or in groups of 2 or 3 following tangential to oblique divisions prior to the emission of a leaf trace (Fig.5; Plate II, 1-5). There is no evidence of fusion between two strands. Xylem maturation is difficult to determine in most strands since they are usually formed by only a few tracheids. It appears to be mesarch in the largest strands (Plate II, 3). Metaxylem tracheids have an average diameter of 24  $\mu\text{m}$  (maximum observed size 44  $\mu\text{m}$ ) and are sometimes difficult to distinguish from the pith cells in transverse section.

Several departing vascular traces to lateral organs are visible on each transverse section (Fig 4, 5; Plate I, 1, 3, 5). The mode of production of these traces was studied on a series of transverse sections. While a similar pattern is repeated for all the observed leaf traces, some points are not entirely clear, in particular the existence of a true sympodial system with a vertical continuity of caulinar strands. The various stages observed are detailed below and illustrated on plate II and on figures 4 and 5.

First, a small sunken medullary strand (arrow, plate II, 1-2) begins to enlarge and divides twice in a tangential to oblique plane. An arc-shaped group of three primary xylem strands is formed, with the median strand remaining more sunken than the two lateral ones ("Sn" on Fig. 5, A1-B1; Plate II, 5). The resulting arc-shaped group then moves outwards toward the secondary xylem and forms a large strand of primary xylem about 400  $\mu\text{m}$  in diameter in contact with the secondary xylem, in which the exact number of protoxylem pole is not



176 always clear (Plate II, 6). Files of secondary xylem tracheids surrounding the future leaf trace  
177 take a curved aspect. There is no evidence of the existence of a primary xylem strand facing  
178 the departing trace or in a close lateral position to it, in the region where a reparatory/cauline  
179 strand would be expected in a sympodial system (Fig. 5, A, B; Plate II, 6-8). However, at this  
180 stage a new, very small primary xylem can be observed on the sections. This “lateral strand”  
181 is located relatively far laterally from the departed trace and does not correspond to a strand  
182 present on the previous, more proximal thin-section (Fig. 5, “LS” on A2 and B2). While it is  
183 always located on the same side of the departing trace, in a highly predictable position, the  
184 origin of this “lateral strand” remains unclear. A first possibility is that it is related to the three  
185 strands observed in the first stages but that the connection could not be observed due to its  
186 small size and/or very horizontal divergence from the location of the leaf trace. In this case,  
187 there would be a classical permanent system of caulinar bundles (sympodial). However we  
188 cannot exclude the possibility that this “lateral strand” arises *de novo*. In that case, there  
189 would be no vertical continuity of the primary vascular system, which would thus be non-  
190 sympodial.

191 The departing leaf trace contains a single primary xylem strand, resulting either from the  
192 fusion of the three original strands or from the disappearance of one or two of them. In some  
193 cases, a few tracheids are seen facing the departed trace (Plate II, 6 arrows) but these tracheids  
194 are gone on the following sections. Finally, the location of the departed trace is only indicated  
195 by an outwards protuberance or indentation of the pith. The “lateral strand” increases in size  
196 and will start dividing at a higher level (Fig 5, C).

197 Leaf traces cross the secondary xylem almost horizontally (Plate I, 3; Plate II, 8). They are not  
198 occluded within the 5 mm of secondary xylem and some can be seen within and beyond the  
199 secondary phloem, indicating that the stem bore leaves at that developmental stage (Plate I, 5;  
200 plate III). A preserved portion of the cortex shows the next stages in the production of the

traces. As it crosses the outer part of the secondary phloem, the trace takes a fan shape on transverse sections of the stem (Plate III, 1). At this stage it is about 1 mm across in its narrowest part and a little under 3 mm across in its widest part. The trace then divides in the cortex in two bundles less than 1 mm wide that continue their horizontal to oblique course (Plate III, 2, 3).

The phyllotaxis is complex and could not be determined exactly. Four leaf traces at different stages of emission can be seen on each transverse section and there is evidence that the internodes were very short, less than 5 mm (Fig 4 A-D). Leaf traces are not emitted according to a simple spiral but there is also no convincing evidence of a more complex (e.g., bijugate) mode of emission.

#### 3.4. Secondary xylem (Plate IV)

The secondary xylem has a maximum thickness of only 5 mm (Fig.3; Plate II). It is composed of tracheids and parenchymatous rays and shows no sign of compression. Some details of the tracheid pitting and ray anatomy are, however, not well-preserved due to the mineralization of the tissue.

In transverse section, the tracheids have a square to rectangular, more rarely polygonal shape.

Their diameter ranges from 27 x 28  $\mu\text{m}$  (maximum 46  $\mu\text{m}$ ) close to the pith to 32 x 32  $\mu\text{m}$  (maximum 65  $\mu\text{m}$ ) in the external part of the secondary xylem cylinder (plate IV 1-2).

Increase in width happens by a small increase of the tracheid diameter but mostly by the formation of new files of tracheids. Some zones where tracheids have a reduced radial diameter are present but there is no true growth ring boundary.

In the inner part of the wood, close to the pith, rays are 1-5 cells in width and separate 1 -3 files of tracheids (e.g., Plate II 4). In this area the rays are larger than in the rest of the wood; they have more cells in width and these cells are larger. This gives a very parenchymatous

aspect to the innermost part of the wood. Beyond this inner zone, rays are often less well preserved and more difficult to observe (Plate IV 3, 4). In tangential section, they are usually uni- or biseriate and 10-20 cells high, more rarely up to 50 (Plate IV 3). Ray cells are better preserved in the smallest rays (Plate IV 3); they are 27-61  $\mu\text{m}$  high. In larger rays only the general outline tends to be visible (plate IV2).

In radial section, the wall of the tracheids bears multiseriate bordered pits (Plate IV 5). No tangential pitting has been observed. Ray cells are longer than high in radial section (plate IV 5) (52-115  $\mu\text{m}$ ), except close to the pith where they are square. Cross-field pitting could not be observed.

### 3.5. Extraxylary tissues (Plate III, Plate IV)

The secondary phloem of the stem has already been described and illustrated (Decombeix et al 2014) so only a short description is provided here. The zone corresponding to the location of the cambium is not well preserved (Plate IV 1) and is usually indicated by a thin dark layer. The secondary phloem is about 4 mm in thickness. It is composed of fibers, rays, axial parenchyma, and putative sieve cells, but, as in the secondary xylem, thin-walled cells are not well preserved. In the innermost (youngest) part, the phloem appears mostly composed of fibers and rays, with a few putative sieve cells and axial parenchyma cells (Plate IV 6). The fibers are arranged in layers that are up to nine cells in radial thickness. These layers of fibers alternate with thinner layers of thin-walled cells that are not preserved (Plate IV 6). In the older phloem multicellular layers of axial parenchyma cells with a few dispersed fibers are clearly visible between the multicellular layers of fibers (plate IV 7). As a result, the outer part of the phloem has a more parenchymatous aspect than the inner part. This is interpreted as the combination of a better preservation of axial parenchyma cells in the outer phloem and of their proliferation as the tissue matures. Phloem rays also tend to enlarge slightly towards

the outside of the secondary phloem ([Plate IV 7](#)). Cellular divisions within some of the thin-walled cells layers indicate the probable level at which a periderm layer would have been formed ([Plate IV 8](#)).

The outermost part of the stem (cortex) on the most complete sections consists of a parenchymatous tissue containing a few sclerotic nests comparable to those in the pith ([Plate I 1](#); [Plate III 1, 2](#)).

#### **4. Anatomical comparisons**

The main anatomical characters of the specimen are (1) a large parenchymatous pith with sclerotic nests, (2) primary xylem strands composed of a few tracheids and separated from the secondary xylem by a small amount of parenchyma, (3) simple leaf traces with no clearly associated caulinar (or “reparatory”) strand, (4) picnoxylic type of wood with rays that are generally uni-biseriate and of medium height, (4) a secondary phloem with alternating tangential multicellular layers of fibers and thin-walled cells, (5) a cortex with sclerotic nests.

The large eustele and relatively dense wood with small tracheids indicate an affinity with putative arborescent seed plants of Mississippian age ([Galtier and Meyer-Berthaud, 2006](#)).

The stele to stem diameter ratio of the specimen (1:1.7) also supports this affinity: [Galtier \(1988\)](#) has shown that this ratio is comprised between 1:5 and 1: 10 in Calamopityaceae and greater than 1:5 in Buteoxylonaceae, Lyginopteridaceae, and in the putative arborescent seed plants of the Mississippian. This informal group, reviewed by Galtier and Meyer-Berthaud in [2006](#), is known from anatomically preserved stems, sometimes with attached leaf bases, from Early to Late Mississippian deposits of Europe, North America, and Australia.

##### *4.1. Primary vascular architecture and leaf trace production*

275 Anatomical characters of the pith and primary vascular system are traditionally considered to  
276 be the most important to distinguish within the different genera of Mississippian putative  
277 arborescent seed plants and will thus be considered first. The new specimen possesses a wide  
278 parenchymatous pith with sclerotic nests and no tracheids. In this later aspect, it differs from  
279 the Mississippian genera *Bilignea* (Scott, 1924), *Megaloxylon wheelarae* (Mapes, 1985), and  
280 *Stanwoodia* (Galtier and Scott, 1991) whose pith contains short pitted cells interpreted as  
281 tracheids. Conspicuous sclerotic nests such as the ones observed in the stem from Algeria are  
282 present in the pith of *Eristophyton beinertianum*, *E. waltonii*, and *Cauloxylon* (Scott, 1902;  
283 Lacey, 1953; Cribbs, 1939). Some authors consider sclerotic nests to be the result of a  
284 physiological reaction to an attack by insects or micro-organisms and not a true systematic  
285 feature of the plants (e.g., Beck and Stein, 1987). It must however be noted that structures  
286 similar to the "sclerotic nests" reported here are present in the pith of some extant angiosperm  
287 stems that do not show any sign of attack and that they appear to be a consistent feature  
288 within some species (ALD personal observation on *Guarea guidonia*, Meliaceae). Given this  
289 and the lack of evidence of animal or fungal damage in the pith of the stem from Algeria, we  
290 follow previous authors who have considered medullar sclerotic nests as a significant  
291 taxonomic character, at least at the species level.

292 Regarding the primary xylem anatomy, the new specimen lacks true medullary strands deeply  
293 immersed in the pith such as the ones found in *Archaeopitys* (Scott and Jeffrey, 1914). Such  
294 strands are also reported in all species of *Pitus* but apparently do not occur in all specimens  
295 (Gordon, 1935, p.284). Because of this uncertainty, we cannot exclude an affinity with *Pitus*  
296 based solely on this absence of deeply immersed strands. In addition to *Pitus*, small primary  
297 vascular strands in a peri-medullary position such as the ones in the stem from Algeria are  
298 also found in the monospecific genera *Faironia* from the middle Tournaisian of France  
299 (Decombeix et al., 2006), in *Cauloxylon*, *Picnoxylon*, and *Megalomyelon* from the upper

300 Tournaisian of Missouri (Cribbs, 1938, 1939, 1940), and in some but not all species of  
301 *Eristophyton* (Scott, 1902; Lacey, 1953; Galtier and Scott, 1990; Galtier et al., 1993  
302 Decombeix et al., 2007, 2008). A comparison of the primary vascular system of these genera  
303 with the new stem from Algeria indicates the presence of differences, especially in the course  
304 of the strands and the mode of leaf trace production.

305 In addition to the fact that no true medullary strands were observed, differences with *Pitus*  
306 include the small size of the primary xylem strands, the lack of a clear cauline (sympodial)  
307 strand from which the leaf trace diverges, and the more complex phyllotaxis. *Megalomyelon*  
308 *myriodesmon* (Cribbs, 1940) does not possess sclerotic nests in the pith and has primary  
309 xylem strands that can reach 200  $\mu\text{m}$  in diameter. A notable difference with the new specimen  
310 from Algeria is the mode of leaf trace emission: in *Megalomyelon* a primary xylem strand  
311 divides tangentially once and produces a departing trace and a conspicuous reparatory strand  
312 that lies opposite the departed trace. Similar differences can be found with *Faironia*  
313 *difasciculata* (Decombeix et al., 2006) which also lacks sclerotic nests in the pith, has primary  
314 xylem strands up to 280  $\mu\text{m}$ , and a conspicuous reparatory strand lying obliquely to the  
315 departing leaf trace. *Picnoxylon leptodesmon* (Cribbs, 1938) also lacks sclerotic nests in the  
316 pith. While different from that of *Megalomyelon* and *Faironia*, its mode of leaf trace emission  
317 also differs from what is seen in the new stem. In *Picnoxylon*, primary xylem strands divide  
318 tangentially once before the emission of a leaf trace and one of the two strands remains visible  
319 on the side of the departed trace before entering the secondary xylem 1 to 10 mm above the  
320 first trace.

321 *Cauloxylon ambiguum* (Cribbs, 1939) has sclerotic nests in its pith. However, it differs from  
322 the stem from Algeria in having frequent fusions between neighboring primary xylem strands  
323 and a maturation that appears endarch in the largest strands.

324 Among species of *Eristophyton*, *E. beinertianum*, and *E. feistii* differ from the new stem by  
325 their primary xylem strands always in contact with the wood (Scott, 1902; Decombeix et al.,  
326 2008). *Eristophyton fasciculare* has a much smaller pith (2-3 mm in diameter), larger primary  
327 xylem strands (up to 200  $\mu$ m), and no sclerotic nests in the pith (Scott, 1902). The fourth  
328 species, *Eristophyton waltonii*, is the one with the most similarities to the stem from Algeria  
329 in terms of primary vascular system organization, with a wide pith with sclerotic nests and a  
330 few small strands separated from the wood (Lacey, 1953). Another similarity is the division in  
331 two of the leaf trace after it has exited the secondary xylem (Long, 1987). However, there is  
332 no descriptions of primary xylem strands dividing prior to leaf trace emission in *Eristophyton*  
333 *waltonii*: each strand apparently moves towards the secondary xylem and is directly emitted  
334 as a leaf trace. This was confirmed by the detailed reconstruction of the vascular system by  
335 Galtier and Scott (1990). The primary vascular system of *E. waltonii*, like that of some  
336 cordaites (Trivett and Rothwell, 1985), thus appears to be non-sympodial. There are  
337 nonetheless suggestions of tangential divisions in some strands.

338 In summary, although the new stem from Algeria shows important similarities with  
339 previously described taxa such as *Cauloxylon ambiguum* or *Eristophyton waltonii*, it seems in  
340 the current state of our knowledge to have a distinct primary vascular architecture. It is  
341 possible that it represents an intermediary stage between the non-sympodial architecture  
342 observed in taxa like *E. waltonii* and the classical sympodial system of most seed plants.  
343 Another possibility is that this situation is linked to the young developmental age of the new  
344 stem.

345 It must be noted at this point that, with the exception of *Pitus* and *Eristophyton*, all the  
346 Mississippian taxa mentioned above have been described as having leaf traces emitted in  
347 pairs. In the case of *Faironia*, the pair of traces is known to vascularize a single petiole base  
348 (Decombeix et al., 2006). *Cauloxylon*, *Picnoxylon*, and *Megalomyelon* on the other hand are

decorticated (Cribbs, 1938, 1938, 1940) and it is unknown whether the paired traces also vascularized a single organ or if they corresponded to two distinct organs emitted at a same level. In *Eristophyton waltonii*, no pairing of traces have been reported but the phyllotaxis is interpreted as a complex spiral (Lacey, 1953), probably 8/21 (Galtier and Scott, 1990). Transverse sections of the Algerian stem often show two traces that can appear at a similar stage of emission (Fig. 4). Closer examination however shows that they are at a different stage in trace of emission. In addition, the wide angle formed by the two traces in those “pairs” also suggests that they did not vascularize a same lateral organ.

#### 4.2. Secondary vascular tissues

Considering the characters of the secondary vascular system, most of the putative arborescent seed plants of the Mississippian have wood tracheids with multiseriate crowded bordered pits such as the one observed in the new specimen. Only *Bilignea* and *Dameria* can be excluded based on this character (Scott, 1924; Galtier et al., 1993; Scott et al., 1994; Decombeix et al., 2011b). The presence of mostly uni- to biseriate rays of the new specimen distinguishes it from taxa such as *Cauloxylon*, *Megalomyelon*, *Pitus dayi*, *P. primaeva*, or *P. antiqua*, which all have larger and/or higher rays (Cribbs, 1939, 1940; Gordon, 1935), as well as from *Endoxylon*, which has uniseriate and very low rays (Scott, 1924; Lacey 1953). *Picnoxylon* has rays relatively comparable to those of the new stem, uni to biseriate and usually 10-15 cells high (Cribbs, 1938). However it possesses ray tracheids, which were not observed in the new specimen. *Eristophyton waltonii*, one of the most similar taxon in terms of primary vascular architecture, has rays that are 1-7 cells wide and 1-50 high (Lacey, 1953; Galtier and Scott, 1990). While the range of ray size is not very different from the new specimen, the latter has generally narrower and lower rays than *E. waltonii*.



The secondary phloem of Mississippian lignophyte trees is a complex tissue containing sieve cells, axial and radial parenchyma, sclereids, and fibers. In this aspect it is similar to that of Devonian Aneurophytalean and Archaeopteridalean progymnosperms (Beck, 1957; Scheckler and Banks, 1971a, 1971b; Stein and Beck, 1983; Galtier & Meyer-Berthaud, 2006; Decombeix & Meyer-Berthaud, 2013; Decombeix et al., 2014). The organization observed in the specimen from Algeria, with tangential layers of fibers that are several cells thick alternating with bands of thin-walled cells is relatively unusual. It is quite similar to the organization seen in Middle Tournaisian trunks from Australia that have a *Pitus/Eristophyton* type of wood but an apparently more complex type of leaf trace emission (Decombeix et al., 2011b; Decombeix, 2013). It differs from the secondary phloem organization of all other Mississippian lignophytes in which this tissue is known, i.e., *Bilignea*, *Calamopitys* (and the other calamopityales *Diichnia* and *Triichnia*), *Eristophyton fasciculare*, *Faironia*, *Lyginopitys*, and *Stanwoodia* (Decombeix et al., 2014). Secondary phloem in *Pitus* is not well-known but Gordon (1935) only reported thin-walled cells in the poorly preserved phloem of *P. dayi*. Secondary phloem anatomy is unknown in the taxa that have the most similarities with new stem such as *Eristophyton waltonii* and *Cauloxylon ambiguum*.

## 5. Systematic paleobotany

### ***Ahnetia* Decombeix et Galtier gen. nov.**

*Type species: Ahnetia conradii* Decombeix and Galtier sp. nov.

*Diagnosis:* Stem with primary and secondary vascular tissues and primary cortex. Eustele consisting of small discrete axial strands of primary xylem at the periphery of a broad circular pith with sclerotic nests. Ratio of primary xylem diameter to stem diameter high (about 1:1.7). Axial primary xylem strands widely spaced, composed of a few tracheids, and separated from the secondary xylem by several layers of parenchyma cells. Leaves arranged in a complex

spiral. Leaf emission starting with two divisions of a primary xylem strand and formation of an arc-shaped group of three strands that moves towards the secondary xylem. One of these strands emitted as a simple leaf trace with one protoxylem strand. No evidence of a sympodial nature of the vascular system. Leaf trace dividing in two in the cortex. Secondary xylem tracheids with multiseriate bordered pits on radial walls. Rays uni- to multiseriate, not high. Secondary phloem present, including fibres arranged in tangential layers several cells in thickness. Evidence of periderm formation within the secondary phloem. Cortex consisting of parenchyma with sclerotic nests.

*Etymology*: after the Ahnet region in which the specimen was collected.

***Ahnetia conradii* Decombeix et Galtier sp. nov.**

*Holotype*: Specimen UM ALG-JC874 (Figures 3-5; Plates I-IV).

*Repository*: Specimen and slides stored in the AMAP Laboratory, CIRAD, are part of the Paleobotanical collections, Service des Collections, Université Montpellier, France.

*Type locality*: Hassi Ti-n-Etenäi, Central Ahnet region, Algeria.

*Horizon*: Tibaradine Sandstones, Late Tournaisian (Tn3).

*Etymology*: after Jacqueline Conrad, who collected the specimen during her pioneering work on the Early Carboniferous stratigraphy of Algeria.

*Specific diagnosis*: Stem with a circular eustele about 20 mm wide, composed of about 13 axial strands and incipient leaf traces. Primary xylem strands peri-medullar, separated from the secondary xylem by several layers of parenchyma cells. Distance between strands up to 6 mm. Primary xylem strands small, typically less than 200 µm in diameter and usually consisting of a few tracheids. Pith of polygonal parenchyma cells and about 20-60 sclerotic nests up to 2 mm in diameter and composed of thick-walled cells of similar dimension than the pith parenchyma cells. Tracheids of secondary xylem rectangular to polygonal, with

average diameter equal to slightly larger than the metaxylem tracheids. Rays up to five cells wide, expanded in the innermost part of secondary xylem, 10-20 cells in height, rarely up to 50. Ray parenchyma cells procumbent. Secondary phloem with axial elements of parenchyma, ray cells, probable sieve cells, and fibers. Fibers arranged in tangential layers up to nine cells thick. Proliferation of axial parenchyma cells and enlargement of rays in old secondary phloem. Departing leaf traces about twice the size of the largest strands, dividing in the cortex in two bundles less than 1 mm wide.

## 6. Growth potential (Table 1)

The new taxon has a relatively large pith, over 2 cm in diameter. Such a large central pith offers the advantage of requiring little energy for its construction and allows a fast and metabolically cheap vertical growth (Mosbrugger, 1990). Among Paleozoic lignophytes, this type of anatomy is found in the Devonian progymnosperm tree *Archaeopteris*, in most putative arborescent seed plants of the Mississippian (Galtier and Meyer-Berthaud, 2006), and in cordaites (Rothwell, 1988). Among extant plants, angiosperm trees with a wide pith tend to be found in pioneer species that develop early in ecological successions (ex: *Cecropia*, *Pittocaulon* (*Senecio*) *praecox*, *Aralia* *spinosa*). Their rapid vertical growth allows them to establish their crown quickly and reduces light access for other species.

The presence of well-preserved extraxylary tissues in the new taxon from Algeria provides important information about the secondary growth of the specimen by allowing us to know the exact thickness of the wood cylinder, an information which is lacking in decorticated specimens. It allows a comparison of secondary growth processes with *Pinus dayi* and *Faironia difasciculata*, two Mississippian stems of comparable diameter with preserved outer tissues (Table 1). The presence of a narrow ring of wood suggests that the specimen from Algeria corresponds to a physiologically young stem, but there are indications of the

development of a periderm in the secondary phloem. This is in contrast with *Faironia*  
*difasciculata*, from the Tournaisian of France, which has a stele diameter, secondary xylem  
thickness, and total diameter comparable to that of the new taxa but still retains its primary  
cortex and has no sign of the development of a periderm. In contrast, while its stele and total  
diameter are a little smaller, *Pitus dayi* produces a periderm early in its development (Gordon,  
1935). A biomechanical analysis of young *P. dayi* twigs by Speck and Rowe (1994) has  
shown that this species was self-supporting and that the periderm quickly replaces the primary  
cortex. *P. dayi* is interpreted by these authors as representing a young axis of a large woody  
tree. From the similarities in distribution and relative amount of tissues, we can infer a  
comparable nature for the new stem. A difference however is that in *Pitus dayi* the periderm is  
produced in a very superficial position in the periphery of the cortex, while in *Ahnetia* it  
appears to have a deeper origin, within the secondary phloem. A similar mechanism is found  
in several other arborescent lignophytes of Early Carboniferous age: *Endoxylon* (Scott, 1924;  
Lacey, 1953), *Eristophyton* (Scott, 1902; Galtier et al., 1993), *Stanwoodia* (Galtier et Scott,  
1991), and an unnamed taxon from Australia (Decombeix, 2013). It must, however, be noted  
that in some plants the production of a first external periderm is followed by the production of  
deeper periderms (e.g., Roth, 1981). It is possible that this was also the case in some of the  
Mississippian taxa but that the first (external) periderm has been lost or is not preserved.  
It is interesting to note that the number of primary xylem strands in *Ahnetia* is low compared  
to some other Mississippian taxa with a comparable organization. While *Ahnetia* only has 13-  
15 strands around a pith that is 2.1 cm in diameter, *Faironia* and *Picnoxylon* both have around  
45 for a comparable pith diameter (Decombeix et al., 2006; Cribbs, 1938). *Cauloxylon*, which  
is 2.5 times larger, has around 100 (Cribbs, 1939). Since the strands in *Ahnetia* are also very  
small, the surface of primary xylem in the stem appears quite reduced compared to other  
Mississippian taxa. The situation is more similar to that observed in the holotype of

*Eristophyton waltoni*, which has only 7-10 strands for a 1 cm wide pith (Lacey, 1953). However, specimens of *E. waltonii* later described by Galtier and Scott (1990) had more strands: 20 for a 1 cm wide pith and up to 40 in larger specimens. In *Faironia*, attached petiole bases indicate that the leaves were quite large compared to the stem diameter (Decombeix et al., 2006). In *Ahnetia* we do not have any complete petiole base attached, but it is possible that the small amount of primary xylem is linked to the possession of smaller leaves than in the other taxa.

## 7. Paleogeographical significance of the new specimen and conclusions

After the extinction of the cosmopolitan progymnosperm tree *Archaeopteris* around the Devonian-Carboniferous boundary, over 20 species of arborescent lignophytes have been reported in Early Carboniferous localities. Most of the specimens are from Europe and North America (Galtier & Meyer-Berthaud, 2006; Decombeix et al., 2011a). However, recent work has shown the presence of arborescent lignophytes in Russia (Orlova, 2010) and Australia (Decombeix et al., 2011b). A similar pattern of transition from *Archaeopteris* to diversified new arborescent lignophyte taxa after the D-C boundary is thus observed in both Laurussia and northeastern Gondwana.

Fossil of *Archaeopteris* are abundant in North Africa, especially in Morocco where they occur in Frasnian and Famennian marine deposits (Meyer-Berthaud et al., 2000, 2004). *Ahnetia* is to date the oldest evidence for the presence in that region of lignophytes capable of a significant amount of secondary growth after the extinction of *Archaeopteris*. It helps extend geographically the pattern of transition observed in deposits of Europe, North America, and Australia. *Ahnetia* is typically an example of a taxa not represented or recognized in compression floras, as is the younger gymnosperm trunk described by Chalot-Prat and Galtier (1989). This suggests that the picture of poorly diversified, lycopsid-dominated Early

Mississippian floras in North Africa is to be considered with caution. It is likely that, as with Australia (Galtier et al., 2007; Decombeix et al., 2011) and South America (Prestianni et al., 2015), future investigations will reveal a more diverse and complex Early Mississippian vegetation in that region.

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642

## Figure legends

**Fig. 1.** Carboniferous basins of North Africa and location of the Ahnet region. The star indicates the Hassi-Tin-Etenai locality where *Ahnetia* was collected (redrawn from [Conrad, 1984](#)).

**Fig. 2.** Late Fammenian (dark grey) and Tournaisian (light grey) lithostratigraphy of the Ahnet region. The lighter area within the Upper Khenig Sandstones indicates a probable gap. *Ahnetia* was collected in the Tibaradine Sandstones (redrawn from [Conrad et al., 1986](#))

**Fig. 3.** *Ahnetia conradii* from the Early Carboniferous of Algeria: camera lucida drawing of a typical transverse sections of the stem (UM-JC784-Ai01) showing the pith (P), sclerotic nests (SN, dark grey), secondary xylem (X2, light grey), leaf traces (LT), and bark tissue (secondary phloem and periderm, B).

**Fig 4.** Camera lucida drawings of the stele in 4 successive transverse sections showing the location of the primary vascular strands and outgoing leaf traces (LT). Only the sclerotic nests located at the periphery of the pith are represented. The location of primary xylem strands on A are indicated by arrows for clarity. Brackets indicate the location of the detailed drawings on Fig. 5; “Sn” , “Sn+1” , and “LS” indicates the strands detailed on Fig.5 A and B, see legend of Fig.5 for explanation. Slides A: UM-JC784-A<sub>2</sub>01, B: UM-JC784-A<sub>2</sub>02; C: UM-JC784-A<sub>2</sub>04; D: UM-JC784-A<sub>2</sub>05. Vertical distance between the sections: 1-2: c.a. 2 mm, 2-3: c.a. 4 mm, 3-4: c.a. 2 mm. Scale bar = 5 mm

**Fig 5.** Details of the drawings on Fig.4 showing the division of strands and emission of leaf traces in selected well-preserved sectors of the sections. A-B: early stages of leaf trace emission, C: later stages of leaf trace emission. (1) is more proximal than (2) on all drawings. Scale bar for A-C = 2 mm.

A1): the future emission of a leaf trace at the location of a strand ( $S_n$ ) is indicated by the presence of an arc-shaped group of 3 strands. The next strand on the right side ( $S_{n+1}$ ) is dividing in two. A2): the arc-shaped group of 3 strands in position  $S_n$  is in contact with the secondary xylem and the files of secondary xylem tracheids are curved at the location of the departing leaf trace.  $S_{n+1}$  has divided in two. A “lateral strand” (LS) that was not present on the previous section is located on the right side of the departing trace, between  $S_n$  and  $S_{n+1}$ . B. Illustrate a similar situation than A but in another part of the stem. At the location  $S_n$ , an arc-shaped group of primary xylem strands moves towards the secondary xylem to produce a leaf trace, at the location  $S_{n+1}$  the strand is dividing in two then three strands. A lateral strand (LS) not visible on the first section is produced between  $S_n$  and  $S_{n+1}$ . C. Shows the next stages of leaf trace emission: C1): the trace at location  $S_n$  starts to cross the secondary xylem. C2) the leaf trace is gone and the “lateral strand” LS increases in size.

**Plate I.** *Ahnetia conradii* from the Early Carboniferous of Algeria: general aspect

1. Transverse section of the stem showing the large parenchymatous pith with sclerotic nests, the secondary xylem with a departing leaf trace, the cambium region, and the bark.

Slide UM-JC784-A<sub>2</sub>04. Scale bar = 2 mm.

2. General view of the pith showing the distribution of the sclerotic nests. Slide UM-JC784-A<sub>2</sub>04. Scale bar = 2 mm.

692 3. Detail of the previous section showing a departing leaf trace (t). Primary xylem strands are  
693 very small and cannot be observed at this magnification. Slide UM-JC784-A<sub>2</sub>04. Scale bar = 1  
694 mm.

695 4. Radial section showing the pith, sclerotic nests and secondary xylem. UM-JC784-B<sub>1</sub>iL01.  
696 Scale bar = ca 1 mm

697 5. Slide UM-JC784-A<sub>2</sub>02. Scale bar = 1 mm

698 Legend: B: bark; ca: cambium zone; P: pith; Ph2: secondary phloem; sn: sclerotic nest; t: leaf  
699 trace; X2: secondary xylem.

700

701 **Plate II.** *Ahnetia conradii* from the Mississippian of Algeria: primary xylem strands and leaf  
702 traces. The center of the stem is towards the bottom on all photos.

703 1. Small primary xylem strand (arrow) composed of only a few tracheids and immersed in the  
704 pith. Note the small sclerotic nest near the strand. Slide UM-JC784-Ai01. Scale bar = 100 µm.

705 2. Primary xylem strands (arrow) with an endarch maturation. Slide UM-JC784-Ai01. Scale  
706 bar = 100 µm.

707 3. One of the largest observed primary xylem strands, likely corresponding to the early stage  
708 of a division (arrows). Slide UM-JC784-B<sub>1</sub>i01. Scale bar = 100 µm

709 4. Small strand and groups of tracheids (arrows) close to the secondary xylem. Slide UM-  
710 JC784-B<sub>1</sub>i01. Scale bar = 100 µm

711 5. Group of 3 strands (arrows), plus maybe some tracheids close to the sclerotic nest. Slide  
712 UM-JC784-Ai01. Scale bar = 100 µm

713 6. Departing leaf trace. Note some putative tracheids in a “band” in the pith facing the trace  
714 (arrows). Slide UM-JC784-Ai01. Scale bar = 500 µm.

715 7. Detail of another departing leaf trace with no identifiable primary xylem strand close to the  
716 departing trace. Slide UM-JC784-B<sub>1</sub>i01. Trace in wood 500 µm

717 8. More advanced departing leaf trace showing the parenchyma on the adaxial side of the  
718 trace and the lack of conspicuous primary xylem strand located close to the trace emission.  
719 Slide UM-JC784-Ai01. Scale bar = 500  $\mu\text{m}$ .

720

721 **Plate III.** *Ahnetia conradii* from the Mississippian of Algeria: leaf traces in the cortex. The  
722 center of the stem is towards the bottom on all sections.

723 1. Trace traversing the outer part of the secondary phloem and the cortex. Note the fan shape  
724 of the trace and the presence of sclerotic nests in the cortex. UM-JC784-A<sub>2</sub>02. Scale bar =  
725 1mm

726 2. Outer part of the secondary phloem and cortex a with a leaf trace that has divided in two  
727 bundles with an horizontal course. Slide UM-JC784-B<sub>1</sub>i01. Scale bar = 1mm

728 3. Detail of one of the two bundles on 2 showing the scalariform pitting of the tracheids. Slide  
729 UM-JC784-B<sub>1</sub>i01. Scale bar = 25  $\mu\text{m}$ .

730

731 **Plate IV.** *Ahnetia conradii* from the Mississippian of Algeria: secondary xylem, cambium,  
732 and secondary phloem. The center of the stem is towards the bottom on transverse sections  
733 and towards the left on tangential sections.

734 1. Transverse section of the secondary xylem and inner part of the secondary phloem Slide  
735 UM-JC784-B<sub>1</sub>i01. Scale bar = 250  $\mu\text{m}$ .

736 2. Secondary xylem in transverse section showing uni-, bi-, and partly triseriate rays. Slide  
737 UM-JC784-Ai01. Scale bar = 100  $\mu\text{m}$ .

738 3. Tangential section of the secondary xylem seen in reflected light and showing uni- to  
739 biseriate rays, most filled or replaced with minerals. Slide UM-JC784-B<sub>2</sub>Tg01. Scale bar=  
740 100  $\mu\text{m}$ .

741 4. Detail of rays in tangential sections. Slide UM-JC784-B<sub>2</sub>Tg01. Scale bar= 50  $\mu\text{m}$

742 5. Radial section of the secondary xylem showing a small ray and uni- to triseriate crowded  
743 bordered pits. Slide UM-JC784-B<sub>2</sub>iL01. Scale bar = 50 µm.

744 6. Detail of inner part of the secondary phloem in transverse section. Most of the thin-walled  
745 cells are not preserved and only the fibers and location of the rays are visible. Slide UM-  
746 JC784-Ai01. Scale bar = 100 µm.

747 7. Older portion of the secondary phloem showing compressed layer of thin wall-cells in  
748 between the successive bands of fibers. Note the expansion of rays between the fibers. Slide  
749 UM-JC784-Ai01. Scale bar = 100 µm.

750 8. Well-preserved layer of parenchymatous tissue between two layers of fibers in the old  
751 secondary phloem. Note the abundant cell divisions. Slide UM-JC784-Ai01. Scale bar = 100  
752 µm.

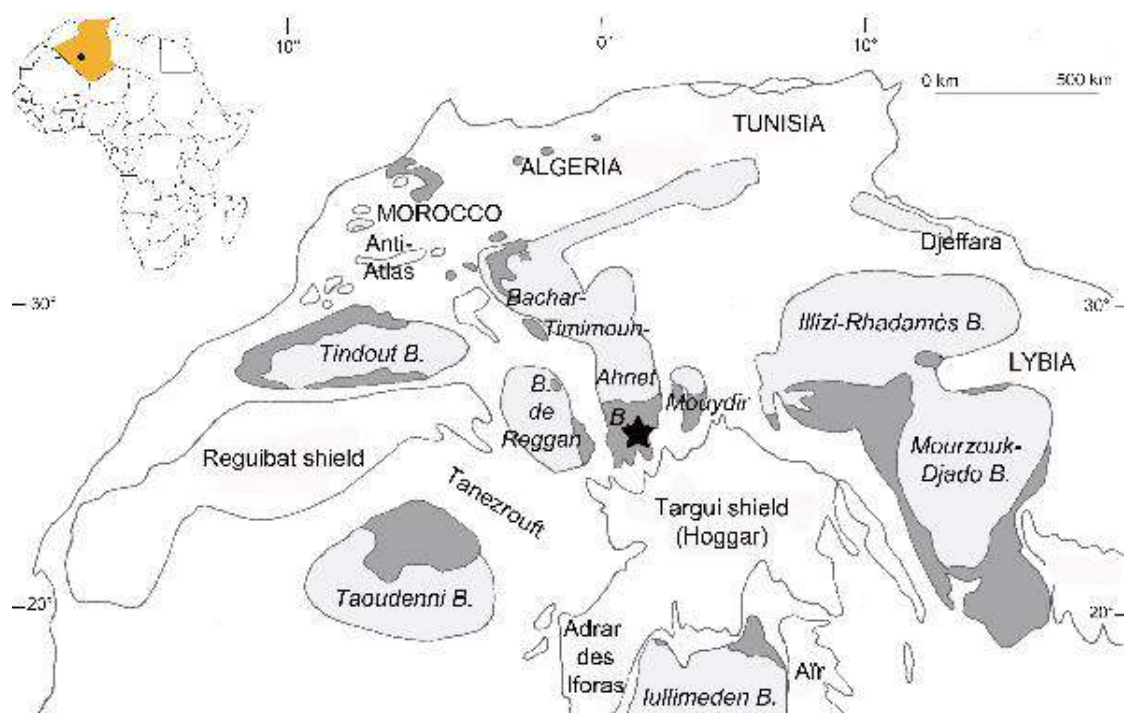
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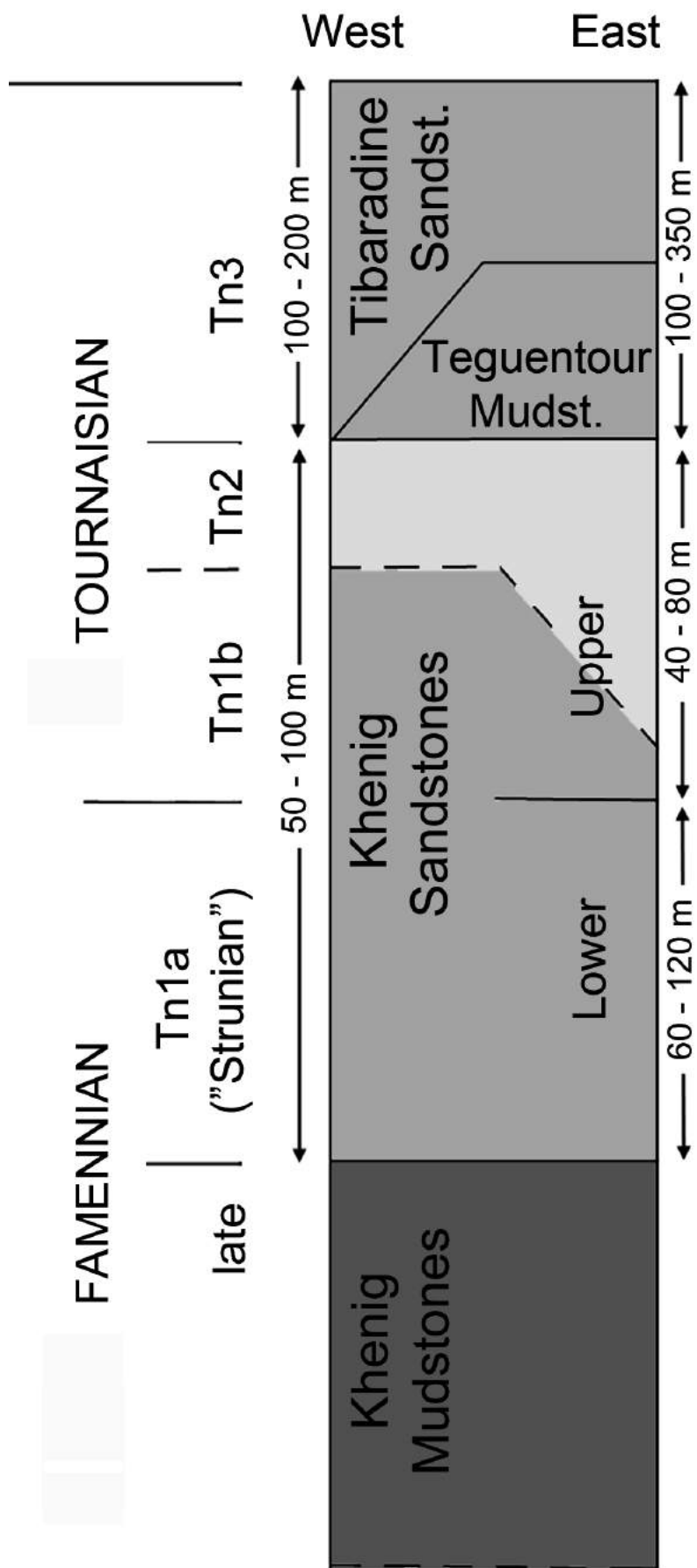
754 **Table legend.**

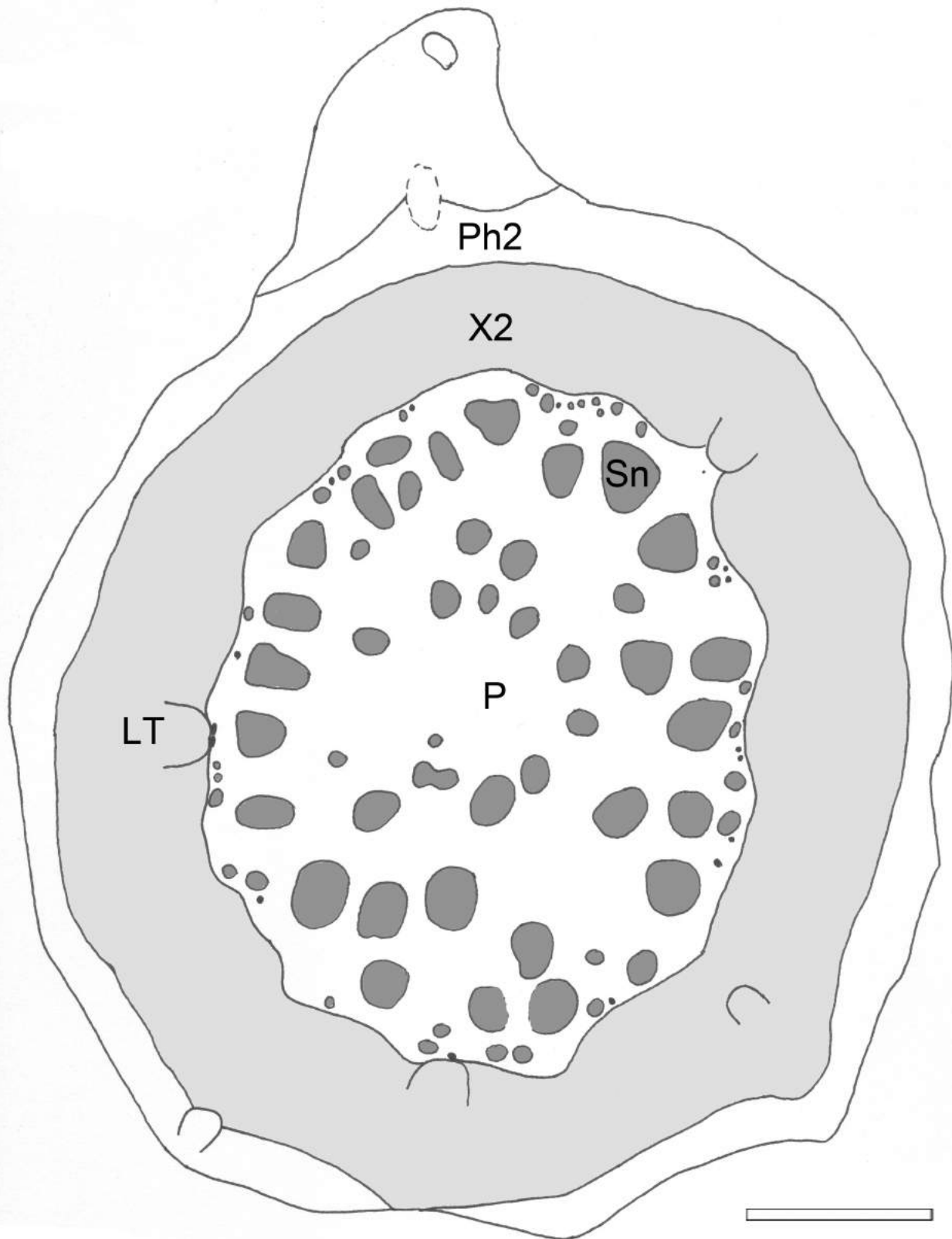
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756 **Table 1.** *Ahnetia conradii* from the Mississippian of Algeria: comparison of tissue ratio and  
757 periderm development with the Mississippian stems *Pitus dayi* (Gordon, 1935) and *Faironia*  
758 *difasciculata* (Decombeix et al., 2006).

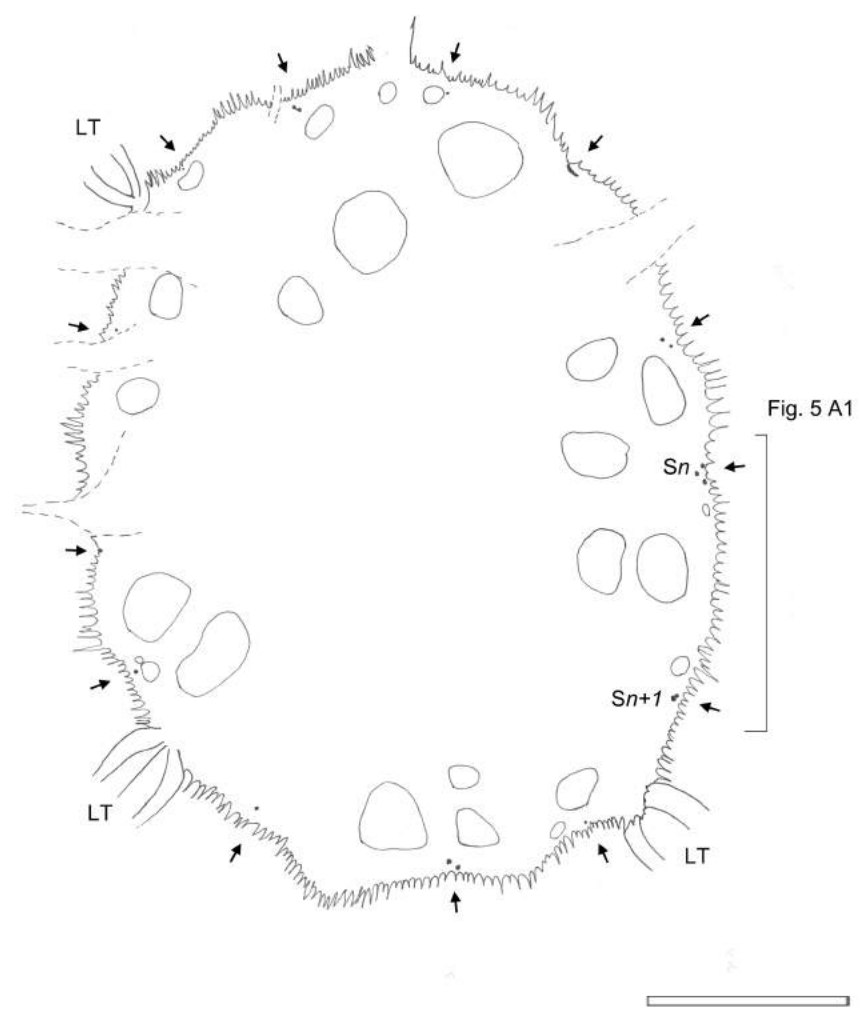




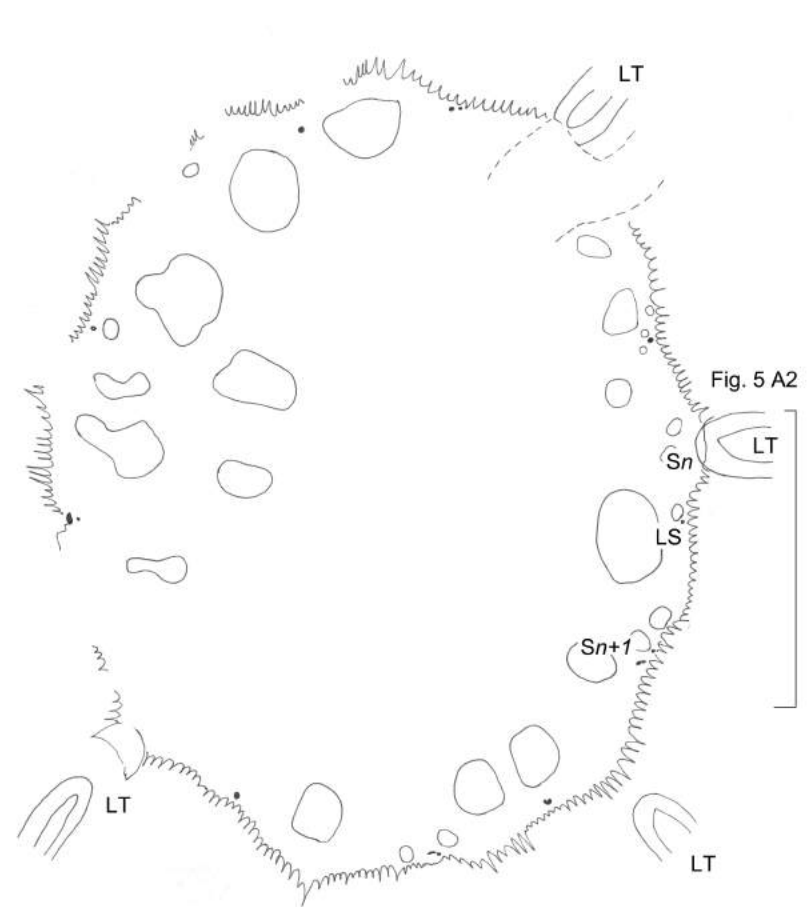




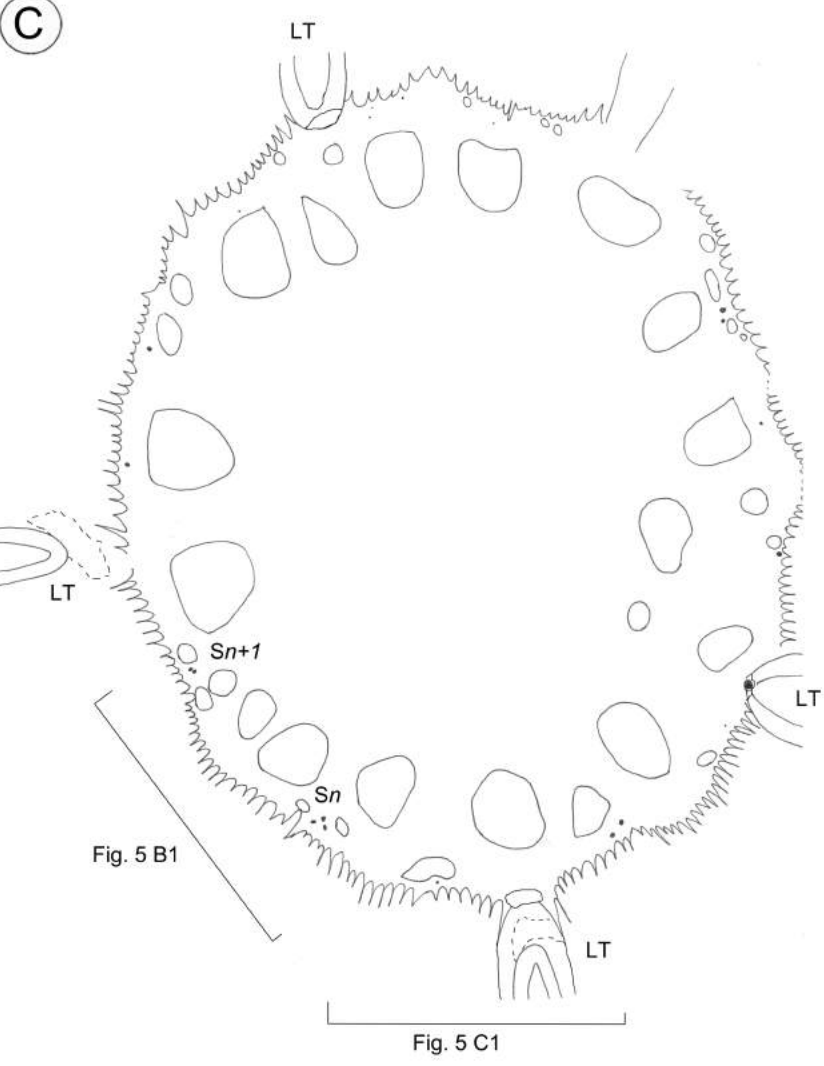
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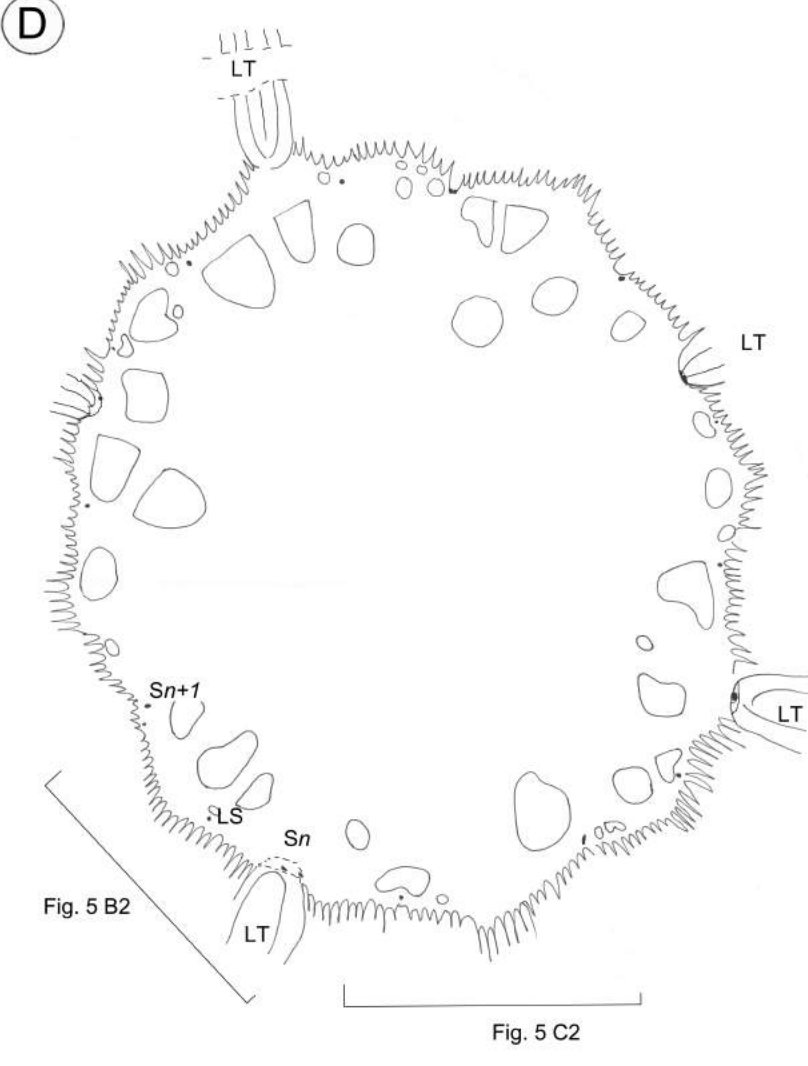
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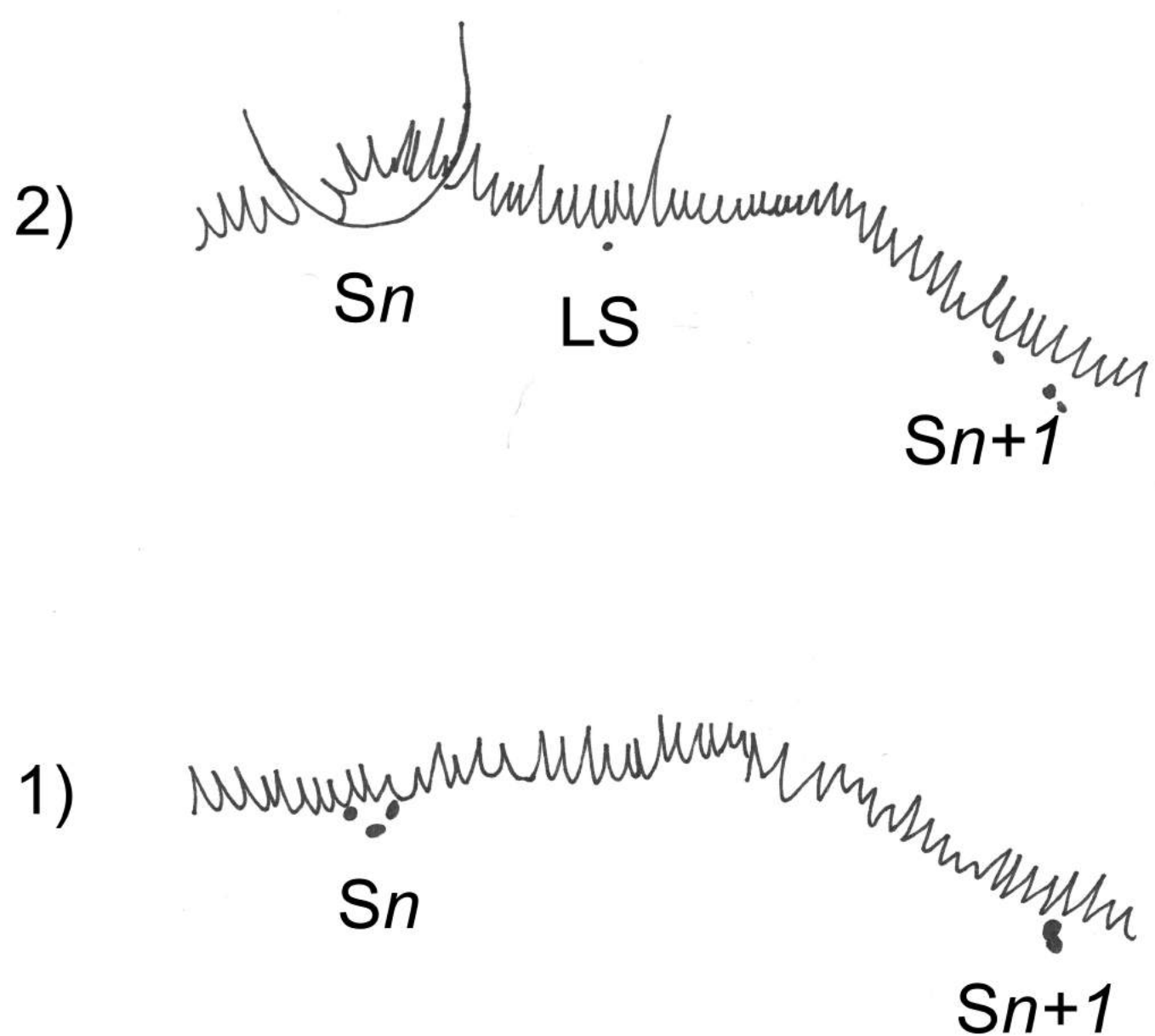
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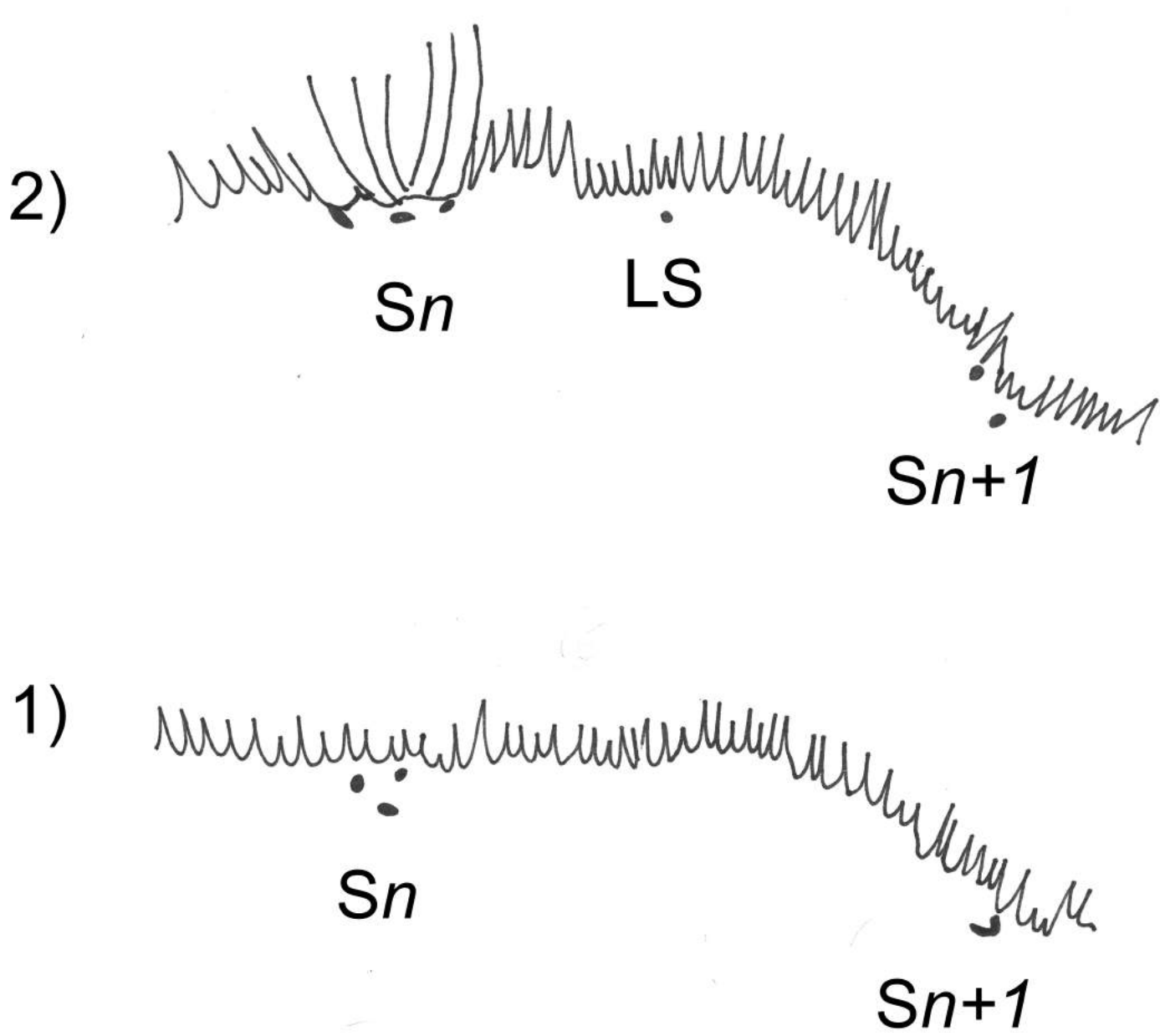
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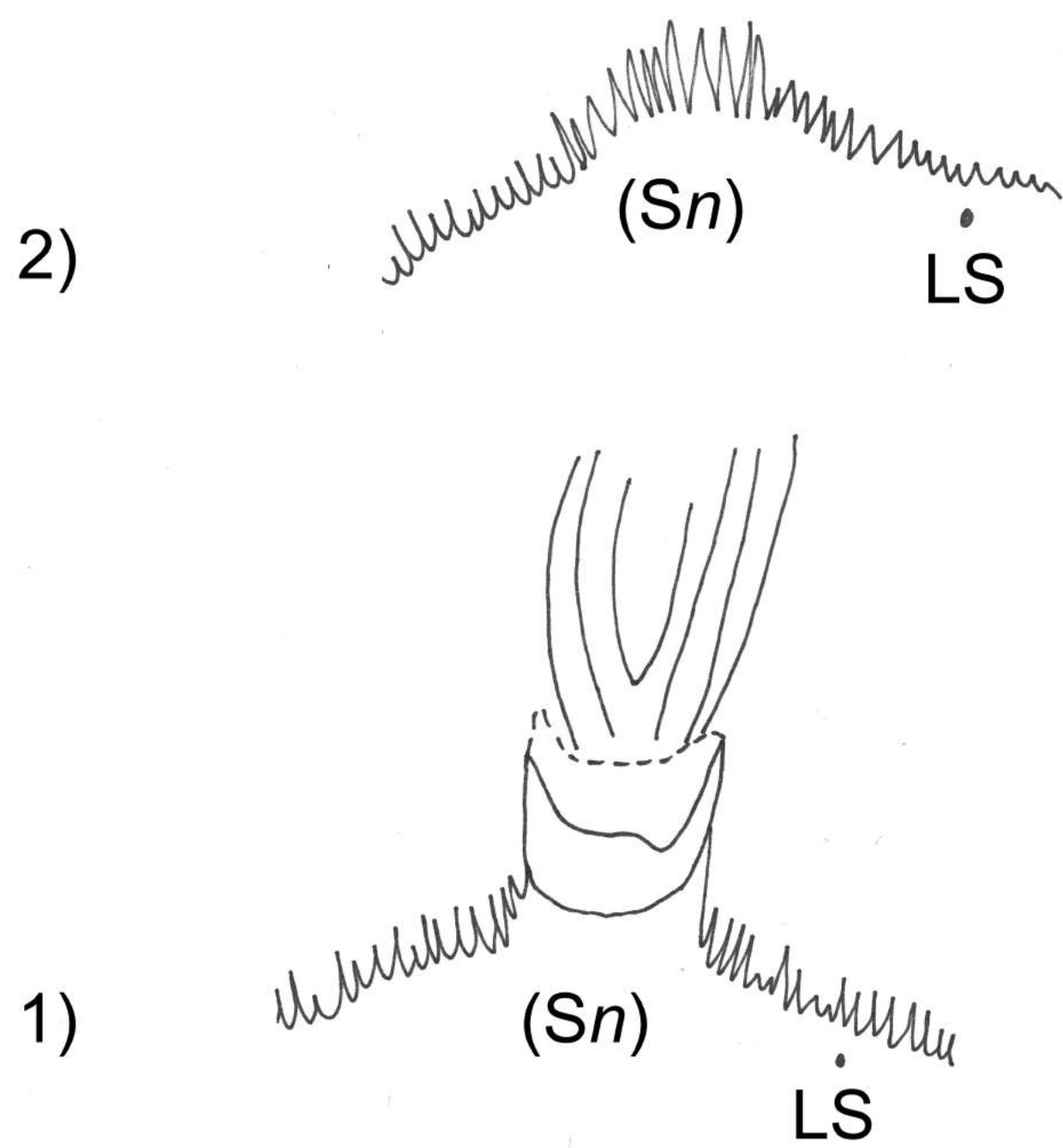
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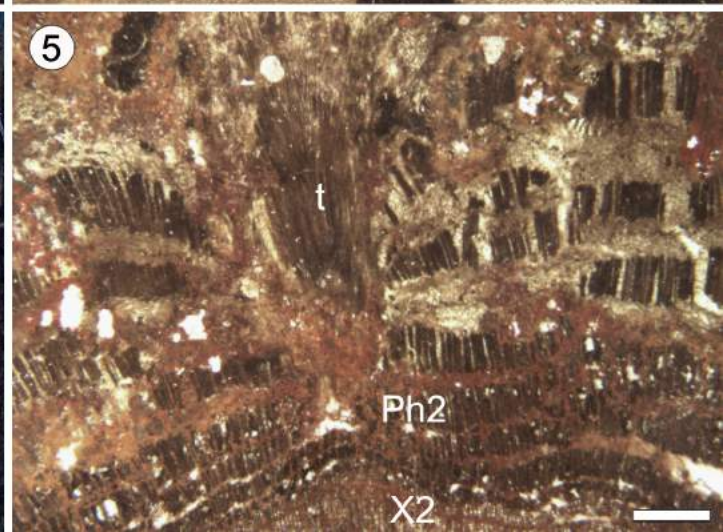
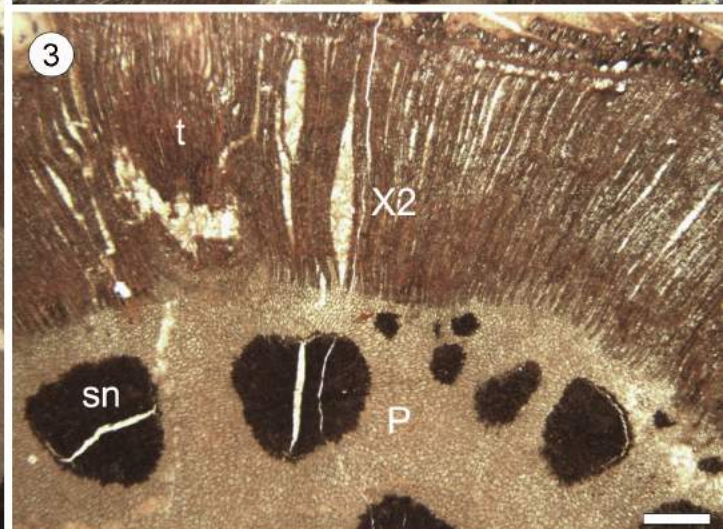
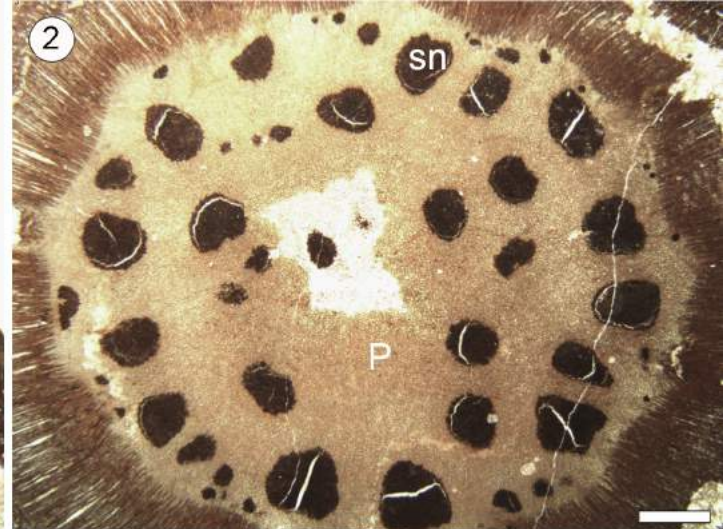
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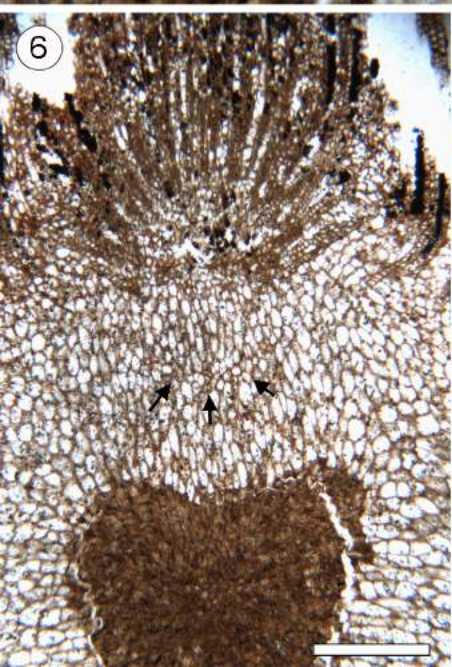
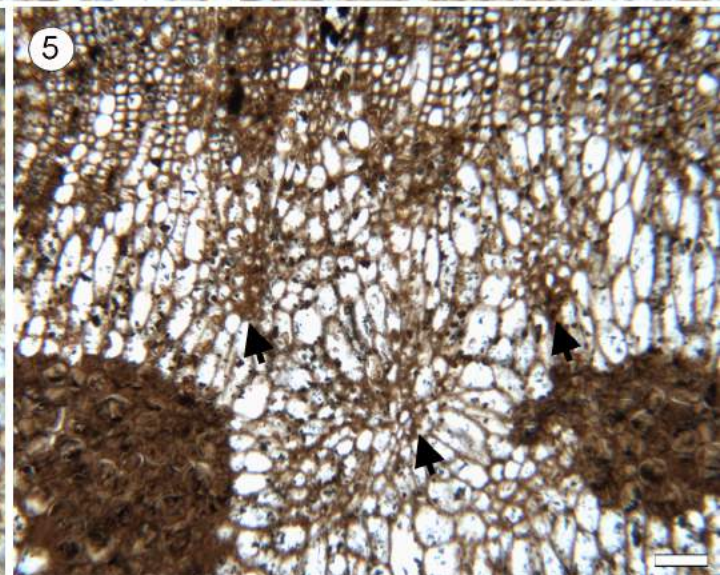
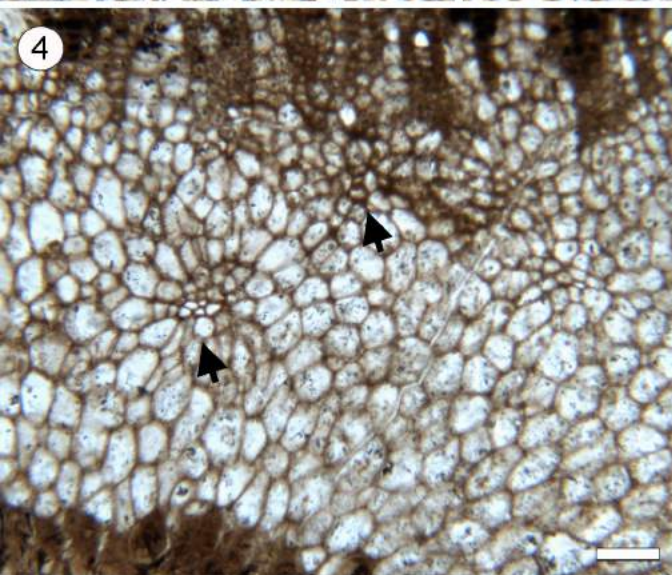
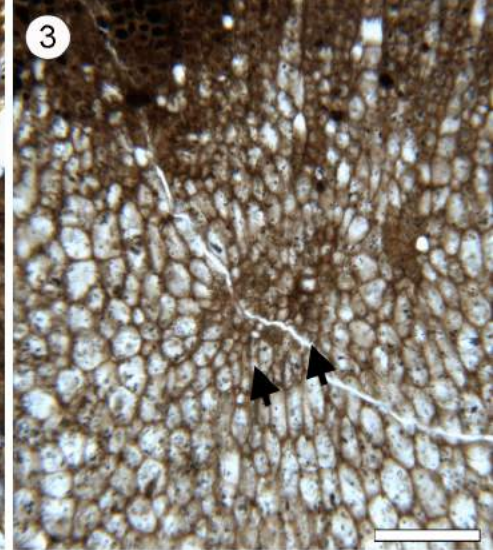
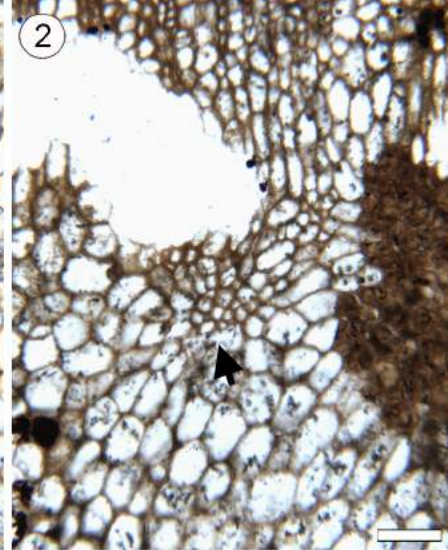
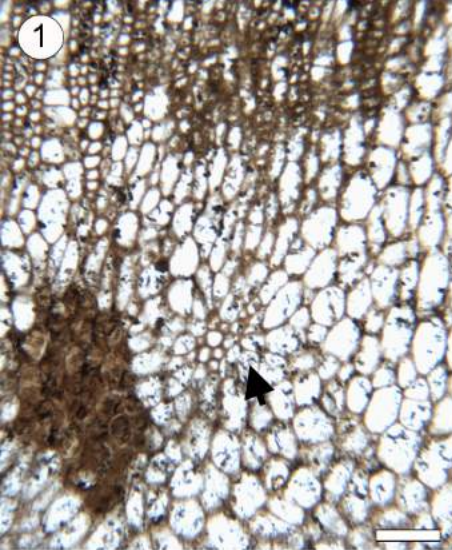
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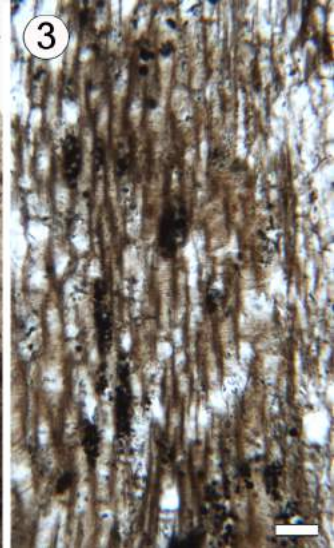
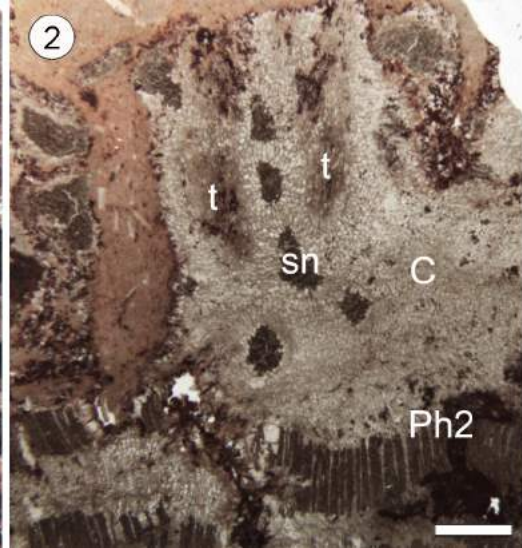
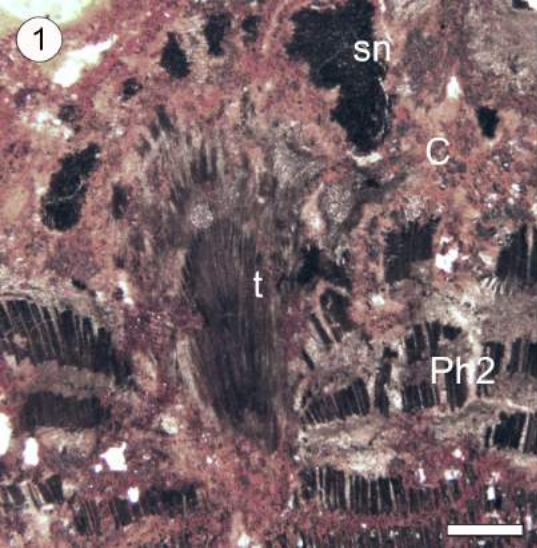




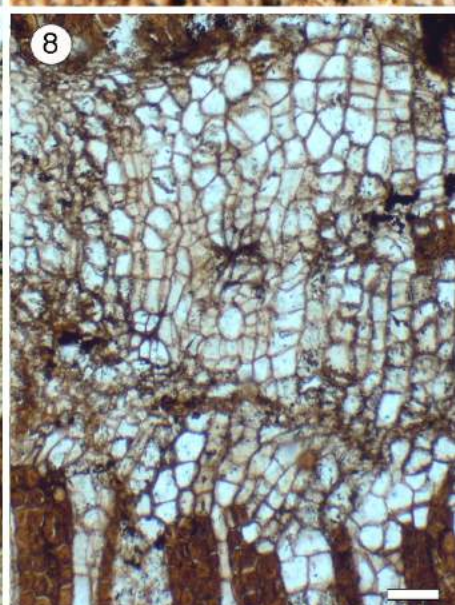
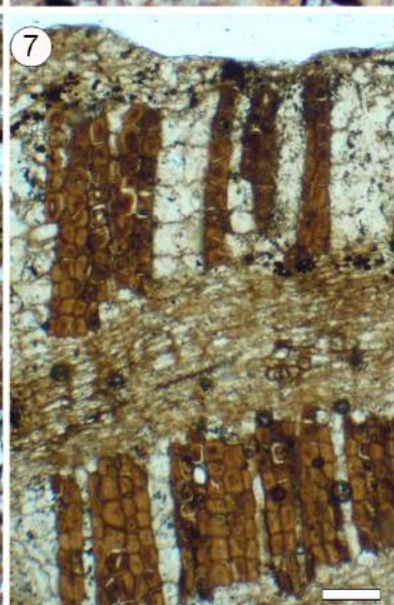
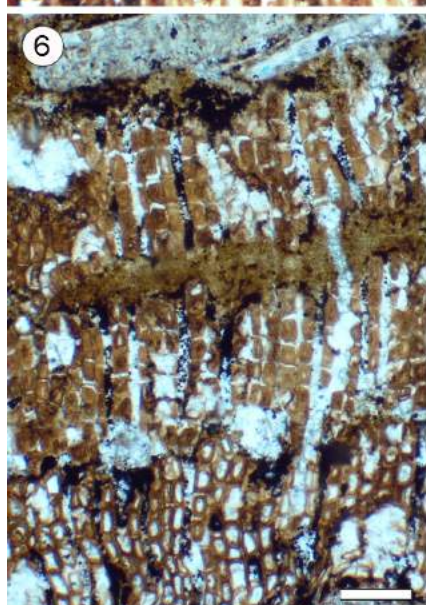
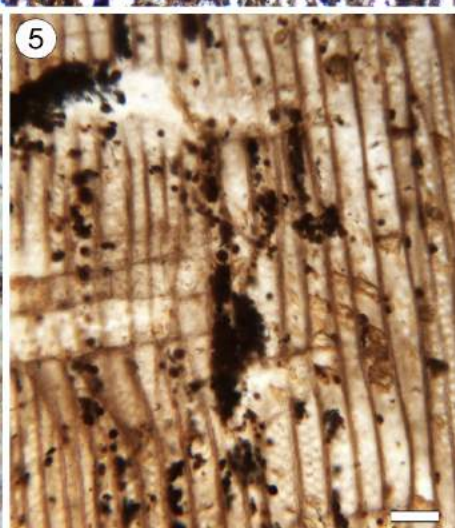
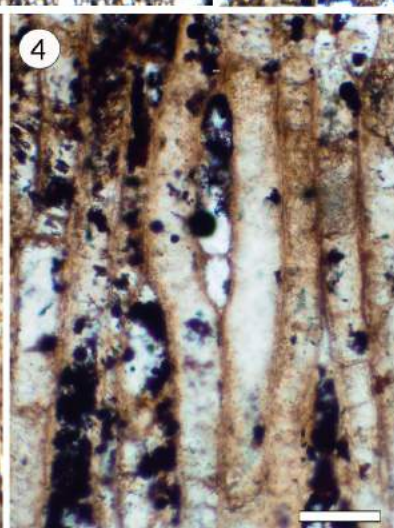
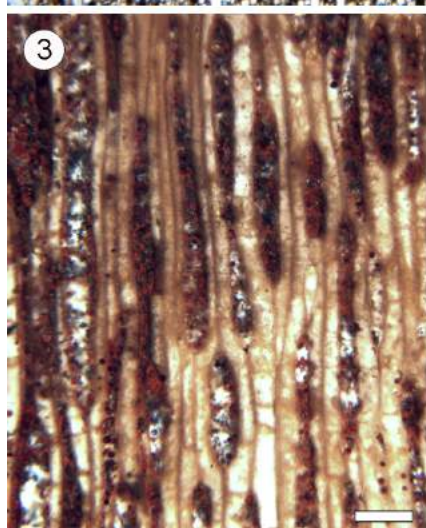
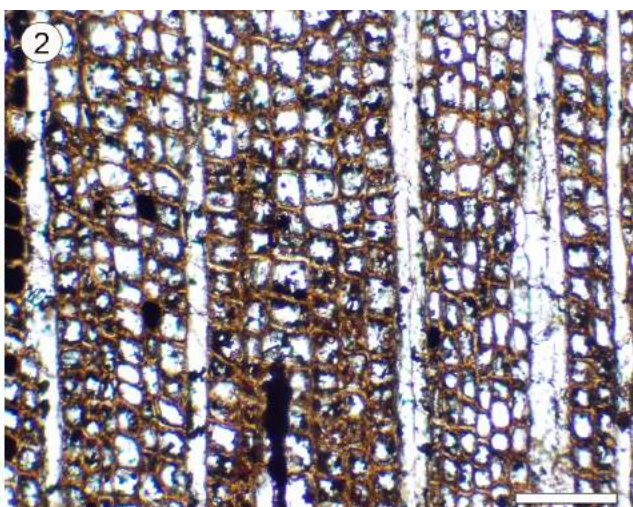












**Table 1.** Comparison of tissue ratio and periderm development in the Mississippian stems *Pitus dayi* (2 specimens figured by Gordon, 1935), *Faironia difasciculata* (Decombeix et al., 2006), and *Ahnetia conradii* (this paper)

	<i>Pitus dayi</i>	<i>Faironia difasciculata</i>	<i>Ahnetia conradii</i>
Ratio stele diameter /total diameter	1 : 3.8 1 : 2.3	1 : 2	1 : 1.7
Axis diameter (mm)	25 25	34	37
Pith diameter (mm)	6.5 11	21	21
Secondary xylem thickness (mm)	6 2	6	5
Secondary phloem thickness (mm)	–	0.5	1.5
Periderm	Yes Yes	No	Yes