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To cite this version:

Bertrand Laloux, Anne-Laure Decombeix. New Pitus and Eristophyton-type woods from the Tournaisian of Queensland, Australia: taxonomic, biogeographic, and palaeoclimatic implications. Comptes Rendus. Palevol, 2022, 21 (42), pp.927-938. 10.5852/cr-palevol2022v21a42 . hal-03895728

comptes rendus
palevol

2022 • 21 • 42

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art. 21 (42) — Published on 12 December 2022
www.cr-palevol.fr

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Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

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ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

New *Pitus* and *Eristophyton*-type woods from the Tournaisian of Queensland, Australia: taxonomic, biogeographic, and palaeoclimatic implications

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Submitted on 3 December 2020 | Accepted on 4 October 2021 | Published on 12 December 2022

urn:lsid:zoobank.org:pub:F6F772EB-F527-470A-9469-201EA9199E17

Laloux B. & Decombeix A.-L. 2022. — New *Pitus* and *Eristophyton*-type woods from the Tournaisian of Queensland, Australia: taxonomic, biogeographic, and palaeoclimatic implications. *Comptes Rendus Palevol* 21 (42): 927-938. https://doi.org/10.5852/cr-palevol2022v21a42

ABSTRACT

The fossil record of arborescent lignophytes shows an increasing anatomical diversity during the Tournaisian (360-347 Mya), suggesting a morpho-anatomical diversification following the extinction of the progymnosperm *Archaeopteris* Dawson, 1871 at the Devonian-Carboniferous boundary. This view has been partly constructed on recent investigations of Early Carboniferous deposits in eastern Australia. In this paper, we describe new silicified wood remains from the Tournaisian of the Burdekin Basin, northeastern Queensland, Australia, that are anatomically close to the genera *Pitus* Zalessky, 1911 and *Eristophyton* Gordon, 1935. While uncertain, the taxonomic affinities of these wood remains have several implications for future studies of Early Carboniferous arborescent lignophytes. First, the taxonomy of *Eristophyton* and *Pitus* has become increasingly problematic as reports of fossil wood assigned to these genera have extended beyond Laurussia. Second, Eastern Gondwanan and Laurussian floras display a convergent pattern of diversification from the Devonian, with the probable presence of a diversity of lignophyte trees in the Early Carboniferous. Third, convergence between Laurussia and Australia with respect to wood anatomy and discrete growth rings may be consistent with past suggestions of a monsoonal circulation during the Early Carboniferous.

KEY WORDS
Early Carboniferous,
Gondwana,
trees,
lignophytes,
palaeoecology,
palaeogeography.

RÉSUMÉ

Nouveaux bois de type Pitus *et* Eristophyton *provenant du Tournaisien du Queensland, Australie : implications taxonomiques, biogéographiques et paléoclimatiques.*

Le registre fossile des lignophytes arborescentes témoigne d'une diversité anatomique grandissante au cours du Tournaisien (360-347 Ma), ce qui suggère un renouvellement morpho-anatomique à la suite de l'extinction de la progymnoperme *Archaeopteris* Dawson, 1871 à la limite Dévonien-Carbonifère. Cette vision s'est partiellement construite sur de récentes investigations dans des dépôts est-australiens du Carbonifère inférieur. Dans cet article, nous décrivons des restes de troncs silicifiés retrouvés dans le Tournaisien du bassin de Burdekin, nord-est du Queensland, Australie, dont l'anatomie se rapproche des genres *Pitus* Gordon, 1935 et *Eristophyton* Zalessky, 1911. Bien qu'incertaines, les affinités anatomiques de ces restes de bois ont différentes implications pour les études futures portant sur les lignophytes arborescentes. Premièrement, la taxonomie des genres *Pitus* et *Eristophyton* apparait de plus en plus problématique à mesure que le registre fossile s'étend au-delà de la Laurussia. Deuxièmement, les flores de la Laurussia et du Gondwana oriental présentent un scénario de diversification convergent dès le Dévonien, probablement en présence d'une diversité de lignophytes arborescentes au cours du Carbonifère inférieur. Troisièmement, la convergence entre ces deux régions tant au niveau de l'anatomie du bois qu'au niveau de cernes de croissance discrets s'accorderait avec de précédentes suggestions d'une circulation de mousson au cours du Carbonifère inférieur.

MOTS CLÉS
Carbonifère inférieur,
Gondwana,
arbres,
lignophytes,
paléogéographie.

INTRODUCTION

The Early Carboniferous (360-323 Mya) is a key period for the evolution of the arborescent lignophytes (progymnosperms and seed plants) that saw a significant morpho-anatomical diversification of vegetative structures in the group (Galtier & Meyer-Berthaud 2006; Hilton & Bateman 2006; Decombeix *et al.* 2011a, 2015). This diversification followed the extinction around the Devonian-Carboniferous boundary of the progymnosperm tree *Archaeopteris* Dawson, 1871 (Dawson 1871), the first known lignophyte to reach the tree habit and a major component of Late Devonian (380-360 Mya) floras worldwide (Meyer-Berthaud *et al.* 1997, 2004, 2008, 2013; Berry *et al.* 2000; Fairon-Demaret *et al.* 2000; Guo & Wang 2009, 2011; Orlova & Jurina 2011; Decombeix *et al.* 2011a; Tanrattana *et al.* 2018). Although the extinction of *Archaeopteris* appears to be coeval with a substantial biotic reorganization around the Hangenberg Event (Streel *et al.* 2000; House 2002; Sallan & Coates 2010; Kaiser *et al.* 2016), it has not been possible to detect a net reduction in plant macrofossil diversity at the Devonian-Carboniferous boundary (Streel *et al.* 2000; McElwain & Punyasena 2007; Cascales-Miñana & Cleal 2014).

Traditionally, the Early Carboniferous lignophyte trees were thought to have diversified only after the Late Tournaisian (353-347 Mya), with the extinction of *Archaeopteris* being followed by a period devoid of lignophyte trees (Behrensmeyer *et al.* 1992). Recently, however, a more transitional scenario has been proposed, based on the facts that:

– lignophyte trees distinct from *Archaeopteris* are present and already diversified in the Middle Tournaisian (Decombeix *et al.* 2005, 2006, 2011a, 2019);

– some of these taxa might have been present during the latest Devonian (Matten *et al.* 1980; Prestianni *et al.* 2010);

– most Early Carboniferous lignophyte trees are found in taphonomic conditions suggesting the colonization of well-drained "uplands", possibly disturbed by volcanism and/or fire (Scott & Galtier 1996; Falcon-Lang 2000b; Meyer-Berthaud *et al.* 2003; Prestianni *et al.* 2010; Decombeix *et al.* 2011a, b).

In this context, Decombeix and collaborators hypothesized the existence of non-archaeopteridalean lignophyte trees before the Devonian-Carboniferous boundary (Decombeix *et al.* 2011a). A climatic amelioration (Raymond 1985; DiMichele *et al.* 2006) could have enabled their diversification in the Early Carboniferous (Galtier & Meyer-Berthaud 2006; Decombeix *et al.* 2011a).

Permineralized plant remains from Early Carboniferous basins of Queensland, Australia, support this hypothesis. Arborescent lignophytes were probably already diversified in northeastern Gondwana during the Middle Tournaisian, as attested by the presence in this region of *Dameria* Decombeix *et al.*, 2011 and *Protopitys* Goeppert, 1850 (Goeppert 1850), and at least one new taxon with a *Pitus*-like wood (Decombeix *et al.* 2011b; Decombeix 2013). Interestingly, at least one of these genera (*Protopitys*) is also found in Laurussia at that time, which strengthens the idea of a pre-Middle Tournaisian origin for some of the arborescent lignophytes that diversified after the extinction of *Archaeopteris*.

In the present paper, we describe the anatomy of additional Tournaisian silicified woods collected in the Burdekin Basin, northeastern Queensland, Australia. Comparison with previously described arborescent lignophytes indicates that they are anatomically close to the Laurussian genera *Eristophyton* Zalessky, 1911 and *Pitus* Gordon, 1935 but likely represent new taxa. We then review the promising perspectives and challenges raised by these Australian specimens in terms of taxonomy, paleophytogeography, and palaeoclimatology.

MATERIAL AND METHODS

The four specimens described in this study are silicified decorticated trunk remains. They were collected in July 2008 at Mount Saint Michael, near Dotswood, in the Burderkin Basin, northeastern Queensland, Australia (19°37'S, 146°17'E). This locality was previously described by Hueber & Galtier (2002) and Decombeix *et al.* (2011b). It is located 50 km north of Charters Towers and about 60 km southwest of Townsville. The area includes Middle Devonian to Permian volcanic deposits (Mawson & Talent 1997; Talent *et al.* 2002; Decombeix *et al.* 2011b). The silicified specimens were found rafted in Cenozoid alluvial sediments, below Devonian-Carboniferous deposits dated from conodonts: Myrtlevale and Julia Formation for the Famennian, Hardwick Formation and Percy Creek Volcanics for the Tournaisian, and Carboniferous-Permian rhyolites (Mawson & Talent 1997). Although the stratigraphic origin of the specimens could not be directly assessed, the occurrence of similar fossil wood preserved in volcanoclastic sediments in the Tournaisian formations above the collection site indicates that the Tournaisian is the most plausible one (Hueber & Galtier 2002; Decombeix *et al.* 2011b).

The four specimens were prepared as classical thin sections in the transverse, tangential, and radial planes (Hass & Rowe 1999). Observation and photography were conducted using a Sony XCD-U100CR digital camera attached to an Olympus SZX12 stereomicroscope and an Olympus BX51 compound microscope. Images were captured using Archimed imaging software (Microvision Instruments, Evry, France). When necessary, the multifocus tool included in Archimed was used to provide a better image. Measurements were carried out using ImageJ software (U.S. National Institutes of Health, Bethesda MD, United States). Unless stated otherwise in the text, all average values and percentages are based on a minimum of 50 measurements. Images were processed using Photoshop (Adobe Systems, San Jose CA, United States). The specimens and corresponding slides are deposited in the AMAP Research Unit, Collections de Paléobotanique, Université de Montpellier, under accession numbers MSM08-14 (six slides), MSM08-20 (six slides), MSM08-171 (five slides), and MSM08-172 (eight slides).

DESCRIPTIONS

Two of the specimens, MSM08-171 and MSM08-172, have part of their pith and primary vascular system preserved. The other two, MSM08-14 and MSM08-20, are only composed of secondary xylem.

MSM08-171

This specimen is 3 cm long and 5.3 × 4 cm in diameter. Part of the central pith is preserved and its radius is estimated to be 1.1 cm, surrounded by 2.2 to 3.6 cm of wood (Fig. 1A, B). The pith shows variations in opacity but no conspicuous structures such as sclerotic nests or medullary strands (Fig. 1A-D).

Primary xylem and lateral organs

Parenchyma cells in the pith are 105-174 µm with irregular shapes. Three types of cells can be distinguished:

- dark and thick cells, interpreted as secretory cells;
- brown cells with thick walls;
- light cells with thin walls (e.g. Fig. 1C).

In tangential section, pith cells are arranged in vertical to oblique files (Fig. 1D). Because only part of the stele's circumference is preserved only a few primary xylem strands have been observed. They range 90-115 µm in diameter (n = 5) (Fig. 1C, E). Primary xylem cells range 14-52 µm (n = 33) and the endarch vs mesarch maturation is not clear. The strands are typically not in contact with the secondary xylem but are separated by a few parenchyma cells and located 360-610 µm from the wood (Fig. 1C: right arrow, E). One strand in contact with the secondary xylem (Fig. 1C: left arrow) could represent a future departing trace to a lateral organ. The pith-secondary xylem outline is irregular, due to the presence of slightly dilated cells in the medullary rays (Fig. 1A, C). Two departing vascular traces to lateral organs were observed, one on a transverse section that is 490 µm in diameter and one on a longitudinal section that is 325-360 µm.

Secondary xylem

The wood is composed of rays and tracheids. The later are polygonal to almost circular in transverse section (Fig. 1F). Their tangential diameter ranges 10-67 µm (average 35 µm) and the radial diameter 13-64 µm (average 41 µm). Rays separate 1-10 files of tracheids in transverse section. While there are some false rings, no true growth ring boundary was recognized.

In tangential section (Fig. 1G, H), 90% of the rays are biseriate, the others uniseriate. They are 1-42 cells high (average eight cells). About 60% are 1-5 cells high and 24% are 7-10 high. Ray cells have a width of 6-38 µm (average 17 µm) and a height of 20-55 (average 35 µm). No pitting is visible on the tangential wall of the tracheids. Ray density is about 19 rays/mm^2.

In radial section, the wall of the tracheids bears bordered pits that are uniformly distributed in alternate rows (Fig. 1I). Most cells (85%) have two rows of pits, others have three. The pits are hexagonal to circular and 9-19 µm (average 14 µm) in diameter. Pit apertures are oval, oblique to horizontal. Ray cell length is 38-315 µm (average 152 µm). Very locally a few cross field pits are visible (Fig. 1J). They are araucarioid, oval oblique with oval apertures. Their maximum diameter is 10-15 µm (n = 8).

MSM08-172

This specimen is about 3 cm long and 6 × 6 cm wide. In transverse section it displays a 3 cm wide pith with conspicuous sclerotic nests, surrounded by a small amount of wood showing faint growth ring boundaries (Fig. 2A, I).

Stele and leaf traces

The pith is composed of parenchyma cells that are 86 × 164 µm in diameter and contains 13 to 16 conspicuous sclerotic nests (Fig. 2A-E). The later are composed of cells that have thicker

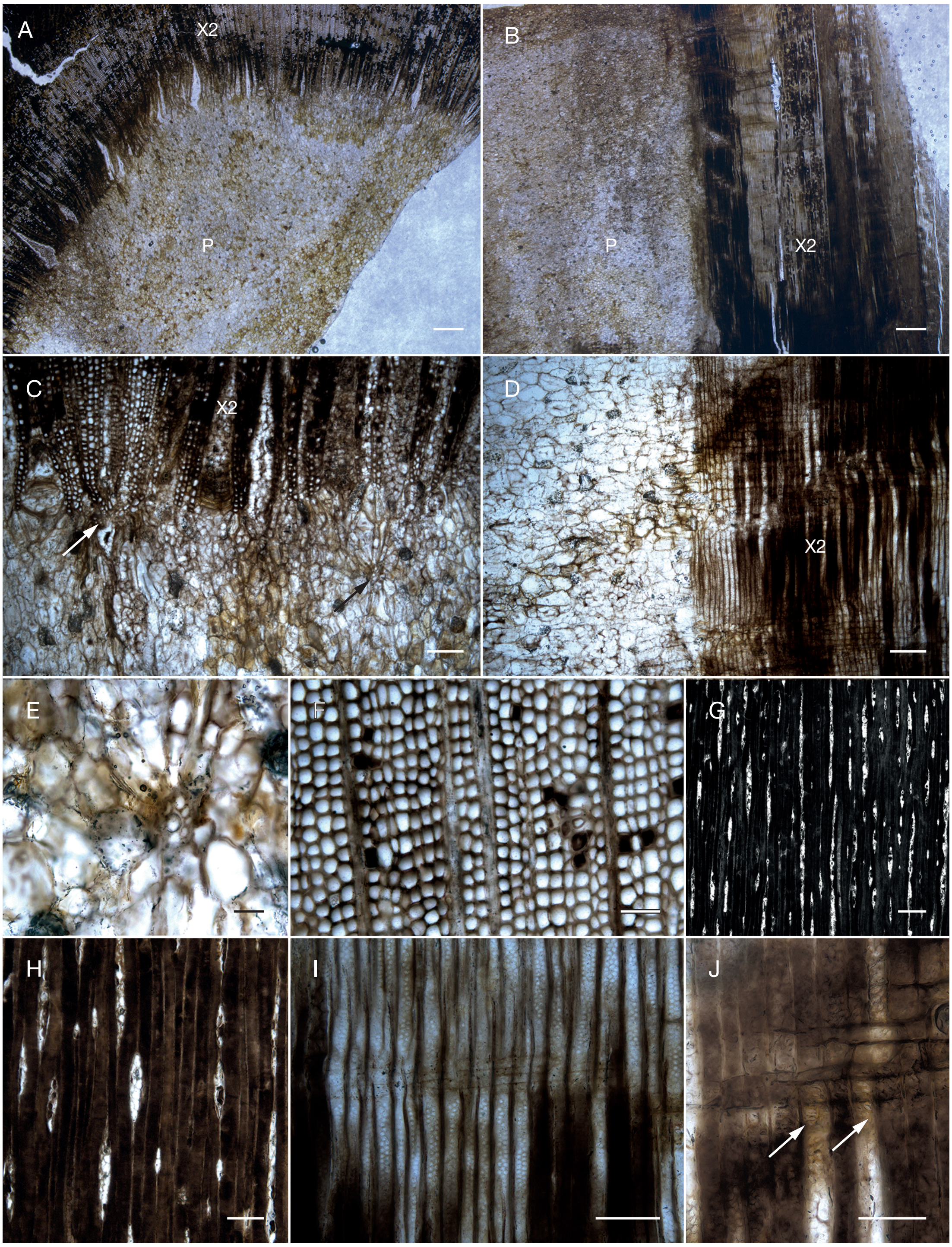

Fig. 1. — MSM08-171: **A**, general view of the specimen in transverse section showing the wide pith (P) and inner part of the secondary xylem (X2), slide MSM08-171-CT1; **B**, general view of the specimen in radial section. Slide MSM08-171-CLR3; **C**, detail of the pith periphery in transverse section with two small primary xylem strands (arrowheads), slide MSM08-171-CT1; **D**, detail of the pith periphery in radial section, slide MSM08-171-CLR3; **E**, small primary xylem strand, slide MSM08-171-CT1; **F**, secondary xylem with biseriate rays in transverse section, slide MSM08-171-CT1; **G**, tangential section of the wood, slide MSM08-171-CLT2; **H,** close up of poorly preserved uni and biseriate rays in tangential section, slide MSM08-171-CLT2; **I**, radial section of the secondary xylem showing biseriate bordered pits, slide MSM08-171-CLR3; **J**, cross-field pitting, slide MSM08-171-CLR3. Abbreviations: **P**, pith; **X2**, secondary xylem. Scale bars: A, B: 1 mm; C, D, G: 250 µm; E, J: 50 µm; F, H, I: 100 µm.

walls, are smaller, darker, and with a more circular outline than the parenchyma cells (Fig. 2C-E). Only a few primary xylem strands have been observed in detail due to the poor preservation. Their diameter range 68-119 µm (n = 8) and they are composed of cells that are 9-32 µm (average 20 µm, n = 31) (Fig. 2F, G). Three of them have a mesarch maturation, while it is less clear in the others. Some are separated from the secondary xylem by a distance of 103-580 µm (e.g. Fig. 2F),

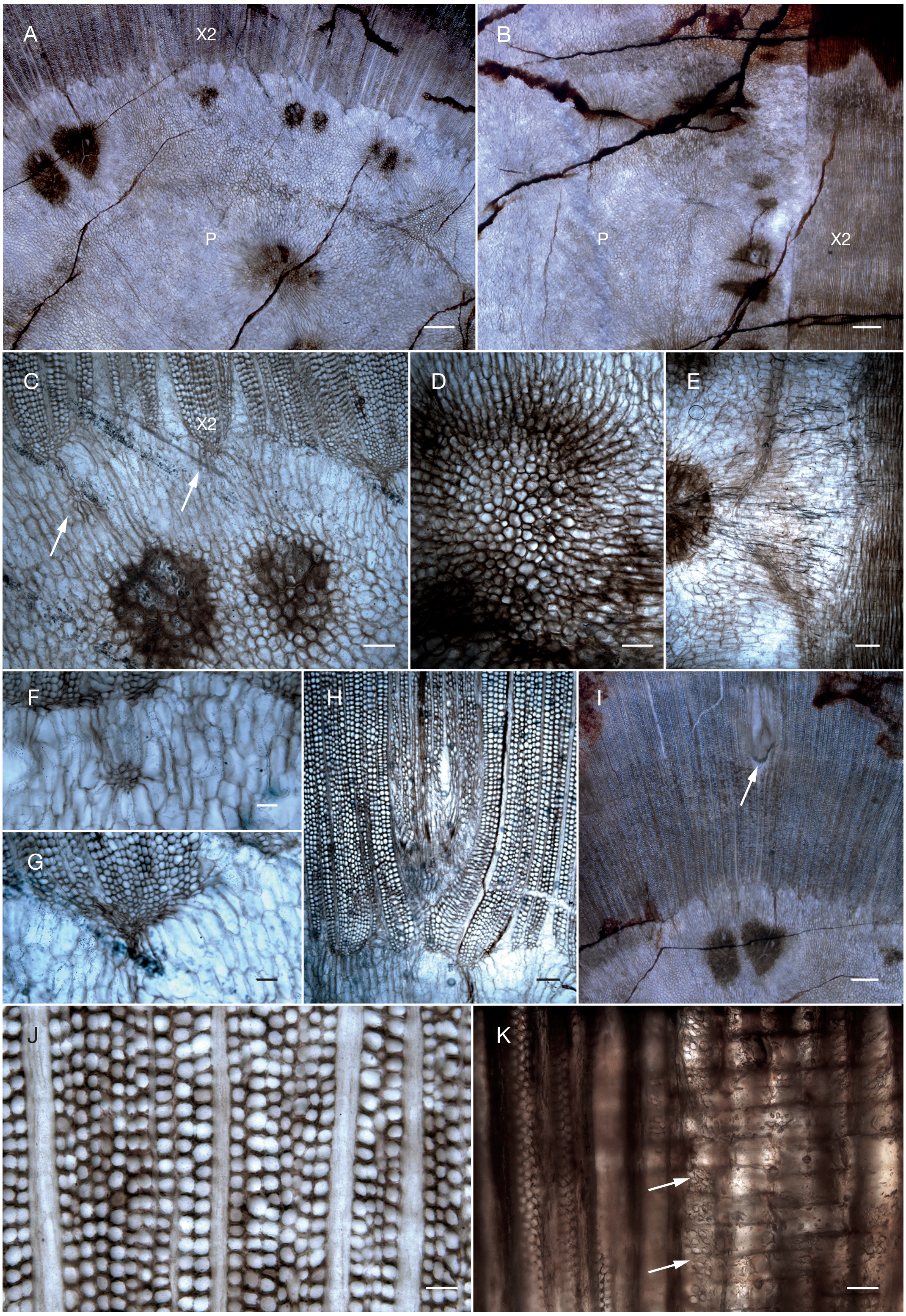

FIG. 2. — MSM08-172: **A**, general view of the specimen in transverse section showing the pith (P) with sclerotic nests and the inner part of the secondary xylem (X2), slide MSM08-172-CT1; **B**, general view of the specimen in radial section, slide MSM08-172-CLR1; **C**, detail of the pith periphery in transverse section with two sclerotic nests and two small primary xylem strands (**arrowheads**), slide MSM08-172-CT1; **D**, detail of a sclerotic nest in transverse section, slide MSM08-172-CT1; **E**, detail of the pith periphery in radial section, slide MSM08-172-CLR1; **F**, small primary xylem strand immersed in the pith, slide MSM08-172-CT1; **G**, small primary xylem strand in contact with the secondary xylem, slide MSM08-172-CT1; **H,** departing vascular trace to a lateral organ, slide MSM08-172-CT1; **I**, small vascular trace to a lateral organ crossing the secondary xylem (**arrowhead**), slide MSM08-172-CT1; **J**, secondary xylem with bi and triseriate rays in transverse section, slide MSM08-172-CT1; **K**, radial section of the secondary xylem showing the multiseriate bordered pits and cross-field pitting (**arrowheads**), slide MSM08-172-CLR1. Scale bars: A, B, I : 1 mm ; C, D, E, H: 250 µm ; F, G, J: 100 µm ; K: 50 µm.

while others are in contact with it (Fig. 2G). Medullary rays are less conspicuous than in the previous specimen and so the pith-wood boundary has a more regular outline (Fig. 2A). Three vascular traces to lateral organs were observed in transverse section. Two of them are still very close to the stele (e.g. Fig. 2H). There is no primary xylem strand facing them, but one can be seen lying on the side close to the departing trace. The trace is 605 × 700 µm and surrounded by secondary xylem. A third trace can be seen within the secondary xylem (Fig. 2I), beyond a faint growth ring boundary.

Secondary xylem

In transverse section, the tracheids are more or less rectangular. Their tangential diameter is 17-95 µm (average 43 µm) and their radial diameter 24-58 µm (average 39 µm). Rays separate 2-25 files of tracheids (Fig. 2J). Two growth ring boundaries are visible; the rings are respectively 1.6 cm and 0.8 cm in thickness. Rays are one to four cells wide, with most of them (70%) being triseriate (Fig. 2J). Ray cells are 7-34 µm (average 17 µm) wide, 33-230 µm long (average 78 µm) and 28-59 µm high (average 43 µm). The radial wall of tracheids bears crowded alternate bordered pits that are hexagonal to circular and 9-19 µm (average 14 µm) in diameter (Fig. 2K). Pit apertures are elliptical to circular. About two thirds of the tracheids have two rows of pits, the others have three. A few cross-field pits were observed, they are about 10 µm wide and are oval and oblique.

MSM08-14

The specimen is 4 cm long and 8 × 10 cm in diameter. Only secondary xylem is preserved. Tracheids are often distorted. They have a rectangular to irregular polygonal shape in cross section (Fig. 3A, B). Their tangential diameter ranges 12-63 µm (average 33 µm) and their radial diameter 23-107 µm (average 50 µm). Rays separate two to 13 files of tracheids. Two growth rings are visible (e.g. Fig. 3A); they are 1.4 and 0.5 cm in thickness. Rays are one to three cells wide (Fig. 3B, C), with 52% being biseriate. They are 2-41 cells high (average 11 cell), with over 60% being 2-10 cells high (Fig. 3C). Ray cells are 10-55 µm wide (average 28 µm) and 12-52 µm high (average 33 µm) (Fig. 3C). Ray density is about 9 rays/mm^2 Hexagonal to circular alternate bordered pits occur on the radial wall of tracheids (Fig. 3E, F). About 90% have two rows of pits, the others having either one or three rows. Radial pits are 10-21 µm in diameter (average 15 µm). Their apertures are oval, of various sizes, and oblique to horizontal. Ray cells are 58-311 long in radial section (average 152 µm). A few small and crowded cross-field pits were observed (Fig. 3F arrowhead).

MSM08-20

This specimen is 8 cm long and 1.1 × 2.3 cm in diameter. It is composed only of secondary xylem. Some false rings are present. Tracheids are polygonal to almost circular in cross section. Their tangential diameter 36-87 µm (average 58 µm) and their radial diameter 26-94 µm (average 56 µm). Rays separate 2-13 files of tracheids in cross section (Fig. 3G). Because of the poor preservation only the biggest/largest rays were distinguishable in tangential section. They are 6-35 cells high (average 16 cells) (Fig. 3H) and 70% are triseriate, the others being biseriate (Fig. 3G). Ray cells are 18-44 µm wide (average 28 µm) and 13-41 µm high (average 27 µm). Radial tracheid pitting consists of alternate rows of crowded bordered pits, typically triseriate (Fig. 3I). Pits are 8-19 µm in diameter (average 12 µm) and have an oval aperture that is oblique or horizontal. Ray cells are 26-113 µm long (average 59 µm). No cross-field were observed.

DISCUSSION

Comparison of the specimens with previously described Early Carboniferous lignophyte trees

We based our anatomical comparisons with previously described Early Carboniferous arborescent lignophytes on the taxonomically significant features reviewed by Galtier & Meyer-Berthaud (2006). We concluded that:

– most of these morphospecies can be directly excluded from our study, except *Eristophyton* and *Pitus*;

– specimens MSM08-14, 20 and 172 display *Eristophyton*-like wood, but each in an unusual combination;

– the stele of specimen MSM08-172 has many typical characters of *Eristophyton*;

– specimen MSM08-171 displays a *Pitus*-like pith with an original set of wood characters.

Several taxonomically significant characters are absent in the four specimens described here, excluding affinities with some Early Carboniferous arborescent lignophytes (Galtier & Meyer-Berthaud 2006, and references therein). Our specimens are devoid of tracheids in the pith, which contrasts with *Bilignea* Scott, 1924, *Megaloxylon* Mapes, 1985, and *Stanwoodia* Galtier & Scott, 1991 (Galtier & Meyer-Berthaud 2006). It lacks “intramedullary” primary vascular strands like in *Archaeopitys* Scott & Jeffrey, 1914 (Galtier & Meyer-Berthaud 2006). We found no double nor even more complex vascular traces to the leaves, as reported in, e.g., *Cauloxylon* Cribbs, 1939, *Megalomyelon* Cribbs, 1940, *Pycnoxylon* Cribbs, 1938, or *Faironia* Decombeix *et al.*, 2006 (Decombeix *et al.* 2006; Galtier & Meyer-Berthaud 2006). The secondary xylem does not display the short and mainly uniseriate rays found in *Araucarites* Goeppert & Stenzel, 1988, *Endoxylon* Lacey, 1953, *Stanwoodia* (Galtier & Meyer-Berthaud 2006), *Dameria* (Decombeix *et al.* 2011b), *Protopitys* (Decombeix *et al.* 2015), or *Tovoxylon* (Orlova 2009). The absence of scalariform pits on the secondary xylem tracheids is not consistent with the arborescent progymnosperm *Protopitys* (Decombeix *et al.* 2015). Characters described in specimens MSM08-14, 20 and 172 are incompatible with *Aporoxylon* (Galtier & Meyer-Berthaud 2006; Decombeix *et al.* 2007).

Specimens MSM08-14, MSM08-20 and MSM08-171 show a wood comprising small to medium-sized parenchymatous rays (up to 50 cells high and four cells wide) and narrow tracheids with multiseriate circular bordered pits.

Fig. 3. — **A**, **F**, MSM08 14; **G**, **I**, MSM08-20: **A**, secondary xylem of MSM08-14 in transverse section showing bi to triseriate rays and a possible growth ring boundary, slide MSM08-14-CT1; **B**, detail of secondary xylem of MSM08-14 in transverse section, slide MSM08-14-CT1; **C**, tangential section showing bi to triseriate rays, slide MSM08-14-CLT2; **D**, general view of the wood in radial section, slide MSM08-14-CLR1; **E**, detail of radial section showing the bi to triseriate bordered pits, slide MSM08-14-CLR1; **F**, detail of radial section with radial pits and cross-field pitting (**arrowhead**), slide MSM08-14-CLR1; **G**, secondary xylem of MSM08-20 in transverse section showing one uniseriate and two biseriate rays, slide MSM08-20-CT2; **H**, general view in radial section showing ray height, slide MSM08-20-CLR3; **I**, detail of radial section with poorly preserved multiseriate bordered pits, slide MSM08-20-CLR3. Scale bars: A, D, H: 250 µm; B, C, G: 100 µm; E, F, I: 50 µm.

All these wood characters are compatible with *Eristophyton* (Lacey 1953; Decombeix *et al.* 2007), but each specimen shows an unusual combination. Unfortunately, the primary vascular tissues are not preserved for specimens MSM08-14 and MSM08-20. Thus, the assignment of these specimens to *Eristophyton* is uncertain.

The stele of specimen MSM08-172 shows a parenchymatous pith with sclerotic nests, numerous mesarch primary xylem strands typically separated from the secondary xylem but coming in contact occasionally, and a small leaf trace undivided proximally. These features are found in *Eristophyton beinertianum* Scott, 1902 and *E. waltonii* Galtier & Scott, 1990 (Lacey 1953; Decombeix *et al.* 2007). Integrating both stele and wood characters, specimen MSM08-172 could be tentatively diagnosed as *Eristophyton* sp.

Specimen MSM08-171 pith lacks intramedullary tracheids. However, it displays a pith with parenchymatous cells of three kinds, i.e. thin-walled ground parenchyma, secretory, and storage cells, revealing a strong similarity with *Pitus* (Gordon 1935). Interestingly, specimen MSM08-171 has a dense wood with straight and short rays (Zalessky 1911), which contrasts with large rays and multiseriate pits classically attributed to *Pitus* (Gordon 1935). Considered as a whole, specimen MSM08-171 could therefore be tentatively diagnosed as cf. *Pitus*.

TAXONOMIC UNCERTAINTIES

Among the Early Carboniferous arborescent lignophytes, *Pitus* and *Eristophyton* are the two genera that combine the largest geographical distribution, stratigraphic distribution, and number of species (Decombeix *et al.* 2007, 2011b). Several difficulties have appeared in the last thirty years as both genera were constructed based on remains from western and central Europe a century ago (Gordon 1935; Decombeix *et al.* 2007, 2008).

In Laurussia, except *Eristophyton feistii* from Montagne noire, France (Decombeix *et al.* 2008), the latest described specimens attributed to *Eristophyton* could not be determined at the species level due to lack of preservation of the primary tissues (Galtier *et al.* 1998; Orlova 2010; Decombeix *et al.* 2017). In Pitus woods from Ireland and eastern Canada, taxonomic difficulties appear increasingly obvious when ontogenetic variability is considered (Falcon-Lang & Galtier 2010; Falcon-Lang *et al.* 2010; Henderson & Falcon-Lang 2011). In Australia, several Early Carboniferous woods have been assigned to *Pitus* primarily on the basis of multiseriate rays and multiseriate radial pitting on the tracheids but their primary vascular structures are unknown (Walkom 1928; Morris 1985). Recently investigated specimens with a *Pitus*-like wood from Queensland revealed some differences with this genus when the bark or leaf trace emissions could be investigated in detail (Decombeix *et al.* 2007, 2011b, 2013, 2019). In North Africa, only two Early Carboniferous arborescent lignophytes remains have been reported:

– a Late Tournaisian axis from the Khenig Formation, Algeria, showing an original set of characters somewhat close to *Eristophyton* and *Pitus* but with a very distinct mode of leaf trace production and representing a new genus, *Ahnetia* (Decombeix & Galtier 2017);

– an Early Serpukhovian wood from Tazekka, Morocco, close to *Eristophyton* but devoid of preserved primary vascular tissues (Chalot-Prat & Galtier 1989).

Besides, between-specimen comparisons from incomplete sets of characters impedes the assumption of similar habit, i.e., the Australian specimens could represent large trees but also smaller woody shrubs.

In the light of these studies and in order to avoid further confusion, we chose not to assign the new specimens described here to *Pitus* and *Eristophyton*. We strongly feel that revisions of *Pitus* and *Eristophyton* are needed before assigning any new fossils to these genera, especially those with no preserved primary tissues. Several taxa exhibiting ambiguous affinities with *Eristophyton* and *Pitus*, such as *Aporoxylon*, *Cauloxylon*, *Paleoxylon*, or *Picnoxylon* (Galtier & Meyer-Berthaud 2006), should also be included in these revisions.

PHYTOGEOGRAPHY

In spite of a substantial geographical gap (Decombeix *et al.* 2011a; Xue *et al.* 2015), the Australian floras known from Devonian (McCoy 1876; Dun 1897; Cascales-Miñana & Meyer-Berthaud 2015; Meyer-Berthaud *et al.* 2015, 2021a, b; Evreïnoff *et al.* 2017; Champreux *et al.* 2020) and Early Carboniferous localities (Sahni 1932; Hueber & Galtier 2002; Galtier *et al.* 2007; Decombeix *et al.* 2011a, 2019) suggest an apparent synchronism of diversification at the generic level with contemporaneous Laurussian floras. In contrast, fossil seeds from the Early Carboniferous of western Gondwana tentatively indicate a delayed diversification in that region (Prestianni *et al.* 2015). Morpho-anatomical connections between stem, foliage, and reproductive structures would allow undisputable identification of the taxa present and a better understanding of the degree of endemism between the different regions (Galtier & Meyer-Berthaud 2006; Decombeix *et al.* 2007).

IMPLICATIONS FOR PALEOENVIRONMENTAL AND PALEOCLIMATIC RECONSTRUCTIONS

The presence of putatively large woody trees comparable to *Pitus* and *Eristophyton* in Eastern Gondwana does not support previous "megabiased" reconstructions (Behrensmeyer *et al.* 2000) toward rather uniform wetland landscapes, based on a fossil record dominated taxonomically by lycopsids and taphonomically by compressions-impressions (Gould 1975; Morris 1985; Pant 1996; Anderson *et al.* 1999; Evreïnoff *et al.* 2017). The discovery in the Tournaisian deposits of Australia of hydrasperman seed ferns and zygopterid tree ferns in the same region would rather indicate complex succession in volcanically disturbed habitats, as suggested from the study of different British sites (Galtier *et al.* 1993; Scott & Galtier 1996; Falcon-Lang 2000b; Phillips & Galtier 2005; DiMichele *et al.* 2006).

Falcon-Lang (1999a, b) interpreted the presence of subtle growth rings in the lignophyte woods from the Viséan of the British Isles as indicating a global monsoonal circulation during the Early Carboniferous (Parrish 1990). This hypothesis is founded on two analogies regarding:

– the phenology between the Carboniferous British taxa and extant Australian conifers (negative correlation between growth ring markedness and foliar persistence; Falcon-Lang 2000a);

– an apparent symmetry between continental mass distribution during the Early Carboniferous and today (Falcon-Lang 1999b).

Because the important annual reversal of low and high pressure areas is influenced by the difference in heat capacity between oceans and the immense continental surface of Asia (Parrish 1993), it could be predicted from the surface of the supercontinent Gondwana that general air and oceanic circulation during the Early Carboniferous may have generated a similar monsoonal circulation (Kutzbach & Gallimore 1989; Parrish 1993; Falcon-Lang 1999b; Wang *et al.* 2005).

In our study, this hypothesis may be supported by:

– the faint rings observed in our specimens, suggesting a tropical climate with alternating wet season and dry season (Creber & Chaloner 1984; Falcon-Lang 2005a, b);

– the possible taxonomic affinities and/or convergent evolution with Laurussian woods.

We expect that the increasing wood fossil record from Gondwana, as well as further lithological, paleogeographical and paleontological evidence (Wang *et al.* 2005; Fielding *et al.* 2008; Fang *et al.* 2018), will enhance new opportunities to test the hypothesis of a global moonsonal climate regime in northeastern Gondwana during the Early Carboniferous.

CONCLUSION

In this paper, we described silicified fossil woods from the Tournaisian of the Burdekin Basin, northeastern Queensland, Australia, that are anatomically close to *Eristophyton* and *Pitus*. As part of recent investigations of Early Carboniferous deposits of this region, these descriptions are consistent with previous evidence for:

– an increasing complexity of plant communities, including forests probably adapted to well-drained and/or volcanically disturbed uplands;

– an apparently synchronous diversification of Eastern Gondwanan and Laurussian floras, in spite of a substantial geographic gap;

– a rapid diversification of the arborescent lignophytes during the Tournaisian.

For future work, we suggest a focus on the following directions:

– extending the geographic distribution of the fossil record of the arborescent lignophytes to other regions of Gondwana;

– a revision of *Pitus* and *Eristophyton*, both defined in Laurussia, as well as potentially related morphotaxa;

– testing the hypothesis of a monsoonal circulation in eastern Gondwana during the Early Carboniferous.

Acknowledgements
We are grateful to the editor, Cyrille Prestianni, and the anonymous reviewer for their insightful suggestions to improve our manuscript. This work was conducted during B. Laloux's master project in 2015 at UMR AMAP and Biodiversity Research Centre, Earth and Life Institute, UCLouvain (co-supervised by A.-L. Decombeix and R. Wesselingh). Technical support for the observation of the specimens was kindly provided by the Unité des Eaux et Forêts (Earth and Life Institute, UCLouvain). We thank J. Talent, B. Meyer-Berthaud and J. Galtier for their help in the field and during this project. AMAP (botAny and Modelling of Plant Architecture and vegetation) is a joint research unit which associates Montpellier University (UM), CNRS (UMR 5120), CIRAD (UMR 51), INRAe (UMR 931) and IRD (R123).

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Submitted on 3 December 2020;
accepted on 4 October 2021;
published on 12 December 2022.