



Record of *Brachyoxylon patagonicum*, a Cheirolepidiaceae wood preserved by gelification in the Aptian Maceió Formation, Sergipe–Alagoas Basin, NE Brazil

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ABSTRACT

A gelified wood from the late Aptian Maceió Formation (Sergipe–Alagoas Basin, northeastern Brazil) was studied under scanning electron microscopy and organic petrography allowing for the record of the fossil-species *Brachyoxylon patagonicum*, likely belonging to the Cheirolepidiaceae family. The anatomical structure of the secondary xylem is characterized by mixed type of radial tracheary pitting, composed exclusively by uniseriate bordered pits, in separated, contiguous and compressed arrangements. Cross-field pits are of the araucarioid type, xylem rays are uniseriate or rarely partially biseriate, and probable sporadic traumatic resin canals are present. The present record expands the paleobiogeographic distribution of the fossil-genus in South America and amplifies its climatic tolerance, since the parent plants lived in the Aptian Tropical Equatorial Hot arid belt. The presence of fungal remains within the wood tissue, and the absence of signs of plant defense against fungal decay suggest saprophytic fungus–wood interactions that likely occurred during a stage of aerobic exposure before burial.

1. Introduction

Fossil wood assemblages are one of the best sources of data for assessing plant biogeographic patterns at the continental scale. For the Mesozoic, wood anatomical analysis provides important answers regarding systematics, evolution of forested environments, paleobiogeography and paleoclimate (Philippe et al., 2004). However, the scarcity of nomenclatural and taxonomic information about Gondwanan Jurassic – Early Cretaceous wood genera in the Brazilian Mesozoic basins precludes assessing important information about forest composition and consequences of the Gondwana break-up on the paleobiogeography.

Most systematic analysis of Brazilian Mesozoic wood assemblages

are focused on the Triassic of the southern Paraná Basin (Crisafulli and Dutra, 2009; Crisafulli et al., 2016, 2018; Pires et al., 2005; Siegloch et al., 2021) and the available formal systematic analyses for younger intervals are restricted (Araújo et al., 2011; Batista et al., 2017; Mohr et al., 2012; Pires, 2008; Pires and Guerra-Sommer, 2011; Pires et al., 2011).

This article describes a dispersed, large-sized wood fragment selected from an assemblage of specimens in assorted shapes and sizes previously cited as “coaly fragments” by different authors (Almeida et al., 2017; Arienti, 2006; Feijó, 1994; Nascimento and Lima Filho, 2005), included in a turbidite system of the Morro do Camaragibe Outcrop (Maceió Formation, Sergipe–Alagoas Basin). The material identification as either

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coalified or charred (burned) wood, however, has not been verified so far.

The main goals of this study were to decipher the preservation process of the wood fragment and to establish a taxonomic assignment based on anatomical parameters, contributing to the knowledge of forest flora composition, and to gain insights on its paleobiogeographic, paleoclimatic and paleoenvironmental significance in the context of the Aptian interval of the Sergipe–Alagoas Basin.

2. Geologic and paleontological synthesis

The Sergipe–Alagoas Basin, located in northeastern Brazil, covers a total area of 44,370 km² and has the most complete stratigraphic sequence of the eastern Brazilian continental margin (Campos Neto et al., 2007) (Fig. 1).

The basin presents five tectonic supersequences: a Paleozoic synclise overlying the Pre-Cambrian basement, pre-rift, rift, transgressive drift, and regressive drift from the Jurassic throughout the Pleistocene (Azambuja Filho et al., 1998; Campos Neto et al., 2007; Feijó, 1994; Mohriak et al., 1997, 1998; Souza-Lima et al., 2002).

The analyzed material was collected in the Maceió Formation (Fig. 2), which is included in the Rift Supersequence, with a subsurface thickness ranging from a few meters to 3000 m, and a thickness of approximately 600 m in the emerged area (Abreu, 1990; Campos Neto et al., 2007). It is composed of sandstones, shales, evaporites and calcilutites.

In this formation there are marine and non-marine ostracods (Galm, 1997), freshwater cyczicidean spinicaudata (Carvalho and Arai, 2001) and actinopterygian fishes (Jordan, 1910; Santos, 1985). The clupeomorph species pointed to a probable freshwater environment (Malabarba et al., 2004) and coprolites of probable carnivorous fishes to freshwater or brackish waters.

The age deposition of the Maceió Formation is considered as late Aptian (115.80–111.30 Ma) due to the occurrence of *Sergipea tenuiverrucata* pollen grains (Arai et al., 2013; Carvalho, M.A., 2004; Heimhofer et al., 2010), present in the *Dejaspollenites microfoveolatus* biozone (Regali et al., 1974).

The main outcrop of this lithostratigraphic unit occurs in the Praia Morros de Camaragibe locality, which is an anticline with an approximate length of 800 m. The deposition is linked to a turbidite system (Almeida et al., 2017; Arienti, 2006; Nascimento and Lima Filho, 2005) related to subaerial sediment gravity flows triggered by catastrophic floods. The freshwater influx entered into the seawater forming sediment-laden hyperpycnal flows or shallow-water turbidity currents

able to transport a large amount of sediment into oceanic deep marine environments (Arienti, 2006). However, the interpretation based on Conchostraca and fishes points to turbidites influx into a shallow lacustrine system (Malabarba et al., 2004).

The analyzed wood specimen was collected from the basal horizon of the central domain of the Morro do Camaragibe outcrop (09°20′06.43″ S, 35°26′25.97″ W), in a medium-grained sandstone with a large amount of dark wood clasts (Fig. 3).

3. Material and methods

The wood specimen consists of a black, elongated and laterally compressed fragment (20.6 cm length × 3.10 cm width × 2.8 cm depth). The sample was horizontally oriented to the bedding plane, intercalated between the underlying medium-grained sandstone with abundant dark wood clasts and the overlying medium-grained sandstone showing fining-upward cycles.

No anatomical analysis under transmitted light microscopy was carried out due to the extreme friability of the material, which prevented the production of thin slides. The observation was then conducted by scanning electron microscopy (SEM) at the Centro de Microscopia e Microanálises IDEIA at Pontifícia Universidade Católica do Rio Grande do Sul, Brazil, associated with organic petrography analysis using incident light in polished blocks under oil (Immersol 518 F). The blocks were also analyzed to obtain reflectance data as a proxy for estimating the degree of coalification and/or charring temperature (e.g., McParland et al., 2009).

Processing techniques for organic petrography were performed through a 50x objective using an AxioSkop 2 Plus Zeiss microscope calibrated with a Sapphire standard (0.595% Ro) and equipped with spectrophotometer J&M (MSP200) at the Palynofacies and Organic Facies Laboratory (LAFO), Department of Geology/UFRJ.

The wood specimen, fossil chips, stubs and polished block are housed in the Macrofossil Collection, Department of Geology of the Instituto de Geociências, Universidade Federal do Rio de Janeiro (IG/UFRJ) under the acronym UFRJ-DG 2859-Pb (hand specimen UFRJ-DG 2859a-Pb; fossil chips UFRJ-DG 2859b-Pb – 2859d-Pb; stubs UFRJ-DG 2859e-Pb – 2859m-Pb; polished block UFRJ-DG 2859n-Pb).

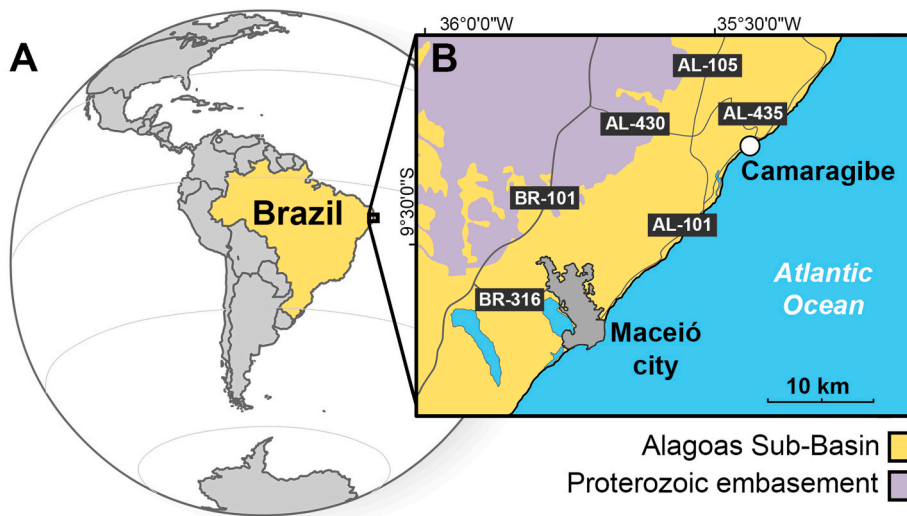


Fig. 1. Location map. (A) Sergipe–Alagoas Basin; (B) Morro do Camaragibe Outcrop (modified from Carvalho, M.A. et al., 2006).

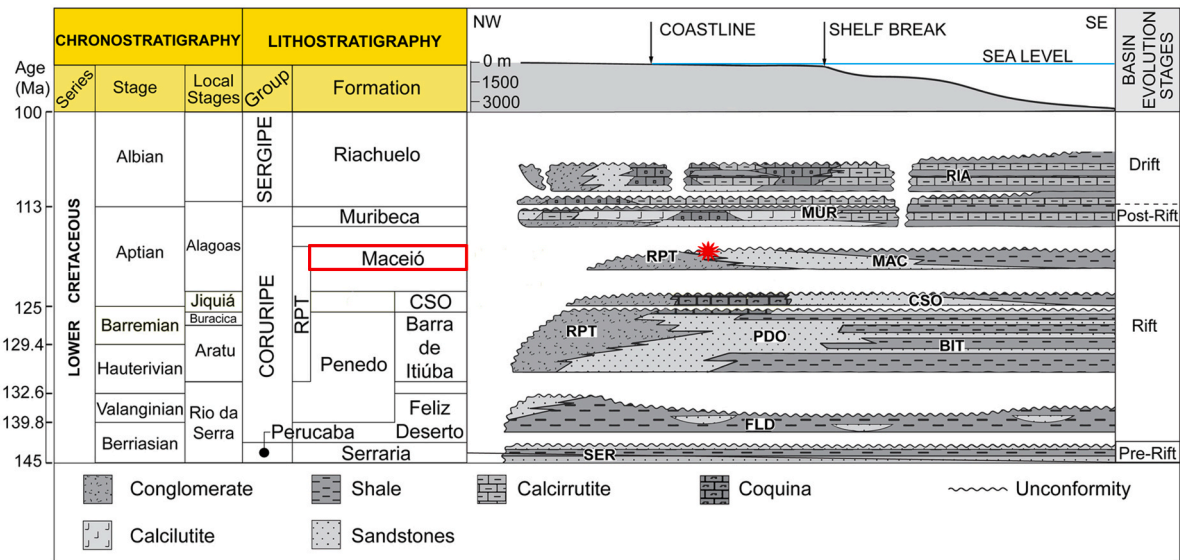


Fig. 2. Stratigraphic context of the Maceió Formation and position of the sample (red star) analyzed in this study. Formation abbreviations: RIA, Riachuelo; MUR, Muribeca; RPT, Rio Pitanga; MAC, Maceió; MCH, Morro do Chaves; CSO, Coqueiro Seco; PDO, Penedo; BIT, Barra de Itiúba; FLD, Feliz Deserto and SER, Serraria (modified from Mendes et al., 2022).

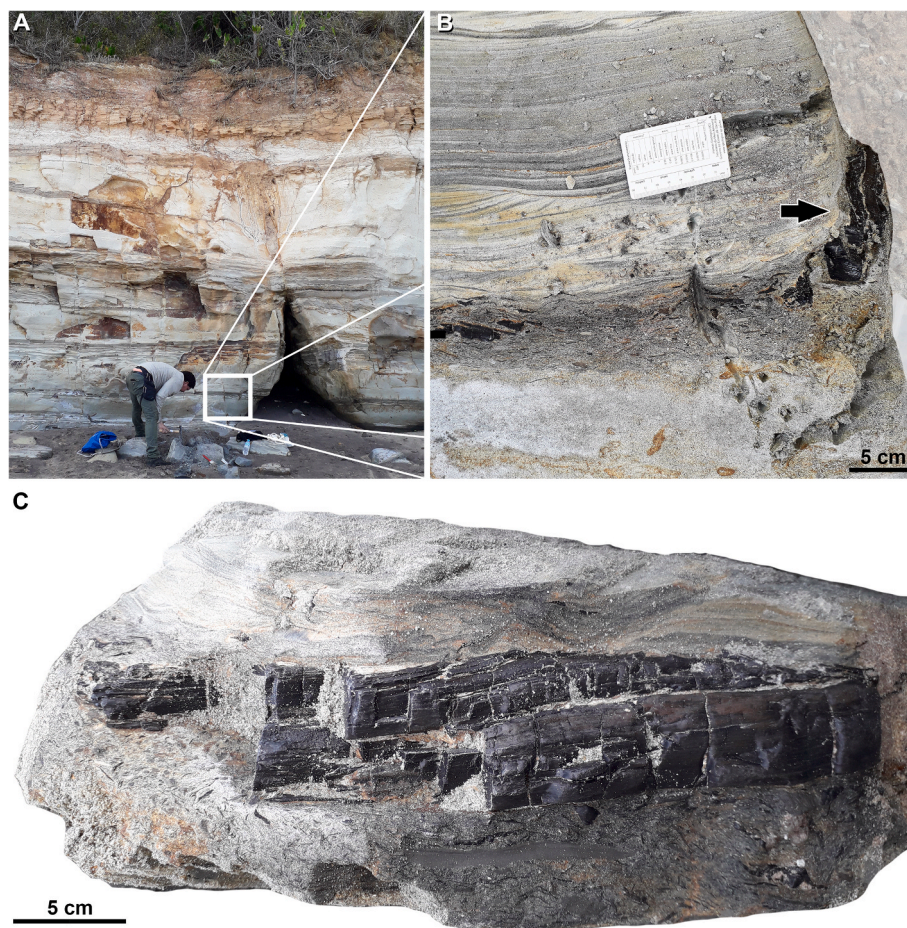


Fig. 3. Morro do Camaragibe outcrop and the wood sample as a clast in the medium-grained sandstone. (A) General view of the studied level; (B) detail from A showing the wood sample (arrow); (C) wood sample included in medium grained sandstones with large amount of dark wood clasts.

4. Results

4.1. Wood preservation process

4.1.1. Incident white and blue light excitation

The black elongated wood specimen shows lustrous sheen, does not soil the hands when rubbed and exhibits a vitreous fracture similar to that of vitrain in bituminous coal (Fig. 3C).

Analysis under incident white light and incident blue light excitation on different regions of the single wood revealed different preservation conditions. Cell structures are preserved and visible to varying degrees. Original cell shapes and cell wall architecture were observed, but partially to fully compressed cells, sometimes lacking details of original cell wall structures due to cell wall thickening were also common (Fig. 4).

The mostly uncompressed parenchymatous ray tissue (0.383–0.40% Ro) (Fig. 4A) exhibited similar reflectance values to the highly compressed xylem tissue (0.332% Ro) (Fig. 4B), as well as to that obtained in tracheids in the wood regions showing total obliteration of any original cell wall structure (0.358–0.40% Ro) (Fig. 4C). No wood section exhibited autofluorescence under incident blue light excitation (Fig. 4D).

The classification adopted by ICCP – International Committee for Coal and Organic Petrology (1971) accepted the gradual morphological change of the original cellular structure through gelification process as defined by Cohen (1968), Spackman and Barghoorn (1966) and Stach et al. (1982). Different maceral names were adopted by ICCP – International Committee for Coal and Organic Petrology (1971) for huminite and vitrinite given the limited resemblance between their coalification products.

In the classification adopted by the ICCP System 1994, the maceral group huminite has been revised from the previous classification (ICCP – International Committee for Coal and Organic Petrology, 1971) to accommodate the nomenclature to changes in the vitrinite classification (ICCP – International Committee for Coal and Organic Petrology, 1998). In the new classification, the vitrinite and huminite systems have been correlated to the level of sub-macerals groups, and the two systems can now be used in parallel, according to the nature of the coal and the purpose of the analysis. Huminite and its macerals are applied only to lignite/soft brown coals, and for subbituminous coal the vitrinite nomenclature is used (Sýkorová et al., 2005).

The average reflectance (0.365% Ro), in addition to the preservation of cell structures in varying degrees and the loss of tissue organization in some areas of the wood revealed the dominance of the huminite maceral group, which is formed as a result of anaerobic preservation when the organic and mineral matter are deposited rapidly. The preservation of cell structures varied according to the degree of decomposition, humification and gelification, and to the rank (Taylor et al., 1998; Sýkorová et al., 2005).

4.1.2. Scanning electron microscopy

The presence of a distinctive middle lamella between walls of adjacent cells revealed by SEM (Fig. 5A) in several regions of the wood indicated the preservation of cell wall structure. The lack of detailed cell wall structures in some areas of the wood (Fig. 5B) was attributed to a consequence of the evolution of the gelification process.

4.2. Systematic paleontology

Fossil-genus: *Brachyoxylon* Hollick & Jeffrey

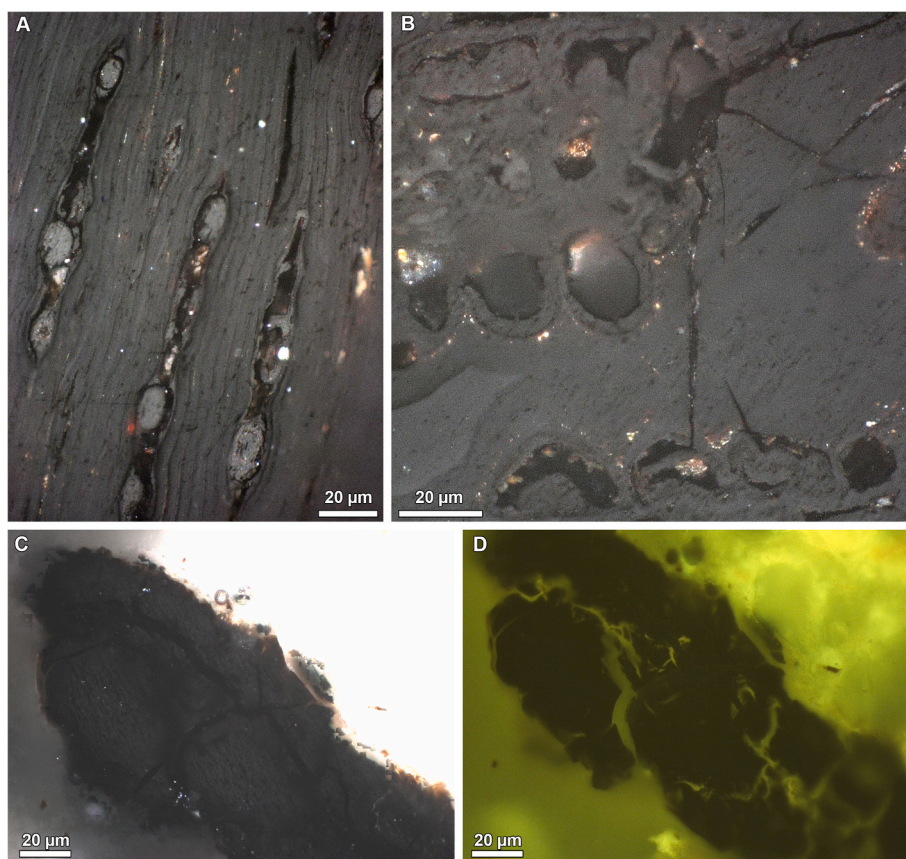


Fig. 4. Photomicrographs of polished sections of the gelified wood. A–C: incident white light; D: incident blue light excitation (fluorescence mode). (A) different compression stages of xylem with uncompressed ray tissue in tangential view; (B) different compression stages of xylem in transverse view; (C, D) highly compressed wood.

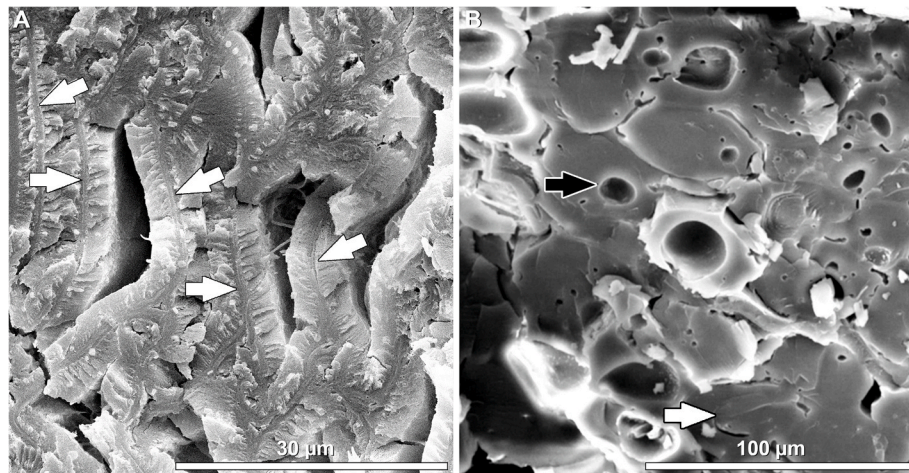


Fig. 5. Tissue preservation in transverse section under SEM. (A) Preservation of distinctive middle lamella (arrows) between cell walls of compressed tracheids; (B) progressive reduction of cell lumen (black arrow), and obliteration of recognizable plant cellular structure (white arrow).

Type species: *Brachyoxylon notabile* Hollick & Jeffrey
Brachyoxylon patagonicum Rombola, Greppi & Pujana
 Studied specimen: UFRJ-DG 2859-Pb
 Geographic occurrence: Praia Morros de Camaragibe locality (09°20'06.43" S, 35°26'25.97" W), NE Brazil.
 Stratigraphic occurrence: Maceió Formation (upper Aptian) Paranaíba Basin.
 Description and taxonomic assignment

The studied fragment is a black, elongated hand specimen (20.6 cm long × 3.10 cm wide × 2.8 depth) of preserved secondary xylem. The specimen corresponds to a homoxylous wood (Decombeix et al., 2019; IAWA Committee, 2004) composed by tracheids as conducting cells, showing a typical gymnospermous pycnoxylic pattern. Axial parenchyma, Sanyo bars, secondary spiral thickening, and trabeculae are absent.

In transverse section tracheids of the inner part of wood are deformed, mostly collapsed, and their configuration could not be reconstructed. Consequently, transverse sections were difficult to analyze, and the wood growth pattern could not be recognized. Many cell walls were deformed and flattened, frequently broken. However, the doubled thickness of tracheid walls 7.5 (6.5–8.4 µm) and the middle lamella 3.3 µm (2.7–3.3 µm) thick could be clearly identified (Fig. 6A). In superficial regions of the sample, tracheids are uncompressed, and are round to oblong in shape, measuring 24.4 (18.7–30) µm in radial diameter and 32.5 (28.7–36.2) µm in tangential diameter. Intercellular spaces are preserved (Fig. 6B).

Probable sporadic axial resin canals (sensu Wiedenhoef and Miller, 2002) were observed. They are round, weakly compressed, 116.2 (111.2–121.5) µm in diameter and are lined by specialized epithelial cells (Fig. 6C). Given their sparse distribution, the arrangement of these canals could not be established.

In radial section oblique ruptures can be observed in tracheid cell walls damaged by compression (Fig. 6D). The intertracheary radial pitting is characterized by round, uniseriate bordered pits 14.5 (14–15) µm diameter, with circular pit aperture, 4 (3.5–4.5) µm in diameter, in spaced (25%) or contiguous (70%) disposition (Fig. 6E–F, H) and unfrequently slightly compressed (5%) (Fig. 6G). The torus is sometimes preserved as a disc-shaped body, 5.5 (5–6) µm diameter) at the center of the pit aperture (Fig. 6H). Tangential tracheid wall pitting, axial parenchyma and septate axial tracheids are absent.

Homocellular rays (as seen in radial section) are composed by thin-walled, 5 (4.5–5.5) µm thick, smooth rectangular parenchymatous cells 39 (23–55) µm long. Most of the tangential walls are straight (90%), and a few are oblique (10%). Cross-fields show 2 to 6 circular 5.9

(5.7–6.1) µm in diameter to oval (5.9–6.5 × 4.7–4.8 µm), sometimes polygonal pits, (IAWA Committee, 2004). Pits occur dominantly in continuous araucarioid organization, half-bordered, mostly unordered (Fig. 7A). The pit aperture is an oblique ellipsoid, smaller than the pit border, measuring 0.6 (0.5–0.6) µm long (Fig. 7B). Ray tracheids are absent.

In tangential section, the homocellular rays of the secondary xylem are frequently uniseriate (90%) and infrequently partially biseriate (10%), averaging 9 (2–14) cells high. The ray cells are barrel-shaped, 18.7 (17–20) µm high and 16.25 (15–17.5) µm wide on average (Fig. 7C and D). The transverse and tangential walls of the parenchyma cells are smooth. Bordered pits are absent on the tangential walls of the tracheids. Resin plugs were not observed.

The anatomical characteristics of the wood specimen were included in the Group D (mixed type of radial pitting) following the criteria of Philippe and Bamford (2008) for Mesozoic gymnosperms, based on tracheidoxyl parataxonomy.

The secondary wood is similar to *Brachyoxylon* Hollick & Jeffrey and *Protocupressinoxylon* Eckhold which are both characterized by mixed type or intermediate-type or transitional type (Übergangstypus, Eckhold, 1923) of bordered radial pitting in tracheids, identified as Brachyoxylean type by Boura et al. (2021). Nevertheless, the araucarioid cross-field type of disposition (IAWA Committee, 2004) found in our specimen characterizes the fossil-genus *Brachyoxylon* (Hollick and Jeffrey, 1909). This type of organization is distinct from that found in the cross-fields of *Protocupressinoxylon* Eckhold (according to Bodnar, 2017, Müller-Stoll and Schultze-Motel, 1989, Philippe, 2002 and Vogellehner, 1968), which shows spaced, cupressoid oculipores, usually ordered in columns, in a cupressoid type of organization.

Agathoxylon Hartig, included in the Group B according to Philippe and Bamford (2008), which has been linked to Araucariaceae (Santos et al., 2021 and citations therein) shows araucarioid organization in the cross-field pits similarly to *Brachyoxylon*. However, these two fossil-genera differ mainly by the radial intertracheary pit arrangement, since *Agathoxylon* has araucarian radial pits, with more than 90% of the pits on the radial wall of tracheids being contiguous to neighbouring pits.

Among the selected Mesozoic species in Table 1, so far accepted for the genus *Brachyoxylon* (updated from Greppi et al., 2020, 2021 and Rombola et al., 2022), the present wood shares most of the diagnostic characteristics with *B. patagonicum* Rombola, Greppi & Pujana described for the Upper Cretaceous Cerro Fortaleza Formation (Rombola et al., 2022), also recorded for the Bajo Barreal Formation (Greppi et al., 2022), from southern and central Argentinean Patagonia respectively. Our specimen also shares characteristics with *B. raritanense* Torrey,

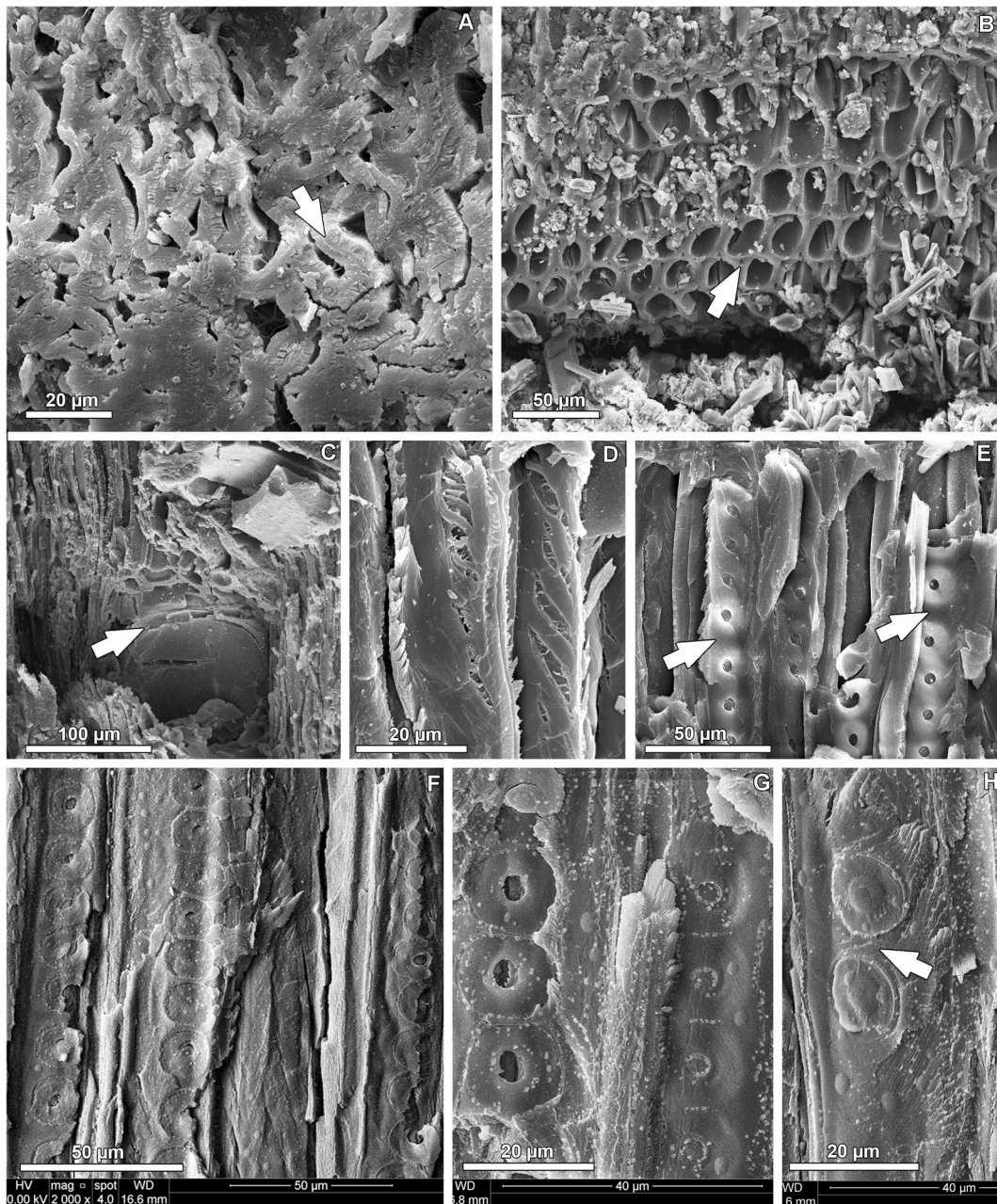


Fig. 6. Anatomical details under SEM. (A) Transverse section of the inner part of the wood with deformed tracheids and preserved middle lamella (arrow); (B) preserved intercellular spaces (arrow); (C) intertracheary axial canal lined by epithelial cells (arrow); (D) oblique ruptures in tracheid cell walls damaged by compression in radial section; (E) spaced radial pitting (arrows); (F) contiguous radial pitting; (G) slightly compressed radial pitting; (H) radial pitting with preserved torus. Arrow points to spaced arrangement of pitting.

firstly described for the Upper Cretaceous of North America, and recently recognized from the Lower Cretaceous Tres Lagunas (Greppi et al., 2020) and Castillo Formation (Greppi et al., 2021) of Argentinean Patagonia. Both *B. patagonicum* and *B. raritanense* are very similar to each other, characterized by the occurrence of exclusively uniseriate series of radial tracheid pitting, and the occurrence of cupressoid cross-field type in araucarioid arrangement, associated to the absence of tangential tracheid pitting and axial parenchyma.

There is a notable similarity between the cross-field pit patterns of *B. patagonicum* from the Upper Cretaceous of Patagonia and the wood described here. The former was observed under SEM and transmitted light microscopy (Fig. 4I of Greppi et al., 2022), while in the present study the anatomical analysis was carried out exclusively under SEM (Figs. 5–7).

The probable axial canals observed here were absent in *B. raritanense* and present in *B. patagonicum*. However, these canals were not considered of diagnostic value by Rombola et al. (2022), given that they were traumatic, i.e., were only secondarily formed in response to biotic or abiotic factors. The characterization of the two species was then based on distinct growth ring boundaries, which, however, depend fundamentally on environmental factors (e.g., temperature, rainfall, available water, among others according to Fritts, 1976). While *B. raritanense* was characterized by its indistinct (or absent) growth ring boundaries, *B. patagonicum* showed distinct growth rings.

The preserved torus in the bordered pits of the specimen under study was not used as a systematic parameter because it is a potentially synapomorphic character among conifers and other gymnosperms from the Mesozoic (Bodnar et al., 2013; Magallón and Sanderson, 2002).

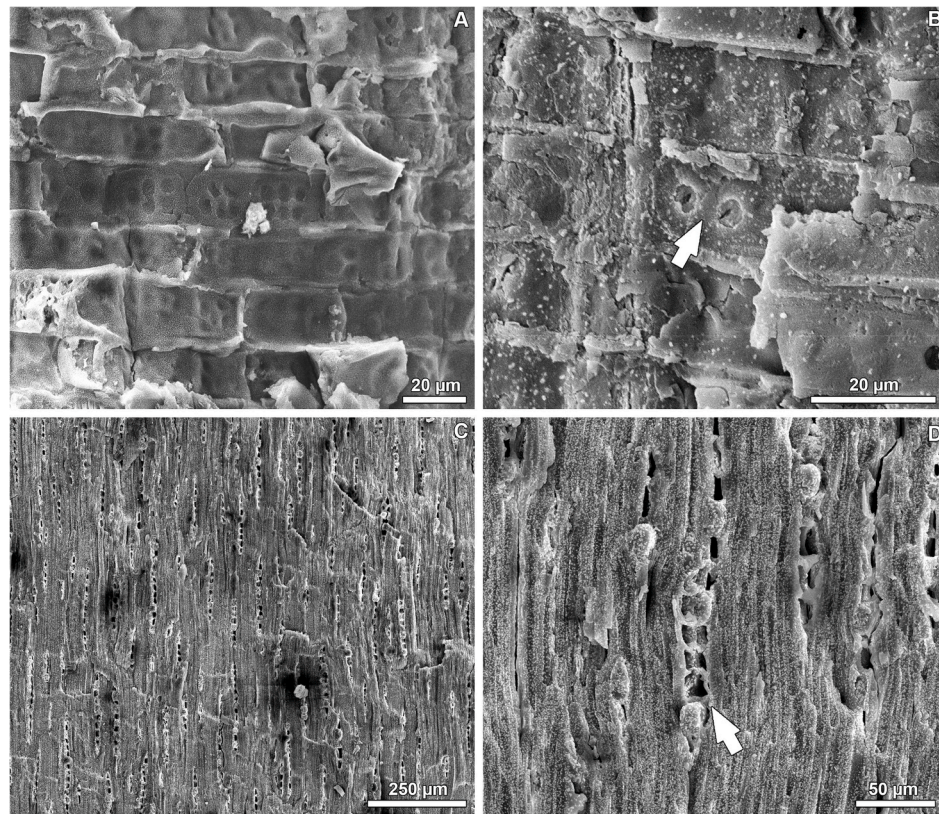


Fig. 7. Anatomical details under SEM. (A) Cross-fields in radial section; (B) detail of cross-field pit aperture, arrow points to spaced pit arrangement; (C) general view of tangential section; (D) detail of tangential section showing partially biseriate rays (arrow).

Table 1

Comparison of the main anatomical features available for the Jurassic – Cretaceous *Brachyoxylon* fossil-species with those described in the present study (after Greppi et al., 2020, 2021 and Rombola et al., 2022). Abbreviations: GRB = Growth ring boundary; IPS = Intertracheary pitting seriation; PxCF = Pit per cross-field; RS = Ray seriation; RH = Ray height [cells]; AP = Axial parenchyma; C = Crassulae; RC = Resin canal; D = Distinct; I = Indistinct; A = Absent; P = Present; ? = doubtful/unknown; T = Traumatic; (T) = Rarely traumatic; e.g.: 1 (2)s = Mainly uniseriate, rarely biseriate pits.

Fossil-species	Age	Country	GRB	IPS	PxCF	RS, RH [cells]	AP	C	RC
<i>B. avramii</i> Iamandei & Iamandei (2005)	Early Cretaceous	Romania	D	1–2s	1–8	1 (2)s, 1–21	A	A	T
<i>B. baqueroensis</i> Vera & Césari (2015)	Late Cretaceous	Argentina	D	1–3s	8–26	1s, 1–9	A	A	A
<i>B. brachyphylloides</i> (Torrey) Kräusel (1949)	Cretaceous	USA	D	1–2s	1–10	1 (2)s, 1–20	A	A	T
<i>B. comanchense</i> Torrey (1923)	Cretaceous	USA	D	1–(2)s	Up to 12	1s, 1–6	A	?	T
<i>B. cristianicum</i> Iamandei, Iamandei & Grădinaru (2018)	Lower Jurassic	Romania	D	1–2s	1–6	1 (2)s, 1–20	P	A	A
<i>B. currumillii</i> Bodnar, Escapa, Cúneo & Gnaedinger (2013)	Early–Middle Jurassic	Argentina	D	1–2s	4–11	1s, 1–10	P	A	A
<i>B. dobroglacum</i> Iamandei & Iamandei (2005)	Early Cretaceous	Romania	D	1–3s	1–6	1s, 1–10	P	P	A
<i>B. eboracense</i> (Holden) Philippe (2002)	Jurassic	England	D	1–2s	Numerous, cupressoid	1s, low	A	A	A
<i>B. holbavicum</i> Iamandei, Iamandei & Grădinaru (2018)	Lower Jurassic	Romania	I–D	1 (2)s	1–6 (9)	1–2s, 1–25	A	A	A (T)
<i>B. lagonense</i> (Laoudouéneix) Dupéron-Laoudouéneix (1991)	Cretaceous	Chad	?	2–3s	Cupressoid	1s, low	A	A	T
<i>B. liebermannii</i> Philippe (1995)	Jurassic	France	I	1s	5–12 cupressoid to podocarpoid	1s, low	A	A	A
<i>B. notabile</i> Hollick & Jeffrey (1909)	Late Cretaceous	USA	D	1–2s	5–11	1s, 1–8	A	P	T
<i>B. raritanense</i> Torrey (1923)	Cretaceous	USA	I?	1s	1–9	1s, 1–15	A	A	A
<i>B. raritanense</i> Torrey (in Greppi et al., 2021)	Early Cretaceous	Argentina	I	1s	3–10	1s, 1–10	A	A	A
<i>B. saurinii</i> Boureau & Serra (1961)	Jurassic (?)	Cambodia	D	1–2s	2–12	1s, 1–31	A	A	T
<i>B. serrae</i> Philippe, Suttethorn & Buffetaut (2011)	Early Cretaceous	Thailand	D	1–2s	5–16	1s, 1–15	A	A	T
<i>B. traatii</i> (Barale) Philippe (1995)	Middle Jurassic	France	I–D?	1–2s	4–9	1s, 1–10	A	A	A
<i>B. voisinii</i> Thévenard, Philippe & Barale (1995)	Jurassic	France	A	1s	3–8	1s, mean 5.8	A	A	A
<i>B. woodworthianum</i> Torrey (1923)	Early Cretaceous	USA	D	1 (2)s	Cupressoid	1–4s, 1s high, 2–4 low	A	A	T
<i>B. zhejiangense</i> Tian, Zhu, Wang & Wang (2018)	Early Cretaceous	China	D	1–2s	2–7	1 (2)s, 1–16	A	A	A
<i>B. zhouii</i> Jiang, Wu, Tian, Wang & Xie (2021)	Early Cretaceous	China	S	1–2s	7–11	1 (2)s, 3–50	A	A	P
<i>B. patagonicum</i> Rombola, Greppi & Pujana (2022)	Late Cretaceous	Argentina	D	1s	1–8	1s, 1–18	A	A	P
<i>B. patagonicum</i> Rombola, Greppi & Pujana (2022)	Late Cretaceous	Argentina	D	1s	4–8	1s, 1–10	A	A	P
<i>B. patagonicum</i> present study	Aptian	Brazil	?	1s	2–11	1s, 2–14	A	A	?P

The set of anatomical characteristics in the material from the Sergipe–Alagoas Basin, NE Brazil, led to its identification as *B. patagonicum*. The lack of information regarding the wood growth pattern in the Brazilian specimen was not considered relevant for the taxonomic assignment.

The frequent co-occurrence of the wood fossil-genus *Brachyoxylon* with plant fossils identified as Cheirolepidiaceae has led to its inclusion in this Mesozoic conifer family (Alvin, 1982; Alvin et al., 1981; Greppi et al., 2020, 2021, 2022; Hieger et al., 2015; Limarino et al., 2012; Machhour and Pons, 1992; Rombola et al., 2022; Rothwell et al., 2007; Zhou, 1983).

Records of the Permian *Brachyoxylon*, e.g., *B. nummularium* (White) Kurzawe, Iannuzzi & Merlotti (Kurzawe et al., 2012) and *B. semibiseriatum* (Pant & Singh) Kurzawe & Merlotti (Kurzawe and Merlotti, 2010) were not included in Table 1 and probably are not members of Cheirolepidiaceae (Greppi et al., 2020, 2021, 2022; Rombola et al., 2022).

4.3. Fungus–wood interactions

Fungal remains were observed in the xylem tissue in longitudinal and cross sections. Fungal hyphae are smooth-walled, unornamented, filamentous, sometimes showing clear septation (Fig. 8A). They occurred in a relatively straight or curved course, showing angle branching (Fig. 8B–F).

The hyphae are mostly tridimensional and tubular in shape, 2.4 (1.9–2.9) µm diameter, but flattened when attached directly to the cell walls (Fig. 8D and E). They could be observed penetrating the cell through pit apertures (Fig. 8F). Occasionally, spherical structures probably corresponding to terminal chlamydo spores, were found isolated or physically connected to a portion of the parental hyphae (Fig. 8C, E).

Physical evidence of plant defense against fungal decay, represented by deposition of resins in the wood tissues around damaged regions were absent.

5. Discussion

5.1. The wood preservation process

Although certain macroscopic characteristics of wood such as dark color and lustrous sheen could lead to a preliminary characterization as charcoal, the performance of organic petrography analysis was definitive for the identification of the huminite maceral group according to the criteria of ICCP – International Committee for Coal and Organic Petrology (1998) and the corresponding preservation process of the coaly wood as gelification.

It is important to note that the lack of details in the cell walls under SEM is a common characteristic of both gelified and charcoalfied (charred) tissues. On the one hand, in gelified tissues this lack of details is due to cell wall thickening and to the loss of its structural integrity, resulting in low reflectance under organic petrography analysis. Generally, in gelified cells the open lumina are infilled with residues, which are product of the secondary wall degradation resulting in a homogeneous surface observable in polished sections (Sýkorová et al., 2005). On the other hand, in the charcoalfication process, the identification of fusinite and semifusinite macerals of the inertinite maceral group (ICCP – International Committee for Coal and Organic Petrology, 2001) leads to the identification of open cellular structure and homogenized cell walls, contrastingly with a notable increase in reflectance.

According to Taylor et al. (1998), the transformation of cell walls of wood into tellinite occurs by the processes of humification and gelification, while the alteration in early stages such as charring caused by forest fires may lead to the formation of fusinite and semifusinite.

The dominant huminite maceral group in the wood sample was formed as a consequence of anaerobic preservation when the organic and mineral matter are deposited rapidly (Taylor et al., 1998). This preservation process fits well with the turbidite depositional process for the Morro do Camaragibe outcrop as inferred by Almeida et al. (2017) and Nascimento and Lima Azambuja Filho et al. (1998). This process would have allowed for the sudden burial of the wood by catastrophic floods of hyperpycnal flows, halting the chemical degradation of the

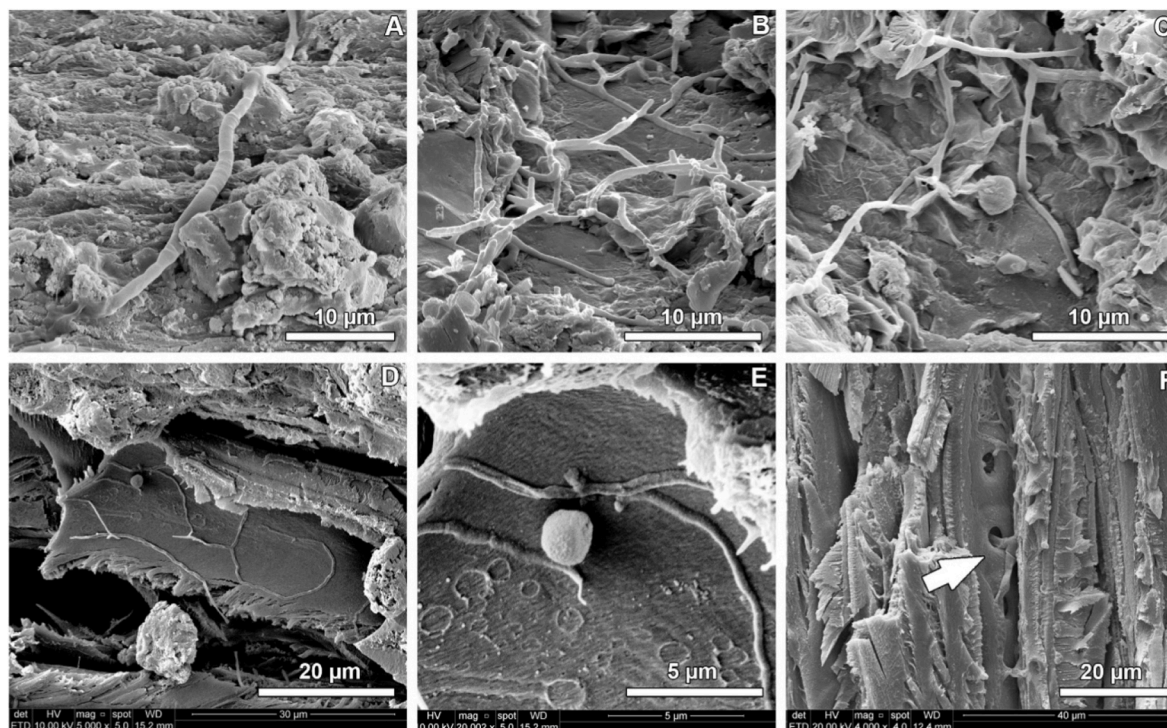


Fig. 8. Fungal remains within the wood. (A) Filamentous septate hyphae; (B) branching hyphae; (C) branching hyphae with connected spherical structure; (D) flattened hyphae attached to the cell wall; (E) detail of (D) with isolated spherical structure; (F) hyphae penetrating the tracheid through pit apertures (arrow).

humified wood tissues, thus favoring the gelification.

This type of preservation shows similarities with the preservation of the inner part of the wood of *Duartenia araripensis* Mohr, Schultka, Süss & Bernardes-de-Oliveira, a probable Cheirolepidiaceae from the Aptian Crato Lagerstätte (Araripe Basin, NE Brazil) that showed a “brown coal” or “lignite” type of preservation (Mohr et al., 2012). Transverse sections showed frequently broken, collapsed, deformed, flattened tracheids and non-homogenized cell walls (Plate 4, Fig. 3 of Mohr et al., 2012), comparable to the material described here.

5.2. Paleoclimate and paleoenvironmental considerations

The fossil-genus *Brachyoxylon*, likely included in the Cheirolepidiaceae, was cosmopolite during the Mesozoic, from the Triassic (Playford and Dettmann, 1965) to the Cretaceous – Paleogene boundary, frequently occurring in low latitudes, in subtropical to tropical climates (Abbink et al., 2004; Doyle et al., 1982; Watson, 1988).

Based on the widespread co-occurrence of Araucariaceae and Cheirolepidiaceae in Cretaceous fossil assemblages, Vakhrameev (1991) suggested that this family was also adapted to temperate climates. This has been ratified by the global map of *Brachyoxylon* spp. of Greppi et al. (2021), which showed the broad latitudinal distribution of the genus during the Cretaceous.

The presence of *Brachyoxylon* in Patagonia, South America, during the Lower/Middle Jurassic and Lower and Upper Cretaceous (Bodnar et al., 2013; Greppi et al., 2020, 2021; Rombola et al., 2022; Vera and Césari, 2015; Vera et al., 2019) and also in Antarctica (Torres et al., 1997) led Greppi et al. (2022) to infer the expansion of tropical to subtropical paleofloras towards high latitudes in South America, Antarctica and Australia during the Cretaceous, ratifying previous inferences of Passalúa (2009) and Iglesias et al. (2011). In these high latitude regions, conifers formed tall forests in fluvial, lacustrine and deltaic paleoenvironments (Rombola et al., 2022 and citations therein).

The record of *Brachyoxylon* presented here expanded the paleobiogeographic distribution of the genus in South America and amplified its climatic tolerance, since the parent plants survived in the Aptian Tropical Equatorial Hot arid belt of Chumakov et al. (1995). Thus, based on fossil wood records, the climatic conditions prevailing in the western part of the Southern Hemisphere during the Early Cretaceous favored the development of cheirolepidiacean conifers from periequatorial through high latitudes.

It is important to observe that reliable records of the Cheirolepidiaceae family have been reported for the Cretaceous interval of northeastern Brazilian Basins. The genera *Brachyphyllum* (Lindley & Hutton) Harris, *Duartenia* Mohr, Schultka, Süss & Bernardes-de-Oliveira, *Lindleycladus* Harris, *Pseudofrenelopsis* Nathorst, and *Tomaxellia* Archangelsky were described for the Crato Formation, Araripe Basin (Batista et al., 2017, 2018; Kunzmann et al., 2006; Mohr et al., 2012; Sucerquia et al., 2015) and considered as adapted to semi-arid to arid climate, living in mesophytic, riverside, sandy regions or marshy saline environments (Bernardes-de-Oliveira et al., 2014; Ribeiro et al., 2021).

Despite the absence of records of *Brachyoxylon* in the Brazilian Cretaceous basins until now, the occurrence of this wood fossil-genus in the Aptian of the Araripe Basin is very likely, considering the anatomical details documented in Fig. 6 of Batista et al. (2017) for branches of *Brachyphyllum obesum* (specimens LPU 242 PL and MPSC PL 580), which were linked to Araucariaceae by the authors mainly by the leaf anatomical traits. A revision of the xylem anatomical pattern of those samples certainly would clarify the systematic position of the specimens.

This is the first formal description of plant remains for the Sergipe–Alagoas Basin so far; the only fossil remains from this basin related to Cheirolepidiaceae have been *Classopollis* pollen grains (Carvalho, M.A., 2004; Heimhofer et al., 2010), associated with hot and dry conditions (Carvalho et al., 2019).

Global paleoenvironmental inferences for the Jurassic–Cretaceous interval have been linking the parent plants of *Brachyoxylon* to plant

communities adapted to borders of channels and riparian areas in lacustrine to fluvio-deltaic environments (Francis, 1983, 1984; (Gallois et al., 2018) ; Vera and Perez Loinaze, 2022).

However, the catastrophic process of organic matter transport defined as turbiditic for the Morro do Camaragibe (Arienti, 2006; Nascimento and Lima Filho, 2005) precludes further inferences about the original habitat of the parent plant. Nevertheless, some affinity with a riparian habitat could be speculated from the study of Almeida et al. (2017), who considered the deposition of the central dominium of the Morro do Camaragibe outcrop as part of the predominantly river-deltaic portions of the system that could be closer to the source area. The gelification process of wood preservation would have occurred as result of a rapid burial of the organic matter under anaerobic conditions.

Some morphological features in the fungal bodies preserved within the wood, such as hyphae septation, suggest a wood decaying process caused by Ascomycota and/or Basidiomycota. Nevertheless, the occurrence of clamp connections, which are typical of Basidiomycota, could not be clearly seen.

Evidence of biological remains (hyphae) and wood fungal degradation patterns were also reported for *B. patagonicum* from the Upper Cretaceous (Cerro Fortaleza and Bajo Barreal Formations) by Rombola et al. (2022) and Greppi et al. (2022). Fungus-plant interactions were attributed to white rot and the occurrence of probable sporadic traumatic resin canals, tracheids with ergastic substances and wall apposition in their interior were inferred as development of defensive responses by the host (Greppi et al., 2022).

Since reaction zones and barrier zones are absent along the wood from the Sergipe–Alagoas Basin, it could be speculated that a saprophytic process was the likely cause of degradation. Thus, fungal decay activity would have occurred during a stage of exposition before burial and occurred in aerobic environments. Such evidence of probable saprophytic fungal activities in wood implies intermittent periods of favorable moisture inputs in potentially dry environments in the Tropical Equatorial Hot arid belt.

6. Conclusion

The record of the wood fossil-species *Brachyoxylon patagonicum* from the Maceió Formation, Sergipe–Alagoas Basin, likely belonging to the Cheirolepidiaceae family, expanded the paleobiogeographic distribution of the genus in the Cretaceous of South America and amplified its climatic tolerance, considering that the parent plants lived in the Aptian Tropical Equatorial Hot arid belt. The present record strengthens the evidence that the climatic conditions prevailing in the Southern Hemisphere during the Early Cretaceous favored the development of conifers, particularly Cheirolepidiaceae, from periequatorial to high latitudes.

In a turbiditic system, the wood gelification process, characterized by the occurrence of macerals of the huminite group, occurred as result of anaerobic conditions of preservation following the organic matter deposition.

Fungus-wood interaction was probably saprophytic and occurred during a stage of exposition before burial, implying some environmental forces represented by intermittent wet windows of opportunity in aerobic environments in the Aptian Tropical Equatorial Hot arid belt.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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