



Research paper

A Middle Devonian *Callixylon* (Archaeopteridales) from Ronquières, BelgiumLuc Cornet ^a, Philippe Gerrienne ^{a,*}, Brigitte Meyer-Berthaud ^{b,c}, Cyrille Prestianni ^d^a Paléobiogéologie, Paléobotanique et Paléopalynologie, Département de Géologie, B18, Université de Liège, Sart Tilman, Liège 1, Belgium^b Université Montpellier 2, UMR AMAP, Montpellier, F-34000, France^c CNRS, UMR AMAP, Montpellier, F-34000, France^d RBINS, Rue Vautier, 29, B-1000 Bruxelles, Belgium

ARTICLE INFO

Article history:

Received 6 March 2012

Received in revised form 3 July 2012

Accepted 6 July 2012

Available online 16 July 2012

Keywords:

archaeopteridalean lignophyte

Callixylon

Givetian

pyrite permineralization

Ronquières

tree

ABSTRACT

A permineralized *Callixylon* trunk is reported from Ronquières, a mid to late Givetian (Middle Devonian) locality from Belgium. The specimen consists of an 80 cm long trunk adpression whose central area is preserved as a pyrite permineralization. The pyritized area is composed of a eustele surrounded by secondary xylem. Tracheids show radially aligned groups of pits separated by unpitted regions on the radial walls of tracheids. The specimen belongs to a group of species characterized by a predominance of uniseriate rays and the lack of ray tracheids. This *Callixylon* specimen is one of the earliest representatives of the genus. It coexists at the locality with large cladoxylpsids and provides direct evidence that the tree habit had evolved in the archaeopteridalean progymnosperms by the Givetian.

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1. Introduction

The widely distributed archaeopteridalean progymnosperms were prominent components of the terrestrial ecosystems during the Late Devonian (Meyer-Berthaud et al., 1999); their remains have been abundantly documented. The order Archaeopteridales includes the genera *Actinopodium* Høeg, *Actinoxylon* Matten, *Archaeopteris* Stur, *Callixylon* Zalessky, *Eddyia* Beck, *Siderella* Read and *Svalbardia* Høeg (Beck and Wight, 1988; Taylor et al., 2009), with *Archaeopteris* and *Callixylon* being by far the best known taxa. The genus name *Callixylon* Zalessky (1911) is applied to permineralized archaeopteridalean stem, branch and root fragments whose secondary xylem includes tracheids with radially aligned groups of small circular bordered pits separated by unpitted regions (Beck, 1960). The primary vascular system of *Callixylon* stems and branches is eustelic; it is protostelic in roots (Beck and Wight, 1988). The first diagnosis of the genus was published by Lemoigne et al. (1983). The name *Archaeopteris* Stur (1875) (see Wang, 2011 for the taxonomical background of the genus) applies to lateral branching systems preserved as adpressions, that superficially resemble the compound fronds of ferns. Beck (1960) demonstrated the connection between a specimen of *Callixylon zalesskyi* Arnold and frond-like branches of *Archaeopteris macilenta* Lesquereux from the Late Devonian of New York. Despite this evidence, *Callixylon* and

Archaeopteris are kept separated. They correspond to fossils with different taphonomical histories, which preserve different sets of traits. Within the Archaeopteridales, *Callixylon* is the only genus corresponding to roots, stems, and proximal branches. In contrast, several genera have been erected for leafy branches in relation to the morphology and bi/tri-dimensionality of their units (e.g. *Archaeopteris*, *Svalbardia*, *Actinoxylon*); their congenericity has been questioned but never resolved (Beck and Wight, 1988). It is therefore possible that *Callixylon* does not strictly overlap with *Archaeopteris*.

We report here the discovery of an 80 cm long *Callixylon* specimen collected in 2005 at a newly discovered fossiliferous outcrop located along the “plan incliné de Ronquières” in Belgium. The present paper is a preliminary description of the primary and secondary xylem of the plant; the establishment of the detailed phyllotaxy of the specimen is currently underway at Liège University.

2. Locality and source strata

The locality that yielded the specimen of *Callixylon* studied here is some 300 m northeast from the “Ronquières, tour du plan incliné (tête amont)” locality reported by Stockmans in 1968 (fig. 1). The flora collected at Stockmans' locality is the most diverse Middle Devonian plant assemblage from Belgium (Berry, 2008). It includes zosterophylloids, lycopsids, cladoxylpsids, aneurophytalean and archaeopteridalean progymnosperms, the proto-ovule *Runcaria* Stockmans, as well as various *incertae sedis* taxa (Stockmans, 1968; Fairon-Demaret, 1981; Gerrienne et al., 2004; Scheckler et al., 2006;

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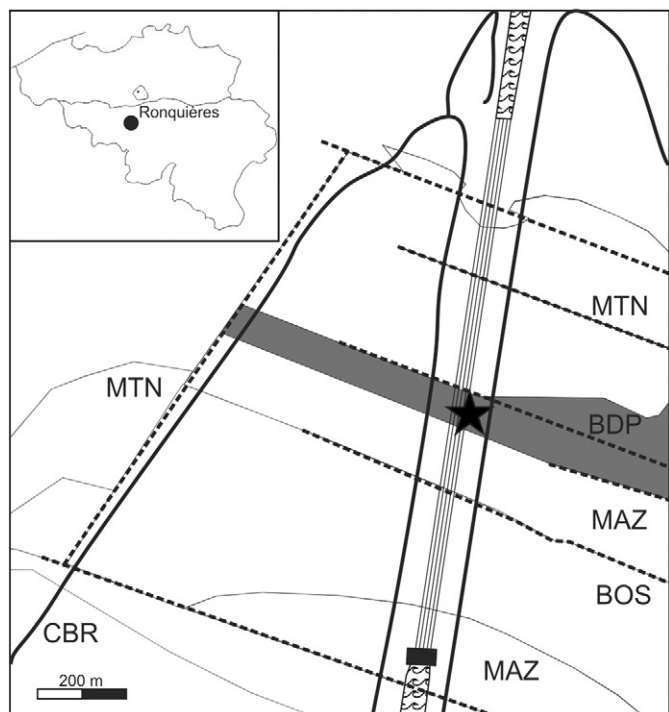


Fig. 1. Simplified geological map of the Plan Incliné area, showing the approximate position of the fossiliferous locality (star). Parallel thin full lines: railway of the “plan incliné”; other thin full lines: limits of the Formation Members; thick full lines: roads; dotted line: faults. BDP = Bois du Planti Member of the Bois de Bordeaux Formation (mid Givetian); BOS = Bossière Member of the Bovesse Formation (early Frasnian); CBR = Combreuil Member of the Bovesse Formation (early Frasnian); MAZ = Mazy Member of the Bois de Bordeaux Formation (late Givetian); MTN = Les Mautiennes Member of the Bois de Bordeaux Formation (early Givetian) (Hennebert and Eggermont, 2002).

Modified from Hennebert and Eggermont (2002).

Gerrienne and Meyer-Berthaud, 2007). Stockmans' flora is in need of an in-depth revision.

The newly discovered fossiliferous outcrop is located along the “plan incliné” (fig. 1). It belongs to the Bois du Planti Member of the Bois de Bordeaux Formation (Bultynck et al., 1991) and mainly consists of alternating grey fossiliferous shale and sandstone. In addition to *Callixylon*, the new outcrop has yielded compression fossils representing cladoxylous trunks, pyritized remains of woody cladoxylous and of stenokolean axes of *Crossia* Beck and Stein, and a large number of as yet unidentified compressions (Gerrienne and Meyer-Berthaud, 2006, 2010; work in progress at Liège University).

The plant fossils which were deposited in a floodplain environment are allochthonous in the two localities.

At both localities, the miospore assemblage includes, among other species, *Acinosporites lindlarensis* Riegel (1968), *Ancyrospora ancyrea* var. *ancyrea* Richardson (1962), *Grandispora velata* (Eisenack) Playford (1971), *Rhabdosporites langii* (Eisenack) Richardson, 1960, *Verrucosporites premnus* (Richardson) Richardson (1965), *Geminospore lemurata* Balme, 1962, *Chelinospore concinna* Allen (1965), *Samarisporites triangulatus* Allen (1965) and *Aneurospore greggsii* (McGregor) Streele (in Becker et al., 1974). On this basis, both localities have been attributed a mid to late Givetian age (TA Opper Zone; Gerrienne et al., 2004; Ville de Goyet et al., 2007).

3. Material and methods

The specimen ULg-13560 consists of an 80 cm long and 12–15 cm wide laterally compressed axis, with a 5.5 cm × 1.8 cm wide central area preserved as a pyrite permineralization. Several bumps, which may represent branch traces, are visible on the surface of the specimen.

This part has been cut into 8 segments, each about 10 cm in length. All segments have been studied either by the thin section and wafering method (78 slides) or by the acetate peel technique (approximately 60 peels) after having been etched by nitric acid (Matten, 1973; Galtier and Phillips, 1999; Hass and Rowe, 1999; Kenrick, 1999).

The nature of this specimen, branch or trunk, is difficult to ascertain. On the basis of its width (12–15 cm) and lack of conicity, we presume that it represents a portion of trunk. The compression of the specimen suggests that it was fossilized parallel to the bedding plane. The primary tissues and secondary xylem of one face are badly preserved (Plate I, 1).

4. Results

4.1. Transverse section

The permineralized central area of the specimen consists of a eustele surrounded by an incompletely and asymmetrically preserved zone of secondary xylem composed of tracheids and rays only (Plate I, 1).

The preserved primary tissues include a parenchymatous pith surrounded by a ring of discrete primary vascular bundles. The specimen has been flattened and the pith is elliptical (Plate I, 1, 2). Its major diameter ranges from 25 to 29 mm, the minor diameter from 4 to 7 mm. This variation is a taphonomic feature, not related to the proximal versus distal position of the section. The cells in the central portion of the pith are badly preserved. Scattered thick-walled cells, some showing black contents, may represent sclereids (Plate I, 2, 3). They are present in all parts of the pith but occur predominantly in the 1–2 mm wide outermost part (Plate I, 2).

Twenty-five primary vascular bundles are visible. The original number of primary bundles was probably around 30. Maturation of the primary xylem is mesarch (Plate I, 2, 4). The protoxylem strand includes thin-walled, possibly parenchymatous, cells (Plate I, 4). Most vascular bundles are not in contact with the inner edge of the secondary xylem (Plate I, 2). Additional minute primary xylem strands are possibly present between the more conspicuous ones (Plate I, 5, arrows). Sclereids may be present around the primary vascular bundles (Plate I, 2). The tracheids of primary xylem are circular to elliptical in section with a major diameter ranging from 6 to 77 μm and a minor diameter ranging from 7 to 60 μm (Plate I, 2).

The thickness of the secondary xylem varies from 4 to 8 mm on one side of the specimen, from 1 to 3 mm on the other side. There is no significant change in the thickness of the preserved part of the wood along the specimen. Tracheids of the secondary xylem are mostly rectangular in section (Plate I, 5). Their radial diameter ranges from 22 to 44 μm ($N=50$; mean: 31 μm ; standard deviation: 5 μm) and their tangential dimension from 13 to 46 μm ($N=50$; mean: 25 μm ; standard deviation: 6 μm). The thickness of the tracheid walls is 3 μm in average. Rays are narrow. They enlarge significantly in the innermost part of the wood. There, groups of 2–7 rows of tracheids are separated by enlarged rays in connection with the pith (Plate I, 1; but see also these inflated rays in longitudinal section in Plate II, 1, 4).

4.2. Longitudinal tangential section

Enlarged rays in the portion of secondary xylem adjacent to the pith range from 326 to 1789 μm in height (Plate II, 1) and 60 to 295 μm in width. In the central part of the secondary xylem there are 10 to 16 rays per tangential mm. There, rays are uniseriate and fusiform, rarely biseriate in part (Plate II, 3) and they are composed of 1 to 13 cells in height, mostly 1 to 7 cells ($N=10$; mean: 12 rays; standard deviation: 2 rays). Ray height (Plate II, 2) varies from 17 to 511 μm ($N=50$; mean: 223 μm ; standard deviation: 142 μm); ray width varies from 12 to 33 μm ($N=50$; mean: 19 μm ; standard deviation: 5 μm). Bordered pits similar in size and arrangement to those

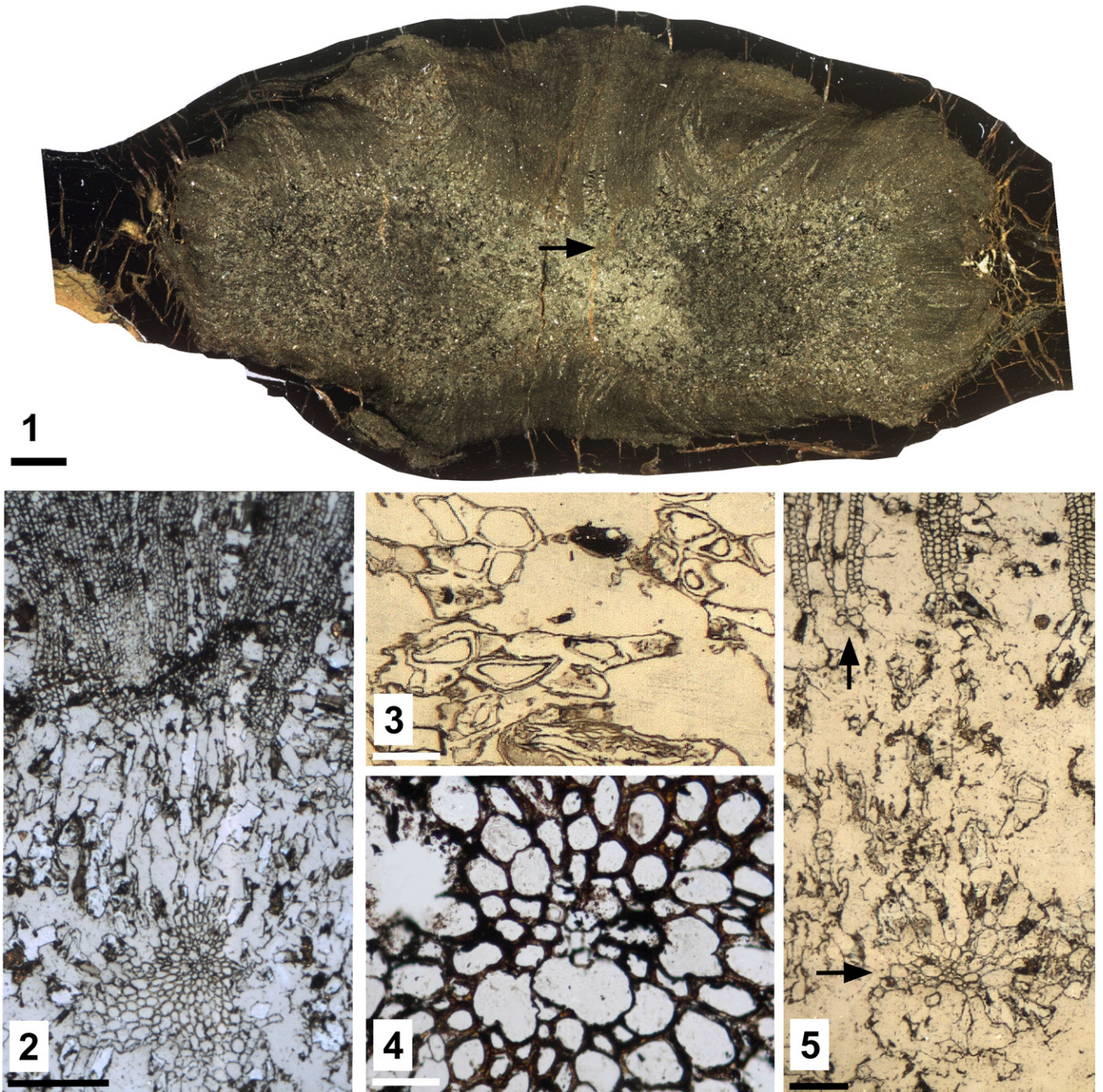


Plate I. *Callixylon* sp. from Ronquières (Belgium); mid to late Givetian (Middle Devonian). Specimen ULg-13560. Transverse sections, except for fig. 4.

1. Gross view showing, from inside to outside: the pith, the primary vascular bundles, the incomplete and asymmetrical zone of secondary xylem. Arrow points at a primary xylem bundle. Scale bar = 2 mm.
2. Primary vascular bundle detached from the inner edge of the secondary xylem. Note cells showing black contents, possibly representing sclereids. Scale bar = 500 μ m.
3. Detail of a primary vascular bundle. Maturation of the primary xylem is mesarch. The protoxylem strand includes thin-walled, possibly parenchymatous, cells. Scale bar = 50 μ m.
4. Sclereids in tangential section. Scale bar = 50 μ m.
5. Possible additional minute primary xylem strands (arrows). Scale bar = 200 μ m.

on the radial walls of the tracheids seem present on the tangential walls in the innermost part of the wood (Plate II, 4). It is possible that this observation is artefactual and actually corresponds to the pitting on radial walls of distorted tracheids. Ray cells are parenchymatous. Sclereids are present in the pith (Plate I, 3).

4.3. Longitudinal radial section

The bordered pits on the radial walls of tracheids are multiseriate (Plate II, 5) and closely adpressed against each other. Their outline is elliptical to circular (Plate II, 5). Their diameter ranges from 7 to

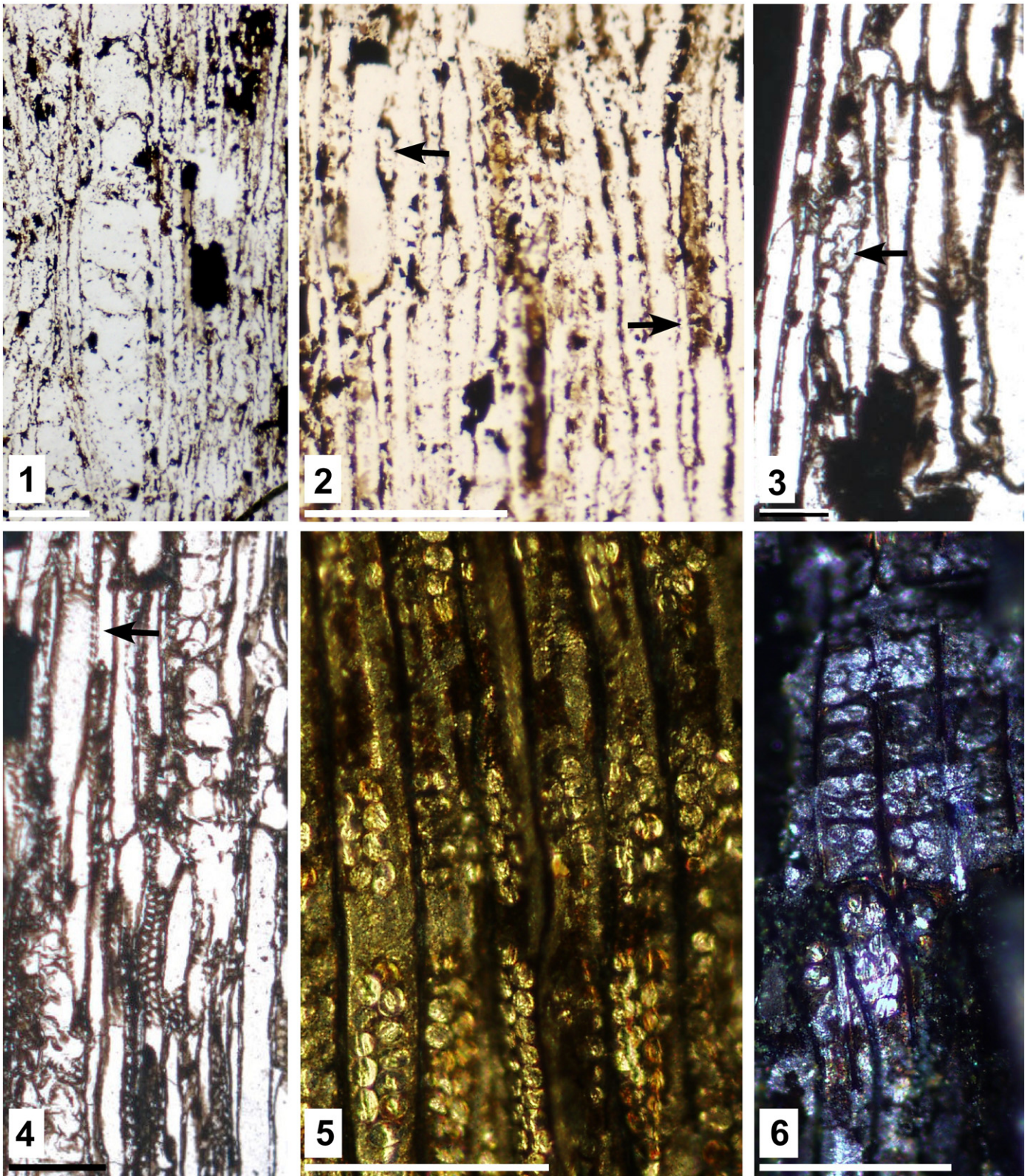


Plate II. *Callixylon* sp. from Ronquières (Belgium); mid to late Givetian (Middle Devonian). Specimen ULg-13560. Longitudinal sections.

1. Tangential section. Enlarged ray in the secondary xylem adjacent to the pith. Scale bar = 200 μm .
2. Tangential view showing the rays. Arrows indicate two rays of different heights. Scale bar = 200 μm .
3. Tangential view showing a partially biseriate ray (arrow). Scale bar = 50 μm .
4. Tangential view showing tangential pitting of the tracheids. The arrow indicates a tracheid with pits on the radial and tangential walls. Scale bar = 100 μm .
5. Radial view showing the bands of pits separated by unpitted areas. Scale bar = 100 μm .
6. Radial view showing cross-fields with 4–5 half-bordered circular pit pairs. Scale bar = 100 μm .

16 μm (N=100; mean: 11 μm ; standard deviation: 1 μm). The pit aperture is elliptical and tilted 45°.

The radial walls of tracheids characteristically show radial bands of grouped pits (Plate II, 5). Each group contains 6 to 24 pits (N=50; mean: 14 pits; standard deviation: 5 pits) and includes most generally alternating biseriate or triseriate rows (Plate II, 5). The height of the pit groups varies from 43 to 134 μm (N=50; mean: 77 μm ; standard deviation: 22 μm); their width varies from 13 to 39 μm (N=50; mean: 77 μm ; standard deviation: 22 μm). The bands of pits are separated by unpitted areas (Plate II, 5) whose height varies from 10 to 77 μm (N=50; mean: 24 μm ; standard deviation: 6 μm). At places, the arrangement of pits in groups is not obvious; this character is probably variable in the specimen.

The rays are composed of rectangular parenchyma cells (Plate II, 6). The size of the few observed cross-fields is variable. Their height varies from 21 to 44 μm and their width from 20 to 47 μm . Half-bordered circular pit pairs are present in the cross-fields. Their number varies from 3 to 9 pits. Their diameter varies from 6 μm to 14 μm . The aperture of the pit is circular to elliptical; in this case, it is either tilted 45° or horizontal. Ray tracheids are absent.

5. Discussion

The presence of radially aligned groups of pits is the main diagnostic feature for identifying the genus *Callixylon* (Arnold, 1929; Orlova and Jurina, 2011). It should nevertheless be noted that Scheckler and Banks (1971) illustrated a radial section of the secondary xylem of *Triloboxylon hallii* (Arnold) Scheckler and Banks [renamed *Triloboxylon arnoldii* by Matten (1974)], with grouped pitting similar to that of *Callixylon*. Stein and Beck (1983), in their revision of the species, found in only one instance a potential grouped pitting, and suggested that this apparently grouped pitting was rather due to the presence of a short vascular ray. Thus, the use of the character “presence of radially aligned group of pits” for the generic identification of *Callixylon* appears justified. The specimen from Ronquières clearly exhibits grouped pitting on the radial walls of the secondary xylem tracheids; consequently, the specimen is attributed to the genus *Callixylon*. Another character of the genus is the presence of mesarch primary vascular bundles at the

periphery of the pith, in contact or not with the secondary xylem (Beck, 1953; Lemoigne et al., 1983). This character is also present in the Ronquières specimen.

Species of *Callixylon* are essentially distinguished from each other by ray characters, such as ray seriation and the presence/absence of ray tracheids (Beck, 1981; Lemoigne et al., 1983; Orlova and Jurina, 2011). In Table 1, we have listed characters of the ray tissue for the species of *Callixylon* recognized as valid by Lemoigne et al. (1983) and Orlova and Jurina (2011). The Ronquières specimen is characterized by (i) a majority of short uniseriate rays and rare partly biseriate rays, and (ii) the lack of horizontal ray tracheids. It is consistent with the “*trifilievii* group” of Orlova and Jurina (2011) that spans the entire Upper Devonian and includes *Callixylon trifilievii* and its “junior synonyms” (*Callixylon marshii*, *Callixylon henkei*, *Callixylon velinense*, *Callixylon clevelandensis*, *Callixylon huronensis*) as well as *Callixylon brownii* and *Callixylon whiteanum* (Table 1). Lemoigne et al. (1983) circumscribe *C. trifilievii* and its possible synonyms (*Callixylon zalesskyi*, *C. whiteanum* and *C. velinense*) to specimens that have uniseriate rays only and that possess ray tracheids, which thus differ from the Ronquières specimen. The occurrence of ray tracheids in the type material of *C. trifilievii* and that of *C. whiteanum* however is contested by Beck and Wight (1988). In addition, rays in *C. whiteanum* can be partly, or entirely biseriate, which adds confusion to the concept of *C. trifilievii* as defined by Lemoigne et al. (1983). The Ronquières specimen has only its innermost, juvenile part of the wood preserved and does not show the whole range of variation originally presented by its wood. In view of these uncertainties, we are reluctant to suggest any specific identification for this specimen and we call it *Callixylon* sp. We, however, suspect that it belonged to a species included in the “*trifilievii* group” of Orlova and Jurina (2011).

Most *Callixylon* sp. are of Late Devonian age (Lemoigne et al., 1983 and references herein). Before this work, direct evidence of the occurrence of *Callixylon* in Givetian plant deposits was few. A 5–7 cm wide specimen of *Callixylon velinense* (Marcelle, 1953) was collected from Sart-Dame-Avelines, a late Givetian locality from Belgium (Stockmans, 1968; Bultynck et al., 1991). *Callixylon marshii* (Hylander, 1922, cited in Arnold, 1930) is based on a small piece of badly preserved wood collected from the Eighteen Mile Creek, Erie County, New York State. The

Table 1

Ray characters for the *Callixylon* species recognized as valid by Lemoigne et al. (1983) and Orlova and Jurina (2011).

Valid species according to 12	Valid species according to 15	Synonymy according to 12	Synonymy according to 15	Ray seriation	Presence of ray tracheids	Age according to 15
<i>C. trifilievii</i> (16)	<i>C. trifilievii</i> (16)	<i>C. velinense</i> (14) <i>C. zalesskyi</i> (1) <i>C. whiteanum</i> (2)	<i>C. huronensis</i> (6) <i>C. henkei</i> (10) <i>C. clevelandensis</i> (5) <i>C. marshii</i> (9) <i>C. velinense</i> (14) <i>C. trifilievii</i> (16)	Strictly uniseriate	Present (12) Absent (15)	Frasnian–Famennian
<i>C. henkei</i> (10) <i>C. petryi</i> (3) <i>C. brownii</i> (8)	<i>C. petryi</i> (3) <i>C. brownii</i> (8)			Strictly uniseriate Strictly uniseriate Uniseriate (80%), occasionally locally biseriate	Absent Present Absent	Famennian Frasnian Upper Devonian–Lower Mississippian
	<i>C. whiteanum</i> (2)	<i>C. trifilievii</i> (16)		Uniseriate, rarely totally biseriate, frequently biseriate in part	Rare or absent (2) No (15) Rare (12)	Upper Devonian–Lower Mississippian
<i>C. erianum</i> (1) <i>C. bristolense</i> (1)	<i>C. erianum</i> (1)		<i>C. bristolense</i> (1)	Uniseriate, occasionally biseriate Uniseriate except the broad ones	Present Present	Frasnian–Famennian Frasnian
	<i>C. zalesskyi</i> (1)	<i>C. trifilievii</i> (16)	<i>C. beckii</i> (6)	Uniseriate, frequently biseriate in part	Present	Frasnian
<i>C. newberryi</i> (7 cited in 12)	<i>C. newberryi</i> (7 cited in 15)	<i>C. marshii</i> (9) <i>C. mentethense</i> (1) <i>C. schmidtii</i> (11)	<i>C. schmidtii</i> (11) <i>C. mentethense</i> (1)	Uniseriate to pluriseriate	Present	Frasnian–Famennian
<i>C. arnoldii</i> (4)	<i>C. kazakhstanum</i> (13) <i>C. arnoldii</i> (4)			Uniseriate to pluriseriate Uniseriate and biseriate	Absent Absent	Frasnian Upper Devonian–Lower Mississippian

1 = Arnold (1930); 2 = Arnold (1934); 3 = Beck (1953); 4 = Beck (1962); 5 = Chitaley (1988); 6 = Chitaley and Cai (2001); 7 = Elkins and Wieland (1914); 8 = Hoskins and Cross (1951); 9 = Hylander (1922); 10 = Kräusel and Weyland (1929); 11 = Kräusel and Weyland (1937); 12 = Lemoigne et al. (1983); 13 = Lepekhina (1963); 14 = Marcelle (1953); 15 = Orlova and Jurina (2011); 16 = Zalessky (1911).

Givetian age of the latter locality was suggested in the protologue (Hylander, 1922), but has not been confirmed since then by any biostratigraphical data. Even more speculative is the report of a *Callixylon*-type of wood from the Givetian of Antarctica (Retallack, 1997). Based on the mid to late Givetian age of the Ronquières locality (Gerrienne et al., 2004; Ville de Goyet et al., 2007), the *Callixylon* specimen described here is therefore one of the earliest representatives of the genus.

Recent information obtained from a paleosol at Gilboa (New York State, USA) provides clear evidence for the existence, during mid-Devonian times, of mixed forests composed of arborescent lycopsids and cladoxyloids, and of woody aneurophytalean progymnosperms (Stein et al., 2012). Based on the presence of characteristic stump casts and attached root systems in three other Givetian paleosols of the Manorkill Formation (New York State, USA), Mintz et al. (2010) suggested that forests inhabited by monospecific stands of arborescent Archaeopteridales occurred in the vicinity of the cladoxyloid forests. According to these authors, those presumed archaeopterid forests grew in more upland positions and better drained environments than the cladoxyloid forests which were established in deltaic and tidal-swamp environments (Mintz et al., 2010). The indirect evidence of tree-sized archaeopterids in the Givetian reported by Mintz et al. (2010) is corroborated by the specimen of *Callixylon velinense* mentioned above and the 12–15 cm wide Ronquières specimen described in this paper. Additional occurrences of Givetian archaeopterids from Belgium include two Stockmans' (1968) localities, namely the "Ronquières, tour du plan incliné (tête amont)" and the "Sart-Dame-Avelines" localities of Stockmans (1968), where archaeopteridalean fossils preserved as adpressions have been collected. These are assigned to *Svalbardia*, suggesting that the Givetian *Callixylon* from Belgium corresponded to archaeopterids with a *Svalbardia* type of leaves. In both localities, *Svalbardia* is found in association with the

cladoxyloids *Wattieza* and *Pseudosporochnus* (Stockmans, 1968; Berry, 2008). Archaeopterids and cladoxyloids also co-occur at the outcrop where the *Callixylon* specimen described here was collected: cladoxyloid specimens preserved as adpressions and as pyrite petrifications were also found there (work in progress at Liege University). All the fossils at those Belgian localities are presumably allochthonous. Other Givetian archaeopteridalean remains (*Archaeopteris* and *Svalbardia*) from New York State are listed by Retallack and Huang (2011). Additional evidence of Givetian archaeopterids includes petrified axes of *Actinoxylon* from New York State (Matten, 1974), compressed specimens of *Svalbardia* from Scotland (Chaloner, 1972), southeastern Altay (Gutak et al., 2011), and Spitsbergen where they occur together with permineralized axes of *Actinopodium* (Høeg, 1942; Schweitzer, 1999). All this information indicates that the transition between the arborescent cladoxyloid forests and the archaeopterid forests occurred during Givetian times, and that both types of vegetation presumably coexisted during several million years.

The Givetian occurrences of Archaeopteridales are plotted in Fig. 2. They are currently situated on the Laurussia palaeocontinent. Most Frasnian occurrences of Archaeopteridales are also provided (Meyer-Berthaud et al., 2004, and references therein; Hammond and Berry, 2005; Guo and Wang, 2011) in order to emphasize the spread of those plants during early Late Devonian times. Even though it might be an artifact due to a regional bias in the progymnosperm macrofossil record because of the lack of available localities on Gondwana, the configuration illustrated in Fig. 2 is suggestive of a center of early radiation of Archaeopteridales roughly located on Laurussia.

6. Conclusion

The mid to late Givetian *Callixylon* sp. from Ronquières represents one of the earliest occurrences of the genus. It is assigned to the "*trifilievii*

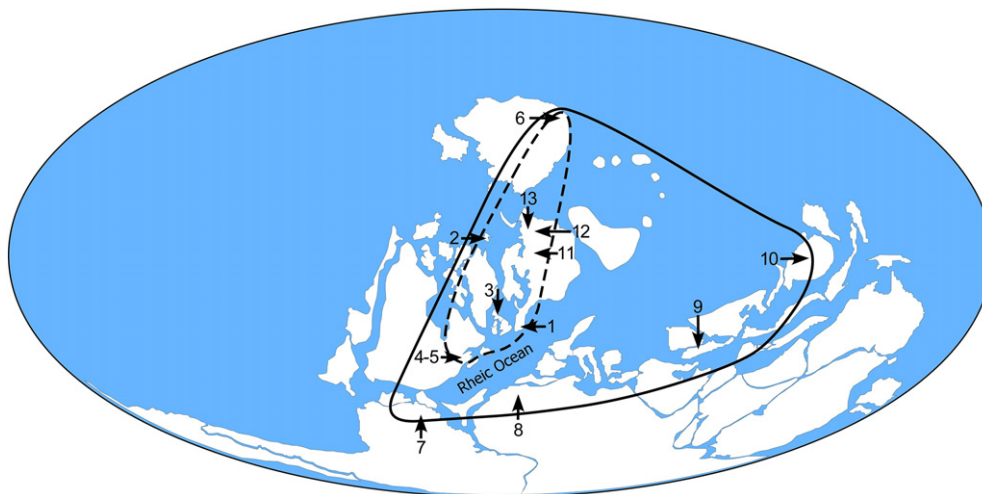


Fig. 2. Givetian (1–6) and Frasnian (5–13) occurrences of Archaeopteridales. Area limited by a dotted line: Givetian distribution of Archaeopteridales; area limited by full line: Frasnian distribution.

1. Belgium: *Svalbardia*, *Callixylon* (Marcelle, 1953; Stockmans, 1968).
 2. Spitsbergen: *Svalbardia*, *Actinopodium* (Høeg, 1942; Schweitzer, 1999).
 3. Scotland: *Svalbardia* (Chaloner, 1972).
 4. New York: *Actinoxylon* (Matten, 1974); stump cast of *Archaeopteris* (Mintz et al., 2010).
 5. New York: *C. trifilievii*, *C. petryi*, *C. erianum*, *C. bristolense*, *Svalbardia*, *Archaeopteris* (references in Lemoigne et al., 1983; Beck and Wight, 1988; Orlova and Jurina, 2011).
 6. Southeastern Altay: *Svalbardia*, *Archaeopteris* (Gutak et al., 2011).
 7. North West Venezuela, Campo Chico formation: *Archaeopteris* (Hammond and Berry, 2005).
 8. Morocco, Anti-atlas: *C. henkei* (Meyer-Berthaud et al., 2004).
 9. China, Xinjiang: *C. clevelandensis* (Chitaley and Cai, 2001).
 10. China, Xinjiang: *Archaeopteris* (Cai, 1981; Hao and Mei, 1987; Guo and Wang, 2011).
 11. Russia, Andonia mountain: *Archaeopteris* (Snigirevskaya and Snigirevsky, 2001).
 12. Kazakhstan: *C. kazakhstanum* (Lepekhina, 1963; Orlova and Jurina, 2011).
 13. Russia, North Timan: *C. trifilievii* (Zalessky, 1911; Orlova and Jurina, 2011).
- Modified from Scotese (2002).

group” circumscribed by Orlova and Jurina (2011). The discovery of this 12–15 cm wide *Callixylon* trunk at Ronquières confirms that the establishment of the tree habit in the lignophyte lineage occurred during Middle Devonian times. The coexistence at the locality of arborescent cladoxyloids and of *Callixylon* remains also suggests that the early steps of the major floristic turnover between cladoxyloids-populated and lignophyte-dominated forests were already perceptible during Givetian times, at least 15 million years before the world-wide dominance of *Archaeopteris* at the end of the Devonian Period.

Acknowledgments

The authors sincerely thank Marcela Mezzatesta-Giraldo and Joel Laval for their help in the preparation of the specimen. PG is a F.R.S.-FNRS Research Associate. AMAP (Botany and Computational Plant Architecture) is a joint research unit which associates CIRAD (UMR51), CNRS (UMR5120), INRA (UMR931), IRD (R123), and Montpellier 2 University (UM27); <http://amap.cirad.fr/>. This work is partly funded by the French National Agency for Research, project ANR No. 2010 BLAN 607 02.

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