

FIRST RECORD OF CONIFER WOOD FROM THE CAÑADÓN ASFALTO FORMATION (EARLY–MIDDLE JURASSIC), CHUBUT PROVINCE, ARGENTINA



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Abstract. A new fossil conifer wood —*Brachyoxylon curruilii* sp. nov.— is described from the Lower–Middle Jurassic of Chubut Province (Argentina). The specimens were collected at a locality where the Cañadón Asfalto Formation is exposed, in the vicinity of the Cerro Cándor village. The studied wood is characterized by mixed pitting in radial tracheid walls (predominantly uniseriate), araucarioid cross fields, low uniseriate rays and the absence of resin canals. The use of transmitted light and epifluorescence microscopy together with SEM imaging allowed the identification of additional characters such as the presence of pitting with torus-margo and compression wood. These characters are discussed in terms of their systematic relevance. On these grounds, the systematic affinity of the studied wood is discussed and linked to the extinct conifer family Cheirolepidiaceae, one of the dominant plant groups during the Jurassic and Cretaceous in Patagonia.

Keywords. Fossil wood. Mesozoic. Patagonia. *Brachyoxylon*. Cheirolepidiaceae.

Resumen. PRIMER REGISTRO DE LEÑO DE CONIFERA DE LA FORMACIÓN CAÑADÓN ASFALTO (JURÁSICO TEMPRANO–MEDIO), PROVINCIA DE CHUBUT, ARGENTINA. Se describe una nueva especie de madera fósil de conífera, *Brachyoxylon curruilii* sp. nov., del Jurásico Inferior a Medio de la provincia de Chubut, Argentina. Los especímenes estudiados fueron coleccionados en una localidad donde aflora la Formación Cañadón Asfalto, en las cercanías de la aldea de Cerro Cándor. Los troncos, estudiados, se caracterizan por el punteado radial de las traqueidas de tipo mixto, predominantemente uniseriado, campos de cruzamiento de tipo araucarioide, radios uniseriados bajos y ausencia de canales resiníferos. La observación bajo MEB y microscopio con luz transmitida y epifluorescencia permitió además la identificación de caracteres tales como la presencia de torus-margo en las punteaduras y estructuras de leño de compresión. Ambos caracteres son discutidos en relación a su relevancia sistemática. Sobre esta base, se discute la afinidad sistemática de la madera estudiada, la cual posee rasgos que la vincularían con la familia de coníferas extintas Cheirolepidiaceae, uno de los grupos de plantas dominantes durante el Jurásico y Cretácico de Patagonia.

Palabras clave. Madera fósil. Mesozoico. Patagonia. *Brachyoxylon*. Cheirolepidiaceae.

THE Jurassic was the period of the Mesozoic Era during which major lineages of modern gymnosperms (*e.g.*, conifers, ginkgoaleans, cycadophytes) diversified and formed the dominant groups of the terrestrial vegetation during the rest of the Mesozoic and part of the Cenozoic. However, these significant evolutionary processes are still poorly understood because of the scarcity and incompleteness of the Jurassic record. This situation is particularly marked in the southern hemisphere, where limited and fragmentary evidence is available for the Early–Late Jurassic.

The Jurassic deposits of the Cañadón Asfalto Basin in Central Patagonia are potentially useful to assess the evolution of the biota throughout the period, given the abundance and richness of fossil-yielding localities with paleofaunas and paleofloras spanning the Early Jurassic–Late Jurassic (Cúneo *et al.*, 2013). This relatively complete record distinguishes the Jurassic deposits of Central Patagonia from all other South-

ern Hemisphere basins. It provides a unique opportunity to tackle an extensive and interdisciplinary study designed to understand biotic evolution in the area during a period of over 50 million years (Escapa *et al.*, 2008a). Recent advances in the knowledge of the Jurassic biota and its diversity in the Cañadón Asfalto Basin include the description of new vertebrates, invertebrates and plants. This has contributed to render this biota one of the richest at a global scale (*e.g.*, Escapa *et al.*, 2008b,c; Sterli, 2008; Gallego *et al.*, 2011; Pol *et al.*, 2011; Escapa and Cúneo, 2012). However, although abundant and potentially diverse, the fossil-wood record remains little known.

Jurassic xylofloras from Argentina have received progressively greater attention over the last century. Early papers dealt with the Middle Jurassic Bahía Laura Group in Santa Cruz Province (southern Patagonia) and include the description of species belonging to *Cupressinoxylon* Göppert 1850

and *Agathoxylon* Hartig 1848 (Jaworski, 1915, 1926a,b; Eckhold, 1921; Calder, 1953). Recent work resulted in a more complete list of taxa (e.g., Zamuner and Falaschi, 2005; Gnaedinger 2006, 2007a,b; Gnaedinger and Herbst, 2006, 2009). The purpose of this contribution is to describe a fossil conifer wood from the Early–Middle Jurassic Cañadón Asfalto Formation, being this the first complete description of fossil wood from the Jurassic of Chubut Province.

MATERIALS AND METHODS

Geologic context

The Patagonian territory in southern Argentina has the largest extent of continental Jurassic outcrops in South America, including siliciclastic, volcanoclastic and volcanic rocks referred to various stratigraphic units (Cúneo *et al.*, 2013). Jurassic deposits in Chubut Province are part of the Somuncurá–Cañadón Asfalto rift basin, which stretches between 40°30'S and 44°30'S and 66°00' and 70°30'W, Central-North Patagonia, Argentina (Stipanovic and Methol, 1980; Cortiñas, 1996). This basin has been interpreted as the result of rifting that began in the Early Jurassic and ending by the Late Cretaceous (Homocv *et al.*, 1991; Figari and Coutarde, 1993).

During the Jurassic, several lithostratigraphic units accumulated as part of the infilling of the Cañadón Asfalto Basin, the first of them in the Early Jurassic and known as Las Leoneras Formation. This is a thin continental unit unconformably overlying the Paleozoic basement (Nakayama, 1973). It is followed by the Lonco Trapial Formation, which is a thick sequence of basalts and volcanoclastic intercalations (Pankhurst *et al.*, 1998). In some areas (e.g., Cerro Cándor) the Lonco Trapial Formation is transitional into the Cañadón Asfalto Formation, represented by lake-deposits including important carbonatic accumulations (Stipanovic *et al.*, 1968). The Jurassic sequence is completed with the Cañadón Calcáreo Formation, originated in prograding fluvial deposits (Proserpio, 1987; Figari and Coutarde, 1993) and distinguished from the Cañadón Asfalto Formation by the total absence of calcareous rocks and its markedly different tectonic style.

The Cañadón Asfalto Formation —where the fossil wood was collected— was for a long time considered Middle-Late Jurassic (Frenguelli, 1949; Tasch and Volkheimer, 1970; Volkheimer, 1971; Silva Nieto *et al.*, 2007; Escapa *et al.*, 2008a). Recent radiometric ages suggest instead that its deposition began by the late Early Jurassic and probably lasted until the early part of the Middle Jurassic (Cúneo *et al.*, 2013).

Fossil preparation

The studied fossil wood was found at the locality known as “Pomelo”, in the lower part of the Cañadón Asfalto Formation, 15 km southeast from Cerro Cándor village, Chubut Province (GPS coordinates available upon request to I.E.). They consist of silicified axes buried in yellowish and grey siltstones and sandstones with a high proportion of pyroclastic material. The stems were preserved parallel or perpendicular to the bedding plane, and represent part of a parautochthonous plant assemblage with no significant lateral transport.

Stems were preserved by siliceous cellular permineralization, with a good to excellent preservation. Transverse, radial-longitudinal and tangential-longitudinal thin sections were obtained from polished surfaces at the Laboratorio de Cortes of the Museo Paleontológico Egidio Feruglio in Trelew (Chubut), and stored in its fossil collection as MPEF-Pb 5626-5629.

Fossils were analyzed using a Zeiss MC80DX stereoscope microscope with attached *camera lucida*. They were observed with transmitted light and epifluorescence. Photographs were obtained using a Nikon camera. Wood fragments were observed under SEM (JEOL JSM-6460), uncoated, at 15kV, 28Pa.

Descriptions follow standardized terminologies of Boureau (1956), Fahn (1990), IAWA Committee (2004) and Philippe and Bamford (2008), and Greguss' Wood Anatomy Atlas (1955). Dimensions of anatomical elements were obtained with 30 measurements in each case. In descriptions, minimum value is mentioned first followed by maximum value. Average values are bracketed.

SYSTEMATIC PALEONTOLOGY

Class CONIFEROPSIDA Gifford and Foster 1989

Order CONIFERALES Engler 1897

Genus *Brachyoxylon* Hollick and Jeffrey 1909

Type species. *Brachyoxylon notabile* Hollick and Jeffrey 1909 ; original designation. Upper Cretaceous, Kreischerville, New York, United States of America.

Brachyoxylon currumilii sp. nov.

Figures 1.1–11, 2.1–5, 3.1–4

Diagnosis. Axes with parenchymatic pith and pycnoxylic homoxylic secondary wood. Growth rings of variable width (80–130 cells), with distinct boundaries and abrupt transition from earlywood to latewood; latewood 1–12 cells wide. Tracheid pitting in radial walls of mixed type, predominant-

ly uniseriate, with a separated, contiguous or compressed arrangement. Pits rounded, with a circular aperture, showing a conspicuous torus. Axial parenchyma scanty and diffuse. Cross-fields of araucarioid type, with 4–11 cupressoid pits in two alternate contiguous rows. Rays homocellular, uniseriate, low, 1–10 cells high.

Age. Early–Middle Jurassic (Cañadón Asfalto Formation).

Type locality. “Pomelo” locality, Cerro Cándor area, Chubut Province, Argentina.

Etymology. The specific name is dedicated to Mr. Godofredo Currumil, the farm owner where the “Pomelo” locality is placed.

Holotype. MPEF-Pb 5626, Fossil Collection of the Museo Paleontológico Egidio Feruglio (Trelew, Chubut).

Paratype. MPEF-Pb 5629.

Description. The four studied wood specimens are 10 to 20 cm in diameter, and exhibit an eccentric pith and secondary xylem (Fig. 1.1–2). Primary vascular tissues, secondary phloem and cortex are not preserved in any sample. The pith is circular, 0.3 mm wide, composed of spherical parenchyma cells, 50 μm in diameter, with thin walls (Fig. 1.2). Secondary xylem shows weakly defined growth rings, with an abrupt reduction of the radial diameter of tracheids towards the ring’s outer margin. Growth-ring thickness varies from 80 to 130 cells (Fig. 1.3). Latewood is 1–12 cells thick. Secondary xylem tracheids are rectangular to round in transverse section (Fig. 1.4). When rounded, they are separated by broad intercellular spaces (Fig. 3.1). The radial diameter of earlywood tracheids is 21.5–35 (29) μm and the tangential diameter is 31–42.5 (38.5) μm . The thickness of the double wall between two earlywood tracheids is 3.5–17.5 (10.5) μm in radial section and 11–17.5 (13) μm in tangential section. The radial diameter of latewood tracheids is 8.5–20 (13) μm and the tangential diameter of tracheids is 25–32 (27) μm . The thickness of the double wall between two latewood tracheids is 6–15 (10) μm in radial section and 7.5–15 (11.5) μm in tangential section. The mean number of tracheids that separate the rays is five, with a range of 2–10 rows of tracheids.

Tracheids show mainly uniseriate (95%), rarely biseriate (5%), bordered pits on radial walls (Fig. 1.5–6). Pits are rounded to flattened, with circular apertures provided with a thick torus (Fig. 1.7–8) and, for the most part, with a contiguous or slightly compressed arrangement (Fig. 1.6), in some cases with a spaced organization (Fig. 1.5–6) even leaving wall zones without pitting (Fig. 2.5). When biseriate, they are sub-alternate to opposite (Fig. 2.3–4). This pattern

belongs to a mixed or transitional type of radial pitting *sensu* Philippe and Bamford (2008).

Tracheid wall pits are 10–30 (13.5) μm high and 11–31 (15) μm wide, with pit apertures of 3–12 (6) μm in diameter. Tangential tracheid walls occasionally show bordered pitting similar to radial pitting, but smaller in diameter. Tracheids have very thick cell walls, with spiral fissures, with a spiral angle about 45° (Fig. 3.2–4).

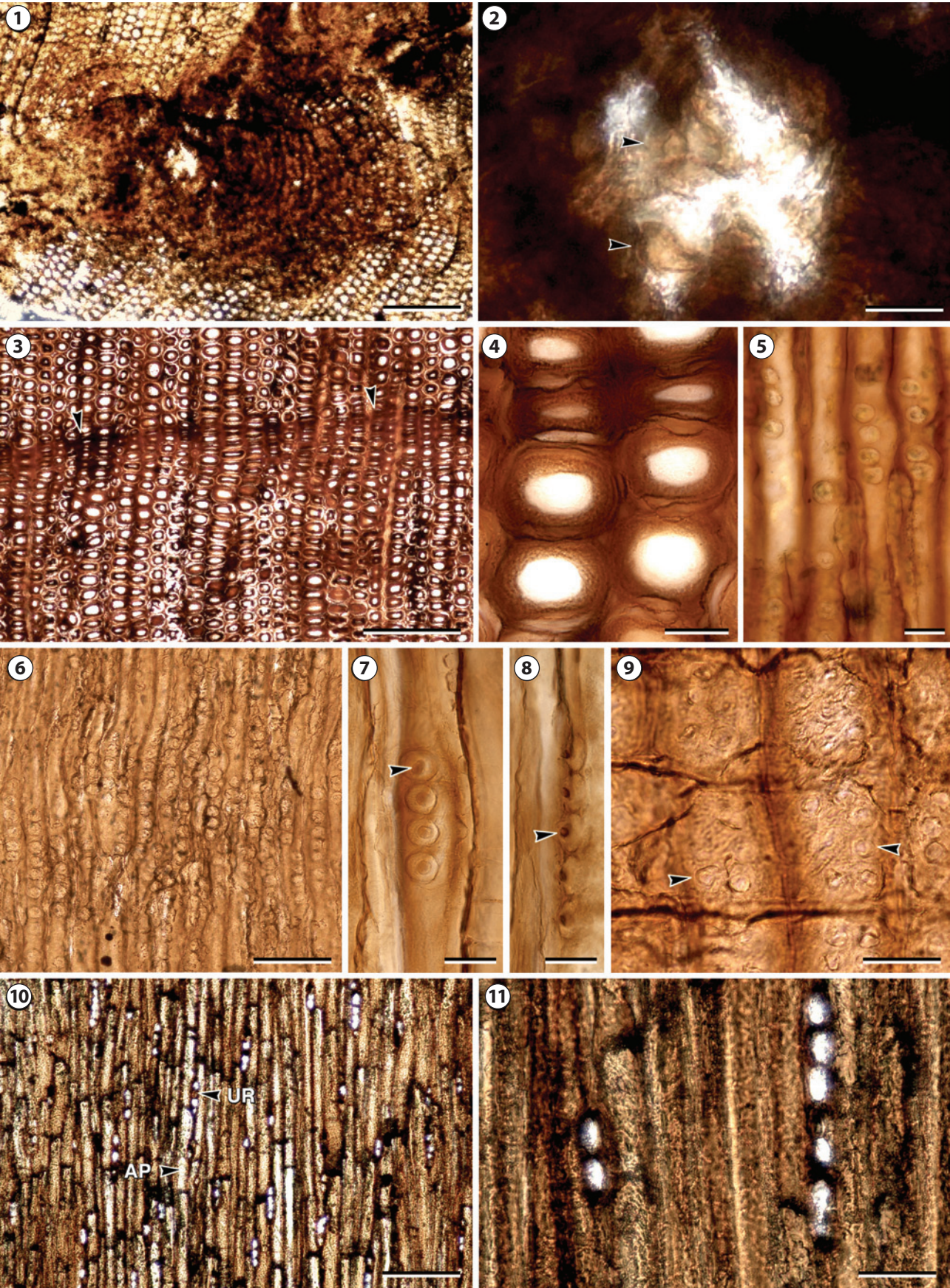
Cross-fields have numerous (4–11) bordered pits with circular or oval outline, 3–14 (7) μm in minor diameter and 4–22 (11) μm in major diameter, contiguous and placed in alternate vertical rows (Figs. 1.9, 2.2). Individual pits are of cupressoid type *sensu* IAWA Committee (2004). Pit aperture is horizontal or oblique. Pit arrangement is of the araucarioid type *sensu* IAWA Committee (2004) (Fig. 1.9).

Secondary xylem rays are homocellular, uniseriate and short with rectilinear trajectory, are 74–234 (102) μm and 1–10 (mode 3; mean 5) cells high (Fig. 1.10–11). They are composed of rectangular parenchyma cells with thin walls, and are 17–33 (27) μm high and 13–32 (21) μm wide. Axial parenchyma is scanty and diffuse (Fig. 1.10) with cells of 234–387 (285) μm high and 33.5–51.5 (42) μm wide.

Branch traces can be recognized in shoots. They are 1 mm diameter in tangential section, and have a rhomboid outline. Around the trace, tracheids and xylem rays are curved or whirled. The centre of the branch trace consists of ray parenchyma cells, many of which have resin contents.

Taxonomic assignment and comparisons

Fossil wood lacking vessels, with bordered pitting on tracheid walls and narrow rays are typical of several Mesozoic wood morphotaxa with coniferophytic affinity (Stewart and Rothwell, 1993). Among them, three morphogenera have been defined to include taxa with mixed radial tracheid pitting and cross-fields with oculipores (=bordered pits) of cupressoid type: *Brachyoxylon* Hollick and Jeffrey (1909), *Zonaloxylon* Grauvogel-Stamm *et al.* (2003) and *Protocupressinoxylon* Eckhold (1921). Mixed radial tracheid pitting distinguishes these three morphotaxa from *Agathoxylon* Hartig 1848, which is characterized by araucarian radial tracheid pitting (see Tab. 1). Nevertheless, according to Philippe and Bamford (2008), *Zonaloxylon* probably have a contiguous pit arrangement, and thus more similar to araucarian pitting. *Protocupressinoxylon* and *Zonaloxylon* are characterized by cross fields with spaced and irregularly arranged oculipores, while *Brachyoxylon* is characterized by cross fields with contiguous and/or compressed and alternately arranged oculipores.



It is interesting to note that Philippe and Bamford (2008) warned that *Protocupressinoxylon* is a nomenclatural synonym of *Protobrachyoxylon* Holden 1913 (Philippe, 1993); as a result, the name *Protocupressinoxylon* is illegitimate. Moreover, the circumscription of its legitimate nomenclatural synonym (*Protobrachyoxylon*) is doubtful since it is a probable junior taxonomical synonym of *Brachyoxylon* (Philippe, 2002).

Brachyoxylon was originally described for Cretaceous wood remains from Kreischerville (New York), and it is defined as a wood with radial tracheid pits not all alternating or mutually flattened, but more frequently of rounded configuration and not contiguous, resiniferous elements characteristically absent, and cross fields with araucarioid type pitting (Hollick and Jeffrey, 1909). On the basis of its broader diagnosis, fossil woods from Permian to Upper Cretaceous rocks in North America, Scandinavia, Great Britain, Central and Southeastern Europe, Southeast and Eastern Asia, North and Central Africa, South America and Antarctica have been assigned to *Brachyoxylon* (see Philippe *et al.*, 2004a). The genus is abundant in Early and Middle Jurassic sediments from all over the world but particularly in the Jurassic summer wet zone; however, *Brachyoxylon* is far less common in Gondwana than in boreal areas (Philippe *et al.*, 2004a).

The presence or absence of axial parenchyma and crassulae, ray heights, and number of pits per cross fields, are used to separate species within *Brachyoxylon* (Tab. 2). Species comparisons are presented in Table 2, excluding those transferred to other genera or not properly described (Iamandei and Iamandei, 2005; Philippe, 1993, 1995). Thus, *B. currumilii* results more comparable and similar to the type species *B. notabile* in ray height and number of cross-field pits, but differs in the presence of axial parenchyma, absence of crassulae, and tracheid pit arrangement (frequently contiguous in the new species, mostly separated in the type species). Consequently, we propose to place the specimens of Chubut in a new species of *Brachyoxylon*.

Previous records of *Brachyoxylon* in Argentina are from the Early Jurassic Roca Blanca Formation and the Early Cretaceous Anfiteatro de Ticó Formation in Santa Cruz Province, southern Patagonia (Gnaedinger *et al.*, 2009; Vera and

Césari, 2012). The first is represented by a fossil wood not identified at the species-level, characterized by the presence of mixed type of radial tracheid pitting, with equally frequent uniseriate and biseriate pits, araucarioid cross-fields with eight cupressoid pits, uniseriate rays, and axial parenchyma (S.G. pers. obs.), differing thus from *B. currumilii* in frequency of biseriate tracheid pits. The Early Cretaceous specimens were assigned with doubts to *B. boureauii* Serra 1966, originally described from the Late Jurassic of Asia (see Philippe *et al.*, 2004b). They are characterized by having mixed radial tracheid pitting with uniseriate and less commonly biseriate and triseriate pits, araucarioid cross-fields with 8–26 pits, and rays exclusively uniseriate, 1–9 cells high (Vera and Césari, 2012). Axial parenchyma was not mentioned. The Cañadón Asfalto species instead has more common biseriate pits and a number of pits per cross-field ranging from 4 to 11.

DISCUSSION

Character considerations

Of particular interest in *Brachyoxylon currumilii* sp. nov. is the presence of a torus-margo structure on radial tracheid walls. Jefferson (1982) observed that the torus can be preserved when the pit aperture is blocked and the pit chamber is unfilled, and fractures between cell walls expose the internal surfaces of both halves of the pit-pair. In this case, the internal surface of the pit-pairs remains concave. The torus is preserved as a circular to disc-shaped body in the center of the pit aperture, as illustrated by Jefferson (1982, text-fig. 3a-d, tab. 1). In *B. currumilii* the torus preservation is comparable with this example.

Torus-margo pit membranes are scarcely mentioned in the literature on Mesozoic woods (*e.g.*, Wheeler and Lehman, 2005; Yoona and Kimb, 2008). However, the development of a torus-margo structure has been crucial in the evolution of conifer secondary xylem, allowing conifers to compete with angiosperms by means of an efficient water transport system (Pitterman *et al.*, 2005; Brodribb *et al.*, 2012).

Torus-margo pits are specializations associated with rounded or oval-shaped pits in narrow xylem conduits, par-

Figure 1. 1–10, *Brachyoxylon currumilii* sp. nov. View under optical microscope; **1**, MPEF-Pb 5626 b Tr II, cross section showing the narrow pith (heads of arrows); **2**, MPEF-Pb 5626 b Tr II, detail of the pith, arrow points to parenchyma cells; **3**, MPEF-Pb 5629 b Tr II, cross section of growth ring boundary (heads of arrows); **4**, MPEF-Pb 5626 a Tr I, detail of tracheid shape in cross section; **5**, MPEF-Pb 5629 a Rd I, radial section of tracheids with spaced to contiguous organization of radial pitting; **6**, MPEF-Pb 5626 a Rd I, general view of radial section, showing the pattern of radial tracheid pitting, which varies from spaced to contiguous and compressed; **7**, MPEF-Pb 5629 a Rd II, detail of radial bordered pits and torus (head of arrow); **8**, MPEF-Pb 5629 a Rd II, torus in lateral view (head of arrow); **9**, MPEF-Pb 5626 a Rd I, araucarioid cross field, arrow points to one individual bordered pit; **10**, MPEF-Pb 5629 a Tg I, tangential section with uniseriate rays (UR) and axial parenchyma (AP); **11**, MPEF-Pb 5629 a Tg I, detail of two uniseriate rays. Scale bar: 60 µm. Scale bar: **1**=600 µm; **2**=100 µm; **3**= 200 µm; **4, 7, 8, 9**= 20 µm; **5**= 30 µm; **6**= 160 µm; **10**= 250 µm; **11**= 60 µm.

ticularly tracheids (Hacke *et al.*, 2004; Bodribb *et al.*, 2012). The torus is an impermeable, typically lignin-based thickening at the center of the pit membrane, which is somewhat larger in diameter than the pit apertures. It is surrounded by the thin part of the pit membrane, the margo, which consists of bundles of cellulose microfibrils, most of them radiating from the torus (Evert, 2006). The function of the torus is to restrict the movement of water through the pit-pair in case of air entry, protecting the membrane from ‘air seeding’ and potential blockage, since water refilling cannot occur if new bubbles and cavitation develop (Evert, 2006; Bodribb *et al.*, 2012). The extremely low resistance of water passing

through torus-margo membrane implies that the hydraulic efficiency of torus-margo bearing plants equals or, in some cases, surpasses that of vessel elements, whose hydraulic efficiency is more connected to their much greater length and width (Hacke *et al.*, 2004; Sperry and Hacke, 2004; Bodribb *et al.*, 2012). It is interesting to note that margo porosity varies substantially among conifer families. The Cupressaceae may exhibit very thick margo regions while the Pinaceae have pits with very porous margos that are clearly differentiated from the torus (Bauch *et al.*, 1972). The margo is a very delicate membrane, and as a result of permineralization (see Jefferson, 1987) it can lose its original structure. Incident-

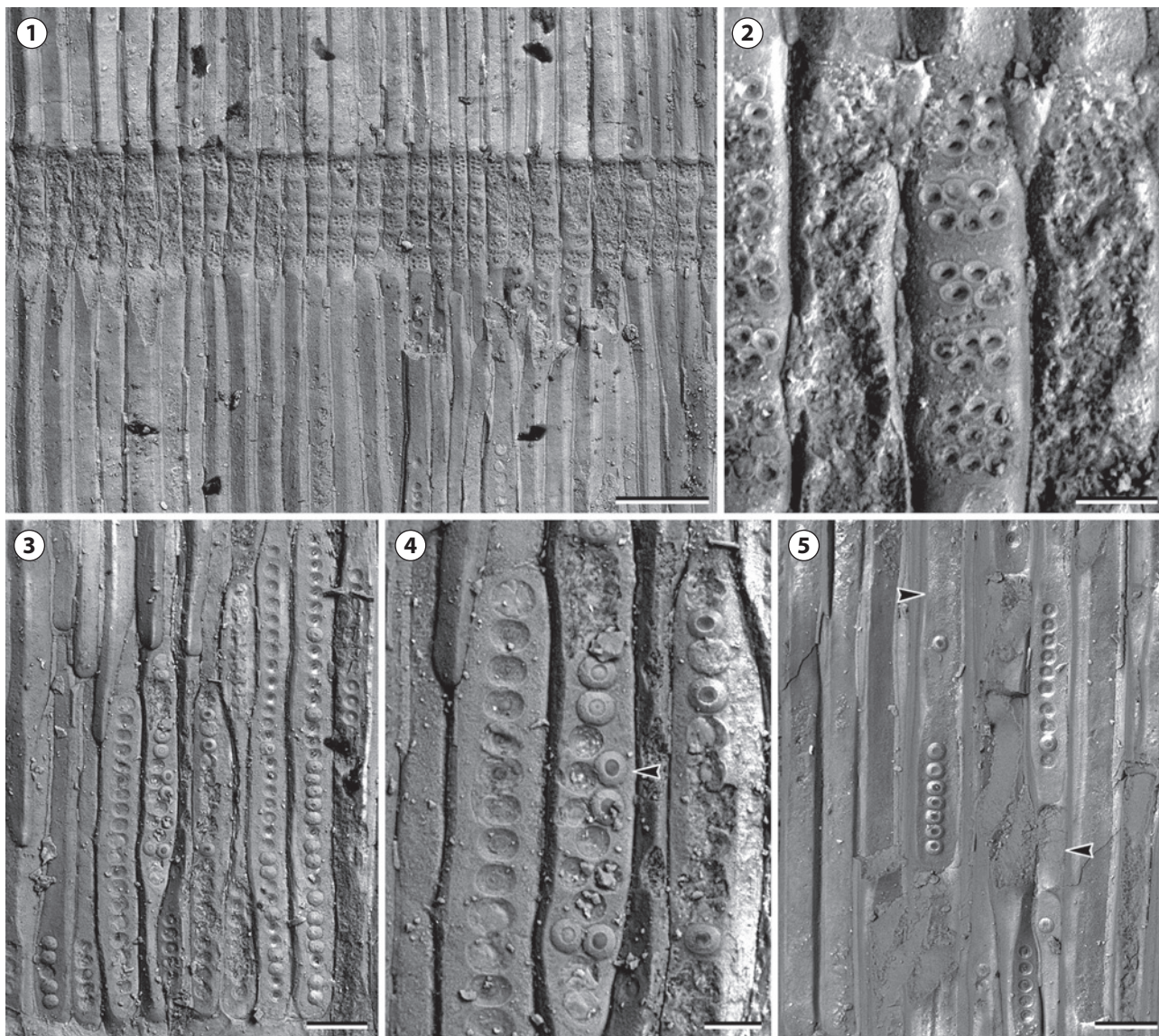


Figure 2. 1-5, *Brachyoxylon currumilii* sp. nov. MPEF-Pb 5629. View under scanning Electron Microscope; **1**, general view of radial section; **2**, detail of araucarioid cross fields; **3**, mixed pattern of radial tracheid pitting; **4**, detail of radial bordered pits and torus (heads of arrows), showing compressed uniseriate pits, and subalternate and opposite biseriate pits; **5**, radial walls of tracheids, showing areas with uniseriate compressed radial pits, and areas without pitting (heads of arrows). Scale bar: **1**= 120 µm; **2**, **4**= 20 µm; **3**= 50 µm; **5**= 100 µm.

tally, margo porosity has not been clearly established in *B. currumilii*.

From a systematic point of view, torus-margo pitting has been mentioned as a potentially synapomorphic character among conifers and other gymnosperms including *Ginkgo* and Gnetales (Magallón and Sanderson, 2002; Doyle, 2006). Torus-like structures have also been found in several species of eudicots (Coleman *et al.*, 2004). Bauch *et al.* (1972) mentioned six structural types of bordered pit membranes in terms of margo and torus morphology and configuration. Subsequently, Doyle (2006) proposed that types 1–4 of bordered pit membranes with a torus to be considered on a single state based on the overlap in the systematic distribution of taxa showing those types. On the other hand, types 5 and 6 were also considered as a single state of pit membranes without torus. A second distinction of torus types considered the presence or absence of a scalloped torus (IAWA Committee, 2004). The presence of a well-developed scalloped torus is a diagnostic character only for the genus *Cedrus* DuRoi (Pinaceae) and therefore it lacks important systematic value in the context of conifer broad evolution.

In addition to margo porosity, other features such as the relative thickness of the torus compared to the margo varies among conifer families (Bauch *et al.*, 1972). For instance, the torus in Araucariaceae and Podocarpaceae seems to be thinner than in Cupressaceae and Pinaceae (Pittermann *et al.*, 2006). In the case of *Brachyoxylon currumilii* the torus looks unspecialized and thick (Fig. 1.7–8, 2.4) and not scalloped. In order to fully understand the systematic value of the torus, a characterization of its occurrence and main features in extinct gymnosperm genera and families needs to be evaluated.

An additional interesting well-preserved character in *Brachyoxylon currumilii* is the presence of compression wood,

megascopically identified by means of eccentric growth rings. Compression wood is present in gymnosperms, and differs from tension wood found in angiosperms (Hellgren *et al.*, 2004). Both of them are types of reaction wood that have the effect of maintaining the position of the axes (Wardrop and Dadswell, 1955) even though increasing weight or other factors tending to change it (Carlquist, 2001). Microscopically, compression wood cells are significantly shorter and more rounded, and show intercellular spaces (Burgert *et al.*, 2004). The innermost layer of the secondary wall —also known as S3 layer (Esau, 1965; Sachs, 1965) or tertiary wall (see Liese and Johann, 1954)— is lacking, whereas the microfibril angle in the middle layer of secondary walls (=S2 layer, see Esau, 1965; Sachs, 1965) and the lignin content are significantly higher than in normal wood tracheids (Côte and Day, 1965). Furthermore, spiral thickenings or helical cavities are observed in the compression wood of gymnosperm species (Yoshizawa *et al.*, 1982; Timell, 1983; Yoshizawa and Idei, 1987). Generally, compression wood is formed on the side exposed to mechanical stress, whereas tension wood forms on the side that is “pulled”. Compression wood forms in the bend on the opposite side of the applied force, thereby lengthening/straightening the bend (Schweingruber, 2007). Consequently, it can be inferred that this side of the shoot was the subject of mechanical stress as it was the lower side of a branch. Typical traits of compression wood, such as very thick cell walls round in cross-section and divided by intercellular spaces, spiral-shaped secondary wall microfibrils with a spiral angle about 45°, and intertracheid spiral fissures, are recognized in the smaller shoots of *B. currumilii* (Fig. 3).

Spiral structures in secondary walls of fossil wood may be product of decay processes (see Jefferson, 1987). Nonetheless, studied specimens exhibit other additional characters that suggest their interpretation as compression wood.

TABLE 1. Comparison between fossil wood morphogenera with mixed or araucarian radial tracheid pitting and cross fields with oculipores of cupressoid type.

	Agathoxylon	Brachyoxylon	Zonaloxylon	Protocupressinoxylon
Tracheid radial pitting	araucarian	mixed	mixed	mixed
Axial parenchyma	occasionally present	generally absent	absent	occasionally present
Cross-field pits	cupressoid	cupressoid	cupressoid	cupressoid
Number of pits per cross-field	numerous	numerous	2–4	2–4
Arrangement of cross-field pits	contiguous, unordered or alternate	contiguous, unordered or alternate	spaced, ordered never alternate	spaced, ordered never alternate
Stratigraphic distribution	Lower Permian–Oligocene	Permian–Upper Cretaceous	Middle Triassic	Lower Jurassic–Lower Cretaceous

Systematic affinity

The genus *Brachyoxylon* was formally described by Hollick and Jeffrey (1909) and characterized by “radial pits not all alternating or mutually flattened as in *Araucarioxylon*

Kraus, but as often or more frequently of rounded configuration and not contiguous; the alternating or flattened condition of the radial pits generally confined to the terminal walls of the tracheids; resiniferous elements characteristically absent; wounds

TABLE 2. Comparative table of species of the genus *Brachyoxylon*.

Species	Age	Distribution	False GR	Resin ducts	Tg TP	Rd TP	Ax Pa	Cr	Rays (height)	CFP
B. notabile Hollick and Jeffrey 1909	Upper Cretaceous	USA	A	T	P	mixed 1–2 seriate	A	P	1 seriate (1–8 cells)	5–11 cupressoid
B. woodworthianum Torrey 1923	Lower Cretaceous	USA	A	A	A	mixed	A	A	1 seriate (high) 2-pluriseriate (low)	cupressoid
B. brachyphylloides (Torrey 1923) Kraüsel 1949	Middle Jurassic-Cretaceous	Tunisia, Nigeria, Chad, USA	A	T	P	mixed 1–2 seriate	A	A	1-partially 2 seriate (1–20 cells)	1–10 cupressoid
B. japonicum (Shimamura 1937) Kraüsel 1949	Lower Cretaceous	Japan	A	At	P	mixed 2–3 seriate	A	A	1 seriate (50–60 cells)	cupressoid
B. saurinii Boureau and Serra 1961	Jurassic (?)	Cambodia	A	T	A	mixed 1–2 seriate	A	A	1 seriate (1–31 cells)	2–12 cupressoid
B. boureauii Serra 1966	Jurassic (?)	Cambodia	A	A	A	mixed 1–2 seriate	A	A	1 seriate (low)	4–36 cupressoid
B. nonakai Yamazaki and Tsunada 1981	Upper Jurassic	Japan	A	A	A	opposite 2–4 seriate	A	A	1 seriate (unknown)	cupressoid
B. lagonense (Laudouéneix 1973) Dupéron-Laudouéneix 1991	Cretaceous	Chad	A	T	A	mixed 2–3 seriate	A	A	1 seriate (low)	cupressoid
B. traatii (Barale 1981) Philippe 1995	Middle Jurassic	France	P	A	P	mixed 1–2 seriate	A	A	1 seriate (low)	4–9 cupressoid
B. liebermanii Philippe 1995	Jurassic	France	P	A	P	mixed 1 seriate	A	A	1 seriate (low)	5–12 cupressoid to podocarpoid
B. eboracense (Holden 1913) Philippe 2002	Jurassic	England	A	A	A	mixed 1–2 seriate	A	A	1 seriate, (low)	numerous cupressoid
B. orientale (Serra 1969) Philippe et al. 2004b	Lower Cretaceous	Tibet	P	A	A	mixed 1–2 seriate	A	A	1 seriate (low)	3–10 podocarpoid
Brachyoxylon sp. A Philippe et al. 2004b	Late Jurassic	Thailand	P	A	P	mixed 1–2 seriate	A	A	1 seriate (low)	up to 12 cupressoid
B. avramii Iamandei and Iamandei 2005	Early Cretaceous	Romania	A	T	R	mixed, 1–2 seriate	A	A	1 seriate (1–21 cells)	1–8 cupressoid
B. dobrogiacum Iamandei and Iamandei 2005	Early Cretaceous	Romania	A	A	P	mixed 1–3 seriate	P	P	1 seriate (1–10 cells)	1–6 cupressoid
B. semibiseriatum (Pant and Singh 1987) Kurzawe and Merlotti 2010	Permian	Brazil	A	P	P	mixed 1–5 seriate	A	A	1 seriate (1–38 cells)	4–16 cupressoid
B. serrae Philippe et al. 2011	Lower Cretaceous	Thailand	A	T	P	mixed 1–2 seriate	A	A	1 seriate (1–15 cells)	5–16 cupressoid

Abbreviations: **GR**, growth rings; **Tg TP**, tangential tracheid pitting; **Rd TP**, radial tracheid pitting **Ax Pa**, axial parenchyma; **Cr**, crassulae; **CFP**, cross field pits; **P**, present; **A**, absent; **T**, traumatic; **R**, rare.

leading to the formation of traumatic resin canals, which are not present under any conditions in *Araucarioxylon Kraus*". Other features pointed out by Hollick and Jeffrey (1909) are the presence of annual rings, tangential pitting of the tracheids, and medullary ray cell walls smooth except those in contact with the tracheids. This last trait is interpreted as cross field of the araucarioid type by Philippe and Bamford (2008).

In terms of its systematic affinity, *Brachyoxylon* was first linked to Araucariaceae (Hollick and Jeffrey, 1909) due to some similarity with *Agathoxylon* (= *Araucarioxylon*)-type woods, and to Cupressaceae (Seward, 1919). More recently it was considered as a conifer *incertae sedis* (Philippe and Bamford, 2008) of the protopinaceous type (*sensu* Kräusel, 1949). However, *Brachyoxylon* has been more frequently related to Cheirolepidiaceae based on its frequent co-occurrence with other organs (*e.g.*, pollen, seed cones, leaves) assignable to this extinct conifer family (*e.g.*, Alvin *et al.*, 1981; Alvin, 1982; Machhour and Pons, 1992; Limarino *et al.*, 2012). In fact, the type species of *B. notabile* Hollick and Jeffrey was related to *Brachyphyllum macrocarpum* Newberry 1896, a possible Cheirolepidiaceae (Alvin, 1982).

Alvin *et al.* (1981) summarized the attributes of the wood assigned to Cheirolepidiaceae as follows: (1) tracheid pitting of mixed type, (2) cross-field pitting of several to numerous cupressoid pits, (3) absence of axial parenchyma (this can be refuted, since many of the cells mentioned as septate tracheids by these authors are actually vertical rows of parenchyma cells), and (4) ray cells with resinous deposits. From these features, mixed tracheid pitting has been reported from all wood attributed to the Cheirolepidiaceae (Axsmith, 2006). Four fossil wood taxa have been related to this family (Tab. 3): *Protocupressinoxylon* Eckhold 1921, *Protopodocarpoxylen* Eckhold 1921, *Brachyoxylon* and *Agathoxylon* Hartig 1848 (Harris, 1979; Alvin *et al.*, 1981; Zhou 1983). The last case has been indirectly linked to Cheirolepidiaceae as a consequence of the transference of the species *Brachyoxylon desnoyersii* Lemoigne 1968 to *Agathoxylon* (Philippe, 1995). Nevertheless, as pointed out by Alvin *et al.* (1981), the wood of neither *Agathoxylon* (= *Brachyoxylon*) *desnoyersii* nor *B. notabile* is associated to the family with certainty. On the other hand, the validity of *Protocupressinoxylon* (see above) and *Protopodocarpoxylen* (see Bamford and Philippe, 2001; Philippe *et al.*, 2002) has been questioned and extensive revision is needed in order to clearly circumscribe the use of these names. In any case, fossil wood assigned to these genera shows features that relate with the Cheirolepidiaceae (Tab. 3).

Additional evidence of the occurrence of Cheirolepidiaceae has been recovered from the Cañadón Asfalto Basin in Chubut Province, Argentina. For instance, cheirolepidiaceous pollen grains (*i.e.*, *Classopollis* spp.) clearly dominate the spectrum in the Cañadón Asfalto and Cañadón Calcáreo formations (Volkheimer *et al.*, 2008; 2009; Olivera, 2012). Moreover, from the same plant horizons of the former unit, cutinized seed cones of possible cheirolepidiaceous alliance have been observed (authors pers. obs.).

The recently described seed-cone species *Pararaucaria delfueyoi* Escapa *et al.*, 2013 from the Upper Jurassic Cañadón Calcáreo Formation has been related to the conifer family Cheirolepidiaceae (Escapa *et al.*, 2013). Together with the type species *Pararaucaria patagonica* Wieland 1929 from the Middle Jurassic of Santa Cruz Province (see Stockey, 1977) they represent the first evidence of cheirolepidiaceous permineralized seed-cones (Escapa *et al.*, 2012), allowing to compare anatomical features in the cone axis with the fossil

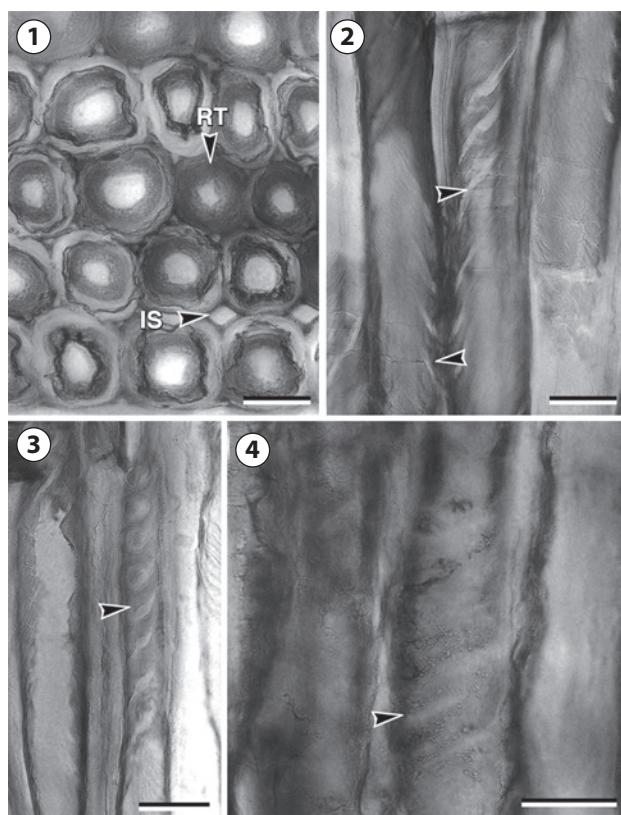


Figure 3. 1-4, *Brachyoxylon currumilii* sp. nov. Compression wood under a fluorescence microscope; **1**, MPEF-Pb 5626 a Rd I, cross section of secondary xylem tracheids, which are markedly rounded (RT) and they have broad intercellular spaces (IS); **2**, MPEF-Pb 5629 a Rd II, radial walls of secondary xylem tracheids, showing spiral fissures in a 45° angle (heads of arrows); **3**, MPEF-Pb 5629 a Rd I, same fissures on the radial wall of latewood tracheids (head of arrow); **4**, MPEF-Pb 5629 a Rd I, internal view of same fissures. Scale bar: **1, 2, 4**= 20 µm; **3**= 40 µm.

wood classically assigned to Cheirolepidiaceae. The central axis on both *Pararaucaria* species presents secondary xylem without resin canals, tracheids with generally uniseriate and circular bordered pitting walls and uniseriate rays (Stockey, 1977; Escapa *et al.*, 2013). Even when these general features are mostly coincident with respect to the wood here described, a more detailed description of central axis anatomy in cheirolepidaceous seed-cones will be necessary in order to establish connections between these organs.

Brachyphyllum Brongniart 1828 is a common fossil genus occurring in most formational units of the Cañadón Asfalto Basin (pers. obs.) and frequently linked to Cheirolepidiaceae (Harris, 1979; Watson, 1988; Taylor *et al.*, 2009). However, the general morphology of *Brachyphyllum* is highly homoplastic; in absence of additional evidence (*i.e.*, anatomy, cuticle) they may represent foliage of different conifer families (*e.g.*, Araucariaceae).

Altogether considered, the fossil record with cheirolepidaceous affinity in the Jurassic of Patagonia is amongst the best represented worldwide, and offers a major opportunity to understand relationships between isolated organs pointing to the recognition of whole plants. In this regard, Jurassic fossil plant localities from the Cañadón Asfalto Basin in central Patagonia, which range in age from the Early through the Late Jurassic, represent a unique chance of uncovering unprecedented evolutionary traits for this extinct conifer family that may hide major surprises in terms of conifer evolution.

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TABLE 3. Comparison between wood of some Cheirolepidiaceae plants and Cañadón Asfalto wood.

Name of reconstruction (wood type)	GR	Latewood width	Rd TP	SPT	Ax Pa	Type of CFP	CFP number	Ray width	Ray height	Resinous ray cells
Hirmerella muensteri (Schenk) Jung 1968 (Protocupressinoxylon sp.)	I	?	mixed	?	A	cupressoid	3–8	probably all 1seriate	1–8 cells	?
Frenelopsis oligostomata Romariz 1946 (Protopodocarpoxylon aveiroense Lauer- jat and Pons 1978)	D	<4 cells	mixed	A	A	podocarpoid	1–13	mostly 1seriate	1–16 cells	P
Pseudofrenelopsis parceramosa (Fontaine) Watson 1977 (Protopodocarpoxylon sp.)	U	2–4 cells	mixed	P	P	podocarpoid to cupressoid	1–17	mainly 1seriate	1–14 cells	P
Suturovagina intermedia Chow and Tsao 1977 emend. Zhou 1983 (Protopodocarpoxylon sp.)	U	4–6 cells	mixed	O	A	podocarpoid to cupressoid and taxodoid	2–8	probably all 1seriate	1–9 cells	P?
Protocupressinoxylon purbeckensis Francis 1983	D	3–4 cells	mixed	A	A	cupressoid	2–7	probably all 1seriate	2–9 cells	P
Brachyphyllum desnoyersii (Brogniart) Saporta 1884 (Agathoxylon (= Brachyoxylon) desnoyersii (Lemoigne) Philippe 1995)	D	3 cells	araucarian	A	A	cupressoid	4–10	all 1seriate	2–4 cells	A
Brachyphyllum macrocarpum Newberry 1895 (Brachyoxylon notabile Hollick and Jeffrey 1909)	D	?	mixed	A	A	cupressoid	5–11	all 1seriate	1–8 cells	A
Brachyoxylon currumili sp. nov	D	1–12 cells	mixed	P?	P	cupressoid	4–11	All 1seriate	1–10 cells	A

GR, growth rings; Rd TP, radial tracheid pitting; SPT, septate tracheids; Ax Pa, axial parenchyma; CFP, cross field pits; P, present; A, absent; I, inconspicuous; D, distinct; U, uneven; O, occasional; ?, with doubts.

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