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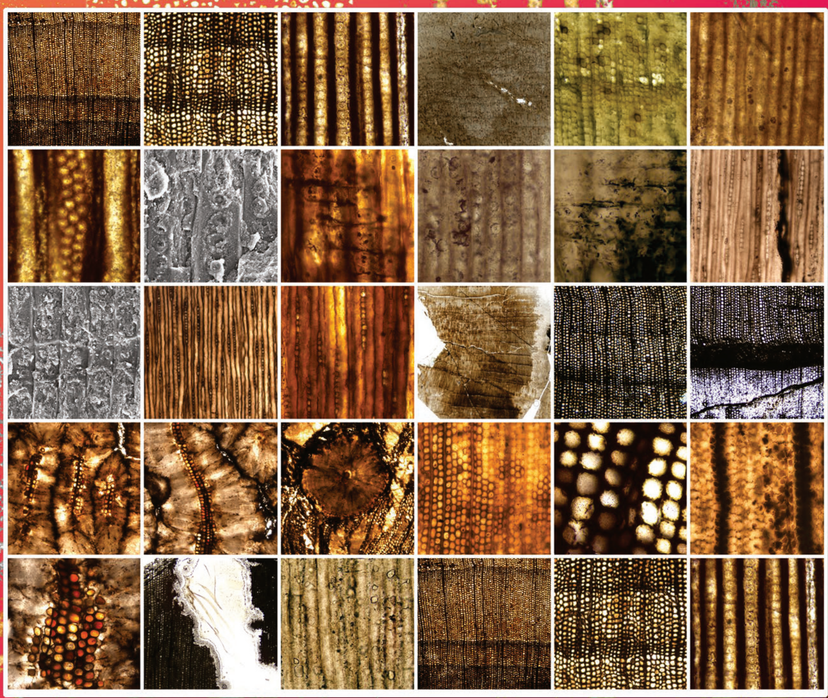

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ABSTRACT

An assemblage of 22 silicified wood specimens collected from the Cerro Grande and Arroyo Blanco localities (Lago La Plata and Tres Lagunas formations, Late Jurassic-Early Cretaceous), in the Fontana Lake area (Chubut Province, Argentine Patagonia), is described. The specimens consist of decorticated secondary xylem. Thirteen specimens have araucarian pits in the radial walls of tracheids and araucarioid cross-fields, allowing their assignment to *Agathoxylon* Hartig, a fossil-genus related to the Araucariaceae Henkel & W. Hochst. Two specimens, with non-contiguous pits in the tracheid radial walls, are assigned to an 'indeterminate abietinean type'. The remaining seven specimens could not be identified taxonomically due to poor preservation, although they have general conifer anatomical features. The size of the specimens and the curvature of their growth rings indicate that they came from large trees. Distinct growth ring boundaries observed in most specimens suggest annual seasonality. In addition, some specimens have false rings and patterns of wood decay. The wood assemblage suggests a forest dominated by Araucariaceae in the Fontana Lake area near the Jurassic-Cretaceous boundary.

KEY WORDS
Agathoxylon,
wood anatomy,
Lago La Plata Formation,
Tres Lagunas Formation,
Kimmeridgian,
Tithonian,
Hauterivian.

RÉSUMÉ

Assemblage de bois de conifères du Jurassique supérieur-Crétacé inférieur de la région du lac Fontana, province de Chubut, Patagonie argentine.

Un assemblage de 22 spécimens de bois silicifiés collectés dans les localités de Cerro Grande et d'Arroyo Blanco (formations Lago La Plata et Tres Lagunas, Jurassique supérieur-Crétacé inférieur), dans la région du lac Fontana (province de Chubut, Patagonie argentine), est décrit. Les spécimens sont constitués de xylème secondaire décortiqué. Treize spécimens présentent des ponctuations araucariennes dans les parois radiales des trachéides et des champs de croisements araucarioïdes, permettant leur attribution à *Agathoxylon* Hartig, un genre fossile apparenté aux Araucariaceae Henkel & W.Hochst. Deux spécimens, présentant des ponctuations non contiguës dans les parois radiales des trachéides, sont attribués à un « type abiétinien indéterminé ». Les sept spécimens restants n'ont pas pu être identifiés taxonomiquement en raison d'une mauvaise conservation, bien qu'ils présentent les caractéristiques anatomiques générales des conifères. La taille des bois fossiles et la courbure de leurs cernes de croissance indiquent que les spécimens proviennent de grands arbres. Les limites distinctes des cernes de croissance observées chez la plupart des spécimens suggèrent une saisonnalité marquée. De plus, certains spécimens présentent de faux anneaux de croissance et des motifs de pourriture du bois. L'assemblage du bois suggère une forêt dominée par les Araucariaceae dans la région du lac Fontana, près de la limite Jurassique-Crétacé.

MOTS CLÉS
Agathoxylon,
anatomie du bois,
Formation Lago La Plata,
Formation Tres Lagunas,
Kimméridgien,
Tithonien,
Hauterivien.

INTRODUCTION

The formation of a volcanic arc on the western edge of Patagonia during the Middle Jurassic-Late Jurassic produced large volumes of lava that covered the pre-existing topography (Macdonald *et al.* 2003; Spalletti & Franzese 2007). In addition, Jurassic marine ingressions from the Pacific Ocean produced climatic changes that favored the creation of new regional paleoenvironments that impacted the development and distribution of flora throughout the Late Jurassic-Early Cretaceous in the southwestern part of Gondwana (Del Fueyo *et al.* 2007; Iglesias *et al.* 2011).

Megafloristic and palynological studies from the Jurassic and Cretaceous of Patagonia show that continental paleoecosystems were composed of gymnosperms (conifers, cycads, pteridosperms, and ginkgoaleans), ferns, lycophytes, equisetaleans, and freshwater phytoplankton (Del Fueyo *et al.* 2007; Iglesias *et al.* 2011). Conifers related to the Araucariaceae Henkel & Hochst., Hirmeriellaceae Harris (= Cheirolepidiaceae Turotanova-Ketova), and Podocarpaceae Endl. would have dominated the arboreal stratum, forming monospecific or mixed forests (Del Fueyo *et al.* 2007; Iglesias *et al.* 2011).

Fossil wood records from the Late Jurassic and the lowest Early Cretaceous of Argentine Patagonia are scarce and isolated. To date, only woods related to the Araucariaceae have been described from the Middle Jurassic-Late Jurassic (Chon Aike Formation, Santa Cruz Province) by Sagasti *et al.* (2019). The lowest Early Cretaceous records are represented by fossil woods related to *Podocarpoxylon* Gothan from Mulichinco Formation (Valanginian, Neuquén Province) (Gnaedinger *et al.* 2017), *Agathoxylon* Hartig, *Brachyoxylon* Hollick & Jeffrey, putative *Cupressinoxylon* Göppert, and indeterminate conifers from Tres Lagunas Formation (Tithonian-?Hauterivian, Chubut Province) (Greppi *et al.* 2020), and *Agathoxylon* and an indeterminate gymnosperm from Springhill Formation (Berriasian-Valanginian, Santa Cruz Province) (Carrizo & Del Fueyo 2015; Del Fueyo *et al.* 2021).

This contribution describes an assemblage of fossil woods from the Fontana Lake area (Late Jurassic-Early Cretaceous). The assemblage is compared with coeval records from South America and Antarctica, contributing to a better understanding of the Mesozoic forests from southern South America.

GEOLOGICAL SETTING

The study area is framed within the so-called Aysén Basin/Río Mayo Embayment (ARB) in the Patagonian Andes of the Chubut Province. The stratigraphy of the ARB comprises the volcanic rocks of the Lago La Plata Formation and the sedimentary and volcanic rocks of the Coyhaique Group, defined in Chile (Fig. 1; Ramos 1981; Suárez *et al.* 1996; Iannizzotto *et al.* 2004).

In Argentina, the Coyhaique Group crops out southwest of Chubut Province and comprises the Tres Lagunas, Katterfeld, and Apeleg formations (Fig. 1; Ramos 1981). It corresponds to a Tithonian-Aptian (Late Jurassic-Early Cretaceous) sedimentary cycle (Olivero 1982; Scasso 1987, 1989; Depine & Ramos 2004; Rolando *et al.* 2004; Gianni *et al.* 2020). In addition, in Chile, the Ibáñez and Toqui formations are respectively equivalent to the Lago La Plata and Tres Lagunas formations (Escosteguy *et al.* 2024).

The studied fossil woods come from the Cerro Grande and Arroyo Blanco localities in the southern margin of Fontana Lake (Fig. 2). The succession in both localities is mainly characterized by thick beds of tuffs, breccias, lavas, and conglomerates with some interbedded sandstones and shales (Olivero 1982; Marshall *et al.* 1984). The Cerro Grande succession, assigned to the Lago la Plata Formation (Rolando *et al.* 2004), is composed of breccias with large silicified trunks, some in possible life position, together with shale beds with abundant fossil leaves (Marshall *et al.* 1984). The beds of Arroyo Blanco locality, assigned to the Tres Lagunas Formation, contain abundant sandstone beds with marine fauna (e.g., cephalopods, bivalves, corals, etc.), while the fossil woods are found in conglomerates (Olivero 1982).

Studies indicated an age between 136-151 Ma (Kimmeridgian-Valanginian) for the Ibáñez and Lago La Plata Formations (Rolando *et al.* 2004; Suárez *et al.* 2009). However, SHRIMP U-Pb studies on zircons from tuffs of the equivalent Toqui Formation in Chile provided ages between 132-153 Ma and, together with the ammonite fauna, point to a Tithonian-?Hauterivian age (Suárez *et al.* 2009, 2015), the age currently assigned to the Tres Lagunas Formation (Escosteguy *et al.* 2024). According to the radiometric ages, the Tres Lagunas and Lago La Plata formations are almost synchronous and were deposited during the Tithonian-Valanginian/Hauterivian? (Escosteguy *et al.* 2024). Consequently, a Late Jurassic-Early Cretaceous age is assigned to the fossil woods.

According to Olivero (1982) and Scasso (1987, 1989), the Lago La Plata and Tres Lagunas formations were deposited in a shallow marine environment around volcanic islands with active volcanism contemporaneous with the sedimentation. High relief due to synchronic tectonism led to marked lateral facies changes and deposition was partially driven by gravity flows, in the Late Jurassic-Early Cretaceous stage of the basin evolution (Scasso 1987, 1989). Rapid volcaniclastic sedimentation and diastrophism led to marked relative sea-level variations, and intercalations of terrestrial sediments are not rare, as is shown in the Cerro Grande locality, where large silicified trunks in possible a life position are immersed in volcanic rocks lacking marine fossils, suggesting fully continental deposition (Quartino 1952; Olivero 1982; Marshall *et al.* 1984).

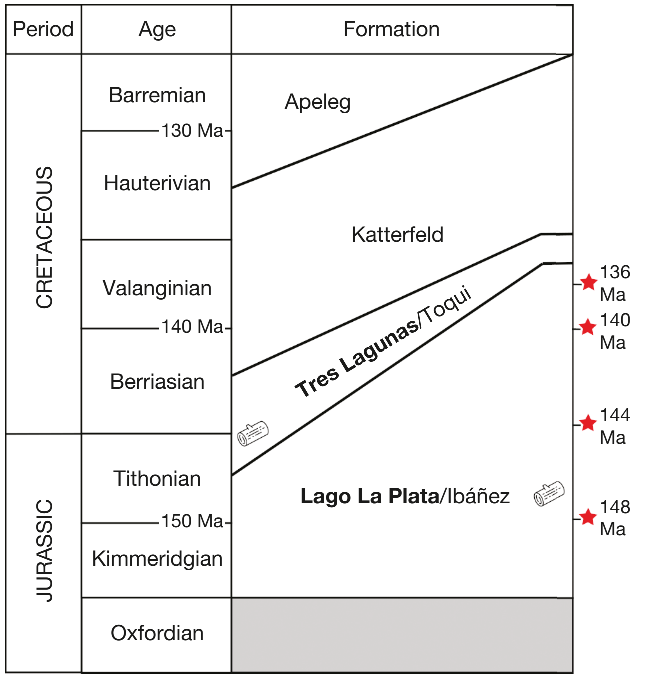

Fig. 1. — Stratigraphic chart of Fontana Lake area (modified from Suárez *et al.* 2009). **Red stars**, SHRIMP U-Pb studies from Lago La Plata/Ibañez Formation (Rolando *et al.* 2004; Suárez *et al.* 2009); **Wood symbol**, stratigraphic position of the fossil woods studied in this work.

MATERIAL AND METHODS

An assemblage of 22 specimens of permineralized fossil woods was collected in Cerro Grande and Arroyo Blanco localities (44°59'43"S, 71°28'48"W and 44°58'38"S, 71°34'59"W, respectively) on the southern margin of Fontana lake, Chubut Province, Argentina (Figs 2; 3). Twenty-one specimens are from Cerro Grande locality (Lago La Plata Formation) and one specimen is from Arroyo Blanco locality (Tres Lagunas Formation) (Table 1). The specimens are housed in the paleobotany collection (acronym MPEF-Pb) of the Museo Paleontológico Egidio Feruglio, Trelew City, Chubut Province, with numbers 10663-10683 and 13151 (Table 1). Microscopic slides bear the same number as the hand specimen, followed by a lowercase letter.

The specimens were sectioned according to traditional techniques used for the study of wood anatomy (Hass & Rowe 1999), to obtain transverse section (TS), radial longitudinal section (RLS), and longitudinal tangential section (TLS). Thin sections were observed in an optical microscope (Leica DM2500) and photographed with a Leica DFC 1295 camera. In addition, small fragments of the woods (radial views) were observed in a scanning electron microscope (Philips XL30) after being gold-coated.

At least 15 measurements or observations of each character for each specimen were made (Table 1). Measurements are expressed as the weighted mean followed by the range and mean standard deviation (SD) between parentheses. When possible, anatomical characteristics were described using the terminology of the IAWA Committee (2004) and the Si and Cp indices proposed by Pujana *et al.* (2016) for the characterization of radial pits.

We followed Philippe & Bamford (2008) and Boura *et al.* (2021) for delimiting fossil conifer genera and for anatomy terms and definitions (e.g., steinkerne preservation). We used the scheme of Creber & Chaloner (1984) and Brison *et al.* (2001) for growth ring classification. We followed Creber (1977) and Creber & Francis (1999) for calculating mean sensitivity.

Abbreviation
MPEF-Pb Museo Paleontológico Egidio Feruglio, Trelew City, Chubut Province.

SYSTEMATIC PALAEONTOLOGY

Family Araucariaceae Henkel & W.Hochst.

Genus *Agathoxylon* Hartig, 1848

Type species. — *Agathoxylon cordaianum* Hartig, 1848. Triassic, Coburg. Bavaria, Germany.

Table 1. — List of studied specimens. Abbreviations: **MED**, minimum estimated diameter; **Si**, seriation index; **Cp**, contiguity percentage; **VDRP**, vertical diameter of radial pits (mean); **TTD**, tracheid tangential diameter (mean); **P×CF**, pits per cross-field (mean); **VDCFP**, vertical diameter of cross-field pits (mean); **RH**, ray height (mean); **R×mm**, rays per mm (mean); *****, less than 15 measurements or unclear; **?**, unknown. Formations (**form.**): **LLP**, Lago La Plata; **TL**, Tres Lagunas.

MPEF-Pb	Form.	Taxonomic unit	Fragment size (cm)	MED (cm)	Si	Cp [%]	VDRP [µm]	TTD [µm]	NPxCF [cells]	VDCFP [µm]	RH [cells]	RH [µm]	R x mm	Observations
10663	LLP	Indet. abietinean type	16×13×10	?	1.00	14.28	21.65*	40.21	?	?	7.27	230.67	4.00	*ex situ*
10664	LLP	*Agathoxylon* sp.	7×7×3	?	1.00	100.00	12.04	29.29*	4.00*	?	4.36	164.20	4.13	*in situ*
10665	LLP	Indet. conifer	7×4×4	80	?	?	?	?	?	?	?	?	?	*in situ*; possibly life position
10666	LLP	Indet. conifer	20×6×6	?	?	?	?	42.01	?	?	4.63	167.38	4.6*	*ex situ*
10667	LLP	Indet. conifer	20×7×4	?	1.00	?	?	36.23	?	?	5.46	193.47	4.57	*ex situ*
10668	LLP	Indet. conifer	11×8×5	20	?	?	?	30.82	?	?	4.09	134.54	4.78	*in situ*; possibly life position
10669	LLP	Indet. conifer	13×5×4	?	?	?	?	31.85	?	?	8.14*	303.54*	?	*in situ*
10670	LLP	*Agathoxylon* sp.	16×10×7	30	1.00	91.17	15.90	34.87	2.04	?	7.68	190.56	6.26	*ex situ*
10671	LLP	*Agathoxylon* sp.	8×5×4	?	1.07	97.74	12.72	30.07*	3.33*	?	4.00*	132.54*	?	*ex situ*
10672	LLP	*Agathoxylon* sp.	6×6×4	?	1.00	100	12.74	34.10*	3.50*	8.70*	5.24	216.90	5.25*	*ex situ*
10673	LLP	Indet. abietinean type	17×12×7	?	1.00*	13.33*	19.35*	?	?	?	?	?	?	*ex situ*
10674	LLP	Indet. conifer	6×4×2	?	?	?	?	37.78	?	?	5.50	187.42	5.07*	*ex situ*
10675	LLP	*Agathoxylon* sp.	5×4×1.5	?	1.08	90.28	13.54	35.54	3.83*	?	6.76	182.11	?	*ex situ*
10676	LLP	*Agathoxylon* sp.	8×8×4	?	1.00	99.18	14.61	33.84	3.42	?	4.45	151.03	4.20	*ex situ*
10677	LLP	*Agathoxylon* sp.	14×10×7	?	1.01	87.61	13.57	39.26	2.81	8.5	4.80	170.61	4.80	*ex situ*
10678	LLP	*Agathoxylon* sp.	14×9×9	?	1.00	85.37	14.33	33.57	3.60*	9.30*	4.46	219.44	4.93	*ex situ*
10679	LLP	*Agathoxylon* sp.	11×7×5	18	1.00	95.76	14.33	34.21	3.66	8.97	4.64	139.48	5.09	*ex situ*
10680	LLP	*Agathoxylon* sp.	9×6×6	?	1.00	98.45	13.45	25.66	2.60	8.74	4.76	174.69	6.11	*ex situ*
10681	LLP	*Agathoxylon* sp.	7×3×2	?	1.12	97.65	15.77	?	2.31	?	13.72*	405.61*	?	*ex situ*
10682	LLP	Indet. conifer	9×6×2	?	?	?	?	?	?	?	?	?	?	*ex situ*
10683	LLP	*Agathoxylon* sp.	14×10×5	?	1.16	100	16.07	?	2.13	?	9.72*	318.98*	?	*ex situ*
13151	TL	*Agathoxylon* sp.	14.5×8×1.5	?	1.80	99.45	14.79	35.49	4.40*	?	8.28	215.75	3.75*	*ex situ*

Agathoxylon sp.

Examined specimens. — MPEF-Pb 10664, 10670-10672, 10675-10681, 10683 (Cerro Grande locality), and 13151 (Arroyo Blanco locality) (Table 1).

Geographic occurrence. — Cerro Grande (Lago La Plata Formation) and Arroyo Blanco (Tres Lagunas Formation) localities (Fig. 2), Chubut Province, Argentina.

Stratigraphic occurrence. — Lago La Plata Formation (Kimmeridgian-Valanginian) and Tres Lagunas Formation (Tithonian-?Hauterivian) (Table 1).

Description

Growth ring boundaries are distinct (Fig. 4A). Latewood has 1-6 rows of radially flattened tracheids (Fig. 4B). Tracheids are roundish to polygonal as seen in transverse section (Fig. 4B). Intertracheary pitting in radial walls is araucarian, mostly uniseriate, sometimes biseriate, and very rarely triseriate (Si = 1.10), contiguous (Cp = 95.2%), and alternate when biseriate and triseriate (Fig. 4C-E); some pits have steinkerne preservation (Fig. 4E). Intertracheary radial pits are circular to hexagonal, 14.1 (9.4-20.7, SD = 1.2) µm in vertical diameter. Cross-fields are araucarioid with 3.2 (1-8, SD = 0.9) mostly contiguous pits per cross-field (Fig. 4F-G). Cross-field pits are half-bordered (= oculipores), circular to elliptical, and 8.8 (7.2-9.2, SD = 0.8) µm in vertical diameter. Horizontal and end walls of ray parenchyma cells are smooth. Rays are medium, 6.3 (1-25, SD = 3.7) cells and 216 (27-594, SD = 99) µm high. Rays are exclusively uniseriate (Fig. 4H-I), and have a frequency of 5.0 (3-8, SD = 0.9) rays per mm. Tracheid tangential diameter is 33.6 (15.8-52.0, SD = 5.8) µm.

Remarks

The specimen from the Arroyo Blanco locality is the only one that has rarely triseriate araucarian intertracheary pitting in radial walls.

Comparisons

Araucarian pitting in radial walls, araucarioid cross-fields, and uniseriate rays allow us to place the specimens in *Agathoxylon* (Philippe & Bamford 2008). *Agathoxylon* woods from the Mesozoic and Cenozoic are commonly related to the Araucariaceae (e.g., Pujana *et al.* 2014). However, not all *Agathoxylon* woods from the Paleozoic are related to this family (Rößler *et al.* 2014). In addition, *Araucarioxylon* Kraus and *Dadoxylon* Endlicher are considered synonyms of *Agathoxylon* and have hundreds of fossil species assigned to them (Philippe 2011). In Table 2, *Agathoxylon* sp. from the Fontana Lake area is compared to species of *Agathoxylon* from the Jurassic and Cretaceous of Patagonia and Antarctica. However, due to the poor preservation of the specimens, we cannot assign them to a particular fossil-species. On the other hand, *Araucaria araucana* (Molina) Koch, from extant Andean-Patagonian forests, has very similar wood anatomy the fossils described in this study (Tortorelli 1956; Rancusi *et al.* 1987).

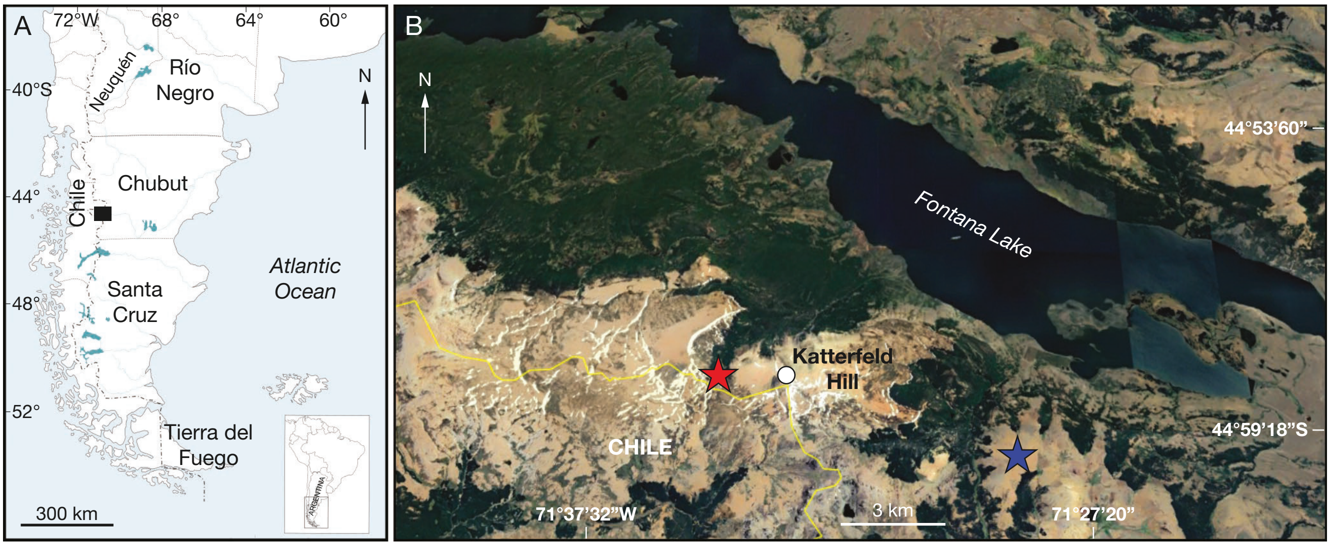

Fig. 2. — **A**, Map of Patagonia showing the Fontana Lake area (rectangle); **B**, satellite image (Google, CNES/Airbus) showing the fossiliferous localities Arroyo Blanco (**red star**) and Cerro Grande (**blue star**). Photo: B, Carlos Daniel Greppi.

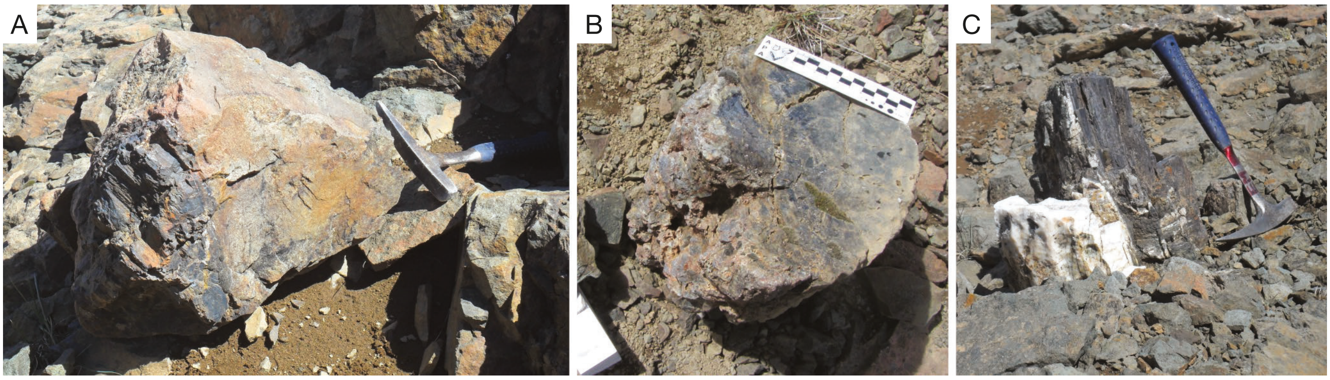

Fig. 3. — **A**-**C**, Fossil woods from Cerro Grande locality: **B**, **C**, fossil woods in possible life position, MPEF-Pb 10664 (**A**), MPEF-Pb 10665 (**B**), and MPEF-Pb 10668 (**C**). Photos: Roberto Román Pujana.

Indeterminate abietinean type

Examined specimens. — MPEF-Pb 10663 and 10673 (Table 1).

Geographic occurrence. — Cerro Grande locality (Fig. 2), Chubut Province, Argentina.

Stratigraphic occurrence. — Lago La Plata Formation (Kimmeridgian-Valanginian).

Description

Growth ring boundaries are distinct (Fig. 5A). Latewood has 1-4 rows of radially flattened tracheids (Fig. 5B). Tracheids are roundish to polygonal as seen in transverse section (Fig. 5B). Isolated tracheids have thick walls and dark lumens (Fig. 5B). Tracheid tangential diameter is 40.2 (31.7-52.7, SD = 5.4) µm. Intertracheary pitting in radial walls is abietinean, exclusively uniseriate (Si = 1.00) and mostly non-contiguous (Cp = 13.8%) (Fig. 5C, D). Intertracheary radial pits are circular, 20.5 (17.0-24.7, SD = 2.1) µm in vertical diameter. Cross-fields are poorly preserved and with pits apparently contiguous and non-contiguous (Fig. 5E). Cross-field pits apparently bordered and *c.* 8 µm in diameter; 2-4 pits per cross-field (Fig. 5E). Horizontal and end walls of ray parenchyma cells are smooth. Rays are medium, 7.2 (1-19, SD = 4.2) cells and 230 (48-524, SD = 114) µm high (Fig. 5F). Rays are exclusively uniseriate (Fig. 5F) and have a frequency of 4.0 (3-6, SD = 0.9) rays per mm.

Comparisons

Diagnostic characters (e.g., intertracheary pitting and cross-field pits) are difficult to observe due to poor preservation, precluding confident assignment of the specimen to a fossil-genus. Occasionally, abietinean intertracheary pitting in radial walls is observed (n = 10 and 9 pits in each specimen, respectively). It is mostly non-contiguous and similar to that present in some fossil-genera such as *Cupressinoxylon*, *Phyllocladoxylon* Gothan, and *Podocarpoxylon* (Philippe & Bamford 2008), which have previously been found in Patagonia (Pujana 2022).

Table 2. — Comparison of *Agathoxylon* sp. from Fontana Lake area with other species of Araucariaceae fossil woods from Patagonia and Antarctica.

Fossil-species	**Reference(s)**	**Main difference(s) with *Agathoxylon* sp.**
Agathoxylon agathioides (Kräusel & Jain) Kloster & Gnaedinger	Kräusel & Jain 1964; Kloster & Gnaedinger 2018	Grown ring boundaries absent; 1(2)-seriate rays
Agathoxylon liguaensis Torres & Philippe	Torres & Philippe 2002	Cross-fields with 1-3 pits per cross-field; rays with 1-56 cells high
Agathoxylon protoaraucana (Brea) Gnaedinger & Herbst	Brea 1997; Gnaedinger & Herbst 2009	Wider tracheid tangential diameter (*c.* 58-69 μm); rare axial parenchyma
Agathoxylon santacrucense Kloster & Gnaedinger	Kloster & Gnaedinger 2018	1-3-seriate radial wall pits; cross-fields with 2-14 pits per cross-field
Agathoxylon santalense (Sah & Jain) Kloster & Gnaedinger	Sah & Jain 1964; Kloster & Gnaedinger 2018	1-2(3)-seriate radial wall pits
Agathoxylon termieri (Attims) Gnaedinger & Herbst	Attims 1965; Gnaedinger & Herbst 2009	1-3-seriate radial wall pits
Araucaryoxylon arayaii Torres *et al.*	Torres *et al.* 1982	1-2(3)-seriate radial wall pits; rays with 2-22 cells high
Araucarioxylon floressii Torres & Lemoigne	Torres & Lemoigne 1989	Axial parenchyma; resin plugs
Agathoxylon kellerense Lucas & Lacey	Lucas & Lacey 1981	1-3-seriate radial wall pits
Agathoxylon mendezii Del Fueyo *et al.*	Del Fueyo *et al.* 2021	Cross-fields with 5-16 pits per cross-field
Agathoxylon ohzuanum (Nishida *et al.*) Gnaedinger & Herbst	Nishida *et al.* 1992; Gnaedinger & Herbst 2009	Grown ring boundaries absent; axial parenchyma
Araucarioxylon pseudochoshiense Nishida & Nishida	Nishida & Nishida 1986	Grown ring boundaries absent; rays with 1-6 cells high
Agathoxylon parachoshiense Nishida & Nishida	Nishida & Nishida 1987	Rays with 1-4 cells high
Araucarioxylon pichasquense Torres & Rallo	Torres & Rallo 1981	Grown ring boundaries absent
Araucarioxylon pluriresinosum Torres & Biro-Bagoczky	Torres & Biro-Bagoczky 1986	1-4-seriate radial wall pits; resin plugs in tracheids
Araucarioxylon resinosum Torres & Biro-Bagoczky	Torres & Biro-Bagoczky 1986	1-3-seriate radial wall pits; cross-fields with 2-3 pits per cross-field; resin plugs in tracheids
Araucaria marenssii Cantrill & Poole	Cantrill & Poole 2005	Axial parenchyma
Agathoxylon pseudoparenchymatosum (Gothan) Pujana *et al.*	Gothan 1908 ; Pujana *et al.* 2014	1-2(3)-seriate radial wall pits; resin plugs in tracheids
Agathoxylon quiriquinaense (Nishida) Gnaedinger & Herbst	Nishida 1984; Gnaedinger & Herbst 2009	Cross-fields with 2-4 pits per cross-field
Araucarioxylon doeringii Conwentz	Conwentz 1885	1-3-seriate radial wall pits; resin plugs in tracheids; rays 1(2)-seriate
Araucarioxylon chilensis Nishida	Nishida 1970	Cross-fields with 2-4 pits per cross-field; Resin plugs
Araucarioxylon chapmanae Poole & Cantrill	Poole & Cantrill 2001	1-3-seriate radial wall pits; resin plugs in tracheids
Agathoxylon allanii (Kräusel) Gnaedinger & Herbst	Kräusel 1962; Gnaedinger & Herbst 2009	1-3-seriate radial wall pits

ADDITIONAL RESULTS

Other specimens

Seven specimens were identified as "Indeterminate conifer" due to their very poor preservation (Table 1). In these specimens, only a general conifer structure could be observed (e.g., some tracheids and rays).

Other characteristics of the fossil woods

Growth reductions are observed in certain areas of the wood (Fig. 6A). False rings are isolated and developed near the growth ring boundaries (Fig. 6A, B). A possible chemical boundary (*sensu* Schweingruber 2007) composed of compact rows of resinous tracheids is observed close to a growth ring boundary and between degraded and unaltered areas of secondary xylem (Fig. 6C). In addition, this area of the wood shows cellular deformation and laterally displacement (Fig. 6C).

Other specimens show areas of completely degraded secondary xylem (Fig. 6D). These areas have tracheids that show a thinning of the cell wall from the lumen toward the outer layers following an erosive pattern with U-shaped notches (Fig. 6E). In some degraded areas of the wood, rows of tracheids adjacent to the rays have dark lumens (probably resin plugs) (Fig. 6F).

The specimen MPEF-Pb 13151 is strongly compacted and has large areas of degraded secondary xylem (Fig. 7A-C). Among these areas, there are chalcedony-filled fractures with silica fibers that surround the domains (Fig. 7C, D), which are bundles of tracheids isolated or arranged in radial rows and rays without apparent alteration. They have an elliptical to circular shape, oblique orientation in transverse section, and are parallel to the longitudinal axis of the wood (Fig. 7C-G). Domains in transverse and longitudinal sections vary in size from *c.* 5 mm to 40 μm.

Other specimens have areas without secondary xylem filled with a radial architecture of chalcedony (Fig. 7H). In addition, numerous polygonal crystals are observed in the lumen of the tracheids of several specimens (Fig. 7I).

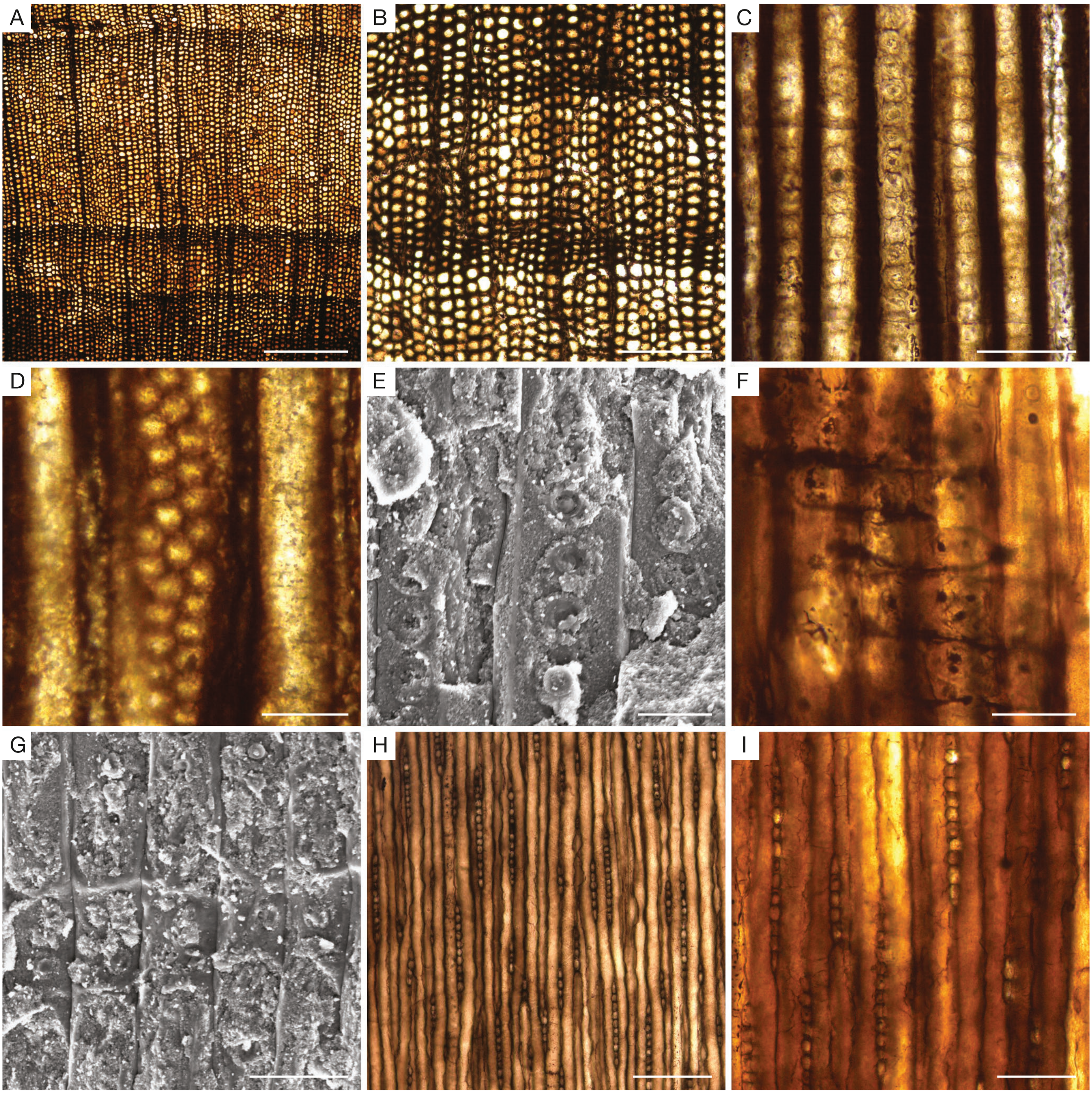

Fig. 4. — *Agathoxylon* sp., MPEF-Pb 10676 (**A**-**C**), MPEF-Pb 13151 (**D**), MPEF-Pb 10679 (**E**-**G**), and MPEF-Pb 10670 (**H**, **I**): **A**, distinct growth ring boundaries (**TS**); **B**, tracheids with circular to polygonal sections (**TS**); **C**-**E**, uni- to triseriate radial pitting (**RLS** in **C** and **D**, radial view in SEM in **E**); **F, G**, araucarioid cross-fields (**RLS** in **F**, radial view in SEM in **G**); **H**, **I**, uniseriate rays (**TLS**). Scale bars: A, 500 µm; B, H, 200 µm; C, D, F, 50 µm; E, 20 µm; G, 45 µm; I, 100 µm. Photos: Carlos Daniel Greppi.

DISCUSSION

Comments on *Agathoxylon* records from South America and Antarctica

The wood assemblage from the Fontana Lake area indicates a conifer dominance of the arboreal stratum. Even though not all the conifer woods could be identified, the wood assemblage shows a dominance of *Agathoxylon* (85%) over abietinean pitting type woods (15%). The identification of only two taxa suggests a low species richness in the assemblage. In addition, the presence of *Agathoxylon* agrees with the distribution and abundance of this fossil-genus throughout the Jurassic-Paleogene of Patagonia and Antarctica (e.g., Philippe *et al.* 2000; Torres *et al.* 2000; Poole & Cantrill 2001; Pujana *et al.* 2014; Mirabelli *et al.* 2018; Pujana 2022; Greppi *et al.* 2023; Vera & Perez Loinaze 2022; Martínez *et al.* 2023a).

In Patagonia, Jurassic wood records are scarce, limited to the Argentinean side (Neuquén and Santa Cruz provinces), and composed mainly of gymnosperms, particularly conifers

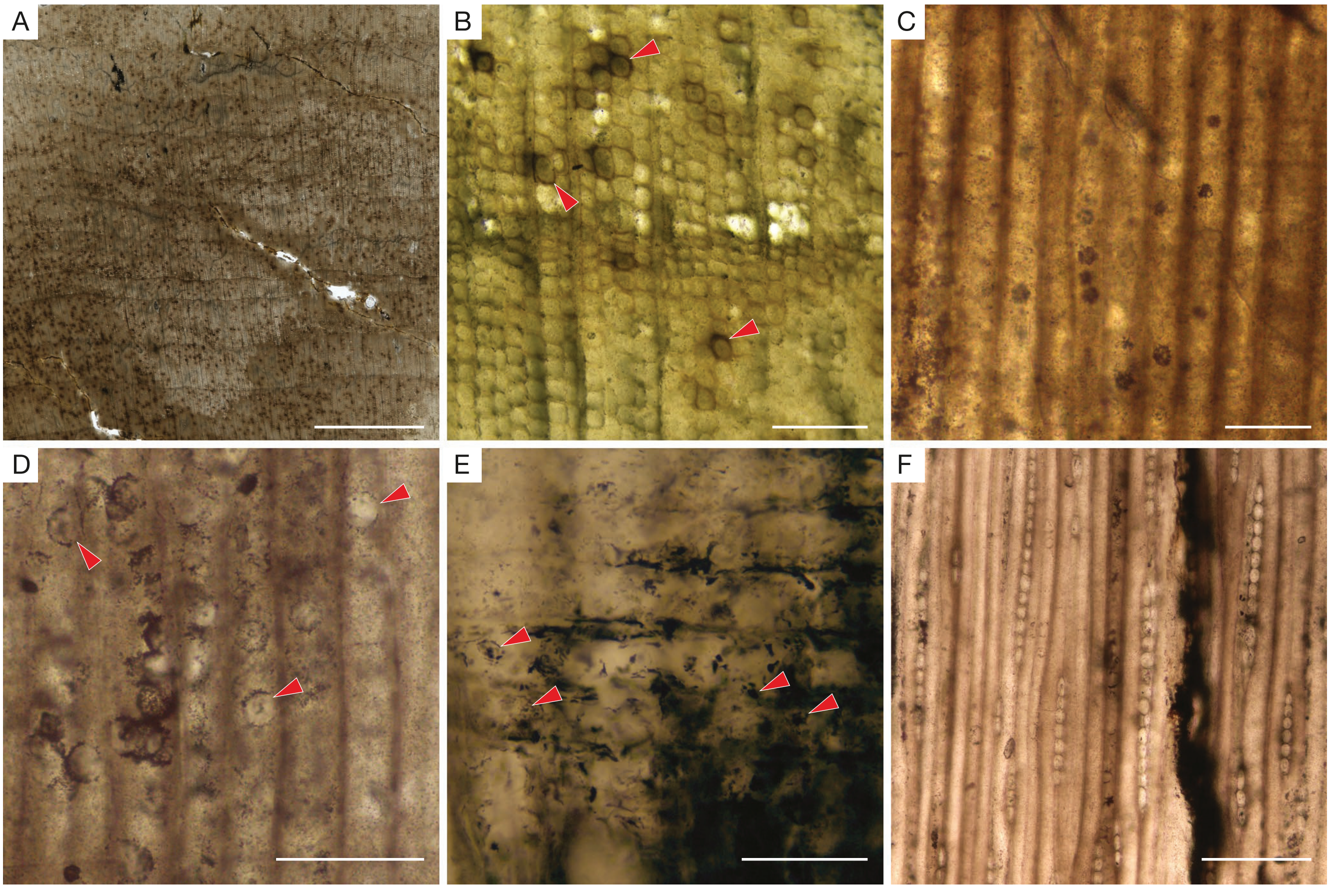

Fig. 5. — Indeterminate abietinean type, MPEF-Pb 10663 (**A**, **B**, **D**-**F**) and MPEF-Pb 10673 (**C**): **A**, poorly distinct growth ring boundaries (**TS**); **B**, tracheids with circular to polygonal sections (**TS**). Note some isolated tracheids with thicker walls and darker lumens (**arrowheads**); **C**, **D**, abietinean radial pitting (**RLS**); **E**, cross-fields with bordered pits (**arrowheads**) (**RLS**). Note the poorly preserved pits (**arrowheads**); **F**, uniseriate rays (**TLS**). Scale bars: A, 3 mm; B, 200 µm; C, D, 100 µm; E, 50 µm; F, 200 µm. Photos: Carlos Daniel Greppi.

such as *Agathoxylon* and *Prototaxoxylon* Kräusel & Dolianiti (later assigned to "Mesozoic *Prototaxoxylon*" by Philippe *et al.* 2019) (Morgans-Bell & McIlroy 2005; Zamuner & Falaschi 2005; Gnaedinger 2006; Gnaedinger & Herbst 2006, 2009; Kloster & Gnaedinger 2018; Sagasti *et al.* 2019). *Agathoxylon* sp. woods from the Fontana Lake area represent the first Jurassic record of this fossil-genus in Chubut Province. Cretaceous fossil wood records are numerous both in Argentinean and Chilean sides of Patagonia, and most wood assemblages are dominated by conifers (e.g., Philippe *et al.* 2000; Greppi *et al.* 2023, 2024; Martínez *et al.* 2023a; Vera *et al.* 2024; Villegas *et al.* 2024).

On the other hand, studies on Jurassic and Cretaceous large fossil wood assemblages from Patagonia (composed of *c.* more than 20 specimens), are not abundant. Most of these assemblages are composed entirely of conifers (Cúneo & Panza 2008; Varela *et al.* 2016; Kloster & Gnaedinger 2018; Greppi *et al.* 2020, 2023; Passalia *et al.* 2023; Rombola *et al.* 2023), and, occasionally, a dominance of conifers over angiosperms (Martínez 2010; Egerton *et al.* 2016; Vera *et al.* 2019, 2020). *Agathoxylon* is usually the only genus or dominant over other conifer fossil-genera, such as *Podocarporxylon* and *Brachyoxylon,* in many assemblages (Zamuner & Falaschi 2005; Gnaedinger 2007a,b; Kloster & Gnaedinger 2018; Greppi *et al.* 2020, 2023).

In Antarctica, there are some records of Jurassic and Cretaceous wood assemblages. These are composed mainly of gymnosperms, especially conifers such as *Agathoxylon*, *Brachyoxylon*, *Cupressinoxylon*, *Phyllocladoxylon,* and *Podocarpoxylon* (Torres *et al.* 2000; Falcon-Lang & Cantrill 2000, 2001; Pujana *et al.* 2017; Toumoulin *et al.* 2023).

In northeast Argentina, a fossil wood assemblage of 22 specimens dominated by *Agathoxylon* was recorded in deposits of the Solari/Botucatu Formation (*c.* 29°S, Late Jurassic-Early Cretaceous) (Martínez *et al.* 2023b). The woods are similar to those from the Fontana Lake area in that they are well silicified and poorly preserved, with only a few specimens assignable to *Agathoxylon* (Martínez *et al.* 2023b). *Agathoxylon* woods have also been described from various localities of Brazil, indicating a distribution toward lower paleolatitudes (e.g., Pires & Guerra-Sommer 2011; Santos *et al.* 2021). The wide distribution of *Agathoxylon* woods reflects the expansion of the Araucariaceae during the Late Jurassic-Early Cretaceous in South America, as evidenced by the abundance of megafossils such as leaves, cones, seeds, and woods (Philippe *et al.* 2004; Panti *et al.* 2012; Cúneo 2021).

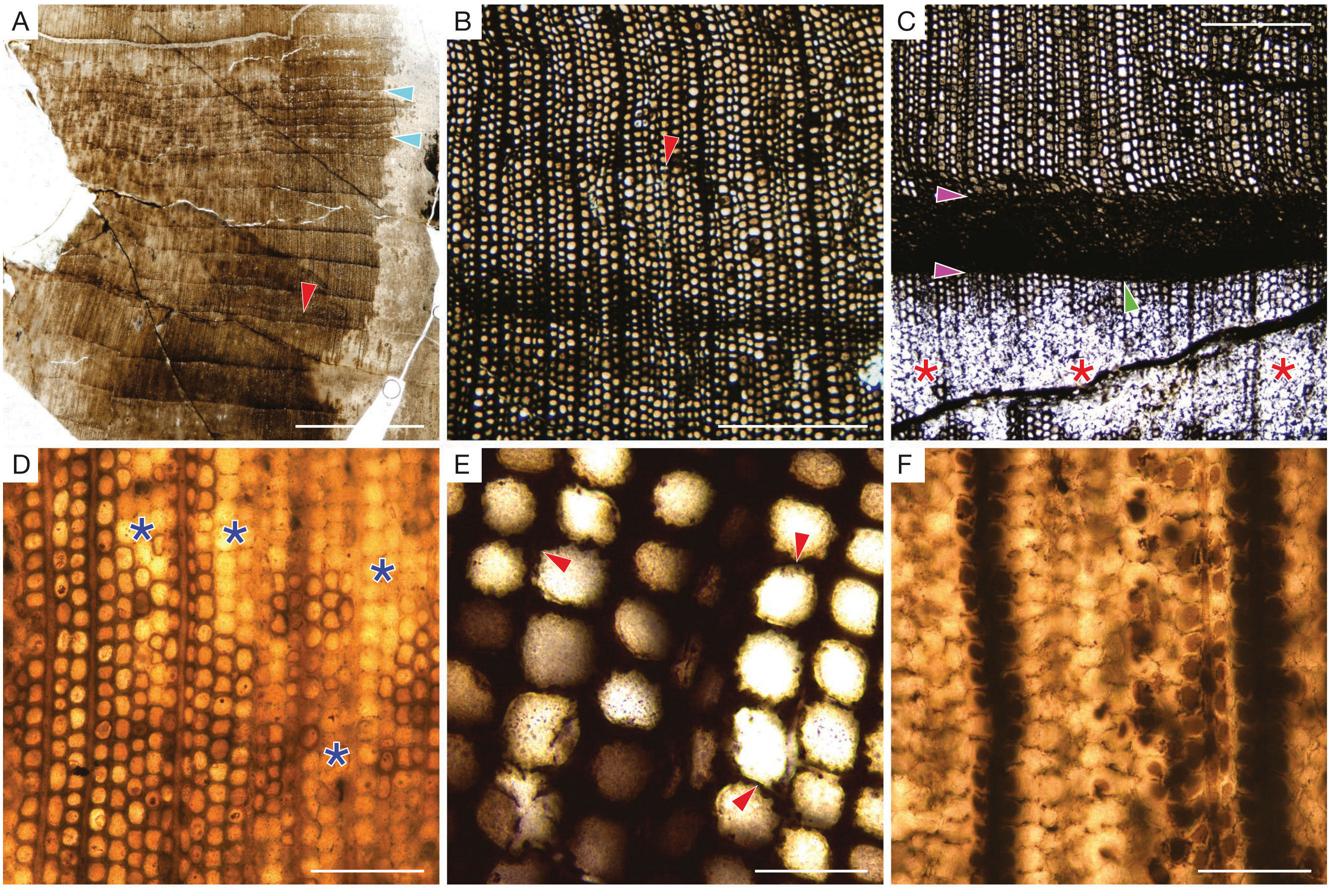

Fig. 6. — Other wood characteristics, MPEF-Pb 10668 (**A**, **D**), MPEF-Pb 10676 (**B**), MPEF-Pb 10670 (**C**), MPEF-Pb 10677 (**E**), and MPEF-Pb 10681 (**F**): **A**, **B**, growth reductions (**between light blue arrowheads**) and false rings (**red arrowheads**) (**TS**); **C**, probable chemical boundary (**between purple arrowheads**), a growth ring boundary (**green arrowhead**), and degraded areas of secondary xylem (**asterisks**) (**TS**); **D**, degraded areas of secondary xylem (**asterisks**) (**TS**); **E**, tracheids degraded from the cell lumen and develop U-shaped notches (**arrowheads**) (**TS**); **F**, rows of tracheids with dark lumens (probable resin plugs) adjacent to the rays (**TS**). Scale bars: A, 5 mm; B, C, 500 µm; D, F, 200 µm; E, 50 µm. Photos: Carlos Daniel Greppi.

Growth rings

In 18% of the fossil woods, growth ring boundaries could not be observed due to the poor preservation. The remaining specimens have distinct growth ring boundaries, which suggest seasonality (Creber 1977; Brison *et al.* 2001). The latewood has a few rows of radially flattened tracheids (*c.* 1-7). Growth rings are comparable with the type E described by Creber & Chaloner (1984) and Brison *et al.* (2001). Measurable growth rings have a mean width of *c.* 1.6 mm (Table 3), suggesting that these trees grew larger than the global mean ring width of extant conifers, estimated at *c.* 1.1 mm (Falcon-Lang 2005). In addition, the width and curvature of the growth rings suggest that the specimens came from large trees (Mosbrugger *et al.* 1994).

Only in a few specimens was the average mean sensitivity (MS) calculated (Table 3). The values obtained indicate that most of the specimens were complacent (Table 3), suggesting that the trees developed under favorable conditions for growth (e.g., water availability, optimal temperature) (Fritts 1976). Other specimens were sensitive (Table 3), suggesting that they were particularly susceptible to limiting factors (e.g., water availability to trees was restricted and variable from year to year) (Creber & Chaloner 1984). Although MS values allow discrimination between complacent and sensitive woods, in general, the distribution of these values is unimodal and normal (Philippe 2023). Therefore, inferences obtained from MS are not suitable for characterizing hypothetical discrete climate classes based on interannual climate variability (Philippe 2023).

Comments on tree-ring structure and silicification of woods

The modification of the tree-ring structure in extant trees is commonly the result of environmental fluctuations, cellular damage by pathogens, or intrinsic plant factors (Schweingruber 1996, 2007). Modification of the tree-ring structure related to the development of false rings are recognized in the woods of the Fontana Lake area, such as intra-annual bands (Fig. 6A, B) (Schweingruber 1996, 2007; Rojas-Badilla *et al.* 2017). Intra-annual bands are false rings developed close to the true rings by fluctuations in cambium activity caused by climatic disruptions, the action of pathogenic organisms, fire, or wind that limit plant growth (Schweingruber 1996; Rojas-Badilla *et al.* 2017). Other modifications of the tree-ring structure are growth reductions which are successive rings of extremely narrow growth resulting from repeated

Table 3. — Growth ring measurements. Abbreviations: **n**, number of rings; **m**, mean ring width; **min**, minimum ring width; **max**, maximum ring width; **MS**, mean sensitivity.

MPEF-Pb	n [rings]	Mean [mm]	Min-max. [mm]	Mean sensitivity	Curvature of rings	False rings
10663	8	1.3	0.8-1.7	0.19	Apparently straight	No
10666	4	1.6	0.9-2.7	0.36	Apparently straight	Yes
10667	6	1.5	1.0-1.9	0.15	Apparently straight	Yes
10668	14	1.4	0.9-1.8	0.18	Apparently straight	Yes
10670	7	2.5	1.6-3.3	0.33	Apparently straight	Yes
10672	7	0.8	0.6-0.9	0.20	Apparently straight	No
10674	4	1.6	0.9-2.3	0.29	Apparently straight	Yes
10675	13	1.0	0.7-1.2	0.22	Apparently straight	Yes
10676	19	0.7	0.4-1.3	0.25	Slightly curved	No
10681	4	3.8	3.5-4.1	0.12	Slightly curved	No

phases of reduced plant growth associated with active volcanism, fire, or low light conditions (Schweingruber *et al.* 2006; Schweingruber 2007) and where observed in some specimens (27%, Fig. 6A). In addition, woods in environments with regular flooding also develop successive rings of extremely narrow growth (Young *et al.* 1993; Falcon-Lang *et al.* 2001). Volcanic activity produces major anatomical changes directly (e.g., defoliation by hot ash, damage to the cambium) or indirectly (e.g., extreme droughts, fire) in the trees involved, reflected in the modification of the tree-ring structure (Schweingruber 2007). Intra-annual bands and successive rings of extremely narrow growth observed in the fossil woods from the Fontana Lake area suggest, in this case, a similarity to that of extant trees affected by volcanic eruptions (Schweingruber 2007; Hernández Vera 2017).

Specimens with areas of decayed wood have patterns similar to white rot produced by modern xylophagous fungi (Schwarze *et al.* 2004; Schwarze 2007). Some fungi causing white rot, attack and delignify the different layers of wood cells simultaneously, following an erosive pattern from the lumen (Anagnost 1998; Schwarze *et al.* 2004; Schwarze 2007), comparable to the pattern observed in our specimens (Fig. 6D, E). In addition, isolated clusters of tracheids and rays with dark contents in their lumens surrounded by degraded tissue in the woods of the Fontana Lake area (Fig. 6F) suggest a nonspecific defensive response by the plant against pathogenicity (Pearce 1991, 1997). A possible chemical boundary is also identified in our woods (Fig. 6C). Chemical boundaries are effective chemical barriers in wood that inhibit or prevent the colonization of saproxylic microorganisms (e.g., fungi) (Pearce 1991; Schweingruber 2007). The cellular lumens of the tracheids are blocked by the production of phenols and resins, forming compact rows of cells along large areas of the wood (Pearce 1991; Schweingruber 2007). Although this zone of the wood is similar to the chemical boundaries in modern woods (Schweingruber 2007), the compact rows of resinous tracheids observed are deformed and laterally displaced, suggesting that greater pressure was exerted on the wood at the time of petrifaction, similar to the so-called shearing zones (Erasmus 1976).

The deformation and preservation of the specimen MPEF-Pb 13151 (Fig. 7A-G) are similar to the contraction of some fossil woods during fossilization (Rößler *et al.* 2021; Mustoe 2023). Well-preserved tracheids within domains or bundles in specimen MPEF-Pb 13151 (Fig. 7D-G) suggest early stabilization by silicification, unlike the highly degraded surrounding tracheids (Rößler *et al.* 2021). Surrounding tracheids with highly degraded wall layers (Fig. 7C) are similar to the activity of xylophagous fungi causing white rot (Anagnost 1998; Schwarze *et al.* 2004; Schwarze 2007) and possibly favored plastic deformation of the wood before fossilization (Rößler *et al.* 2021). Furthermore, rows of sound tracheids have an apparent contraction, suggesting that they did not have total rigidity and experienced differential contraction concerning the surrounding degraded tracheids, which allowed the stability of the domains under plastic deformation (Rößler *et al.* 2021).

Petrification of wood begins when minerals (e.g., silica, calcium carbonate, etc.) fill anatomical spaces, such as the cell lumens and intercellular spaces, fractures, or cavities produced by xylophagous organisms (Mustoe 2017, 2023). Organic tissues may be degraded during fossilization and replaced by minerals (Mustoe 2017, 2023). Chalcedony is the main component of petrified fossil woods worldwide and is characterized by a fibrous silica microstructure and a radial growth architecture (Mustoe & Dillhoff 2022; Mustoe 2023), similar to the preservation of the woods in the Fontana Lake area (Fig. 7H). The development of quartz crystals (Fig. 7I) suggests multiple episodes of mineralization due to the availability of high concentrations of silica (Viney *et al.* 2016). High concentrations of dissolved silica are common in volcanic environments that generate large accumulations of ash and lava flows (Ballhaus *et al.* 2012; Mustoe 2017), similar to the volcanic rock deposits in the Fontana Lake area.

Paleobotanical records in the Fontana Lake area

Previous studies based on fossil leaves from the Fontana Lake area described conifers as an important component of the floras developed during the Late Jurassic-Early Cretaceous (Baldoni & Olivero 1983). The leaf flora was composed of *Equisetites* sp., *Cladophlebis antarctica* (Nath.) Halle, *Coniopteris* sp., *Dictyophylum* sp., *Sagenopteris* cf. *rhoifolia* Presl, *Elatocladus* sp., *Elatocladus* cf. *conferta* (Oldt) Halle, *Araucarites* sp., and *Taeniopteris* sp. (Baldoni & Olivero 1983). Furthermore, Olivero (1982) mentioned the presence of *Brachyphyllum* (?) sp., a genus possibly associated with the Araucariaceae (e.g., Carrizo *et al.* 2019) or the Hirmeriel-

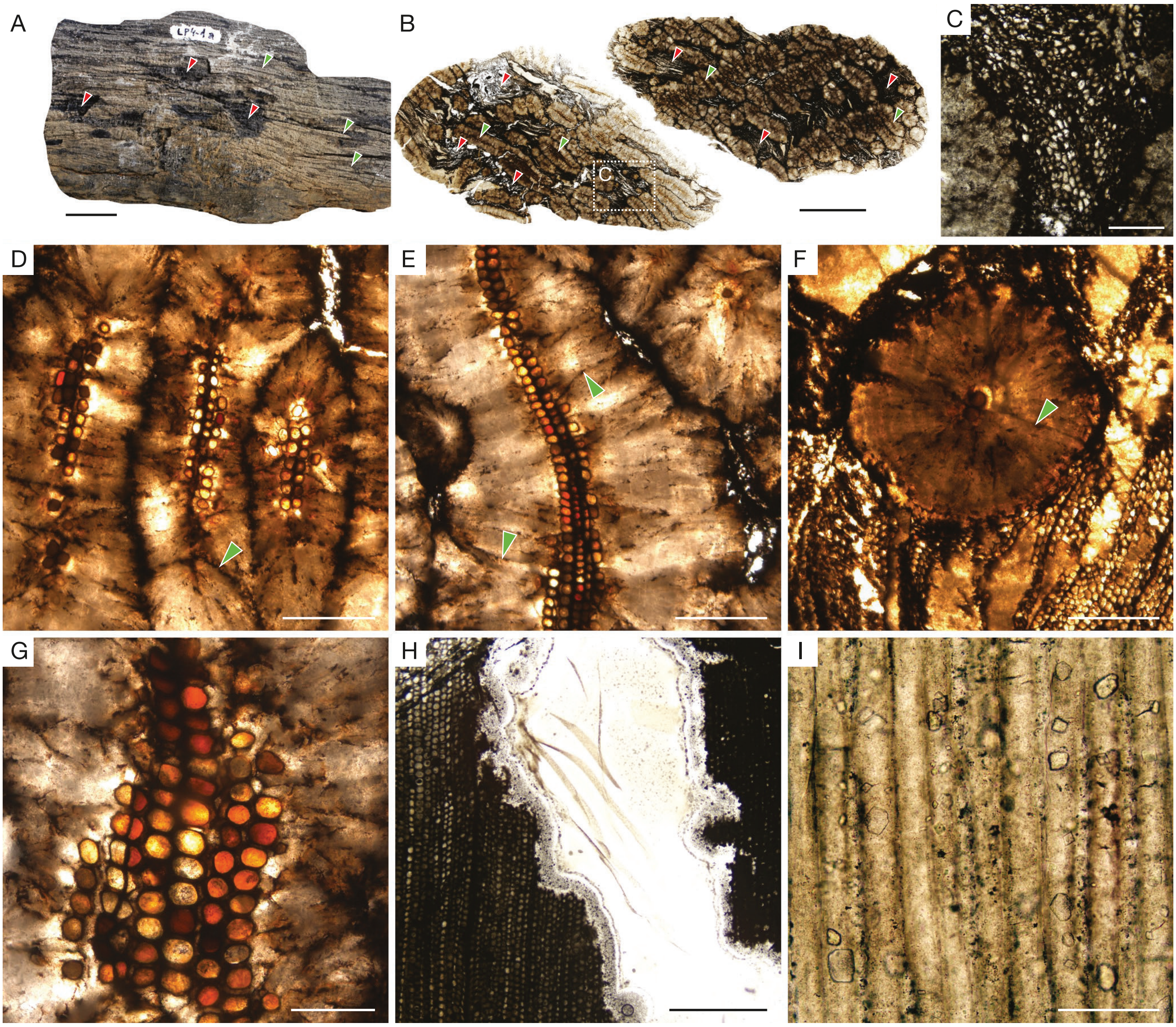

Fig. 7. — Wood preservation, MPEF-Pb 13151 (**A**-**G**), MPEF-Pb 10678 (**H**), and MPEF-Pb 10674 (**I**): **A**, **B**, a fossil wood with domains (**green arrowheads**) and degraded areas (**red arrowheads**) (**A**, **RLS**; **B**, **TS**); **C**, detail of degraded area (**TS**); **D**-**G**, detail of domains composed by tracheids clusters (**D**-**E**, **G**) and single tracheid (**F**) (**TS**). Note the silica fibers in radial projections (**arrowheads**); **H**, fracture filled by radial architecture of chalcedony (**TS**); **I**, numerous crystals in the tracheids (**RLS**). Scale bars: A, 10 mm; B, 5 mm; C, F, G, 200 µm; D-E, H, 500 µm; I, 100 µm. Photos: Carlos Daniel Greppi.

laceae (e.g., Escapa & Leslie 2017). Marshall *et al.* (1984) in the Cerro Grande locality mentioned leaf remains of *Elatocladus* sp. and *Otozamites* sp., fossil-genera usually related to conifers and Bennettitales, respectively.

The ancient forests of the Fontana Lake area were strongly influenced by volcanic activity, as evidenced by the presence of fossil woods within lava flows and pyroclastic breccia deposits (Olivero 1982; Marshall *et al.* 1984; Scasso 1987, 1989). Similar floras that developed near volcanic arcs (paleolatitude 62°S), and composed of coniferous and Bennettitales woods, have also been described from the Early Cretaceous of Livingston Island (Antarctica) (Falcon-Lang & Cantrill 2001). This assemblage is characterized by 52% of fossil wood carbonized by the action of pyroclastic flows (Falcon-Lang & Cantrill 2001). However, the specimens from the Fontana Lake area are strongly silicified and do not present anatomical features typically associated with charring as seen in *Araucaria* spp. (Osterkamp *et al.* 2018), such as homogenization of the cell walls of tracheids, ray burst, etc. In addition, araucarioid cross-field pits of specimens from the Fontana Lake area do not show apparent modifications related to the pit aperture width/pit width and pit aperture height/pit height during carbonization, unlike what is seen in extant Araucariaceae species (Gerards *et al.* 2007). This suggests that fossilization occurred when volcanic activity was low or absent, which also favored the preservation of some specimens in possible life position, preventing their removal (Quartino 1952; Olivero 1982; Marshall *et al.* 1984). Furthermore, the fossil woods preserved in life position suggest an autochthonous deposition.

CONCLUSIONS

An assemblage of 22 fossil woods from the Fontana Lake area (Late Jurassic-Early Cretaceous) was studied. The anatomy of 13 specimens indicates an affinity with *Agathoxylon* sp. Two poorly preserved specimens were assigned to an "indeterminate abietinean type" while the remaining seven correspond to indeterminate conifers.

The forest composition, dominated by *Agathoxylon,* resembles that of numerous assemblages described from Jurassic-Cretaceous deposits in Patagonia and Antarctica (e.g., Philippe *et al.* 2000; Torres *et al.* 2000; Pujana *et al.* 2017; Greppi *et al.* 2020).

Most of the specimens have distinct growth ring boundaries, suggesting seasonality. In addition, many have false rings and growth reductions, suggesting a relationship with environmental stress caused by active volcanism during the Late Jurassic-Early Cretaceous in the area. All the fossil woods are well-silicified, possibly due to diagenetic factors linked to the volcanic environment in which they lived.

Some specimens show decay patterns attributable to the activity of xylophagous fungi. Furthermore, the presence of possible marked chemical boundaries and clusters of resinous tracheids in areas of degraded wood suggests defensive responses by the host plants.

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