

Early Jurassic silicified woods from Carapace Nunatak, South Victoria Land, Antarctica

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<https://zoobank.org/5213691A-5C25-4E71-A74E-FF2CF82C2C16>

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Academic editor: Alexander Schmidt ♦ Received 23 February 2023 ♦ Accepted 5 May 2023 ♦ Published 19 May 2023

Abstract

The Jurassic vegetation of Antarctica remains poorly known and, while there have been several reports of large fossil trees from that time period across the continent, detailed anatomical studies of their wood are extremely scarce. Here we describe new silicified woods of Early Jurassic (probably Toarcian) age from Carapace Nunatak, South Victoria Land. The genera *Agathoxylon* and *Brachyoxylon* are formally recognized for the first time in the Jurassic of Antarctica. The preservation of the woods is imperfect, which is likely explained by the presence in some of the specimens of fungi, whose anatomical structures are described in detail. Combined with previous reports of pollen, leaves, and cones from South and North Victoria Land, these new specimens support the presence of several conifer families in the Early Jurassic floras of the region.

Key Words

Agathoxylon, Araucariaceae, *Brachyoxylon*, conifers, fossil fungi, gymnosperms, Hirmeriellaceae, Mesozoic

Introduction

Abundant fossils indicate that Antarctica was vegetated for most of its history. Permineralized trunks, some of them preserved *in situ*, demonstrate the establishment of forests on the continent from the Permian and their persistence in some areas until the late Miocene (e.g. Cantrill and Poole 2012). Dwarf trees (*Notofagus*) are also documented in the Transantarctic Mountains during the Pliocene (Francis and Hill 1996). Detailed studies of permineralized wood conducted since the early 1900s have provided valuable information on the taxonomic affinities but also on the growth and physiology of these trees (e.g. Kraüsel 1962; Francis 1986; Falcon-Lang and Cantrill 2001; Taylor and Ryberg 2007; Gulbranson et al. 2014; Miller et al. 2016). However, most of these studies have focused on Permian, Triassic, and Cretaceous specimens. Fossil wood and tree trunks are also known from

Jurassic deposits of Antarctica, but they have received comparatively less attention and only a small number of specimens have been described to date. The first detailed description was that of Early Jurassic trunks from the Mesa Range region, in Northern Victoria Land, by Jefferson et al. (1983). The trees were engulfed in lava and are preserved in growth position. They reach 1 meter in diameter. Based on their secondary xylem anatomy, they were compared to the morphogenus *Protocupressinoxylon*, a nomenclatural synonym of *Protobrachyoxylon* Holden, 1913 (Philippe 1993), which might belong to the Hirmeriellaceae (or Cheirolepidiaceae, see Paclt 2011; Doweld 2020 for discussion), i.e. an extinct family of conifers. In the Antarctic Peninsula, del Valle et al. (1997) reported the presence of fossil stems and trunks, some of them up to 50 cm in diameter, within volcanoclastic rocks of the Early to Late Jurassic age from Brebbia Nunatak and Ramírez Nunatak. However, they did not

provide an anatomical description of the specimens. Late Jurassic – early Cretaceous anatomically preserved wood fragments were also reported from Hope Bay (Torres et al. 2000). Large woody axes are also known to occur in Middle Jurassic cherts at Storm Peak, in the Central Transantarctic Mountains (Kellogg and Taylor 2004), but again these specimens have never been formally described. In Northern Victoria Land, new Early Jurassic fossil woods have been collected recently and are under study (Bomfleur et al. 2011; Harper et al. 2012). In Southern Victoria Land, Garland et al. (2007) described an Early Jurassic coniferous stump preserved in a basalt flow at Coombs Hills. The specimen is about 40 cm in diameter and was compared to the Podocarpaceae.

Carapace Nunatak, located about 10 km from Coombs Hills, is known for its well-preserved Early Jurassic fossils plants and animals occurring in lacustrine deposits intercalated between lava flows of the Kirkpatrick Basalt Formation. Various arthropods are present in the deposits, with an abundance of conchostracans and other crustaceans indicating a shallow and/or ephemeral freshwater environment (Ballance and Watters 1971; Ball et al. 1979; Shen 1994). Palynofloras include a relatively high count of *Classopollis* pollen (Bomfleur et al. 2014), which has been related to the Hirmeriellaceae (e.g., Taylor et al. 2009; Thévenard et al. 2022). Plant macrofossils identified to date correspond to fern leaves and rhizomes, isolated ovules, cycadophyte leaves, and conifer foliage and cones. Among the conifers, Townrow (1967a) listed the presence of several fossils of putative podocarpaceous affinities: shoots and seed cones of *Nothodacrium warrenii* and the pollen cone *Masculostrobos warrenii*. He also noted the presence of *Brachyphyllum*- and *Pagiophyllum*-like shoots (Townrow 1967b). More recently, two new pollen cones have been described from Carapace Nunatak: *Classostrobos elliotii*, which has been assigned to the Hirmeriellaceae (Hieger et al. 2015), and *Chimaerostrobos minutus*, with characters reminiscent of both Voltziales and Araucariaceae (Atkinson et al. 2018). Here we describe fossil woods collected at the locality during the austral summer 2014–2015. We discuss their affinities and how they fit within our knowledge of conifer diversity in Antarctica during the Early Jurassic.

Materials and methods

Locality and age of the specimens

The fossil woods described in this study were collected from the moraine located on the E-NE side of Carapace Nunatak, southern Victoria Land, Central Transantarctic Mountains, Antarctica (76°53'S, 159°25'E, elevation 2150 m, Convoy Range Quadrangle; Fig. 1). Two formations outcrop at Carapace Nunatak, the Carapace Sandstone Fm and the overlaying Kirkpatrick Basalt Fm. Radiometric dating and palynological analyses indicate an Early Jurassic age for both formations, with an early Toarcian (ca. 180 Ma) age for the Kirkpatrick Basalt

Fm (Elliot 2013 and references therein; Bomfleur et al. 2014). The woods occurred on the moraine together with blocks of silicified chert containing plant material from the lacustrine beds of the Kirkpatrick Basalt Fm. Based on the matrix surrounding some of the specimens, their location on the moraine, and their co-occurrence with blocks of silicified chert, we consider the specimens to be derived from the Kirkpatrick Basalt Fm and thus to be Toarcian in age.

Specimen preparation and imaging

Of the 10 putative wood specimens collected, four (#270, 271, 272, 274) were preserved well enough to observe all the characters important for wood taxonomy. Specimens 273, 275, 276 and 279 are more distorted and, while qualitative characters can be observed, obtaining a significant number of measurements proved more difficult. Finally, specimen 277 is insufficiently preserved to allow its anatomy description and taxonomic analysis. Specimen 278 lacked anatomical preservation: it consisted of a wood impression on a piece of sedimentary rock containing small fusains.

The specimens are heavily silicified and were prepared as thin-sections in the transverse, tangential, and radial planes following the classical technique (Hass and Rowe 1999). Images were taken in reflected light using ArchiMed software (Microvision Instruments, Evry, France) with Sony XCD-U100CR digital cameras attached to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound microscope, except for Fig. 4A–C, which were taken with a Keyence VHX 7000 digital microscope and the associated imaging software. Plates were composed with Adobe Photoshop version 21.0.1 (Adobe Systems, San José, California, USA). Transformations made in Photoshop included cropping, rotation, and adjustment of exposure, contrast, when needed.

Statistical analyses

Statistical analyses were performed to describe ray height and its variability across the specimens, to better distinguish between wood morphospecies. They were performed using Rstudio software (version 4.0.3; R Core Team 2020, Boston, USA). For each specimen, thirty ray heights were measured on tangential or radial sections. Data normality was tested by a Shapiro-Wilk test and homoscedasticity, with a Levene test (package *car*, version 3.0-10, Fox and Weisberg 2019). Since normality and variance homogeneity hypotheses were most of the time not respected, only non-parametric tests were used to compare ray heights. Differences between specimens were evaluated using Mann-Whitney-Wilcoxon. Kruskal-Wallis and Multiple Comparison Kruskal-Wallis tests (package *agricolae*, version 1.3-3, de Mendiburu 2020) were used to compare specimens (Fig. 5). For the different tests, a significance level, α , of 0.05 was chosen.

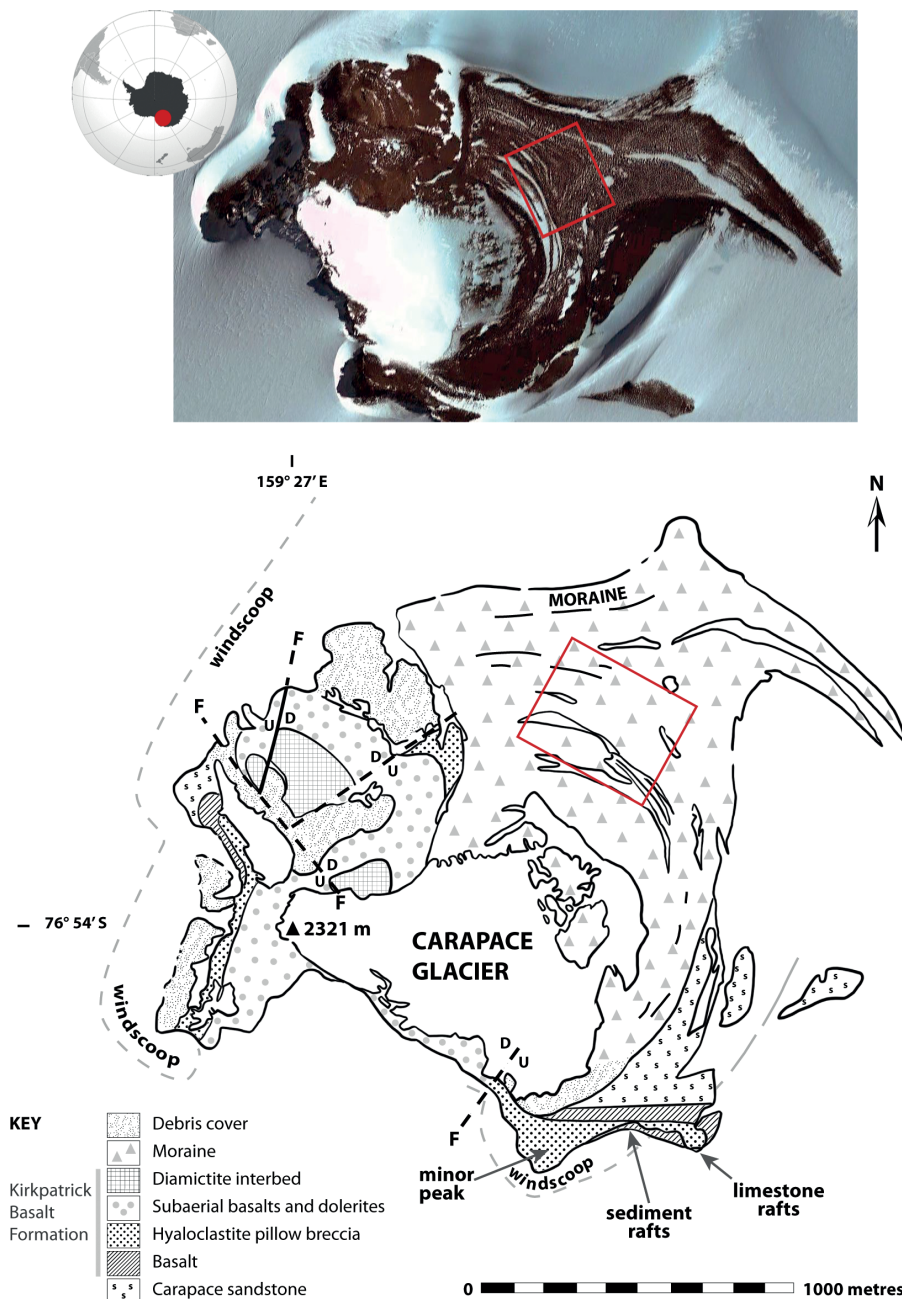


Figure 1. Location of the fossil wood locality. Aerial view of Carapace Nunatak (Source: Google Earth); the red square represents the area where the specimens were collected. Geological map modified after Bradshaw (1987). F: fault, U: up, D: down.

Results

With the exception of specimen 271, which corresponds to a branch about 7 x 5 cm in diameter (Fig. 2A), all the specimens represent pieces of wood with no indication of their origin within the plant. All wood specimens are composed of tracheids and parenchymatous rays. They share a number of characters but differ by ray height and type of radial pitting.

Anatomical characters shared by all samples

Specimen 271 shows several growth rings boundaries (Fig. 2B, C). In all other specimens, the limited extent

of non-distorted wood prevents the detection of potential growth rings. The woods typically appear distorted and poorly preserved, often with the rays darker, more conspicuous, than the tracheids both in transverse (Fig. 2E, F) and in tangential (Fig. 2G–I) sections. The average diameter of tracheids range 25–30 µm depending on the specimens (Fig. 2D–F). Rays are uniseriate (Fig. 2D–I), rarely partly biseriate, and a few, i.e. up to 10, cells high (Figs 2G–I, 3). They have thin, straight unperforated cell walls and often have a dark brown to black content. In radial section, the end wall is perpendicular to sub-perpendicular to the ray (e.g. Fig. 3). There are rare instances of axial parenchyma with no particular organization. When preserved, cross-field pitting is araucarioid, i.e. pits are mostly cupressoid, often in groups of 3 or more, organized in a relatively

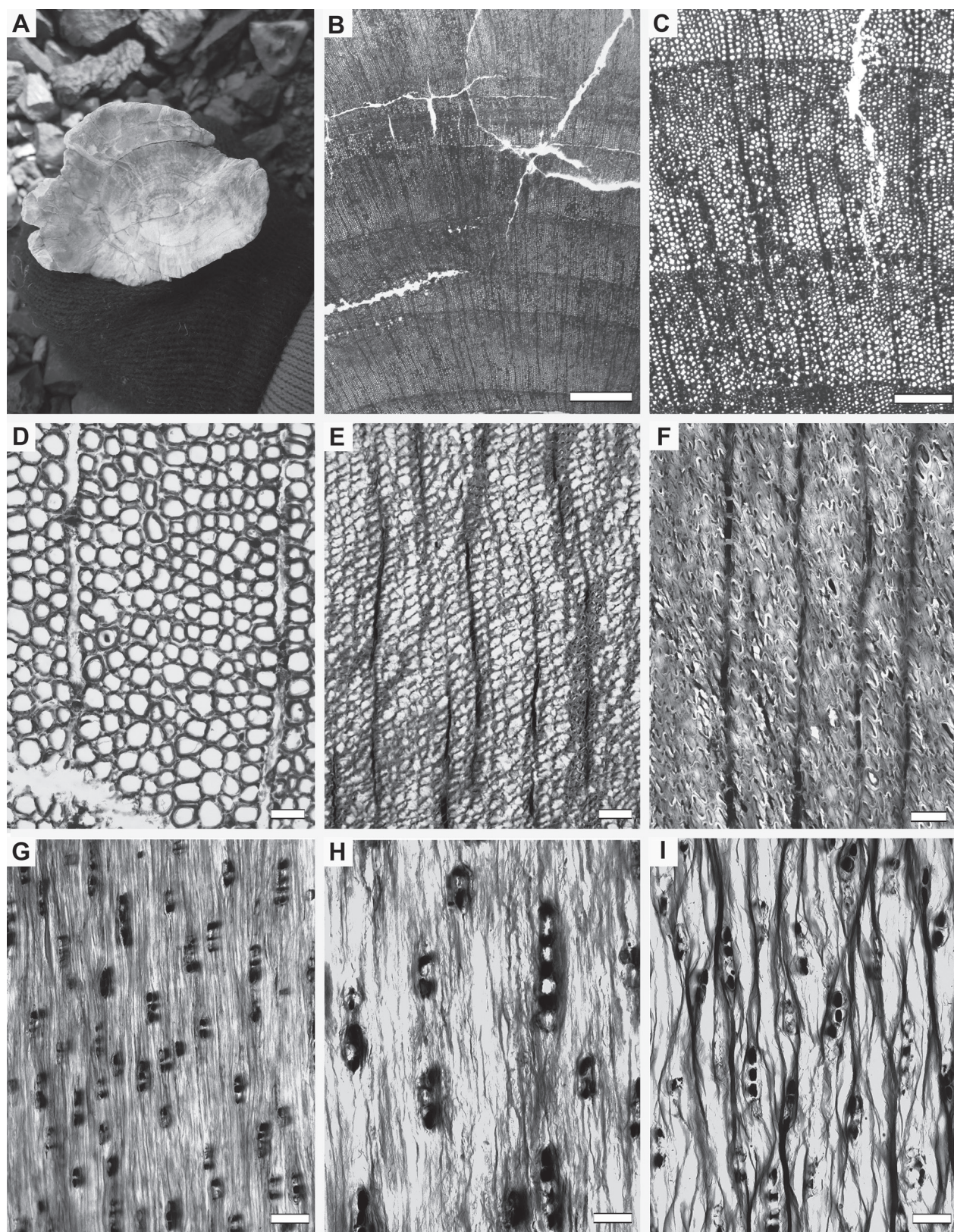


Figure 2. Early Jurassic woods from Carapace Nunatak in transverse and tangential section: **A.** General view of specimen 271 in the field; **B.** Transverse section of the previous specimen showing several growth ring boundaries. Slide 30781; **C.** Detail of two rings with a small amount of late wood. Slide 30781; **D.** Close up of wood anatomy in transverse section showing tracheids and two uniseriate rays. Slide 30781; **E.** Transverse section of specimen 270 showing poorly preserved tracheids and several uniseriate rays. Slide 30775; **F.** Transverse section of specimen 276 showing extremely distorted tracheids and several uniseriate rays. Slide 35934; **G.** General view of specimen 274 in tangential section showing numerous uniseriate and low rays. Slide 35924; **H.** Detail of rays in 274. Slide 35924; **I.** General view of specimen 276 in tangential section showing numerous uniseriate and low rays. Tracheid walls are almost completely degraded. Slide 35931. Scale bars: 2 mm (**B**); 500 μ m (**C**); 50 μ m (**D**, **F**, **H**, **I**); 100 μ m (**E**, **G**).

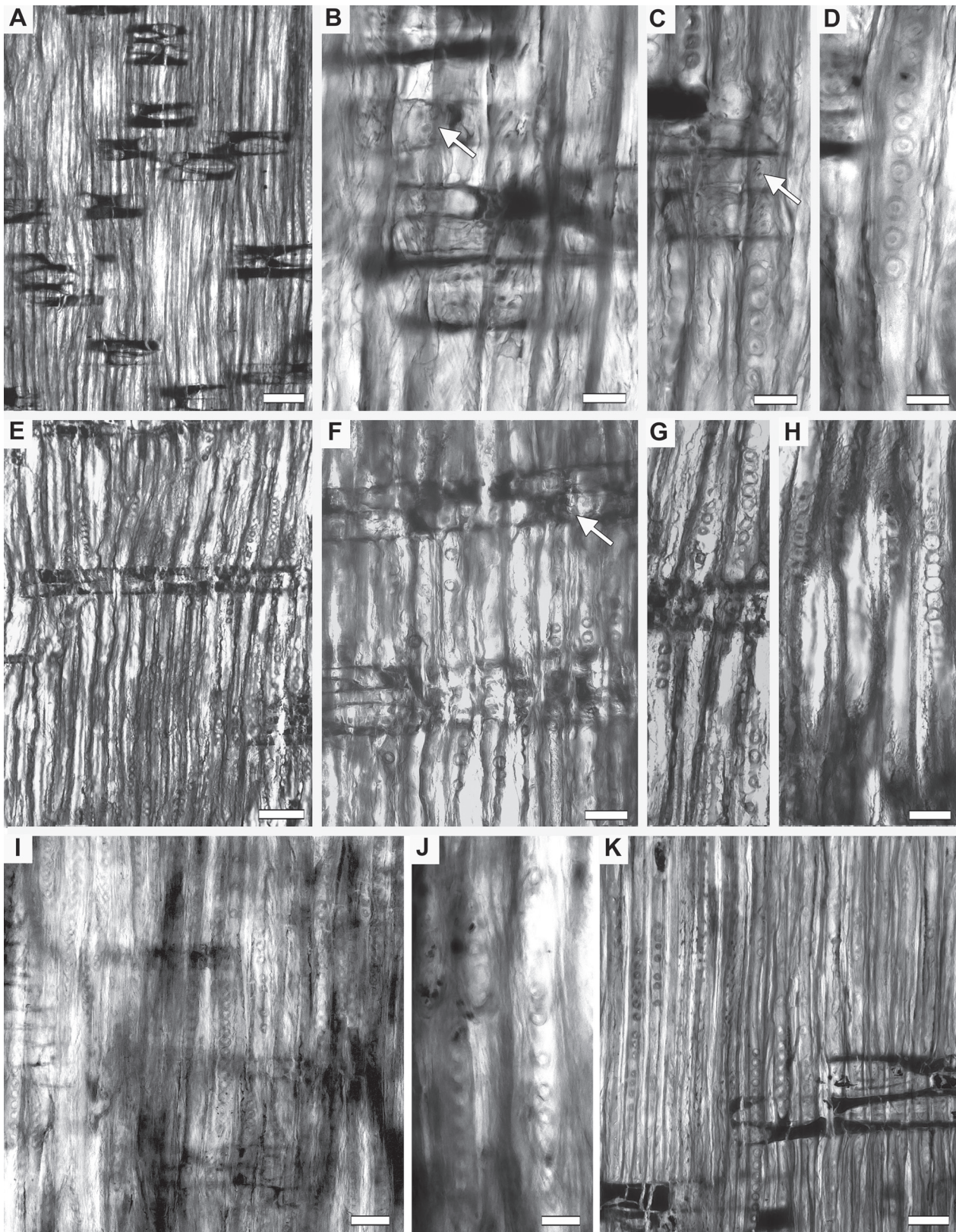


Figure 3. Early Jurassic woods from Carapace Nunatak with mixed pitting in radial section. Specimens 270 (A–D), 271 (E–H), 272 (I–J) and 274 (K). **A.** General view of specimen 270 in radial section showing the low rays. Slide 35913; **B.** Cross-field region in specimen 270. Slide 35913; **C.** Other detail showing the cross-field and relatively crowded radial pitting. Slide 35913; **D.** Detail of a tracheid with abietean pitting. Slide 35913; **E.** General view of specimen 271 in radial section showing the low rays and mixed radial pitting. Slide 30784; **F.** Detail showing the cross-field and radial pitting. Slide 30783; **G.** Detail of E, showing araucarian and abietean radial pitting. Slide 30784; **H.** Detail showing araucarian radial pitting. Slide 30784; **I.** General view of specimen 272 in radial section showing the low rays and mixed radial pitting. Slide 35915; **J.** Detail of abietean pitting. Slide 35915; **K.** General view of specimen 274 in radial section showing the low rays and mixed radial pitting. Slide 35925. Scale bars: 100 μm (A, E); 25 μm (B–D, J); 50 μm (F, H, I, K).

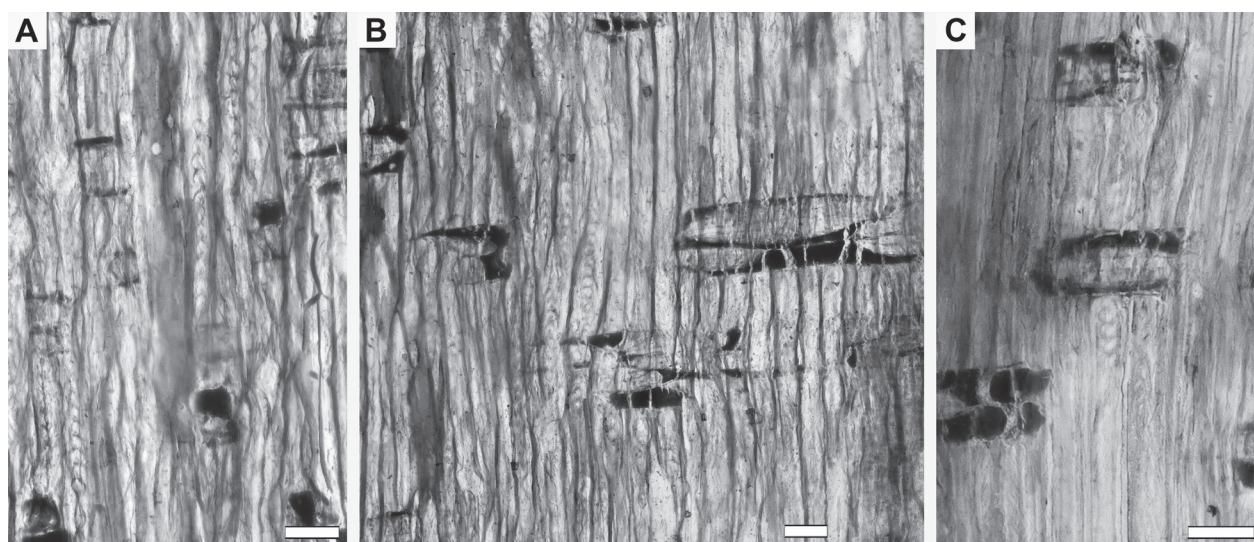


Figure 4. Early Jurassic woods from Carapace Nunatak with only araucarian pitting in radial section. Specimen 276. **A.** Tracheids with araucarian pitting. Slide 35937; **B.** Rays and tracheids with araucarian pitting. Slide 35937; **C.** Rays and tracheids with araucarian pitting. Slide 35938. Scale bars: 50 µm (A–C).

crowded alternate fashion (Fig. 3B, C). Resin canals are absent (e.g. Fig. 2B–F).

Radial pitting

Two major morphotypes of wood can be distinguished based on the pitting on the radial wall of their tracheids:

- n°270, 271, 272, and 274 have mixed pitting, with the presence of both araucarian and abietinean pitting (Fig. 3). The proportion is about 55–60% of araucarian pits on the tracheids where pitting is visible. The distribution of the two types of pitting is not homogeneous through the wood, especially in specimen 270.
- n°273, 275, 276, and probably 279 have araucarian pitting (Fig. 4). Pits appear contiguous in 90% of the cases and are often flattened. When multiseriata, pits are always arranged alternately.

Ray height

Ray height typically ranges 1–10 cells (Figs 2G–I, 3A, F, I, Suppl. material 1). Because the number of cells composing a ray was not easy to assess on all the specimens, comparisons were made using ray height in µm. It ranges 25.5–310.6 µm, with average heights of 61.0–166.6 µm (see Fig. 5). Significant height differences are visible between specimens (Kruskal-Wallis test: chi-squared = 71.148, df = 7, p-value = <0.001; Figs 3, 5A). Ray height is on average higher in specimens with mixed radial pitting than with araucarian radial pitting, with mean heights of 85.5 and 107.2 µm respectively (Wilcoxon test: W = 5758, p-value = <0.001; Fig. 5B).

However, the important across-specimen variability does not enable the use of this anatomical feature to distinguish between the morphogenera (Fig. 5A).

Fungal remains

One of the possible reasons for the poor preservation of the material is that the woods were already partly decayed when they were silicified. This is supported by the presence of abundant fungal remains in some of them (Fig. 6A–N). Direct evidence of fungal remains occurs in highest concentration in the rays and adjacent cells. Fungi consist of fragmented hyphae that are smooth and narrow (2–5 µm in diameter; Fig. 6A) to wider forms (≥6 µm in diameter; Fig. 6I), both types are connected (Fig. 6I) are sparsely septate (arrow in Fig. 6A; black arrow in Fig. 6E). Hyphae frequently produce perpendicular branching at uneven intervals (white arrow in Fig. 6C). Some hyphae are fractured and disarticulated (Fig. 6B; black arrow in Fig. 6C), which is likely a result of preservation. Clamp connections are rare but present (Fig. 6D). Small ellipsoidal (6–8 µm long by 3–5 µm high) to spherical propagules occur terminally (Fig. 6E) or intercalary (Fig. 6F) on hyphae, which can be dark in color (Fig. 6E) to opaque (Fig. 6F). Similar structures do co-occur, or are connected, with fungal mycelia, but it is possible that they may represent preservational artifacts (arrowheads in Fig. 6G) or possible tyloses (Fig. 6H). Like the host wood, fungal mycelia are poorly preserved and degraded (Fig. 6G, I, J₁–J₂, K), which may have happened before burial or during the taphonomic process. Wide hyphae have a rough, crystalline texture (Fig. 6J₁–J₂); it is possible that the thin, smooth hyphae could have been covered in mineral precipitates during

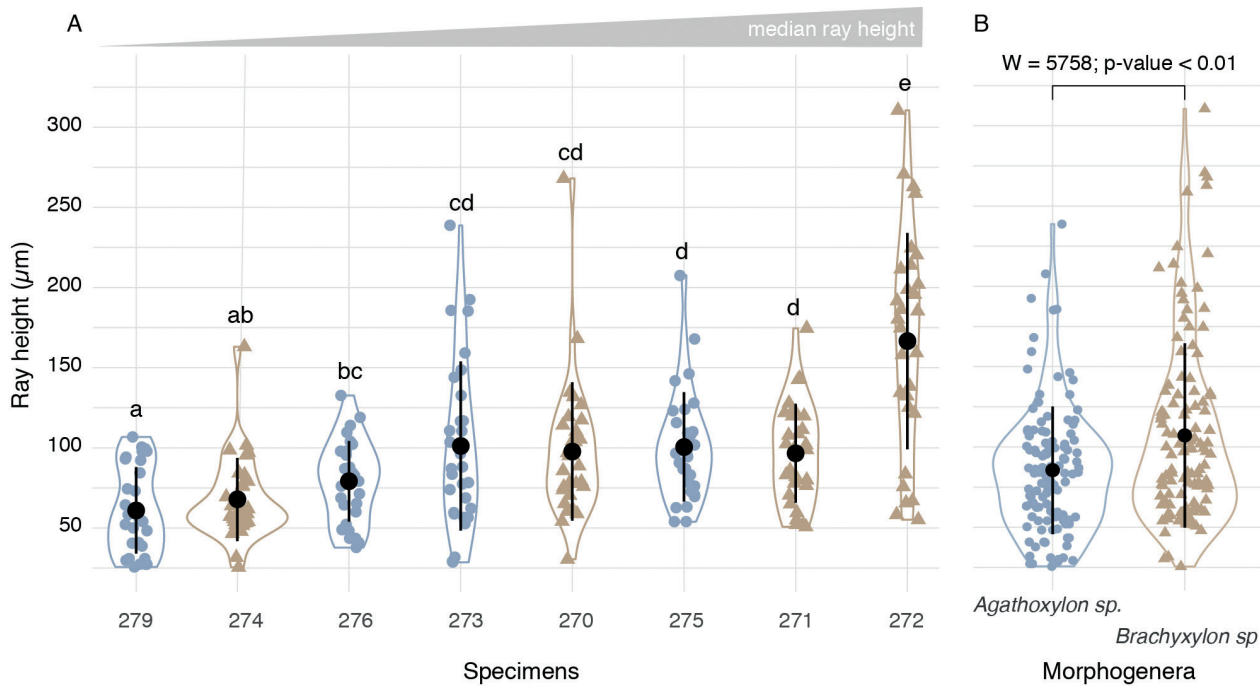


Figure 5. Ray height and pitting type in the specimens from Carapace Nunatak. Ray height across specimens and wood morphogenera (μm). Specimens with mixed (i.e., araucarian and abietinean) and araucarian radial pitting are represented by caffè latte and blue-gray colors respectively. **A.** Size group distinction between specimens based on the Multiple Comparison Kruskal-Wallis test. Groups sharing letters are not characterized by significantly different sizes. Specimens are ordered in ascending order of their median value; **B.** Average ray height within the different wood morphogenera. Significance of the mean ray height was evaluated with a Wilcoxon test. Central black dots and lines indicate means and standard deviation of ray height measurements.

preservation (arrow in Fig. 6J), and ‘wide’ hyphae represent a biomimetic structure. Mycelia occur in multiple orientations in radial and tangential sections and traverse from tracheid to adjacent tracheid via the pits (Fig. 6K, arrows in 6L). Indirect evidence of fungi includes areas in transverse sections of wood that are highly degraded with numerous, and large, erosional notches and cavities (Fig. 6M), which gives lumina a ‘starburst’-like appearance. At higher magnification, erosional troughs are present in all wall layers in adjacent tracheids (Fig. 6N). Although it is impossible to confidently determine the systematic affinity of the fungus (or fungi because there may be multiple species co-occurring within the wood), based on presence of clamp connections, at least one of the fungi is a basidiomycete. The degradational pattern within the wood is similar to decay by some extant soft rot fungi (Schwarze 2017: see figs 52, 54–55, 62–63, 68, 70), which makes the wood soft and spongy, thus, less conducive to preservational processes and making wood anatomical features difficult to discern.

Taxonomic affinities of the woods

Philippe and Bamford (2008) published a key to Mesozoic conifer-like woods that summarizes the diversity known at that time and the characters considered

significant to distinguish the different morphogenera. The new specimens from Carapace Nunatak share the following characters from Philippe and Bamford’s key: (1) all rays uniseriate, except for some local biseriation, (2) radial pits never scalariform, (3) axial parenchyma present or absent, neither particularly associated with the rays nor inflated, and (4) all ray cell walls thin and smooth, unpitted. Although ray height is sometimes used to distinguish taxa, this criterion is not included in the key of Philippe and Bamford (2008) and does not seem to carry additional information in the analysis of our specimens. In addition, since the position within the whole plants of the different wood specimens from Carapace Nunatak is unknown, it is very likely that these variations represent at least in part the normal heterogeneity of wood. Differences in radial pitting on the tracheid walls are taxonomically significant and visible. They are used hereafter to distinguish two types of wood. Because of the small number of specimens and their poor and variable preservation, we choose here to only identify them at the generic level.

Specimens with araucarian pitting on radial wall of tracheids: *Agathoxylon sp.*

Within the group with araucarian pitting specimens, 273, 275, and 276 share the following characters:

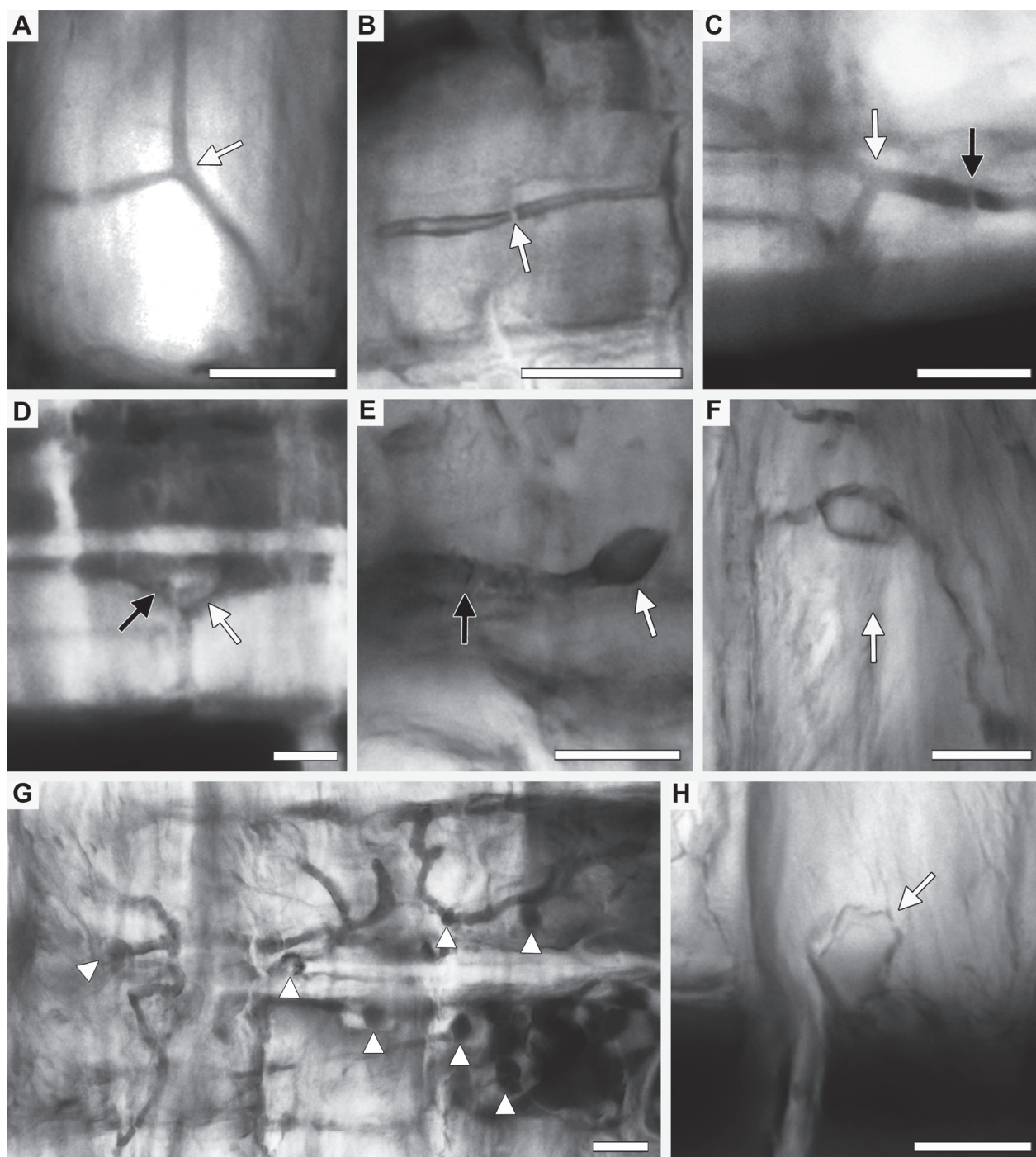


Figure 6. Fungal remains in Early Jurassic woods from Carapace Nunatak. **A.** Perpendicularly branching hyphae with septum (arrow). Slide 30780; **B.** Disarticulated hypha with single fracture. Slide 30780; **C.** Branching hypha (white arrow) with single fracture (black arrow). Slide 35923; **D.** Hypha with clamp connection. Slide 35923; **E.** Septate hypha (black arrow) with terminal propagule (white arrow). Slide 30780; **F.** Intercalary propagule (arrow). Slide 30780; **G.** Multi-branching hyphae with terminal swellings (arrow heads) in rays. Slide 35923; **H.** Ellipsoidal structure, possible tylosis (arrow). Slide 30780. Scale bars: 10 μm (**A–H**).

(1) cross-fields of the araucarian type, i.e. with numerous contiguous unordered cupressoid to taxodioid oculipores, (2) spiral thickening absent, and (3) end wall of ray cells perpendicular or subperpendicular to the ray. They are thus assigned to the genus *Agathoxylon* Hartig, 1848 (Philippe and Bamford 2008; Rößler et al. 2014 and references therein). Specimen 279 also seems to fit this diagnosis but given its poor preservation we assign it to this genus with caution. More than 400 morphospecies

of *Agathoxylon* have been reported, dating from the Carboniferous to the present (Rößler et al. 2014), and *Agathoxylon*-type wood has been associated with various taxa, including cordaites, conifers, and several groups of pteridosperms. Although *Agathoxylon* is known to occur in Gondwana during the Jurassic and in Antarctica during the Cretaceous, it is the first time to the extent of our knowledge that the genus is formally reported from the Jurassic of Antarctica.

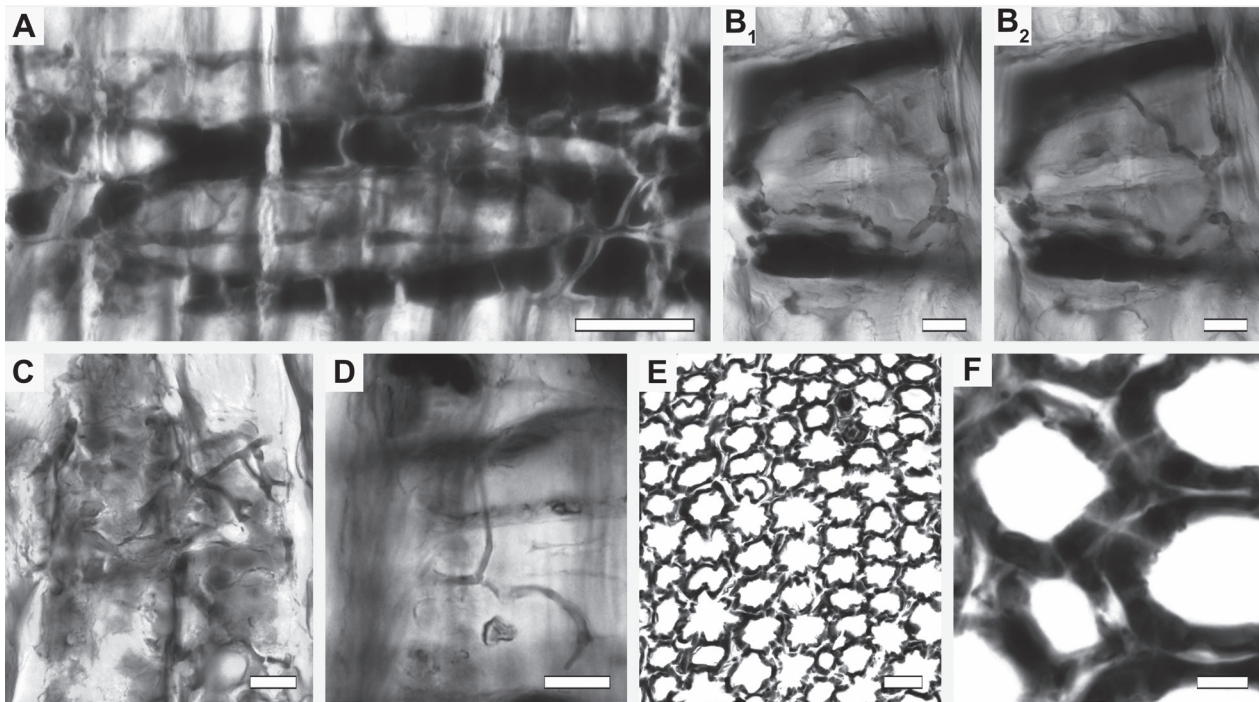


Figure 7. Fungal remains in Early Jurassic woods from Carapace Nunatak. **A.** Wide hypha with branching narrow hyphae (arrow). Slide 274 (radial B1); **B₁**, **B₂**, Multiple focal planes of wide hyphae; note thin structure inside of wide hypha (arrow). Slide 30780; **C.** Degraded hyphae traversing between two adjacent tracheids with abnormal Y-branch (arrow). Slide 30780; **D.** Hypha traversing through pits (arrows). Slide 30780; **E.** Highly degraded tracheids in transverse section. Note starburst pattern in lumina from multiple, and coalescing, erosional cavities. Pattern is similar to extant soft rot fungi. Slide 30781; **F.** Prominent erosional troughs in adjacent tracheids (arrows). Slide 30781. Scale bars: 50 μm (**A**, **E**); 10 μm (**B₁**, **B₂**, **C**, **D**).

Specimens with mixed pitting: *Brachyoxylon* sp.

The three specimens with mixed pitting (araucarian and abietinean; n°270, 271, 272, and 274) share the following characters: (1) in the earlywood oculipores always cupressoid, i.e. with an aperture narrower than one margin, and (2) cross-fields of the araucarian type, i.e. with contiguous unordered and often alternate oculipores. They are thus assigned to the genus *Brachyoxylon* Hollick & Jeffrey, 1909 (Philippe and Bamford 2008). *Brachyoxylon* was originally established for Late Cretaceous woods from the USA (Hollick and Jeffrey 1909). It has since been reported in Jurassic and Cretaceous localities of Europe, Asia, South America and North America (Philippe et al. 2004; Tian et al. 2018; Greppi et al. 2021 and references therein). Kurzawe and Merlotti (2010) also reported *Brachyoxylon* from the Permian of Brazil. *Brachyoxylon* wood has been linked to various conifer families, including Araucariaceae, Cupressaceae, and Hirmeriellaceae. It is, however, more frequently associated with Hirmeriellaceae remains (leaves, *Classopolis* pollen, or *Classopolis* producing cones; e.g. Alvin et al. 1981; Alvin 1982; Machhour and Pons 1992; Limarino et al. 2012; Tian et al. 2018). This is the first report of *Brachyoxylon* from the Jurassic of Antarctica. Like *Agathoxylon*, the genus is known elsewhere in Gondwana during the Jurassic (Philippe et al. 2004; Greppi et al. 2021). In Antarctica, it was only reported previously in Early Cretaceous deposits of the South Shetland Islands (Philippe et al. 1995; Torres et al. 1997).

Discussion

Comparisons with previously described Early Jurassic woods from Antarctica

The woods assigned to *Protocupressinoxylon* (= *Protobrachyoxylon* Holden, 1913 (Philippe 1993)) described by Jefferson et al. (1983) from the Mesa Range region in North Victoria Land have a distinct anatomy from the ones of Carapace Nunatak. A major difference is their cross-field pitting, with 3–6 non-contiguous cupressoid pits vs. crowded pits in the new specimens. Rays are also higher in Jefferson specimens (up to 40 cells) and axial parenchyma is absent while it occurs in some of our specimens.

The stump from Coombs Hills, Southern Victoria Land, reported by Garland et al. (2007) shares numerous characters with the woods from Carapace Nunatak, including uniseriate rays, ray cells that are thin-walled with no pits in horizontal walls, and araucarioid cross-fields with up to 9 crowded cupressoid pits (Garland et al. 2007). Radial pitting in the Coombs Hill stump consists of “mainly non-contiguous” bordered pits that are always uniseriate. Tracheid diameter is very small, 11–15 μm . Rays are slightly higher than in the Carapace Nunatak specimens, with a maximum height of 15 cells with an average height of 66 μm , i.e. 990 μm for an average ray. Garland et al. (2007) compared the stump from Comb Hills to Podocarpaceae but without indicating which character(s) they based this affinity on. Given the lack of data on the

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

We warmly thank the other members of the 2014–2015 G-496 team: Drew Brown, Dave Buchanan, Charles Daghlian, Ignacio Escapa, Erik Gulbranson, Lauren Michel, and Ana Zajivciek for their help in the field. This study would not have been possible without the US Antarctic Program pilots and helo techs who flew us to the capricious place that is Carapace Nunatak, and among them we are especially grateful to Rebecca Voltin (Lyons, OR, USA) who also found one of the first and best-preserved specimens presented in this paper. We thank the anonymous reviewer and Alexander Schmidt for their constructive comments, and editorial handling. This work was partially funded by an award from the US National Science Foundation (#1142495) to Edith L. Taylor (Lawrence, KS, USA), who we thank for her mentorship and support. AMAP (botAny and Modelling of Plant Architecture and vegetation) is a joint research unit that associates Montpellier University, CNRS (UMR 5120), CIRAD (UMR51), INRAe (UMR931) and IRD (UR123). Finally, AT thanks Sandrine Escobar and Morgane Ganault for their help on Fig. 2.

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Supplementary material 1

Table with ray height measurements for the different specimens

Authors: Agathe Toumoulin, Anne-Laure Decombeix, Carla J. Harper, Rudolph Serbet

Data type: table (excel file)

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Link: <https://doi.org/10.3897/fr.26.102570.suppl1>