

Cupressaceous woods in Jurassic geothermal deposits of the Deseado Massif, Patagonia, Argentina with evidence of nurse-log growth strategy

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ABSTRACT

The fossil wood record of Cupressaceae is extensive across the Mesozoic and Cenozoic, with a wide distribution in both hemispheres. However, the affinities of some fossil woods are uncertain due to incomplete descriptions, preservation issues, and anatomical traits of ambiguous interpretation. This study describes the anatomy and discusses the affinities of well-preserved Jurassic silicified woods. Samples were collected from geothermal deposits at the 'Claudia' locality in the Deseado Massif, Santa Cruz Province, Southern Patagonia, Argentina. The material corresponds to pycnoxylic and homoxylic secondary xylem characterized by a distinctive combination of traits, including mixed pitting on tracheids, cupressoid cross-field pits arranged in a cupressoid pattern, and abundant diffuse axial parenchyma. These characteristics are compatible with *Protocupressinoxylon* and suggest affinities with Cupressaceae. Additionally, chert blocks preserving fragments of these woods contain vegetative organs (e.g., leaves, roots) with affinities with this family, supporting the suggested affiliation. The studied woods are assigned to the open nomenclature *Protocupressinoxylon*-type wood, following the IAPT Fossil Committee's recommendations concerning the nomenclature problems of this name, while acknowledging the extensive historical and current use of it. Nurse logs are also recorded based on the presence of several stems and rootlets anchored to some of the studied woods, which expands the fossil record of this growth strategy.

1. Introduction

Cupressaceae s.l. is one of the most widespread conifer families, growing in warm and temperate regions across the world (Page, 1990; Brunsfeld et al., 1994; Gadek et al., 2000; Kusumi et al., 2000; Farjon, 2005; Little, 2006; Schulz and Stützel, 2007; Farjon, 2010; Nunes et al., 2019; Liu et al., 2022). This family comprises 32 genera and more than 130 species that form a monophyletic lineage, including the traditional Cupressaceae sensu stricto and the paraphyletic Taxodiaceae (Bruns-

feld et al., 1994; Gadek et al., 2000; Kusumi et al., 2000; Farjon, 2005; Schulz and Stützel, 2007; Mao et al., 2012; Yang et al., 2012; Atkinson et al., 2014a, 2014b; Nunes et al., 2019; Liu et al., 2022). Based on numerous molecular, morphological, and combined phylogenetic studies, Cupressaceae is divided into seven subfamilies: Cunninghamioideae, Taiwanoideae, Athrotaxidoideae, Sequoioideae, Taxodioideae, Callitroideae, and Cupressoideae (Brunsfield et al., 1994; Tsumura et al., 1995; Stefanović et al., 1998; Gadek et al., 2000; Kusumi et al., 2000; Little, 2006; Farjon, 2010; Atkinson et al., 2014a; Nunes et al., 2019; Liu

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et al., 2022).

The fossil record of Cupressaceae is highly abundant and widely distributed across both hemispheres, extending back to the early Mesozoic (Stockey, 2005; Mao et al., 2012; Leslie et al., 2018). This record primarily consists of isolated organs, with ovulate cones being the most valuable for phylogenetic and systematic studies; however, leaves and woods are more commonly found (Stockey, 2005; Mao et al., 2012; Leslie et al., 2018). The oldest broadly accepted record of Cupressaceae is a whole-plant concept based on impressions and compressions of leafy twigs with attached ovulate cones, pollen cones, and silicified wood, represented by the species *Austrohamia minuta* (Escapa et al., 2008; Rothwell et al., 2012; Bodnar and Escapa, 2016), collected in Chubut Province (Patagonia, Argentina), from rocks interpreted as a lateral equivalent to the Las Leoneras Formation (Lower Jurassic; see Cúneo et al., 2013). Subsequently, the whole-plant concept *Austrohamia asfaltensis*, composed of twigs organically connected to ovulate cones and pollen cones, was described from the Sitio Frenguelli locality within the lower strata of the Cañadón Asfalto Formation (Lower Jurassic; Contreras et al., 2019). Additionally, a Middle Jurassic whole-plant concept based on leafy branches with attached pollen and ovulate cones has been described from the Lower Yima Formation, Yima District, West Henan Province, central China (Yao et al., 1998). However, isolated organs attributed to cupressaceous species have also been reported from older strata. This includes, for instance, leaves, wood, and leafy twigs from the Upper Triassic of France (Lemoigne, 1967) and the Middle and Upper Triassic of Argentina (Bonetti, 1966; Bodnar et al., 2015; Ruiz and Bodnar, 2019).

The Cupressaceae fossil record is broadly congruent with the relationships of basal groups proposed by phylogenetic topologies and the stratigraphic appearance of the different clades (Mao et al., 2012; Leslie et al., 2018; Contreras et al., 2019; Liu et al., 2022). The subfamilies Cunninghamioideae and Taiwanioidae are consistently recovered as early diverging lineages within the family (Gadek et al., 2000; Mao et al., 2012; Leslie et al., 2018; Contreras et al., 2019; Stull et al., 2021; Liu et al., 2022). In this context, the fossil record is concordant with this hypothesis, showing a diverse and widespread occurrence of cunninghamioid and taiwanioid-like conifers during the Jurassic, including *Austrohamia* and other genera of similar morphology, such as *Elatides* Heer spp., *Cunninghamiostrobus* Stöpes et Fujii spp., *Hubbardiostrobus* Atkinson, Rothwell et Stockey, *Hughmillerites* Rothwell, Stockey, Mapes et Hilton, and *Pentakonos* Herrera, Shi, Knopf, Leslie, Ichinnorov, Takahashi, Crane et Herendeen (Harris, 1943, 1953; Yao et al., 1998; Escapa et al., 2008; Rothwell et al., 2012; Atkinson et al., 2014a, 2014b; Shi et al., 2014; Herrera et al., 2017).

Cupressaceous fossil woods are abundant in Mesozoic and Cenozoic deposits (Eckhold, 1922; Kräusel, 1949; Bodnar and Artabe, 2007; Nunes et al., 2019) and has a broad distribution in both the Southern (Bonetti, 1966; Bodnar and Artabe, 2007; Gnaedinger et al., 2013; Ruiz et al., 2017; Nunes et al., 2019; Ruiz and Bodnar, 2019) and the Northern Hemispheres (Eckhold, 1922; Kräusel, 1949; Bodnar and Artabe, 2007; Philippe and Bamford, 2008; Nunes et al., 2019). The affinities of some fossil woods within this family remain uncertain at different systematic levels due to incomplete descriptions, poor preservation, discrepancies in the interpretation of anatomical traits, and ambiguous characters that may support alternative interpretations (Kräusel, 1949; Vaudois and Privé, 1971; Bodnar and Artabe, 2007; Gnaedinger, 2007a; Nunes et al., 2019; Ruiz et al., 2017; Ruiz and Bodnar, 2019; Bodnar et al., 2023).

Although whole-plant hypotheses provide information on several vegetative and reproductive features of the parental plant, isolated organs are by far the most frequent fossil representation for most plant groups (Farjon, 2005; Stockey, 2005; Rothwell et al., 2012; Leslie et al., 2018; Contreras et al., 2019). Therefore, identifying character combinations that allow for unambiguous assignment to systematic groups is essential. In particular, the systematic assignment of fossil woods to different conifer families represents a highly debated topic because

including wood characters in phylogenetic studies is challenging (Olson, 2005; Carlquist, 2012, 2013). Wood traits are highly variable within a single species, and even within specimens, because of ecological, ontogenetic, and habitat differences (Martínez-Cabrera et al., 2012; Carlquist, 2013; Philippe et al., 2019; Wheeler and Baas, 2019; Onyenedum and Pace, 2021). Furthermore, wood features such as the arrangement of axial parenchyma and crossfield pitting pattern, may show a high degree of homoplasy on both extant and extinct species (Olson, 2005; Carlquist, 2012, 2013). Likewise, many wood characters vary on a continuous scale but are usually represented in the literature as discrete variables (e. g., tracheid diameter, cell wall thickness, and ray height; Falcon-Lang, 2005; Olson, 2005; Carlquist, 2013).

Despite these challenges, most of the species within Cupressaceae show a characteristic combination of wood anatomical features, i.e., axial tracheids without helical thickenings, cupressoid or taxodioid cross-field pits, and presence of axial parenchyma, generally with resin contents (Greguss, 1955; Gadek et al., 2000; Román-Jordán et al., 2017; Nunes et al., 2019). Additional traits, such as absence of resin canals and oculipores with a mean diameter of less than 10 µm (Thompson, 1910; Gordon, 1912; Holden, 1913; Belyea, 1919; Peirce, 1937; Greguss, 1955, 1972; Roig, 1992; Pujana et al., 2020), have also been mentioned for several cupressaceous species (Peirce, 1937; Boutelje, 1955; Greguss, 1955; Boureau, 1956; Bonetti, 1966; Vaudois and Privé, 1971; Gadek et al., 2000).

The description and study of fossil woods anatomically preserved in association or connection with organs related to Cupressaceae have the potential to offer valuable insights into the ecological and anatomical evolution of these woods. This is particularly important because, as mentioned above, many features in cupressaceous woods are ambiguous when evaluating affinities (Olson, 2005; Bodnar and Artabe, 2007; Gnaedinger, 2007a, 2007b; Bodnar and Escapa, 2016; Nunes et al., 2019; Bodnar et al., 2023). However, studies that associate well-preserved fossil woods with reproductive or vegetative structures are limited (Harris, 1953; Bodnar and Escapa, 2016).

This study describes the anatomy and discusses the systematic affinities of exceptionally well-preserved silicified woods from Jurassic geothermal deposits at the 'Claudia' locality (Deseado Massif, Patagonia, Argentina), which are in association with vegetative organs attributed to Cupressaceae s.l. (Escapa, personal observation; Molano, 2024). These woods exhibit a distinctive combination of features, which suggests affinities with both basal extant and fossil Cupressaceae genera, offering new insights into the early diversification of the family. Moreover, the presence of anatomically preserved rootlets within some specimens suggests that these woods functioned as nurse logs, expanding the fossil record of this ecological interaction and broadening our understanding of ecological adaptations in Mesozoic Cupressaceae.

2. Geological setting

The samples were collected from hydrothermal cherts at the 'Claudia' locality, from outcrops of the La Matilde Formation, which represents the final stage of the Bahía Laura Complex, in the southern area of the Deseado Massif (See Fig. 1; see also Guido, 2004; Guido and Campbell, 2014). The Deseado Massif is located in the Santa Cruz Province, Southern Patagonia, Argentina. It has an extension of approximately 60,000 km² (Fig. 1). During the Middle to Late Jurassic (~178–151 Ma), this region was affected by intense bi-modal, andesitic (Bajo Pobre Formation) and dacitic to rhyolitic (Chon Aike Formation) volcanic activity associated with the fragmentation of Gondwana and the opening of the South Atlantic Ocean (Riley et al., 2001; Richardson and Underhill, 2002).

During the Late Jurassic, extensive hydrothermal activity occurred in this region, associated with a mature or quiescent volcanic phase, which led to the formation of epithermal metalliferous deposits (mainly gold and silver), widespread silicification, and surface geothermal fields (Schalamuk et al., 1997; Guido and Campbell, 2011, 2014). Numerous

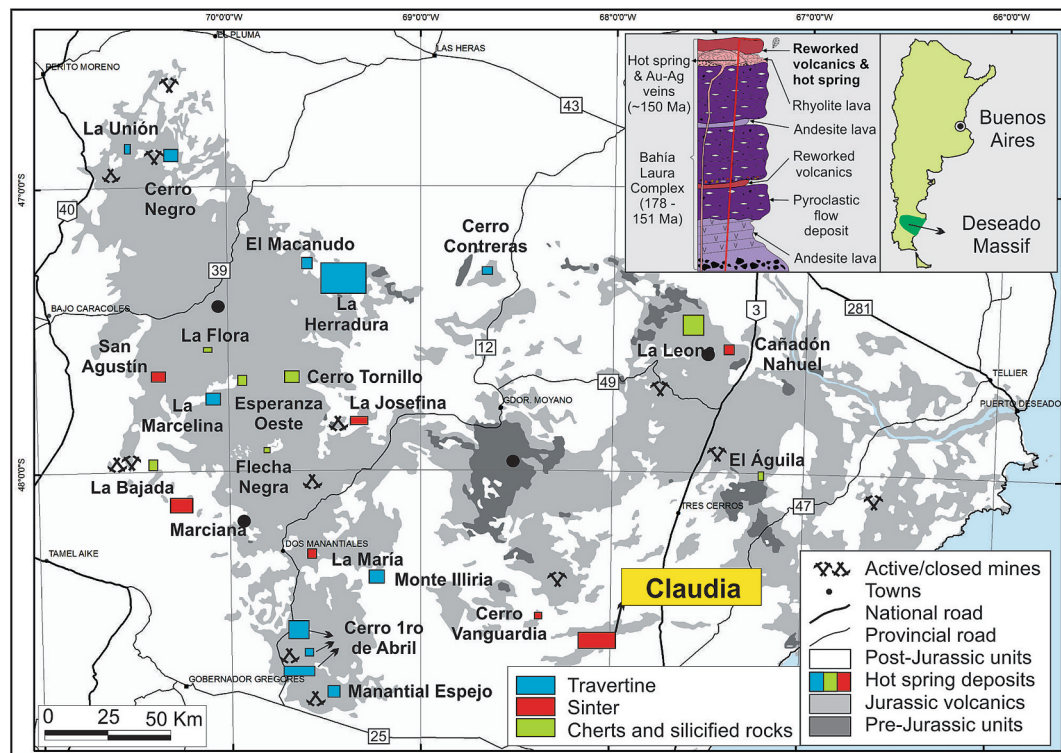


Fig. 1. Location and geological context of the Claudia locality in the Deseado Massif (Patagonia). Jurassic volcanic rocks of the Bahía Laura Complex are shown in gray. Younger ("Post-Jurassic") rocks are shown in dark gray. Geothermal deposits are highlighted in colors: sinter (silica-rich hot-spring deposits) in red, travertine (carbonate spring deposits) in blue, and cherts and silicified rocks (mainly silicified tuffs or travertines) in green. The fossiliferous cherts described in this study were collected from a sinter hot spring deposit at Claudia. The inset (top right) shows the stratigraphic sequence of the Jurassic volcanic complex including the andesitic lavas (Bajo Pobre Formation; lilac color), the intermediate to acid pyroclastic and lava flows (Chon Aike Formation; violet and pink color) and the reworked volcanics of the La Matilde Formation (red color in the column) which hosts the geothermal localities where the studied samples were collected. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fossilized and exceptionally well-preserved geothermal fields within fluvio-lacustrine volcanoclastic strata of the La Matilde Formation have been identified in multiple explorations. These fields are distributed across a 400×250 km area in NNW- and WNW-oriented belts (Fig. 1; Guido and Campbell, 2011, 2014). These deposits represent the only known Mesozoic geothermal fossiliferous deposits with ecosystem-level preservation, filling an important stratigraphic gap between similar Paleozoic and Cenozoic areas (Channing et al., 2007; Guido et al., 2010; García Massini et al., 2012, 2016; Sagasti et al., 2016; Nunes et al., 2020).

The geothermal deposits crop out at 'Claudia', which is located at the eastern end of the southern belt defined by Guido and Campbell (2011) (Fig. 1). The geology of this locality comprises the Bahía Laura Complex, which includes three main formational units: the Bajo Pobre (intermediate volcanic rocks), Chon Aike (acidic volcanic rocks), and La Matilde formations (reworked volcanoclastic material). Regionally, 'Claudia' represents a paleogeothermal system distinguished by extensive deposits of travertine and silicified travertine interbedded with silica sinter accumulations, outlining an area of diverse and widespread geothermal activity during the Jurassic (Guido and Campbell, 2014). The outcrops of these hydrothermal deposits are situated within an ENE-oriented erosional window of the extant Seco River, exposing Jurassic and Cretaceous volcanoclastic formations that would otherwise be partially covered by younger Quaternary deposits (Guido and Campbell, 2014).

In these outcrops, chert deposits associated with the distal areas of hydrothermal influence display signs of early lithification, as indicated by the bending of lacustrine layers around the chert layers (Guido and Campbell, 2014). This likely occurred during the infusion of hydrothermal fluids into sedimentary horizons, followed by differential compaction of the deposit (Guido and Campbell, 2011, 2014). These

hydrothermal cherts are of particular interest due to their exceptional fossil preservation, offering a unique opportunity for paleobotanical studies on well-preserved anatomical and morphological samples. The high level of preservation also allows for the examination of ecological interactions, providing insights into past terrestrial ecosystems (Guido and Campbell, 2011, 2014).

3. Materials and methods

The studied material comprises silica permineralizations of the secondary xylem (Fig. 2a–d). Transverse, tangential and radial longitudinal thin sections were prepared following standard procedures (Archangelsky, 1962; Stockey, 1977; Jones and Rowe, 1999). The slides were observed and photographed under transmitted light or epifluorescence using a Nikon (Tokyo, Japan) DS-Fi3 camera coupled to a Nikon Eclipse 80i microscope. Epifluorescence was achieved through a Nikon C-SHG1 high-pressure mercury lamp power supply. General views of cross sections displaying the presence of rootlets were captured using two KENKO (Tokyo, Japan) extension tubes (36 mm and 12 mm) coupled to a Canon EF-S 60 mm macro lens on a Canon (Tokyo, Japan) EOS 7D DSLR camera. Image stacking was performed by merging partially overlapping photographs to create high-quality images of critical features, using Adobe Photoshop 2024 (v. 26.0) (San Jose, USA), with checking for artifacts. Wood anatomical terminology follows the recommendations of IAWA Committee (2004), Philippe and Bamford (2008), Boura et al. (2021), Esteban et al. (2023), and Bodnar et al. (2023). Measurements are expressed as the mean followed by the range in brackets, with at least 30 observations recorded for each parameter. In the case of the rootlets, the limited availability of structures did not allow for the minimum number of observations, so the measurements

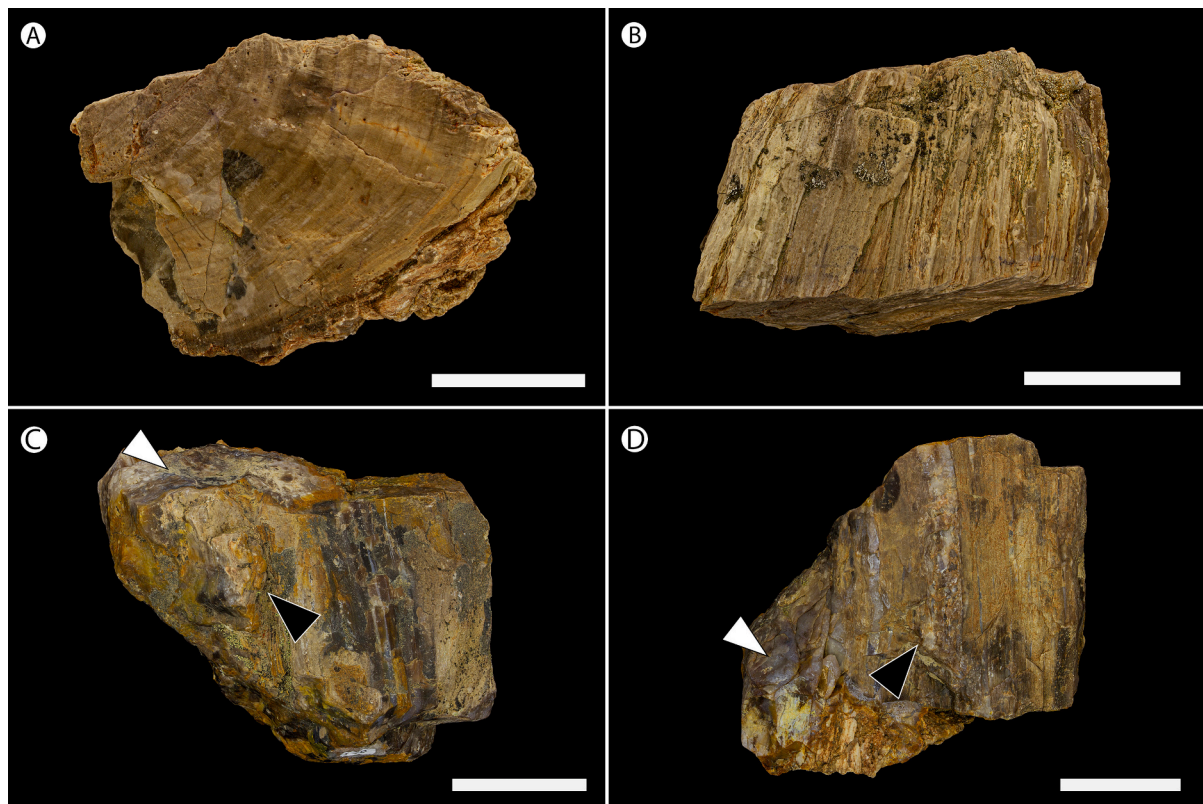


Fig. 2. Specimens of *Protocupressinoxylon*-type wood from Claudia locality. The fossils correspond to silicified secondary xylem; A. MPM-Pb 16110, general view from above of a log isolated from the rock matrix; B. MPM-Pb 16110, general lateral view of a log isolated from the rock matrix; C-D. MPM-Pb 16117, general view of logs preserved as inclusions (black arrow) in the chert blocks (white arrow). Scale bars: A,B,C,D = 4 cm.

are provided as a range.

The macrofossils and thin sections obtained from the specimens are housed in the Paleobotanical Collection of the Museo Regional Padre Molina (MPM; Río Gallegos, Santa Cruz, Argentina), and are cataloged under accession numbers MPM-Pb 16109–16117

4. Systematic paleontology

Order: PINALES Gorozh. (= CONIFERALES)

Family: CUPRESSACEAE SENSU LATO Gray

Genus: *Protocupressinoxylon* Eckhold

Type species: *Typus non designatus* (Philippe, 2002; Philippe and Bamford, 2008).

Protocupressinoxylon-type wood

Stratigraphic unit and age: La Matilde Formation, Bahía Laura Complex, Late Jurassic (Guido and Campbell, 2011, 2014).

Studied material: MPM-Pb 16109–16117

Locality: Claudia, Deseado Massif, Santa Cruz Province, Argentina.

Description: The studied fossils are fragmentary logs, some of which are isolated from the rock matrix (Fig. 2a–b) and others are preserved as inclusions in the chert blocks (Fig. 2c–d). The specimens are permineralized by silicates, preserving only the secondary xylem. They are decorticated and do not preserve the pith and primary vascular tissues. Their diameters range from 8 to 16 cm (Fig. 2a–d).

In the transverse section, the growth rings are indistinct (Fig. 3a–b). False rings are frequently observed in several specimens, consisting of sporadic rather than periodic groups of up to 4 cells wide (Fig. 3a–b), with slightly thicker double walls, forming more or less distinguishable bands, with variable spacing between them and no abrupt variation in cell diameter (Fig. 3a–b). The transverse section of the tracheids is circular to polygonal in outline (Fig. 3a–d, e), and intercellular spaces are frequent (Fig. 3d). The tracheids are 36.00 (17.87–51.60) μm in

tangential diameter, and 37.01 (15.77–62.26) μm in radial diameter. The tracheids are predominantly thin-walled, with a double wall thickness of 2.67 (1.00–5.78) μm . Axial parenchyma is diffuse and abundant (Fig. 3a–b, e), distinguishable in the transverse section by having dark resinous contents (Fig. 3e–f).

In the radial longitudinal section, the tracheid pitting exhibits a mixed pattern (i.e., “brachyoxylean” sensu Boura et al., 2021) (Fig. 4a–e). The pits are bordered, with circular to oval apertures and a well-defined torus (Fig. 4a–e) and are 16.95 (7.44–23.70) μm in radial diameter and 14.89 (7.95–21.30) μm in vertical diameter. The ratio between vertical and horizontal diameters is 0.90 (0.60–1.40). The pits are generally circular and occasionally compressed, arranged contiguous (48%) or spaced (52%) (Fig. 4a–e), predominantly uniseriate (86%) and occasionally biseriate (14%). Biseriate pits display an opposite (61%) or alternate (39%) arrangement (Fig. 4c–e). Tertiary thickenings are not observed in the tracheids. Cross-fields have one to four (generally two to three) spaced oculipores arranged in one to two rows (Fig. 5a–b) (i.e., cupressoid pattern sensu Philippe, 1995; and Philippe and Bamford, 2008). Cross-field pits are bordered, with circular to oval apertures (i.e., cupressoid oculipores sensu Philippe, 1995), horizontal to oblique when oval (Fig. 5a–b). Oculipores are 4.56 (2.06–10.24) μm in radial diameter. Ray parenchyma cells are exclusively procumbent (Fig. 5c–d), with smooth horizontal and terminal walls (Fig. 5d).

In the longitudinal tangential section, rays are exclusively uniseriate and of high average height, consisting of 20 (5–44) cells or 475.53 (153.84–1209.13) μm high (Fig. 6a–b). Septate tracheids are present, with simple-walled septa (Fig. 6c, f). Tangential pits and tertiary thickenings are not observed in the tracheids. Axial parenchyma cells have smooth transverse walls, which are sometimes irregularly thickened (Fig. 6g–h).

In some specimens, preserved as inclusions in chert blocks, there are rootlets embedded within the secondary xylem (Fig. 7a–e). In the

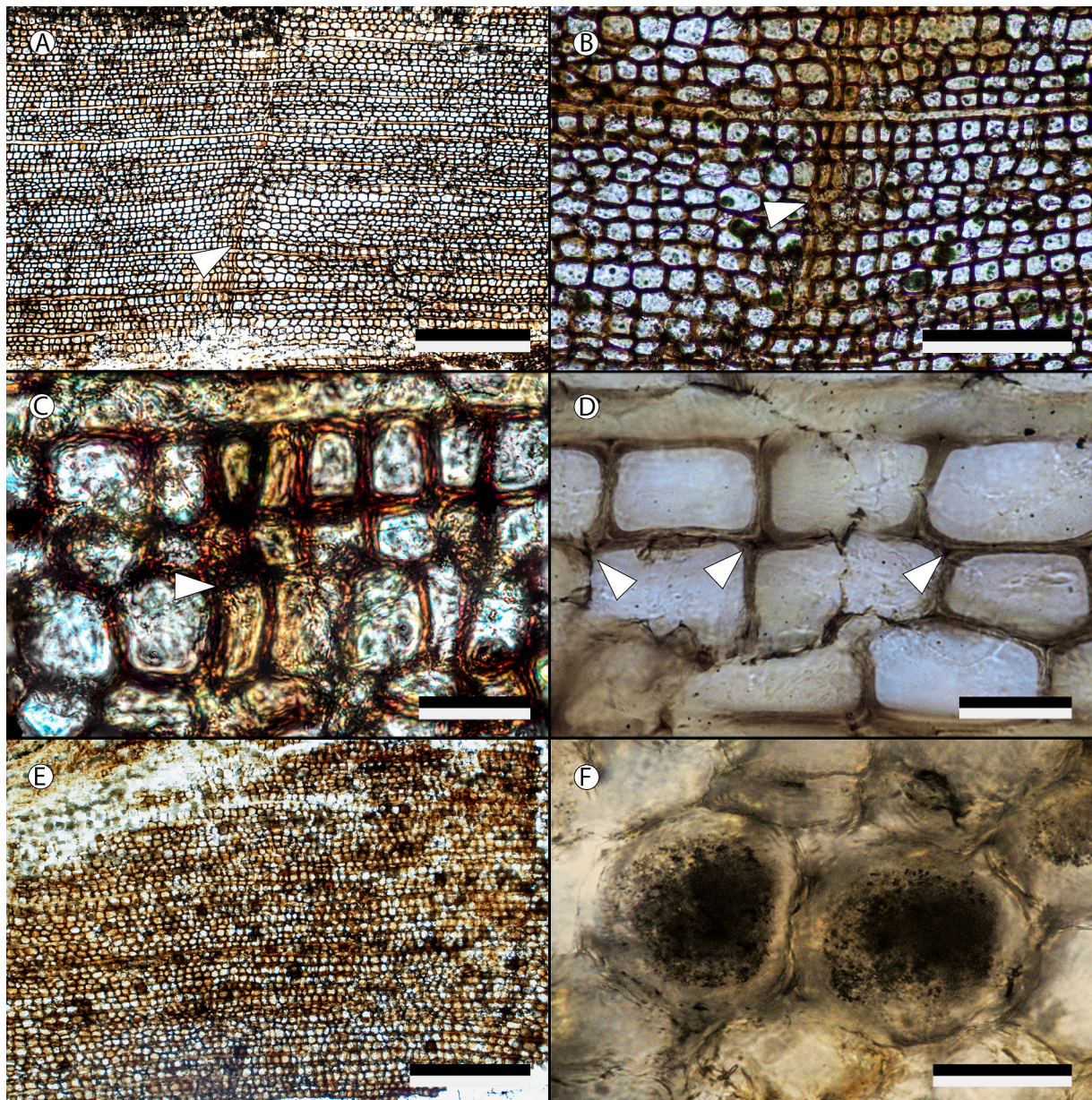


Fig. 3. Specimens of *Protocupressinoxylon*-type wood, from the Jurassic of Patagonia, in cross section. A. MPM-Pb 16109, general view of the cross section, showing a false ring (white arrow); B. MPM-Pb 16109, detail of the false ring (white arrow); C. MPM-Pb 16109, further detail of the tracheids in cross section, showing the cells outline and a false ring (white arrow); D. MPM-Pb 16109, detail of cross section showing Intercellular spaces between tracheids (white arrows); E. MPM-Pb 16109, general view showing abundant, diffuse axial parenchyma (dark cells); F. MPM-Pb 16110, detail of axial parenchyma with resinous content. Scale bars: A = 500 μ m; B = 200 μ m; C,D,F = 40 μ m; E = 500 μ m.

transverse section, they are circular in outline and sometimes they appear flattened or deformed (Fig. 7a–d), with larger diameters varying from 805 to 5069 μ m and smaller diameters between 791 to 1984 μ m (Fig. 7a–d). The rootlets are characterized by a central vascular cylinder, which varies from diarch to hexarch among the different individuals (Fig. 7a–d), with longer diameters ranging from 369 to 1552 μ m and shorter ones from 197 to 1106 μ m. The vascular cylinder is followed by an endodermis composed of a single layer of cells, and this is followed by several layers of cortical cells (Fig. 7b–d). In most of the specimens, only the outer 4 to 5 layers of cortex are preserved and the inner portion of the cortex appears hollowed (Fig. 7b–d). In the cross section, some of the rootlets show secondary branching (Fig. 7b).

5. Discussion

5.1. Systematic affinities

The following combination of characters observed in the studied woods suggests their assignment to Cupressaceae: tracheid radial walls lacking helical thickenings, smooth horizontal walls of the ray parenchyma, cross fields with cupressoid oculipores arranged in cupressoid pattern, and abundant axial parenchyma (Greguss, 1955; Gadek et al., 2000; Román-Jordán et al., 2017; Nunes et al., 2019). Additionally, axial parenchyma in different arrangements (diffuse, tangential and marginal), and oculipores with an average diameter smaller than 10 μ m are common features in this family (Greguss, 1955, 1972; Roig, 1992; Román-Jordán et al., 2017; Pujana et al., 2020; Esteban et al., 2023).

Cupressaceae woods are usually associated with abietinean tracheid

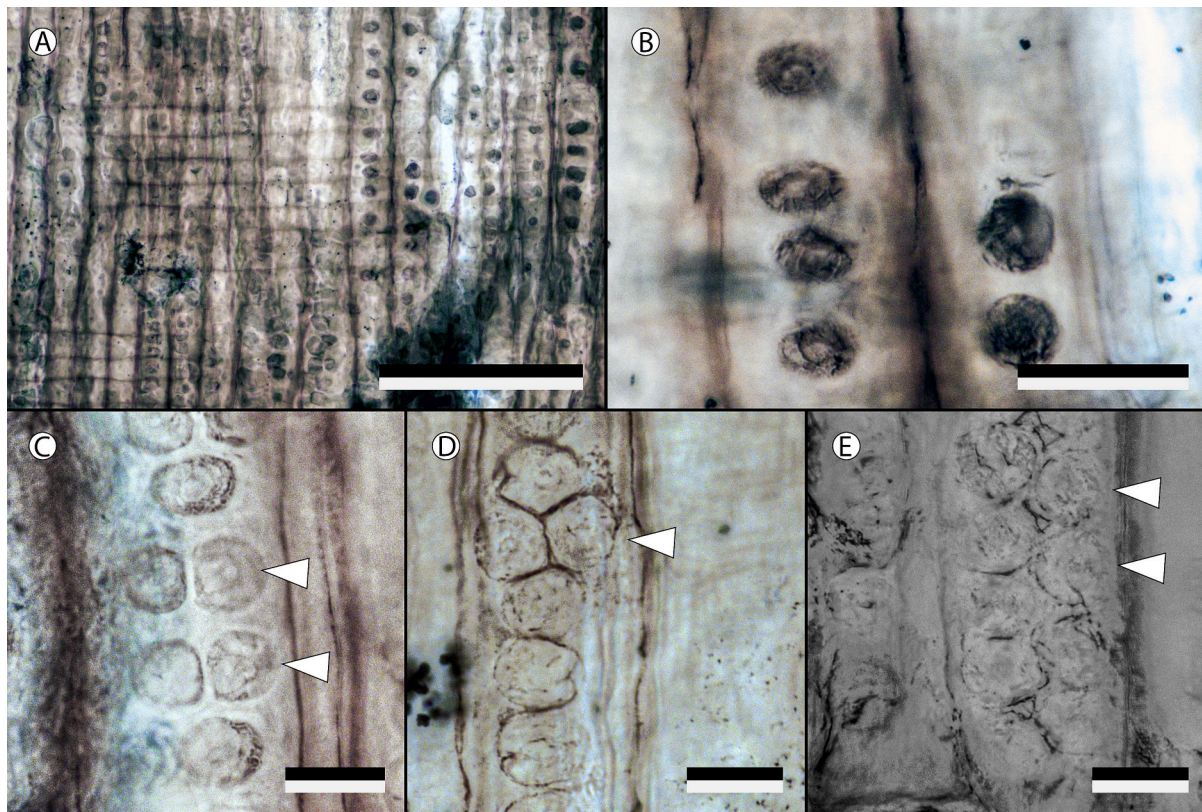


Fig. 4. Radial longitudinal sections of *Protocupressinoxylon*-type wood from the Jurassic of Patagonia, showing radial tracheid pitting. A. MPM-Pb 16109, general view of a radial longitudinal section, showing the tracheid pitting pattern; B. MPM-Pb 16109, detail of tracheids showing uniseriate and spaced radial tracheid pitting; C. MPM-Pb 16109, detail of a tracheid showing partially biseriate, spaced, opposite pitting (white arrows); D. MPM-Pb 16109, detail of a tracheid showing uniseriate, partially biseriate, contiguous pitting with a pair of biseriate, opposite pits (white arrow); E. MPM-Pb 16110, detail of tracheids showing biseriate, contiguous, alternate radial tracheid pitting (white arrows). Scale bars: A = 200 µm; B = 40 µm; C,D,E = 20 µm.

radial pitting (Greguss, 1955; IAWA Committee, 2004; Bodnar and Artabe, 2007; Nunes et al., 2019). However, various fossil woods assigned to this family exhibit, similarly to the samples studied here, mixed or brachyoxylean tracheid pitting (see ‘Comparison with fossil woods’; Eckhold, 1922; Kräusel, 1949; Vaudois and Privé, 1971; Müller-Stoll and Schultze-Motel, 1990; Ru-feng et al., 1996; Bamford and Philippe, 2001; Bodnar and Artabe, 2007; Nunes et al., 2019). Frequently, there are some discrepancies between the terminology used for descriptions of the extant and fossil woods, and certain features used for describing fossils are not considered for living taxa (e.g., patterns of tracheid radial pitting; Bodnar et al., 2023). Nevertheless, available images and descriptions of extant Cupressaceae suggest that mixed pitting is present in some species (see ‘Comparison with extant woods’; Rushton, 1915; Shimakura, 1937; Bannan, 1941; Greguss, 1955).

The taxonomic and systematic relevance of mixed pitting has been debated in literature, as some authors pointed out that the proportion of contiguous and separated pits varies between individuals, and even between branches and stems of the same organism (e.g., Bailey, 1933). In addition, this feature occurs in multiple conifer lineages across a broad temporal range, and its origin within the evolutionary history of conifers is difficult to trace (Bailey, 1933; Shimakura, 1937; Bannan, 1941; Greguss, 1955; Bamford et al., 2016). An additional problem with using this feature for wood taxonomy or systematics, especially in fossil woods, is that preservation can sometimes make it difficult to distinguish between separated and contiguous pits (Bamford et al., 2016; Bodnar et al., 2023). For example, when pits are primarily preserved as internal molds of the pit chamber, araucarian biseriate pits appear slightly smaller than the original ones, leading to their misinterpretation as abietinean (Gothan, 1905; Bamford et al., 2016). Despite these difficulties, interesting trends are observed regarding the presence of mixed

tracheid radial pitting, such as its broad presence in Mesozoic woods and the apparently exclusive combination of this pitting pattern with araucarioid cross fields in Hirmeriellaceae (Philippe, 1992; Bamford et al., 2016; Thevenard et al., 2022).

The anatomy that characterizes the specimens described here is consistent with that of *Protocupressinoxylon* Eckhold (see ‘Generic assignment and specific comparisons’; Vogellehner, 1968; Müller-Stoll and Schultze-Motel, 1989; Philippe, 2002; Philippe and Bamford, 2008; Bodnar, 2017). In early studies, woods with this combination of features were classified under the artificial group “Protopinaceae” (Kräusel, 1917; Eckhold, 1923; Kräusel, 1949; Vogellehner, 1967, 1968; Correa et al., 2019). However, there is no stratigraphic, paleogeographic, systematic, or taxonomic justification for the conservation of this group (Bamford et al., 2016; Correa et al., 2019; Vera and Perez Loinaze, 2022). Additionally, the use of this artificial group has led to wrong and confusing interpretations resulting in its abandonment (see Bamford et al., 2016; Correa et al., 2019; Vera and Perez Loinaze, 2022).

Likewise, the set of traits of *Protocupressinoxylon* Eckhold has been associated with Cupressaceae (e.g., *P. munense*, *Protocupressinoxylon*-type wood; Blokhina, 1975; Oh et al., 2024), but also frequently with Hirmeriellaceae (=Cheirolepidiaceae; Alvin et al., 1981; Zhou, 1983; Axsmith, 2006; Bodnar et al., 2013; Correa et al., 2019; Vera and Perez Loinaze, 2022). Accordingly, several species of *Protocupressinoxylon* have been found in association with vegetative and reproductive remains attributed to Cheirolepidiaceae (e.g., *P. rhaeticum* Vogellehner, *P. purbeckensis* Francis, *P. carentanensis* Barale, and *P. munense* Shilkina and Blokhina; see Vogellehner, 1967; Francis, 1983; Barale, 1987; Thevenard et al., 2022). However, this set of features is not exclusively present in Hirmeriellaceae. For example, the woods *Protocupressinoxylon* *baii* Jiang et al., *P. bhivkundense* (Agashe and Prasad) Kurzawe y

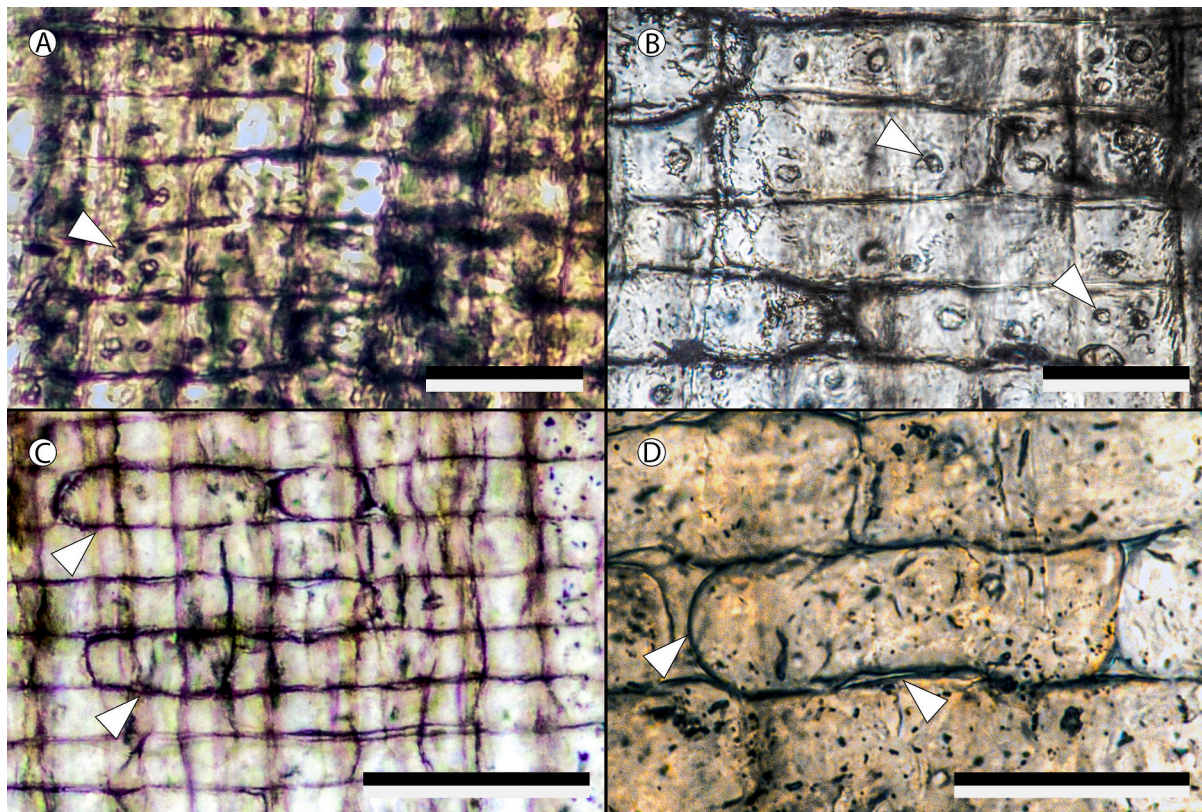


Fig. 5. Radial longitudinal sections of *Protocupressinoxylon*-type wood, from the Jurassic of Patagonia, showing features of the cross fields and the ray parenchyma. A-B. MPM-Pb 16110, general view (A) and detail (B) of cupressoid cross fields comprising 1–4 cupressoid oculipores (white arrows) C. MPM-Pb 16110, detail of ray parenchyma composed of procumbent cells (white arrows); D. MPM-Pb 16110, detail of ray parenchyma cells with smooth walls. Scale bars: A = 50 µm; B,D = 40 µm; C = 100 µm.

Merlotti, and *P. surangei* (Agashe, Prasad and Suresh) Kurzawe and Merlotti have been reported from the Permian, preceding the stratigraphic record of this conifer family (Kurzawe and Merlotti, 2010; Thevenard et al., 2022; Vera and Perez Loinaze, 2022; Jiang et al., 2024).

Affinities with Hirmeriellaceae are less probable for the woods described here due to some anatomical differences between the mesozoic woods linked to this family and the specimens described here. For instance, abundant axial parenchyma, a feature that characterizes the Patagonian specimens, is not common in the wood of this family (Philippe and Bamford, 2008; Tian et al., 2018; Thevenard et al., 2022). Moreover, the cross-field pits in araucarioid pattern, exhibited, at least partially, by Mesozoic woods unambiguously attributed to the Hirmeriellaceae (Tian et al., 2018; Thevenard et al., 2022), are not present in the woods described here. Overall, the anatomical concordance with Cupressaceae supports assigning the Patagonian woods studied here to this family. Furthermore, the samples studied in this work are preserved in association with organs anatomically and morphologically related to Cupressaceae sensu lato (Molano, 2024; see figure supplementary 1). Likewise, in the study area there is no additional evidence suggesting the presence of Hirmeriellaceae (Molano, 2024).

As stated above, wood fossils attributed to Cupressaceae are widely recorded in Mesozoic localities worldwide; however, the taxonomic affinities of some specimens remain uncertain (Kräusel, 1949; Vaudois and Privé, 1971; Bodnar and Artabe, 2007; Gnaedinger, 2007a; Nunes et al., 2019; Ruiz et al., 2017; Ruiz and Bodnar, 2019; Bodnar et al., 2023). The Jurassic Patagonian specimens described here exhibit a distinctive combination of anatomical features characteristic of Cupressaceae. These traits agree with those observed in other cupressaceous fossils (e.g., *Protaxodioxylon patagonicum*; see ‘Comparisons with fossil woods’; Bodnar and Escapa, 2016; Oh et al., 2024) and also correspond to the

wood anatomy of extant genera within taxodiaceous Cupressaceae, particularly *Taiwania* (see ‘Comparisons with extant woods’; Román-Jordán et al., 2017; Esteban et al., 2023). The features documented in these specimens suggest a basal placement within the Cupressaceae lineage. This interpretation aligns with the early-diverging position of Jurassic fossil taxa and extant basal genera in the phylogenetic topologies proposed for this family (Gadek et al., 2000; Escapa et al., 2008; Mao et al., 2012; Leslie et al., 2018; Contreras et al., 2019; Liu et al., 2022).

5.1.1. Comparisons with fossil woods

The specimens described here mainly share features with other fossils linked to Cupressaceae (Table 1). Cupressoid oculipores in cupressoid arrangement are consistently present in fossil woods assigned to this family (Vaudois and Privé, 1971; Philippe et al., 1999; Bodnar and Artabe, 2007; Bodnar and Escapa, 2016; Nunes et al., 2019). In some cupressaceous woods, the cupressoid cross fields co-occur with other patterns, such as circoporoid in *Sequoioxylon* (Torrey, 1923), dacrydioid in *Protelicoxylon* and *Herbstiloxylon* (Gnaedinger, 2007a), taxodioid in *Juniperoxylon* (Ruiz and Bodnar, 2019), *Libocedroxylon* (Penny, 1947; Greguss, 1967), *Thuioxylon* (Penny, 1947; Vaudois and Privé, 1971), *Taxodioxylon* (Kräusel, 1949; Van der Burgh and Meijer, 1996; Yang and Zheng, 2003; Philippe and Bamford, 2008; Ding et al., 2016), and *Protaxodioxylon* (Bamford and Philippe, 2001; Vozenin-Serra et al., 2011; Bodnar and Escapa, 2016; Chinnappa et al., 2019), as well as araucarioid in *Austrocupressinoxylon* (Nunes et al., 2019).

Abietinean tracheid radial pitting is commonly associated with Cupressaceae fossil woods (e.g., IAWA Committee, 2004; Bodnar and Artabe, 2007; Philippe and Bamford, 2008; Nunes et al., 2019). However, some taxa related also exhibit mixed tracheid pitting like the samples studied here (e.g., Eckhold, 1922; Kräusel, 1949; Boureau,

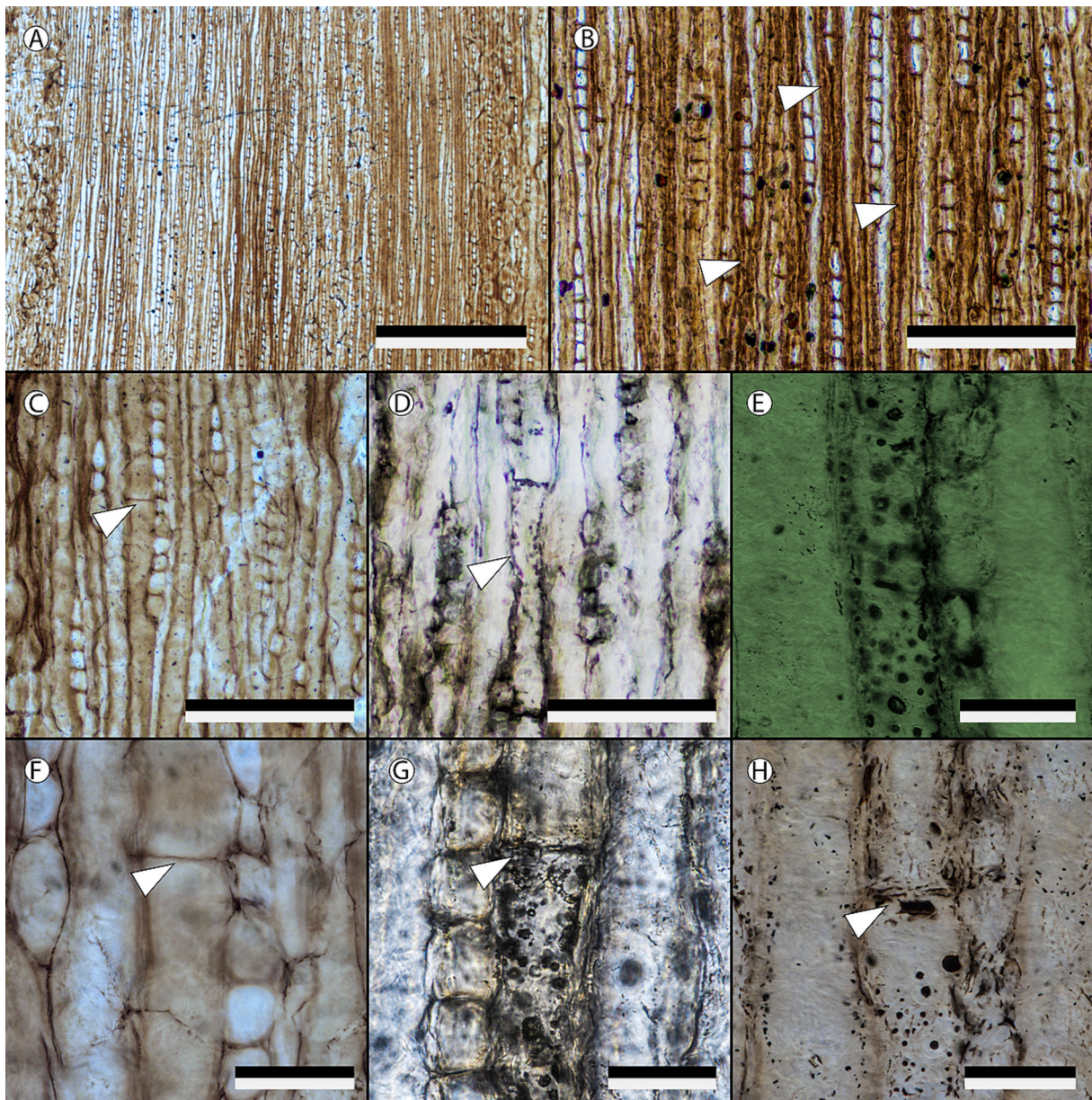


Fig. 6. Tangential longitudinal sections of *Protocupressinoxylon*-type wood, from the Jurassic of Patagonia. A. MPM-Pb 16109, general view of a section showing uniseriate rays; B. MPM-Pb 16109, general view of a section showing uniseriate rays, and tori (white arrows) of the radial tracheid pits; C. MPM-Pb 16109, detail of a section showing septate tracheid with a simple transverse septum (white arrow); D. MPM-Pb 16110, detail of a section showing axial parenchyma with resinous content (white arrow); E. MPM-Pb 16111, detail of a section under epifluorescence, showing resinous content in axial parenchyma; F. MPM-Pb 16109, detail of a tracheid showing simple and thin transverse septum (white arrow); G. MPM-Pb 16110, detail of the axial parenchyma cells, with smooth transverse wall (white arrow); H. MPM-Pb 16111, detail of the axial parenchyma cells showing smooth and irregularly thickened transverse wall (white arrow). Scale bars: A = 500 µm; B,C,D = 200 µm; E,F,G,H = 40 µm.

1956; Vaudois and Privé, 1971; Bamford and Philippe, 2001; Bodnar and Artabe, 2007; Nunes et al., 2019), including species of *Protajuniperoxylon* (Bonetti, 1966), *Protochamaecyparixylon* (Giraud and Hankel, 1985), *Protelicoxylon* (Gnaedinger, 2007a; Akkemik et al., 2022), *Herbstiloxylon* (Gnaedinger, 2007a), and *Protaxodioxylon* (Vozenin-Serra et al., 2011; Bodnar and Escapa, 2016; Chinnappa et al., 2019). Likewise, woods assigned to *Protocupressinoxylon*, which have also been related to Cupressaceae, display mixed tracheid radial pitting (e.g., Oh et al., 2024).

Similar to the samples in this study, axial parenchyma, smooth horizontal walls of the ray parenchyma cells, as well as tracheid radial walls without helical thickenings are commonly observed in cupressaceous fossil woods (e.g., Vaudois and Privé, 1971; Philippe et al., 1999;

Bodnar and Artabe, 2007; Nunes et al., 2019), although, some exceptions are observed. For instance, spiral thickenings are present in *Protelicoxylon* Philippe, *Herbstiloxylon* Gnaedinger (Gnaedinger, 2007a), and *Protaxodioxylon* (Chinnappa et al., 2019). Furthermore, axial parenchyma is absent in some *Thujoxylon* specimens (Bodnar and Artabe, 2007; Ding et al., 2016; Nunes et al., 2019).

The combination of abundant axial parenchyma and septate tracheids is not frequently reported in literature for conifers. Interestingly, this combination is shared by the Jurassic wood *Protaxodioxylon patagonicum*, which is part of the *A. minuta* whole-plant concept (Bodnar and Escapa, 2016), and the *Protocupressinoxylon* described by Oh et al. (2024). The identification of these two traits may be confusing, as they are similar structures characterized by transverse walls inside the cells

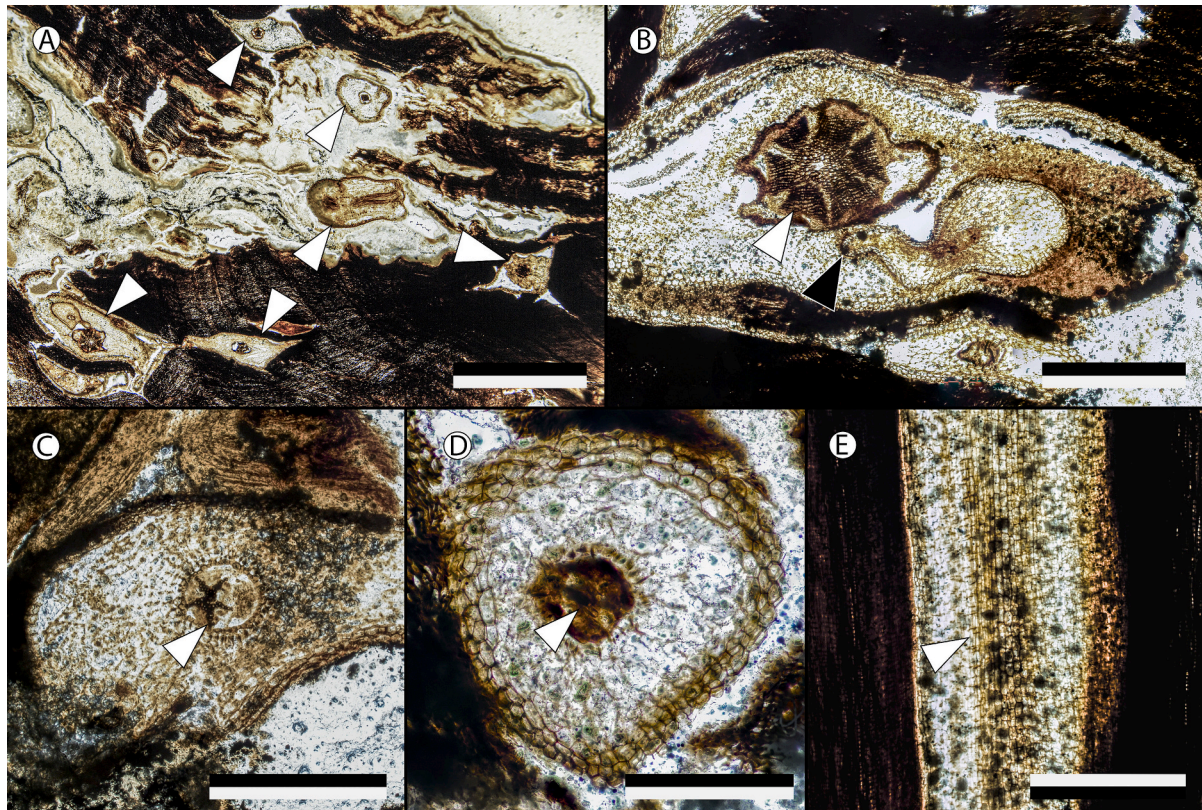


Fig. 7. Rootlets anchored to secondary xylem of *Protocupressinoxylon*-type wood from the Jurassic of Patagonia; A. MPM-Pb 16109, general view of a cross section showing rootlets inside the secondary xylem (white arrows); B. MPM-Pb 16109, detail of a rootlet in cross-section with a hexarch vascular arrangement (white arrow) and branching secondary rootlet (black arrow); C. MPM-Pb 16109, detail of a pentarch rootlet in cross section (white arrow); D. MPM-Pb 16109, detail of a diarch rootlet (white arrow); E. MPM-Pb 16109, longitudinal section of wood and rootlet, showing primary anatomy of the rootlet (white arrow). Scale bars: A = 5 mm; B,C, E = 1 mm; D = 200 μ m.

(IAWA Committee, 2004; Beck, 2010; Bodnar and Escapa, 2016). Despite their similarities, these structures can be distinguished, as septate tracheids have simpler and thinner septa (Fig. 6c, f) compared to the transverse walls found in axial parenchyma (Fig. 6g–h), which possess a double wall and a lamella that come from contiguous cells (Bodnar and Escapa, 2016). Additionally, in the woods from this study, axial parenchyma is characterized by resinous material and shorter spaces between transverse walls (Fig. 6d–e, g–h) than those found in the septa of septate tracheids.

The mixed or brachyoxylean tracheid pitting has been frequently associated in the literature with Hirmeriaceae (=Cheirolepidiaceae). The samples in this study share this tracheid pitting arrangement with cheirolepidiacean woods from the genera *Protopodocarpoxylon* Eckhold and *Brachyoxylon* Hollick and Jeffrey (Alvin et al., 1981; Correa et al., 2019; Thevenard et al., 2022). Similarly, they share cupressoid oculipores with cheirolepidiacean *Brachyoxylon* and some Cretaceous *Agathoxylon* Hartig woods (Gerards et al., 2007; Néraudeau et al., 2009, 2012; Tian et al., 2018; Thevenard et al., 2022). In contrast, some characters observed in the woods described here are not present in cheirolepidiacean woods. For example, axial parenchyma is absent in woods that have been unambiguously assigned to this family through organic connections with other vegetative or reproductive structures, or related to it through mutual presence type of association (e.g., Harris, 1957; Vogellehner, 1965, 1967; Alvin, 1982; Barale, 1987; Zhou and Kirchner, 1992; Hill et al., 2012; Sucerquia et al., 2015; Thevenard et al., 2022; Moreau et al., 2019; Thevenard et al., 2022). However, there are some exceptions, such as *Protocupressinoxylon purbeckensis*, which is preserved along with *Cupressinocladus* foliage (Francis, 1983; Philippe et al., 2010). Interestingly, *Agathoxylon* woods unambiguously related to the Hirmeriaceae do not indicate whether axial parenchyma is present

or absent (Gerards et al., 2007; Néraudeau et al., 2009, 2012; Thevenard et al., 2022).

Furthermore, woods related to the Hirmeriaceae through organic connection (Hill et al., 2012; Sucerquia et al., 2015; Thevenard et al., 2022) or mutual presence association (Harris, 1957; Vogellehner, 1965, 1967; Alvin, 1982; Francis, 1983; Barale, 1987; Zhou and Kirchner, 1992; Philippe et al., 2010; Moreau et al., 2019; Thevenard et al., 2022) show, at least partially, an araucarioid cross-field pits arrangement. This trait is not observed in the woods here assigned to *Protocupressinoxylon*.

The woods described here are anatomically most similar to the Jurassic *Protocupressinoxylon* from Antarctica (Oh et al., 2024) and to *Protaxodioxylon patagonicum*, the latter of which is part of the *Austrohamia minuta* whole plant concept (Bodnar and Escapa, 2016). They share the uniseriate to biseriate brachyoxylean radial tracheid pitting, absence of ray tracheids, abundant and diffuse axial parenchyma abundant with smooth transverse walls, septate tracheids, and oculipores with a spaced distribution and no more than four pits per cross field. Additionally, these wood taxa are preserved in rock formations that reflect humid Jurassic environments (Bomfleur et al., 2011; Guido and Campbell, 2014; Bodnar and Escapa, 2016; Contreras et al., 2019; Oh et al., 2024).

5.1.2. Comparisons with extant woods

As mentioned at the beginning of this section, several features observed in the woods described here are consistently found across the different genera of extant Cupressaceae (Table 2). For example, contiguous and separated pits, as well as opposite and alternate arrangements when biseriate, are present in *Cupressus*, *Cunninghamia*, *Fokienia*, *Glyptostrobus*, *Juniperus*, *Libocedrus*, *Metasequoia*, *Platycladus*, *Sequoiadendron*, *Taiwania*, *Taxodium*, and *Thuja* (see images and

Table 1

Comparison of *Protocupressinoxylon*-type wood with similar fossil genera. Abbreviations: TTS = Tracheid transverse section; RTPP = Radial tracheid pitting pattern; RTPS = Radial tracheid pitting seriation; TTP = Tracheid tangential pitting; AP/APHW = Axial parenchyma/Axial parenchyma horizontal walls; CFT/CFNP = Cross field type/Cross fields, number of pits; RPHW/RPEW = Ray parenchyma horizontal walls/ray parenchyma end walls; RT = Ray tracheids. The characters in parentheses occur occasionally. Characters with (?) represent inferences from descriptions and images, but without explicit designation from original authors. References: [Vaudois and Privé \(1971\)](#), [Bodnar and Artabe \(2007\)](#), [Gnaedinger \(2007a, 2007b\)](#), [Philippe and Bamford \(2008\)](#), [Brea et al. \(2009\)](#), [Vozenin-Serra et al. \(2011\)](#), [Pujana and Ruiz \(2017\)](#), [Tian et al. \(2018\)](#), [Chinnappa et al. \(2019\)](#), [Nunes et al. \(2019\)](#), [Oh et al. \(2020\)](#), [Akkemik et al. \(2022\)](#), [Thevenard et al. \(2022\)](#).

	Age	Location	TTS	RTPP	RTPS	TTP	AP/APHW	CFT/CFNP	RPHW/RPEW	RT
<i>Protojuniperoxylon</i> Eckhold	Triassic, Cretaceous	South America, Europe	Polygonal	Abietinean or mixed	Uniseriate or biseriate	Absent	Scarce/Nodular (?)	Cupressoid/2 to 6	Nodular/Nodular with indentures	Present
<i>Callitrixylon</i> Privé and Boureau	Paleogene	Europe	Circular	Abietinean	–	Absent	Present/Smooth	Cupressoid/–	Smooth or nodular/Smooth	Present
<i>Chamaecyparixylon</i> Chudajberdyev in Vakhrameev et al.	Paleogene, Neogene	Western Europe and former USSR	Polygonal	Abietinean	Uniseriate	Present	Present/Nodular (?)	Cupressoid/2 to 4	Smooth/Smooth	Absent
<i>Cupressinoxylon</i> Kräusel	Jurassic, Cretaceous, Paleogene	Widespread	Circular or polygonal	Abietinean	Uniseriate to triseriate	(Present)	Abundant/Nodular	Cupressoid/–	Smooth/Smooth	Absent
<i>Juniperoxylon</i> Houlbert en Lecointre emend Kräusel	Triassic?, Cretaceous, Paleogene	Europe, Argentina	Circular or polygonal	Abietinean	Uniseriate to triseriate	Absent	Present/Smooth or thickened	Cupressoid or taxodioid/–	Smooth or nodular/Smooth, (indentures)	Present
<i>Libocedroxylon</i> Greguss	“Paleogene	Western Europe	Polygonal	Abietinean	Uniseriate	Present	Abundant/Nodular	Cupressoid or taxodioid/1 to 6	Smooth/Smooth, (indentures)	Absent
<i>Protouchamaecyparixylon</i> Giraud in Giraud y Hankel	Triassic?, Jurassic	Chile, Tanzania	Polygonal	Mixed with araucarian predominance	Uniseriate; (biseriate)	Absent	Scarce/Smooth or nodular	Cupressoid/2 to 4	Smooth/Smooth	Absent (?)
<i>Tetraclinoxylon</i> Grambast	Paleogene	Europe	Circular	Abietinean	Uniseriate to triseriate	Absent	Present/Smooth	Cupressoid/–	Smooth or nodular/Smooth or nodular	Absent (?)
<i>Thuioxylon</i> Unger	Paleogene, Neogene	North America, Europe	Polygonal	Abietinean	Uniseriate	(Present)	Absent or scarce/Nodular	Cupressoid or taxodioid/1 to 4	Smooth/Smooth with indentures	Absent (?)
<i>Widdringtonoxylon</i> Penny	Paleogene	Europe	Polygonal	Abietinean	Uniseriate to biseriate	Absent	Present/Smooth	Cupressoid/–	Smooth/Smooth	Absent (?)
<i>Austrocupressinoxylon</i> Nunes et al	Cretaceous	Argentina	Circular or polygonal	Abietinean	Uniseriate; (biseriate)	Present	Present/Smooth	Cupressoid or araucarioid/1 to 4 cupressoid/ 5 to 10 araucarioid	Smooth or nodular/Smooth with indentures	Present
<i>Protelicoxylon</i> Philippe	Jurassic, Cretaceous	Europe, Asia, Argentina	–	Mixed with abietinean predominance	Uniseriate; (biseriate)	–	Present/–	Cupressoid or dacridioid/1 to 5	Smooth/Smooth	–
<i>Herbstiloxylon</i> Gnaedinger	Jurassic	Argentina	Polygonal	Mixed with abietinean predominance	Uniseriate; (biseriate)	–	Abundant/Smooth	Cupressoid and dacridioid/1 to 2	Smooth/Smooth	–
<i>Protaxodioxylon</i> Bamford and Philippe.	Jurassic, Cretaceous	Mongolia, China, India, Spain, Argentina, France	–	Mixed	Uniseriate to biseriate	Present or absent	Generally present/Smooth	Taxodioid, or taxodioid and cupressoid/1 to 5 (6)	–/–	Absent
<i>Taxodioxylon</i> Hartig	Cretaceous, Cenozoic	Northern Hemisphere	Circular or polygonal	Abietinean?	Uniseriate to biseriate; (multiseriate)	Present or absent	Present/Nodular or smooth	Taxodioid, or taxodioid and cupressoid/1 to 4 (7)	Smooth/Smooth	–
<i>Sequoioxylon</i> Torrey	Cretaceous	United States, China	Circular or polygonal	Abietinean?	Uniseriate to biseriate	Present or absent	Present/Nodular and smooth, or Smooth	Cupressoid or taxodioid; sometimes circoporoid/1 to 6	Smooth/Smooth	Present or absent
<i>Protopodocarpoxyton</i> Eckhold	Jurassic, Cretaceous	Europe, Asia, Antarctica	–	Mixed	Uniseriate to biseriate	(Present)	Absent with few exceptions/–	Podocarpoid or araucarioid/–	Smooth/Smooth	–
<i>Brachyoxyton</i> Hollick and Jeffrey	Permian, Triassic, Jurassic, Cretaceous	Wide distribution	–	Mixed	Uniseriate to triseriate	Present or absent	Absent/–	Araucarioid/1 to 26	–/–	Absent
<i>Agathoxyton</i> Hartig	Triassic, Jurassic, Cretaceous, Paleogene	Wide distribution	–	Araucarian	Uniseriate to multiseriate	Present or absent	–/–	Araucarioid/–	Smooth/–	Absent
<i>Protocupressinoxylon</i> Eckhold	Permian, Triassic, Jurassic, Cretaceous	Wide distribution	Circular or polygonal	Mixed	Uniseriate to biseriate; (triseriate)	Present or absent	Present or Absent/–	Cupressoid, or cupressoid and araucarioid/1 to 11	–/Generally smooth	–

Table 2

Comparison of *Protocupressinoxylon*-type wood from the Jurassic of Patagonia with extant genera of Cupressaceae sensu lato. Abbreviations: TTS = Tracheid transverse section; RTPP = Inferred radial tracheid pitting pattern; RTPS = Radial tracheid pitting seriation; TTP = Tracheid tangential pitting; AP/APHW = Axial parenchyma/Axial parenchyma horizontal walls; CFT/CFNP = Cross field type/Cross field number of pits; RPHW/RPEW = Ray parenchyma horizontal walls/ray parenchyma end walls; RT = Ray tracheids. Radial tracheid pitting arrangement is not explicitly assigned in extant woods; however, it was inferred from descriptions and images in literature. Characters in parentheses occur occasionally. References: Metcalfe (1931), Shimakura (1937), Bannan (1941, 1942), Boutelje (1955), Greguss (1955), Hejnowicz (1973), Sugawa and Fujii (1992), De Magistris (1997), Gadek et al. (2000), Esteban et al. (2002, 2015, 2023), Visscher and Jagels (2003), de Palacios et al. (2014), Román-Jordán et al. (2017), Kitin et al. (2009), Nunes et al. (2019).

	Area	TTS	RTPP	RTPS	TTP	AP/APHW	CFT/CFNP	RPHW/RPEW	RT
<i>Actinostrobus</i>	Australia	Polygonal	Abietinean	Uniseriate, (biseriate)	Occasionally present	Present/Smooth	Cupressoid/2–6 (8–10)	Smooth/Smooth	Absent
<i>Athrotaxis</i>	Tasmania	Polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/Smooth	Cupressoid or taxodioid/1 to 2	Smooth/Smooth, (nodular)	Absent
<i>Austrocedrus</i>	Argentina, Chile	Circular or polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/Smooth	Cupressoid or cupressoid partially taxodioid/2 (1 a 6)	Smooth/Smooth, (nodular)	Absent
<i>Callitris</i>	Australia, Tasmania, Nueva Caledonia	Circular or polygonal	Abietinean	Uniseriate, (biseriate)	Occasionally present	Present/Smooth or nodular	Cupressoid/1 to 4	Smooth, (pitted)/Smooth	Absent
<i>Calocedrus</i>	USA, China, Thailand, Birmania, Laos, Vietnam	Circular or polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/Nodular	Cupressoid or cupressoid partially taxodioid/1 to 5 (7)	Smooth, (pitted)/Smooth or nodular	Absent
<i>Chamaecyparis</i>	USA, Japan, Taiwan	Circular or polygonal	Abietinean	Uniseriate, (biseriate)	Absent or present	Rarely absent/Smooth or nodular	Cupressoid or cupressoid partially taxodioid/1 to 4 (8)	Smooth or pitted/Smooth or nodular	Absent or present
<i>Cryptomeria</i>	Japan	Polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/Smooth or nodular	Cupressoid or taxodioid/1 to 2	Smooth or scarcely pitted/Smooth	Absent
<i>Cunninghamia</i>	China, Japan, Taiwan	Polygonal	Abietinean or mixed	Uniseriate, (biseriate)	Present	Present/Smooth or occasionally nodular	Cupressoid or taxodioid/1 to 4	Smooth/Smooth, (nodular)	Absent
<i>Cupressus</i>	Temperate regions of Northern hemisphere	Circular or polygonal	Abietinean or mixed	Uniseriate	Present	Present or scarce/Smooth or nodular	Cupressoid/1 to 4 (8)	Smooth or pitted/Smooth or nodular	Absent or present
<i>Diselma</i>	Tasmania	Polygonal	Abietinean	Uniseriate	Present	Present/Smooth or nodular	Cupressoid/1 to 2 (3 to 5)	Smooth/Smooth or nodular	Absent
<i>Fitzroya</i>	Argentina, Chile	Polygonal	Abietinean	Uniseriate	Present	Present/Nodular or occasionally smooth	Cupressoid or cupressoid partially taxodioid/1 to 4 (8)	Smooth or pitted/Smooth or nodular	Rarely present
<i>Fokienia</i>	China, Laos, Vietnam	Polygonal	Abietinean or mixed	Uniseriate, (biseriate)	Present	Present/Smooth or nodular	Cupressoid or taxodioid/1 to 3 (6)	Smooth, (pitted)/Smooth	Absent
<i>Glyptostrobus</i>	China, Vietnam	Polygonal	Abietinean or mixed	Uniseriate, (biseriate)	Present	Present/Nodular	Cupressoid or taxodioid/1 to 4	Smooth/Smooth	Absent
<i>Juniperus</i>	Northern hemisphere	Circular or polygonal	Abietinean or brachyoxylean	Uniseriate, (biseriate)	Present	Present or scarce/Smooth or nodular	Cupressoid/1 to 4 (6)	Smooth or pitted/Smooth or nodular	Absent
<i>Libocedrus</i>	New Zealand, New Caledonia	Polygonal	Abietinean or brachyoxylean	Uniseriate, (biseriate)	Occasionally present	Present/Smooth or nodular	Cupressoid or taxodioid/1 to 4 (11)	Smooth/Smooth	Absent
<i>Metasequoia</i>	China	Polygonal	Abietinean or brachyoxylean	Uniseriate to multiseriate	Present	Present/Smooth or nodular	Cupressoid or taxodioid/1 to 2	Smooth, (pitted)/Smooth	Absent
<i>Microbiota</i>	Siberia	Polygonal	Abietinean	Uniseriate	Present	Present/Smooth or nodular	Cupressoid/1 to 2	Smooth, (pitted)/Smooth	Absent
<i>Neocallitropsis</i>	New Caledonia	Circular or polygonal	–	Uniseriate or biseriate, (multiseriate)	Present	Absent or scarce/Smooth	Cupressoid/1 to 2 (4 to 6)	Smooth/Smooth	Absent
<i>Papuacedrus</i>	New Guinea, Maluku Islands	Polygonal	–	Uniseriate, (biseriate)	Present	Present/Smooth	Cupressoid or taxodioid/1 to 2 (4 to 6)	Smooth/Smooth	Absent

(continued on next page)

Table 2 (continued)

	Area	TTS	RTPP	RTPS	TTP	AP/APHW	CFT/CFNP	RPHW/ RPEW	RT
<i>Pilgerodendron</i>	Argentina, Chile	Polygonal	Abietinean or randomly arranged (not contiguous)	Uniseriate or randomly arranged	Present	Present/ Smooth or nodular	Cupressoid or cupressoid partially taxodioid/1 to 3 (4 to 6)	Smooth/ Smooth	Absent
<i>Platycladus</i>	China	Polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/ Nodular	Cupressoid/1 to 4	Smooth or scarcely pitted/ Smooth	Absent
<i>Sequoia</i>	USA	Polygonal	Abietinean	Uniseriate or biseriate	Present	Present/ Smooth or nodular	Cupressoid or taxodioid/1 to 2	Smooth, (pitted)/ Smooth, (nodular)	Absent or present2
<i>Sequoiadendron</i>	USA	Polygonal	Mixed	Uniseriate or biseriate	Present	Present/ Smooth or nodular	Cupressoid or taxodioid/1 to 2	Smooth or pitted/ Smooth, (nodular)	Absent
<i>Taiwania</i>	Taiwan, China	Polygonal	Abietinean or mixed	Uniseriate or biseriate	Present	Present or scarce/Smooth	Cupressoid or cupressoid partially taxodioid/1 to 2	Smooth/ Smooth	Absent
<i>Taxodium</i>	USA, México	Polygonal	Abietinean or mixed	Uniseriate, biseriate or triseriate1	Present	Present/ Nodular or occasionally smooth	Cupressoid or cupressoid partially taxodioid/1 to 4	Smooth, (pitted)/ Smooth	Absent
<i>Tetraclinis</i>	Spain, Morocco, Algeria, Tunisia	Polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/ Smooth	Cupressoid/1 to 4	Smooth/ Smooth	Absent
<i>Thuja</i>	USA, Canada, China, Corea, Japan	Polygonal	Abietinean or mixed	Uniseriate, (biseriate)	Present	Rarely present/ Smooth or nodular	Cupressoid or taxodioid/1 to 4 (8)	Smooth or pitted/ Smooth	Absent
<i>Thujopsis</i>	Japan	Polygonal	Abietinean	Uniseriate, (biseriate)	Present	Present/ Nodular	Cupressoid or cupressoid partially taxodioid/1 to 2 (4)	Smooth, (pitted)/ Smooth	Absent or present3
<i>Widdringtonia</i>	Malawi, Mozambique, Zimbabwe, South Africa	Polygonal	Abietinean	Uniseriate or biseriate	Present	Present/ Smooth	Cupressoid/1 to 2 (3 to 4)	Smooth/ Smooth	Absent

descriptions in Rushton, 1915; Shimakura, 1937; Bannan, 1941; Greguss, 1955; Hejnowicz, 1973).

Interestingly, the features described in the studied Jurassic woods are frequently found in basal Cupressaceae, including *Sequoiadendron*, *Metasequoia*, and *Taiwania*. From these genera, most similarities are found with *Taiwania* (subfamily Taiwanoideae; Gadek et al., 2000; Mao et al., 2012; Leslie et al., 2018; Liu et al., 2022). The shared features include cupressoid cross fields, diffuse axial parenchyma with smooth and irregularly thickened transverse end walls, and ray parenchyma cells with smooth walls. Additionally, descriptions and images of *Taiwania* woods (e.g., Shimakura, 1937; Greguss, 1955) show radial tracheid walls with a mixed arrangement of pits, which can be either contiguous or spaced, and apparently alternate when biseriate. Likewise, occasional polygonal pits are seen in a similar manner to the woods from this study (see fig. 7 in Shimakura (1937) and Fig. 4d in this work).

As discussed in previous sections, the woods described here are very similar to *Protaxodioxylon patagonicum*, fossil taxon for the wood of the *Austrohamia minuta* whole-plant concept (Bodnar and Escapa, 2016), which in turn has also been related to the Taiwanoideae (Escapa et al., 2008; Shi et al., 2014; Herrera et al., 2017; Atkinson et al., 2021). Furthermore, the *Protocupressinoxylon* woods studied here are preserved together with other organs of cupressaceous affinities, including leaves and twigs with phyllotaxis, morphology and anatomy like that of *Austrohamia* species (Figure supplementary 1; Yao et al., 1998; Escapa et al., 2008; Dong et al., 2018; Zhang et al., 2012; Contreras et al., 2019). It is possible that the woods described here are related to the same lineage of *Austrohamia*, which is located at the base of Cupressaceae.

5.2. Generic assignment and specific comparisons

The studied woods are similar to species within the fossil genera *Protocupressinoxylon* Eckhold and *Protaxodioxylon* Bamford and Philippe based on the following combination of characters: indistinct growth rings, diffuse and abundant axial parenchyma, lack of resin canals, mixed type of the radial tracheid pitting, cupressoid oculipores arranged in cupressoid cross fields, uniseriate rays, cells of the ray parenchyma with smooth horizontal walls, and lack of resin canals (Vogellehner, 1968; Müller-Stoll and Schultze-Motel, 1989; Philippe, 2002; Philippe and Bamford, 2008; Bodnar, 2017). Similar combinations of features also characterize the wood of other fossil genera (see Table 3). However, given the presence of mixed type of the radial tracheid pitting, the exclusive cupressoid oculipores arranged in cupressoid cross fields, the smooth ray cell wall, and the lack of resin canals, affinities with *Protocupressinoxylon* are more likely (Vogellehner, 1968; Müller-Stoll and Schultze-Motel, 1989; Philippe, 2002; Philippe and Bamford, 2008; Bodnar, 2017).

Protocupressinoxylon is considered a junior synonym of *Proto-brachyoxylon* Holden (Philippe, 1993; Philippe and Bamford, 2008; Bodnar, 2017; Vera and Perez Loinaze, 2022; Jiang et al., 2024; Oh et al., 2024). Also, *Protocupressinoxylon* has been suggested to be a taxonomical synonym of *Brachyoxylon* Hollick and Jeffrey are (Philippe et al., 2010), although this interpretation remains debated. However, a proposal to conserve this genus was made by Bodnar (2017), considering both the extensive use of *Protocupressinoxylon* in fossil woods from the Permian to the Cretaceous and the lack of use of the respective senior synonym (*Proto-brachyoxylon*). The proposal was not recommended by

Table 3

Comparison of species of *Protocupressinoxylon*-type wood from the Jurassic of Patagonia with other species of *Protocupressinoxylon* Eckhold and *Protaxodioxylon patagonicum* Bodnar and Escapa. Abbreviations: GR = Growth rings; AP = Axial parenchyma; APA = Axial parenchyma arrangement; TRC = Traumatic resin canals; RTPS = Radial tracheid pits seriation; RTPSp = Radial tracheid pits spacing; RTPA = Radial tracheid pitting arrangement; TTP = Tracheid tangential pitting; CFT = Cross field type; Cross fields, number of pits; RCW = Ray parenchyma cell walls; RW = Ray width; RH(Cells) = Ray height; MRH = Mean ray height. References: ¹Savidge et al., 2006; ²Jiang et al., 2024; ³Kurzawe and Merlotti, 2010; ⁴Barale, 1987; ⁵Correa et al., 2019; ⁶Müller-Stoll and Schultze-Motel, 1989; ⁷Attims, 1965; ⁸Shelomenzeva, 1993; ⁹Kräusel, 1949; ¹⁰Iamandei and Iamandei, 1999; ¹¹Iamandei and Iamandei, 2005; ¹²Vera and Perez Loinaze, 2022; ¹³Vogellehner, 1968; ¹⁴Roggeveen, 1932; ¹⁵Zheng and Zhang, 1982; ¹⁶Francis, 1983; ¹⁷Philippe et al., 2010; ¹⁸Vogellehner, 1967; ¹⁹Thevenard et al., 2022; ²⁰Oh et al., 2024; ²¹Bodnar and Escapa, 2016.

Taxon	Age	Location	GR	AP	APA	TRC	RTPS	RTPSp	RTPA	TTP	CFT	CFNP	Oculipore	RCW	RW	RH (Cells)	MRH
<i>Protocupressinoxylon</i> -type wood	Jurassic	Argentina	Indistinct	Present. Abundant	Diffuse	Absent	Uniseriate-biseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid	1–2 (3–4)	Cupressoid	Smooth	Uniseriate	20 (5–44)	High
<i>P. arizonicum</i> Savidge 2006 ¹	Triassic	USA	Distinct	Present	Diffuse	Absent	Uniseriate-rarely biseriate	Contiguous or spaced	Alternate	Present	Cupressoid	1–4	Cupressoid	Smooth	Uniseriate, rarely partially biseriate	1–10	?
<i>P. baii</i> Jiang et al. 2024 ²	Permian	China	Indistinct	Present	Diffuse	Absent	Uniseriate-biseriate	Contiguous or spaced	Alternate, rarely opposite	Absent	Cupressoid	1–2 (3–4)	Cupressoid	Smooth	Uniseriate, partially biseriate	5 (1–24)	Medium
<i>P. bhivkundense</i> (Agashe and Prasad) Kurzawe and Merlotti 2010 ³	Permian	India	Distinct. Abrupt	Absent	–	Absent	Uniseriate-biseriate	Contiguous or spaced	Opposite or alternate	Present	Cupressoid	1–8	Cupressoid	Smooth	Uniseriate-biseriate	8 (1–33)	Medium
<i>P. carentanensis</i> Barale 1987 ⁴	Jurassic	France	Distinct	Absent	–	Absent	Uniseriate-rarely biseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid	(2)4 (8)	Cupressoid	Smooth	Uniseriate	(1–11)	?
<i>P. carrizalense</i> Correa et al. 2019 ⁵	Triassic	Argentina	Distinct. Gradual	Absent	–	Absent	Uniseriate-biseriate	Contiguous or compressed, rarely spaced	Opposite or alternate	Absent	Cupressoid	2–4	Cupressoid	Smooth	Uniseriate	7 (1–19)	Medium
<i>P. catenatum</i> Müller-Stoll and Schultze-Motel 1989 ⁶	Jurassic	Germany	?	Absent	–	Absent	Uniseriate-rarely biseriate	Contiguous	Opposite, sometimes alternate	Present	Cupressoid-Araucarioid	3–10	Cupressoid	Smooth	Uniseriate, partially biseriate	1–14	?
<i>P. chouberti</i> Attims 1965 ⁷	Jurassic	Marocco	?	Absent	–	Absent	Uniseriate-rarely biseriate	Contiguous or compressed, partially spaced	Opposite or alternate	Present	Cupressoid-Araucarioid	2–9	Cupressoid	Smooth	Uniseriate-rarely biseriate	1–13	?
<i>P. cocpatassense</i> Shelomenzeva 1993 ⁸	Cretaceous	Uzbekistán	?	Present	Diffuse	Absent	Uniseriate-rarely biseriate	Compressed-less commonly spaced	Opposite	Absent	Cupressoid	1–3	Cupressoid	Smooth	Uniseriate, partially biseriate	28 (3–46)	High
<i>P. coromandelinum</i> (Sahni) Kräusel, 1949 ^{5, 9}	Jurassic	India	?	Present. Abundant	Diffuse	Absent	Uniseriate-biseriate	Contiguous or spaced	Mainly opposite, sometimes alternate	Absent	Cupressoid	1–2	Cupressoid	Smooth	Uniseriate-rarely biseriate	10 (2–30)	Medium
<i>P. dockumense</i> (Torrey) Kräusel, 1949 ^{5, 9}	Triassic	Estados Unidos	?	Absent	–	Absent	Uniseriate-biseriate	Contiguous or spaced	Alternate	Absent	Cupressoid-Araucarioid (?)	2–9	Cupressoid	Smooth (?)	Uniseriate (?)	1–15(–∞)	?
<i>P. dragastani</i> Iamandei and Iamandei 1999 ^{10, 11}	Cretaceous	Rumania	Distinct	Present or absent	Diffuse	Absent	Uniseriate-biseriate-rarely biseriate	Contiguous or spaced	Opposite to sub-opposite	Present or absent	Cupressoid	1–8	Cupressoid	Nodular or smooth	Uniseriate	1–38	?
<i>Protocupressinoxylon</i> sp. cf. <i>P. dragastani</i> Iamandei et Iamandei 1999 ¹²	Cretaceous	Argentina	Distinct. Abrupt	Absent	–	Absent	Uniseriate-biseriate-rarely biseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid	4–6	Cupressoid	Smooth	Uniseriate-rarely biseriate	6 (1–28)	Medium

(continued on next page)

Table 3 (continued)

Taxon	Age	Location	GR	AP	APA	TRC	RTPS	RTPSp	RTPA	TTP	CFT	CFNP	Oculipore	RCW	RW	RH (Cells)	MRH
<i>P. leonardianum</i> Vogellehner 1968 ¹³	Jurassic	Italy	?	Absent	–	Absent	Uniseriate-biseriate	Contiguous, rarely spaced	Opposite, rarely alternate	Rare	Cupressoid-Araucarioid (?)	5–6	Cupressoid	Smooth	Uniseriate	1–17	?
<i>P. liasinum</i> Müller-Stoll y Schultze-Motel 1989 ⁶	Jurassic	Germany	?	Absent	–	Present	Uniseriate-biseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid-Araucarioid	2–10	Cupressoid	Smooth	Uniseriate, rarely partially biseriate	1–19	?
<i>P. malayense</i> Roggeveen 1932 ¹⁴	Triassic	Indonesia	Indistinct	? Absent	–	Absent	Uniseriate-rarely biseriate	Contiguous or compressed	Opposite	Absent	Cupressoid	1–5	Cupressoid	Smooth	Uniseriate	7 (2–16)	Medium
<i>P. mishanense</i> Zheng y Zhang 1982 ¹⁵	Jurassic-Cretaceous	Mongolia, China	?	? Absent	–	Absent	Uniseriate-biseriate	Mainly compressed or contiguous	Opposite or alternate	Absent	Cupressoid	1–3	Cupressoid	Smooth	Uniseriate, partially biseriate	8–20 (3–48)	?
<i>P. munense</i> Shilkina y Blokhina en Blokhina 1975 ⁵	Jurassic	Siberia	Distinct	Absent	–	Absent	Uniseriate-biseriate	Contiguous or spaced	Mainly opposite	Absent	Cupressoid	2–4 (6)	Cupressoid	Smooth	Uniseriate	10 (1–25)	Medium
<i>P. orientale</i> (Seward) Kräusel, 1949 ^{5, 9}	Jurassic	Afghanistan, Japan	?	Present	?	Absent	Uniseriate-biseriate	Contiguous or spaced, occasionally compressed	Opposite, occasionally alternate	Present	Cupressoid	3 a 4	Cupressoid	Smooth (?)	Uniseriate, rarely partially biseriate	20 (1–30)	High
<i>P. purbeckensis</i> Francis 1983 ^{16, 17}	Jurassic	England, Spain, Switzerland	No definidos	Present	?	?	Uniseriate-rarely biseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid-Araucarioid	2–7	Cupressoid	Smooth	Uniseriate	3 (2–9)	Very low
<i>P. rhaeticum</i> Vogellehner 1967 ^{18, 19}	Triassic-Jurassic	England	?	Absent	–	Absent	Uniseriate	Spaced or compressed	?	Absent	Cupressoid-Araucarioid	3–8	Cupressoid	Smooth	Uniseriate	1–8	?
<i>P. solmsi</i> (Stopes) Kräusel, 1949 ^{5, 9}	Cretaceous	New Zealand	?	Present	–	Present	Uniseriate-rarely biseriate	Mainly spaced, less commonly contiguous	?	Present	Cupressoid	1–2	Cupressoid	Smooth	Uniseriate (?)	(1–6)	?
<i>P. surangei</i> (Agashe, Prasad and Suresh) Kurzawe and Merlotti 2010 ³	Permian	India	Distinct. Gradual	Absent	–	Absent	Uniseriate to tetraseriate	Contiguous or spaced	Opposite or alternate	Absent	Cupressoid-Araucarioid	1–11	Cupressoid	Smooth	Uniseriate-biseriate	2,3,4,10 (1–35)	Very low/medium
<i>P. weidlingense</i> (Jacobson) Kräusel, 1949 ^{5, 9}	Cretaceous	Austria	?	Present	–	Absent	Uniseriate-biseriate	Mainly contiguous or compressed	Alternate	Absent	Cupressoid	3–4	Cupressoid	Smooth	Uniseriate-biseriate	1–14	?
<i>P. wejgaoense</i> (Agashe and Kumar) Kurzawe and Merlotti 2010 ³	Permian	India	Distinct	Absent	–	Absent	Uniseriate-biseriate	Contiguous or spaced	Alternate or subopposite	Present	Cupressoid	1–6	Cupressoid	Smooth	Uniseriate-biseriate	8–12 (2–34)	Medium
<i>Protocupressinoxylon</i> -type wood ²⁰	Jurassic	Antarctica	Distinct	Present. Abundant	Diffuse	Present	Uniseriate-biseriate	Contiguous or spaced	Opposite or alternate	Sometimes present	Cupressoid	1–3 (4?)	Cupressoid	Smooth	Uniseriate, rarely partially biseriate	7 (1–38)	Medium
<i>Protaxodioxylon patagonicum</i> Bodnar et Escapa ²¹	Jurassic	Argentina	Distinct	Present. Abundant	Diffuse	Absent	Uniseriate-biseriate-rarely biseriate	Contiguous or spaced	Opposite to alternate	Absent	Taxodioid	1–4	Taxodioid	Smooth	Uniseriate, rarely partially biseriate	6 (1–26)	Medium

the IAPT Fossil Committee, suggesting that further taxonomic research on the genera *Protocupressinoxylon*, *Protobraxyoxylon*, and *Braxyoxylon* is required to make a definitive decision (Herendeen, 2020). In this study we use the open nomenclature *Protocupressinoxylon*-type wood, reflecting the taxonomic uncertainty highlighted by the IAPT Fossil Committee (Herendeen, 2020) and acknowledging the extensive historical and current use of this name (Philippe, 2002; Greguš et al., 2020; Vera and Perez Loinaze, 2022; Jiang et al., 2024; Oh et al., 2024).

Protocupressinoxylon is a fossil genus with over thirty assigned species, many of which do not fit within the original diagnosis (Kräusel, 1949; Philippe et al., 2010; Correa et al., 2019). Comparisons with twenty five species, consistent with the diagnosis made by Eckhold (1923) (Correa et al., 2019), and other recently described woods from the Permian of China (Jiang et al., 2024) and the Jurassic of Antarctica (Oh et al., 2024) were established with the fossils described here (see Table 3). Additionally, comparisons with the Jurassic Argentine *Protaxodioxylon patagonicum* Bodnar et Escapa (see Bodnar and Escapa, 2016) were carried out due to similarities in anatomical traits.

The 'Claudia' woods are most similar to the Jurassic specimen of *Protocupressinoxylon* from Antarctica (Oh et al., 2024) and the Permian *Protocupressinoxylon baii* Jiang et Wan from China (Jiang et al., 2024). It differs from *P. baii* by its exclusively uniseriate rays, larger ray height, and the proportion of opposite and alternate tracheid radial pitting when biseriate, and from the *Protocupressinoxylon*-type wood described in Oh et al. (2024), by the absence of tangential tracheid pitting, exclusively uniseriate rays, absence of traumatic canals, and greater average ray height.

In summary, the combination of features supports the assignment of the woods to *Protocupressinoxylon*. Moreover, the unique combination of characters observed in the studied specimens does not support their assignment to any previously described species. Therefore, we propose the recognition of a new species, pending resolution of the taxonomic uncertainties associated with *Protocupressinoxylon* (Philippe, 2002; Philippe and Bamford, 2008; Bodnar, 2017; Herendeen, 2020).

5.3. Ecology

The utility of wood anatomical traits for climatic and ecological inferences has been frequently discussed, as these traits provide valuable insights into the environmental conditions in which the organisms live (Creber and Chaloner, 1984; Francis, 1984; Falcon-Lang, 1999; Copenheaver et al., 2006; Artabe et al., 2007; Vaganov et al., 2011; Morino et al., 2021). For example, absent or indistinct growth rings are considered indicators of regions with no marked seasonality in rainfall or temperature (Brison et al., 2001; Vaganov et al., 2011). Although, some conifers may lack growth rings even in clearly seasonal climates (e.g., Brison et al., 2001). On the other hand, false rings, which comprise cell bands of slightly thick-walled cells without abrupt changes in size at their boundaries, are generally regarded as indicators of unseasonal and biotic or abiotic disruptive events (Creber and Chaloner, 1984; Cherubini et al., 2003; Copenheaver et al., 2006; Vaganov et al., 2011). Intermittent drought periods are considered to be the main cause of false ring formation; however, other factors, such as insect herbivory or periodic flooding are also likely causes (Young et al., 1993; Copenheaver et al., 2006; Gonda-King et al., 2012). Interestingly, it has been reported that some influences can affect the propensity of woody plants to produce false rings (e.g., age, position within the forest canopy, reduction in photosynthetic rate, interruption of cambial activity; Bolton and Petty, 1978; Cherubini et al., 2003; Copenheaver et al., 2006; Gonda-King et al., 2012). Additionally, presence of false rings can alter or prevent the formation of growth rings. Therefore, inferences about seasonality in rainfall or temperature cannot be drawn from the absence of growth rings (Falcon-Lang, 2000; Brison et al., 2001; Falcon-Lang, 2007; Césari et al., 2012).

From an ecological perspective, the presence of axial parenchyma has been linked to xeromorphic adaptations in plants, acting as a

temporary water reservoir in trees adapted to arid environments (Bodnar and Escapa, 2016; Stupianek et al., 2021). But it has also been related to hydromorphic ones, suggesting it is involved in the oxygenation of roots and stems in flooded trees (Carlquist, 1975; Callado et al., 2024). Additionally, the distribution and conformation of axial parenchyma are recognized as variations resulting from biotic and abiotic stresses such as herbivory, pathogens, embolisms, and mechanical damage (Shigo, 1984; Schmitt and Liese, 1993; Deflorio et al., 2008; Sperry, 2013; Wheeler et al., 2013; Chano et al., 2015; Torres-Ruiz et al., 2015; Morris and Jansen, 2016). Furthermore, septated tracheary elements are related to the storage of reserve substances such as starch under stress conditions, including droughts and high temperatures (Frison, 1948; Fahn and Lessem, 1963; Beck, 2010; Carlquist, 2015; Bodnar and Escapa, 2016; Plavcová et al., 2023).

The mutual presence of abundant axial parenchyma with resinous content, septate tracheids, and false rings in the woods described here could be indicative of plant responses to disruptive events, mechanical damage, or stressful physico-chemical conditions associated with the characteristic dynamics of the migrating geothermal landscapes, especially with events of drought and flooding (Jones et al., 1997; Brison et al., 2001; Trapp and Croteau, 2001; Vaganov et al., 2011; Guido and Campbell, 2014; Channing et al., 2007; Sagasti et al., 2024; García Massini et al., 2025). Particularly, the false rings suggest non periodicity of these events (Brison et al., 2001; Vaganov et al., 2011). Likewise, the conspicuous presence of dark contents suggests that these structures could have participated in healing injuries or storing water during dry periods (Schmitt and Liese, 1993; Mauseth, 2014; Chano et al., 2015; Janssen et al., 2020).

5.4. Presence of rootlets and possible role as nursing logs

The fragments of permineralized secondary xylem containing rootlets measure more than 15 cm wide, and the rootlets are irregularly distributed within the tissue, with a variety of diameters, angles, and vascular cylinder arrangements (ranging from diarch to hexarch). These characteristics support the hypothesis of seedling germination within log debris (Hofgaard, 1993; Narukawa et al., 2003; Césari et al., 2010, 2012; Decombeix et al., 2021), and contrast with the anatomical features observed in other possible explanations for the presence of rootlets, such as root natural grafting or adventitious root formation (Bannan, 1942; Bormann, 1966; Lovell and White, 1986; Hamann, 1998; Iijima et al., 2020). This strategy conveys several ecological advantages to the developing plantlets, which increases their fitness (e.g. reduced competition with understory plants, and protection from waterlogged or very compacted soils, pathogenic fungi or herbivory; Harmon et al., 1986; Harmon and Franklin, 1989; Césari et al., 2010, 2012; Fischer et al., 2016; Decombeix et al., 2021; Feng et al., 2022; Harmon et al., 1986; Fischer et al., 2016; Feng et al., 2022).

Nurse logs represent an ecological strategy in which woody debris, such as trunk remnants, serve as a substrate for the germination of tree seedlings (Sánchez et al., 2009; Fukasawa, 2016; Feng et al., 2022; Vera and Perez Loinaze, 2022; Veblen et al., 1979; Harmon and Franklin, 1989; Lusk and Ogden, 1992; Christie and Armesto, 2003; Lack, 1991; Sánchez et al., 2009). In the fossil record, examples of nurse logs have been described from different geographical regions and geological periods (Césari et al., 2010, 2012; Decombeix et al., 2021; Feng et al., 2022; Wang et al., 2024). The importance and relationship of ecological factors with nurse log interactions may vary among taxa, climatic regimes and geographic areas (Santiago, 2000; Sánchez et al., 2009; Decombeix et al., 2021).

Nurse logs may have provided seedlings with a stable substrate, offering protection from soil instability typical of the geothermal systems, likely fluctuating water tables (Daugherty, 1963; Fajon-Demaret et al., 2003; Césari et al., 2010, 2012; Decombeix et al., 2021; Feng et al., 2022; Vera and Perez Loinaze, 2022). The presence of other conifer organs of cupressaceous affinities (see figure supplementary 1)

preserved along the studied fossil woods, and the absence of other conifer families in the locality, suggest possible conspecificity of the rootlets and logs (Daugherty, 1963; Fairon-Demaret et al., 2003).

6. Conclusions

The assignment to Cupressaceae is supported by the distinctive combination of recorded characters and further reinforced by the co-occurrence of organs morphologically and anatomically related to this family. Although some features described herein are also compatible with Hirmeriellaceae, some differences are observed. For instance, abundant axial parenchyma is rarely reported in members of Hirmeriellaceae and the complete absence of araucarioid cross-fields has not been recorded in woods unambiguously assigned to this family.

The general anatomy of the studied samples is consistent with the diagnosis of the fossil genus *Protocupressinoxylon* Eckhold and, based on a unique combination of features not yet reported, they most probably represent a new species within the genus. However, they are assigned to the open nomenclature *Protocupressinoxylon*-type wood, considering the nomenclature problems of this genus, following the recommendations of the IAPT Fossil Committee, and acknowledging the extensive historical and current use of this genus. The establishment of a new species is suggested for these woods once the nomenclature conflicts of this name can be resolved.

The presence of abundant axial parenchyma with resinous content, septate tracheids, and false rings suggests plant responses to disruptive environmental events such as droughts, mechanical damage, or extreme temperatures, possibly linked to the the dynamics of the geothermal system.

The presence of rootlets within the permineralized secondary xylem is consistent with a nurse-log strategy, which may have provided seedlings with a stable, protected, and nutritious substrate. While the conservative nature of primary root anatomy makes it difficult to establish affinities, the presence of further cupressaceous organs in the locality, and the absence of preserved organs from other conifer families, suggest the conspecificity of rootlets and logs.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2025.105400>.

Data availability

Data will be made available on request.

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