Agathoxylon santanensis sp. nov. from the Aptian Crato fossil Lagerstätte, Santana Formation, Araripe Basin, Brazil

Ângela Cristine Scaramuzza Santos [a], Anelise Marta Siegloch [a], Margot Guerra-Sommer [a,*], Isabela Degani-Schmidt [b], Ismar Carvalho [b,c]

[a] *Universidade Federal do Rio Grande do Sul, IGEO, Programa de Pós-Graduação em Geociências, Av. Bento Gonçalves 9500, 91509-900, Porto Alegre, Brazil*
[b] *Universidade Federal do Rio de Janeiro, CCMN/IGEO, Programa de Pós-Graduação em Geologia, Av. Athos da Silveira Ramos 274, Bloco J1, Cidade Universitária, 21941-916, Rio de Janeiro, RJ, Brazil*
[c] *Universidade de Coimbra, Centro de Geociências, Rua Sílvio Lima, 3030-790, Portugal*

ABSTRACT

The study of a petrified twig under high-resolution optical microscopy allowed for the first formal record of the morphogenus *Agathoxylon* for the late Aptian Crato Member (Santana Formation, Araripe Basin, northeastern Brazil) and the description of a new species, *Agathoxylon santanensis*. The wood is characterized by mostly (95%) araucarian triseriate alternate bordered pits with hexagonal boundaries in a compact arrangement, and cross-field pits with araucarioid organization. In addition to *Agathoxyon*-type of xylem, the preservation of a belt of stone cells and axial resin ducts in the non-functional phloem, and an attached leaf with parallel venation showing longitudinally oriented stomata point to a probable Araucariaceae affinity. The presence of *Agathoxylon* xylem associated with phloem of Araucariaceae affinity in the Tropical-Equatorial Hot Arid belt indicate that the parent plants survived in different climatic zones in the Early Cretaceous of Western Gondwana, from peri-equatorial to warm and cool-temperate belts. The general growth pattern suggests that the growth interruptions zones were caused by temporary water stress, which was the limiting factor for favorable growing.

1. Introduction

The macroflora of the late Aptian Lagerstätte of the Crato Member (Santana Formation, northeastern Brazil) was abundant and diversified, according to different authors (Santos et al., 2020 and citations therein). The Araucariaceae and Cheirolepidiaceae conifers represent about 30% and angiosperms are the dominant forms in the fossil plant assemblage (32%), whereas gnetaleans (19%) and lycophytes, sphenophytes, fili-cophytes, pteridosperms, bennettitaleans, and *incertae sedis* gymnosperms (19%) are complementary elements (Bernardes-de-Oliveira et al., 2014). Palynological data support the macroscopic occurrences (Heimhofer and Hochuli, 2010; Souza-Lima and Silva, 2018).

The Crato fossil plants occur mainly as authigenic preservation and more rarely as coalified compressions (sensu Schopf, 1975). Petrified woods have not been described so far; however, given the characteristics of the paleobotanical assemblage, largely composed of fragments of potential arborescent trees, the low representativeness of petrified woods must be attributed to taphonomic bias rather than to scarcity of the parent plants in the source environment.

Previous informal anatomical analysis (Santos et al., 2020) performed on the petrified twig (systematically described here) composed of xylem, bark and connected leaf from the Crato Member allowed for the identification of a probable araucarian affinity.

Among extant conifers the Araucariaceae family has *Agathoxylon*-type wood, but Pteridospermales and Cheirolepidiaceae from the Jurassic – Early Cretaceous also showed this wood type (Philippe et al., 2004; Rößler et al., 2014). Nevertheless, for Del Fueyo et al. (2021) *Agathoxylon mendezii* (Early Cretaceous of Patagonia, Argentina) showed a close affinity with the Araucariaceae based on wood anatomy, fossil records (Leslie et al., 2018), time-calibrated molecular phylogeny of conifers, and combined phylogenetic analyses on extant and fossil plants (Escapa and Catalano, 2013).

The main goal of the present study is to propose a new taxon based on the xylem pattern of a petrified wood with the additional support of the organically connected bark and leaf for probable botanical affinities. The wood growth pattern allows for some speculations about growth adaptations related with the environment of the Crato fossil Lagerstätte.

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2. Geological synthesis

The Santana Formation (Ponte and Appi, 1990) included in the post-rift stage of the Araripe Basin is a 60 m thick succession of finely laminated carbonates interlayered with green shales and fine-to-coarse sandstones. The wood material studied here came from the lowermost Crato Member, which hosts the Crato fossil Lagerstätte, with exquisite preservation of plants, invertebrates, and vertebrates within a carbonate succession (Barling et al., 2015; Carvalho et al., 2019; Grimaldi, 1990; Martill, 1993; Martill and Bechly, 2007; Naish, 2007; Pinheiro et al., 2012). The age of the Santana Formation has been largely discussed (e. g., Martill, 2007), and a late Aptian age (113–119 Ma) was inferred based on the recognition of the palynological subzone P-270-2 (Heimhofer and Hochuli, 2010; Regali and Santos, 1999; Rios-Netto et al., 2012). The laminated carbonate layer (Fig. 1b) was interpreted as a shallow meromictic lacustrine environment (Heimhofer and Martill, 2007; Heimhofer et al., 2010) with episodic freshwater influx (Selden and Nudds, 2012).

The widespread occurrence of evaporites along the evolving South Atlantic rift system, the absence of coal layers, and the dominance of drought-resistant, xerophytic vegetation (Ziegler et al., 2003; Mohr et al., 2007), suggested semi-arid to arid climatic conditions for the
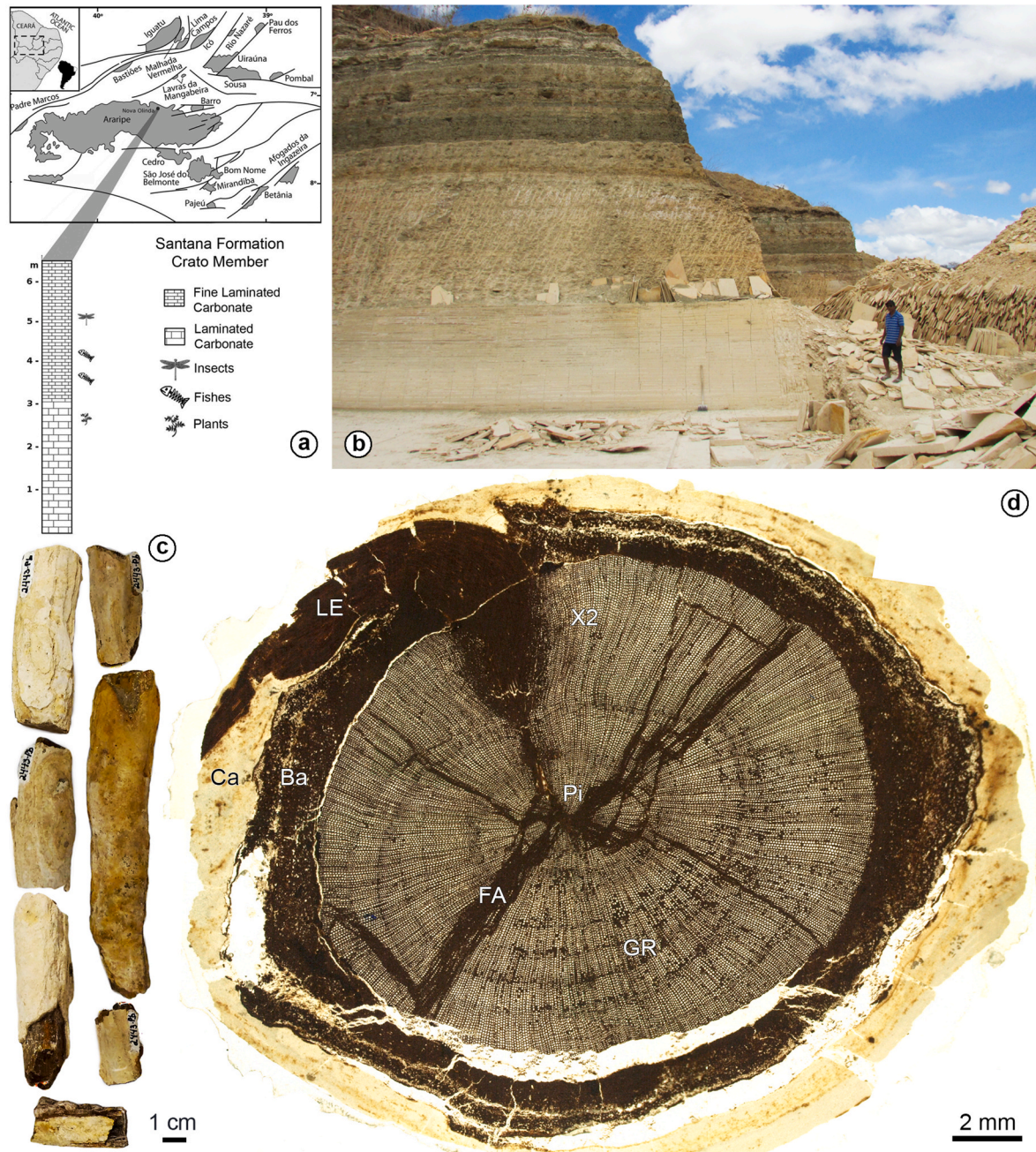

Fig. 1. Location map, collection site and gross morphology of the type specimen 2443 Pb. a) Map of the Araripe Basin in the context of the Cretaceous northeastern Brazilian intracratonic basins and stratigraphic profile of the collection site (Carvalho et al., 2019); b) Pedra Branca Mine fossiliferous outcrop of the Crato Member (Santana Formation) at Nova Olinda County, Ceará state, Brazil. The studied fossil comes from the lower laminated carbonate succession; c) branch fragment (2443 Pb) broken in seven parts; d) composite image of a full cross-section of the branch under stereoscopic microscope showing the surrounding carbonate layer (Ca), small pith (Pi), the massive, homogeneous secondary xylem (X2), growth interruptions of variable width (GR), a leaf emergence (LE), the bark (Ba) and fungal attack (FA) (slide 2443Pb-1).

Aptian deposition interval of the Araripe Basin, included in the Tropical-Equatorial Hot Arid belt of Chumakov et al. (1995).

3. Material and methods

The fossil specimen was likely a secondary branch, measuring 395 mm in length and 21 mm in diameter, containing petrified wood and bark. The studied material was previously analyzed by Santos et al. (2020) aiming to characterize white rot fungal decay in the secondary wood and was informally identified as a probable araucarian wood. Elemental EDS analysis indicated a dominant mineralization by iron (Fe) in the cell walls (Santos et al., 2020). Oxygen (O), in addition to carbon (C), are probable remains of the original organic matter of the cell walls. The mineralization of cell lumina occurred mainly with respect to crystal-shaped calcium (Ca).

The single fossil specimen broke into seven fragments when it was mechanically removed from the carbonate sediment (Fig. 1c). The macroscopic type specimen is housed in the paleontological collection of the Departamento de Geologia, Instituto de Geociências, Universidade Federal do Rio de Janeiro under the acronym 2443 Pb. Thin sections are stored under the codes 2443Pb-1 to 2443 Pb-35.

Different fragments of the single branch were sectioned in transverse, radial and tangential sections and polished, uncoated thin sections (40 µm thick) were produced. Epoxy resin was used as an embedding and mounting medium. The sections were polished using 0.05 mm aluminum oxide powder. The anatomical analysis was conducted under transmitted and reflected light microscopy.

The thin sections were analyzed and photographed with a Leica S8 APO stereoscopic microscope and a Zeiss AxioScope transmitted light microscope with mounted cameras at the Universidade Federal do Rio Grande do Sul (UFRGS).

Zeiss AxioVision 4.8.1 software was used to make measurements, and the plates were composed with Adobe Photoshop CS6 Extended. Transformations done to the images were cropping, rotation, contrast adjustments, focus stacking, and image composition. The terminology used to provide the anatomical details of the wood followed the recommendations of Decombeix et al. (2019), Falcon-Lang (2003), IAWA Committee (2004), and Schweingruber (1992, 1996).

4. Systematic paleobotany

Genus *Agathoxylon* Hartig, 1848
Type species *Agathoxylon cordaianum* Hartig, 1848 (Triassic, Coburg, Germany).
Agathoxylon santanensis sp. nov.
Figs: 1c, d – 5.
Holotype: 2443 Pb (petrified wood fragment).
Etymology: The specific epithet is named after the stratigraphic unit of the specimen occurrence, the Santana Formation of the Araripe Basin (Brazil).
Type locality and horizon: Mina Pedra Branca, Nova Olinda County, Ceará state, Brazil (7°5′40″/39°42′6″); laminated carbonate layer at lowest portion of the late Aptian Crato Member, Santana Formation, Araripe Basin.
Diagnosis: Wood growth interruptions distinguishable; tracheid quadrangular in cross-section. Secondary wood homoxylic, pycnoxylic; tracheid pitting in radial section in araucarian arrangement, bordered pits alternate, mostly triseriate (95%) very rarely alternate bisseriate (5%), in compact arrangement, with the pits completely packing the tracheid radial wall. Resin-filled tracheids present; rays parenchymatous, homogeneous, uniseriate. Cross-field pitting araucarioid with 4–8 cupressoid pits. Resin plugs common.

4.1. Morphological description

The specimen corresponds to a homoxylous wood (Decombeix et al.,

2019; IAWA Committee, 2004) composed of tracheids as conducting cells, measuring 21 mm in mean diameter and 395 mm of preserved length (Fig. 1c), showing a very small pith (394 µm) surrounded by a massive secondary xylem (up to 16 mm wide) and a 2 mm wide bark. The presence of a leaf organically connected to the axis (Fig. 1d) confirmed the identification of the specimen as a branch, but eccentric compression wood is absent.

4.1.1. Transversal section

In the pith there are clusters of sclerenchyma cells (30–43, mean 34 µm wide) (Fig. 2a). Primary xylem was inconspicuous. In one of the cross-sections the pith showed irregular boundaries and was not clearly separated from the xylem (Fig. 2a) probably related with the presence of an abscission zone.

The secondary xylem shows a typical pycnoxylic pattern (Decombeix et al., 2019) composed of tracheids in dense arrangement and uniseriate parenchyma rays. In cross-section, the tracheids are square, arranged in regular rows, limited by elongated, rectangular parenchyma ray cells with thin walls (3 µm). Tracheids with dark fillings, probable relicts of resins, are a common feature within the secondary xylem and are randomly dispersed or in clusters (Fig. 2b). Compression wood formed by eccentric growth is absent.

Cell-by-cell measurements in cross-section detected 5 rings 680–948 mm wide (Fig. 1d). In each ring, the tracheids of the initial wood are 60–95 µm (average 75 µm) in radial diameter and cell walls are 6–13 µm (average 9 µm) thick. In the latewood, 1–3 tracheid rows are flattened, each tracheid measuring 29–50 µm (average 36 µm) in radial diameter and cell walls are 6–13 µm (average 9 µm) thick. These rings are distinguished from growth rings (IAWA Committee, 2004) by the absence of thickened cell walls in the latewood in relation to the earlywood tracheids (Fig. 2b, c, d). In addition to the absence of thickened walls, rings show abrupt decline followed by a rapid rise back up in the tracheid diameter (Fig. 2c). Some rings are inconspicuous or subtle, and the boundaries cannot be completely traced laterally (Fig. 2d). The vascular cambium is indistinct.

4.1.2. Radial longitudinal section

The tracheids of the secondary xylem show crowded, hexagonal bordered pitting and cross-fields with araucarioid pits (Fig. 3a). The intertracheary pits, ranging from 14 to 16 µm in diameter, are mostly triseriate (95%), rarely biseriate alternate (5%), with rounded or elliptical apertures (Fig. 3b and c). Sanyo bars, secondary spiral thickening, and trabeculae are absent. The compact arrangement of the pits (Fig. 3b and c) is a striking anatomical feature that is present from the initial to the outer rows of the secondary xylem along the entire length of the wood specimen (395 mm).

Cross-field pits are small (oculipores) (Fig. 3a), half-bordered, cupressoid (Fig. 3d and e), disposed in araucarioid pattern (sensu Barefoot and Hankins, 1982; Vogel, 1995) with irregularly arranged pits (4–8), smaller (13 µm diameter) than the tracheid pitting (Fig. 3a, d).

Plate-like resin plugs (ca. 39 µm wide) extend fully across the tracheid (Fig. 4a). The rays show exclusively typically elongated parenchymatous cells, with straight horizontal and perpendicular end walls.

4.1.3. Tangential longitudinal section

The exclusively uniseriate rays range from 1 to 14 cells high (average 6 cells), are 39–483 µm (average 174 µm) high, in a density of six rays per millimeter (Fig. 4b–d). Individual ray cells are 9–36 µm (average 20 µm) high and 13–30 µm (average 20 µm) wide. The tangential surfaces of the ray cells are not pitted.

Ellipsoid branch traces, up to 823 µm long, occur in the marginal part of the tangential sections, cross cutting the wood, (Fig. 4c and d). The traces show anatomical organization similar to that of the twig, are composed of a central mass of parenchymatous and sclerenchymatous cells. The central mass (pith) is surrounded by a massive homogeneous
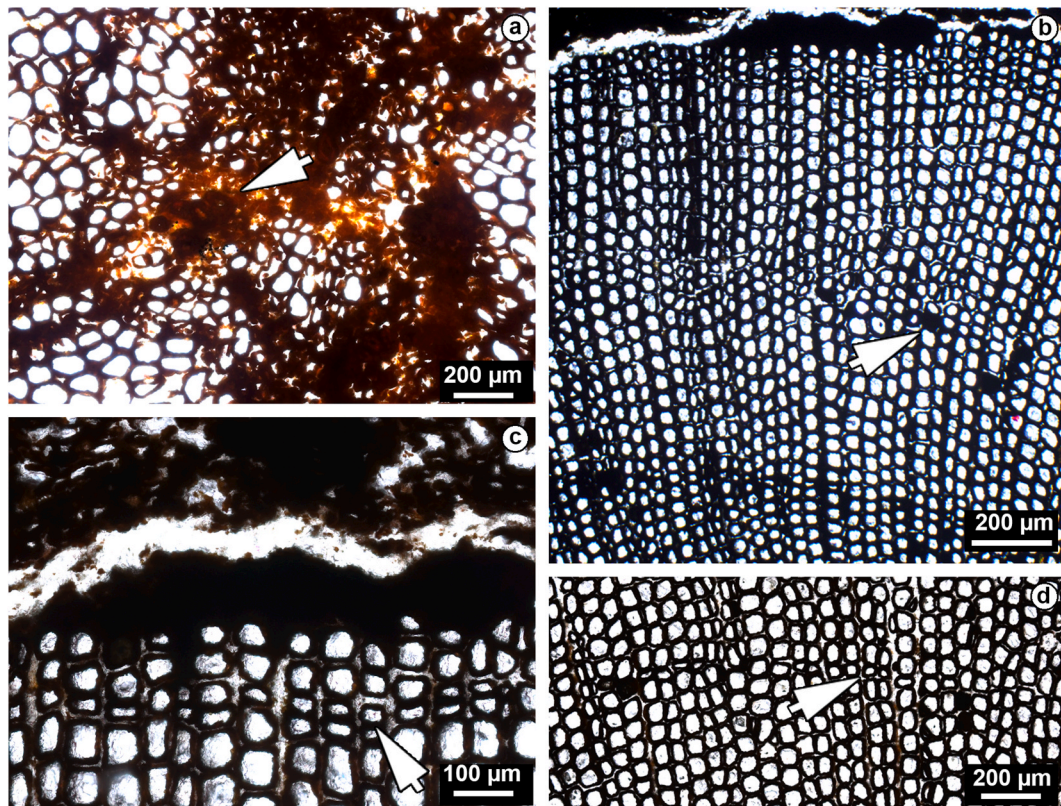
Fig. 2. Anatomical features in cross-section (slide 2443Pb-7). a) Pith with clusters of sclerenchyma cells (arrow); b) secondary xylem with growth interruptions and resin-filled tracheids (arrow); c) detail of growth interruption boundary; d) subtle growth interruption zone with boundaries that cannot be traced laterally.

secondary xylem composed of tracheids with small lumens, 5–13 µm wide (average 9 µm) (Fig. 4c).

4.1.4. Bark

The portion outside the xylem (Fig. 5) measures 1.2–3 mm (mean 2.1 mm) wide and was better observed in transversal section.

The secondary phloem (Fig. 5a) is poorly preserved in comparison to the xylem and is mostly collapsed, probably because the replacement of the thin cell walls of the active phloem by iron minerals disrupted the original organization of this tissue.

The functional phloem was intensely crushed, and its cells were unidentifiable. The boundary between the conducting and non-conducting phloem cannot be clearly seen (as typically occurs in conifer younger branches).

Although the preservation of the non-functional phloem is also poor, it was possible to distinguish dispersed axial resin ducts with round to ellipsoidal lumina (122 µm mean diameter) encircled by poorly preserved epithelial cells, and polygonal to semi-square sclereids (9.6–27 µm diameter) often in irregular groups (Fig. 5b and c).

A tangential band of sclereids occurs at the boundary between the phloem and the cortex; axial resin canals (50 µm mean diameter) are also found randomly in this region. Some of the cortical sclereids show expanded diameters, which surpasses that of some of the resin canals (Chan, 1986) (Fig. 5d).

Phelloderm and phellogen were not clearly observable in the bark of this young branch specimen, however, the thin periderm contains remnants of layered cells which probably belong to the phellem (up to 270 µm thick, Fig. 5e).

4.1.5. Branch surface structures

One attached leaf can be observed in transversal section (Figs. 1d and 6a). It is sessile with acute apex, 10.6 mm long and 3.11 mm wide at the insertion point. Assuming that it is folded at the midrib, a total width of 4.94 mm can be projected at its widest point. The width/length ratio is 0.47 and the distance between the leaf base and the maximum width represents a 55% of the leaf length.

The venation is parallel, maintaining the same caliber along the leaf with 32 ridges per mm (Fig. 6b). The stomata are arranged in longitudinal rows between the ridges. Although the petrification by iron minerals precluded a clear observation of the stomata, some apparati showed a rectangular stomatal pore (25–42.5 µm long and 13–23.5 µm wide) longitudinally oriented parallel to the ridge (Fig. 6b). The stomata are partially covered by 4 papillae, 2 lateral and 2 polar, consistently 14 µm long and 10 µm wide (Fig. 6c). The outline of the epidermal cells was obscured by the authigenic preservation.

5. Discussion

The homoxylic, pycnoxylic wood specimen with araucarian tracheid pitting in the radial walls of the tracheids, homogeneous, uniseriate parenchymatous rays and araucarioid cross-field pitting point to the morphogenus *Agathoxylon* Hartig according to the criteria of Philippe and Bamford (2008) for Mesozoic gymnosperms based on tracheidoxyl parataxonomy. This systematic approach rests in descriptive terms, and it is not based on hypothetical systematic relationships.

Since the radial pits of the tracheids and cross-fields associated with the ray pattern are the most important characteristics in the definition of morphogeneric status (Philippe and Bamford, 2008), the comparison of the wood from the Araripe Basin with *Agathoxylon* species from the Jurassic–Cretaceous of South America (see Del Fueyo et al., 2021) was based on these characteristics (Table 1). The triseriate alternate, hexagonal radial pitting is shared with *Agathoxylon agathiodes* Torres and Biro-Bagoczky (1986) (Middle Jurassic), *A.* (*Araucarioxylon*) *arayaii* Torres et al., 1982 (Jurassic), *A.* (*Araucarioxylon*) *chapmanae* Poole and Cantrill (2001) (Late Cretaceous), *A.* (*Araucarioxylon*) *kellerense* (Lucas & Lacey) Pujana et al., 2017 (Late Cretaceous), *A.* (*Araucarioxylon*)
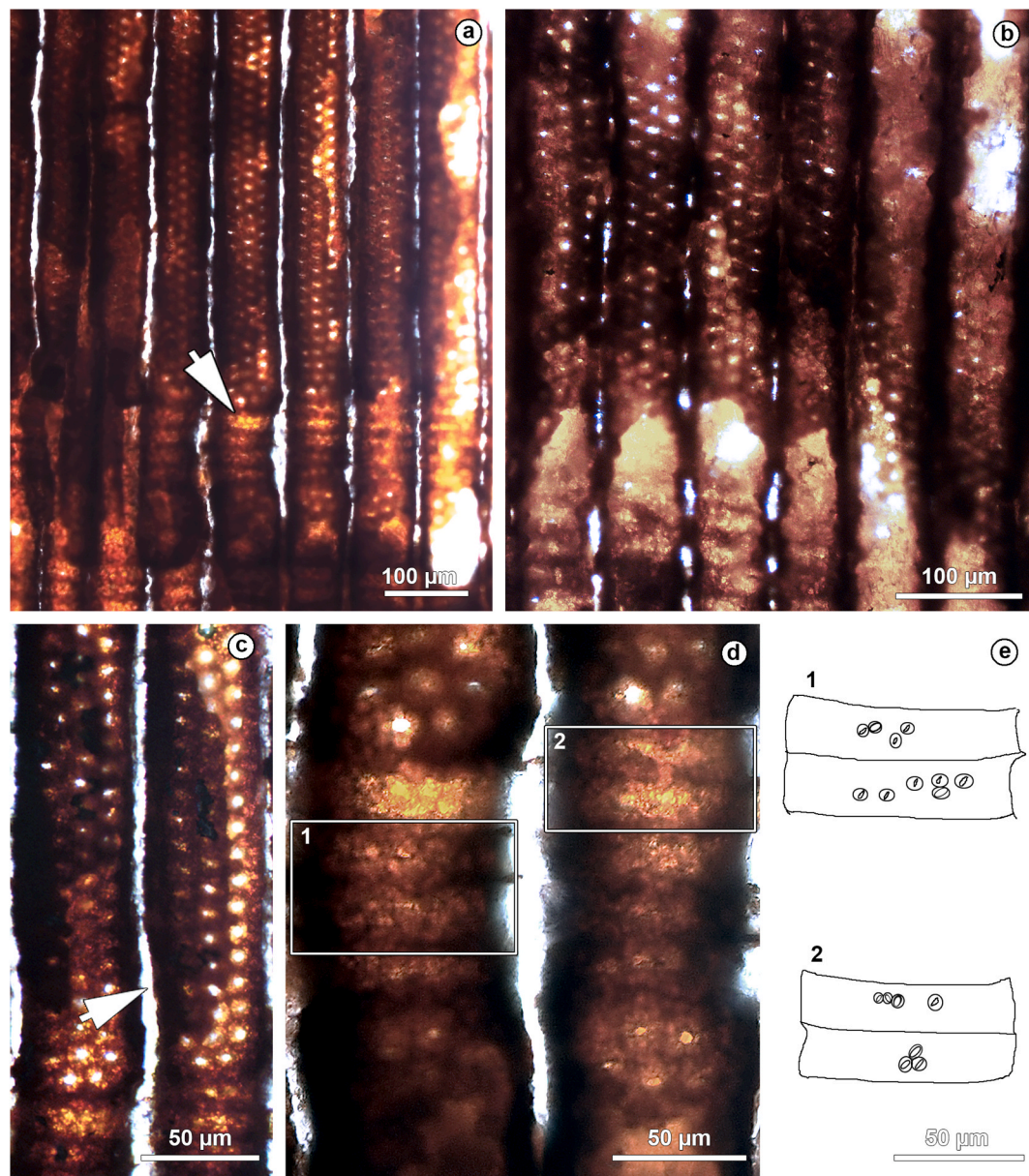
Fig. 3. Main anatomical wood pattern in radial section (slide 2443-Pb-8). a) General view of tracheids with multiseriate hexagonal bordered pitting and cross-fields with araucarioid pitting; b, c) tracheids with multiseriate alternate hexagonal bordered pitting in compact arrangement and continuous degradation of the middle lamella by white rot (arrow); d) detail of (a) showing densely arranged pits with araucarioid organization in cross-fields; e) schematic drawing of observable cross-field pitting from (d).

pluriresinosum Torres and Biro-Bagoczky (1986) (Late Cretaceous), *A.* (*Araucarioxylon*) *resinosum* Torres and Biro-Bagoczky (1986) (Late Cretaceous), *A. santacruzense* Kloster and Gnaedinger (2018) (Middle Jurassic), *A. termieri* Gnaedinger and Herbst (2009) (Middle Jurassic). However, the uniseriate, biseriate, and triseriate alternate pit disposition found in these species contrast with the mostly (95%) triseriate, alternate, compact arrangement found in *Agathoxylon santanensis* sp. nov. (Fig. 3a–d). occurring along the entire wood length (up to 395 mm) and in the outer and inner parts of the xylem. This unique feature distinguishes the species described here from the other taxa.

Half-bordered cross-field pitting showing exclusively araucarioid pattern (Fig. 3d), according to the criteria of IAWA (2004), is shared only with *Agathoxylon santacruzense,* and *A. termieri.* This kind of pitting differs from the cupressoid arrangement present in the remaining taxa. However, resin plugs in tracheids were not observed in these species.

We consider this as the first record of the genus *Agathoxylon* from the

Brazilian Araripe Basin, included in the Aptian Tropical-Equatorial Hot Arid belt of Chumakov et al. (1995), because the very poor preservation and the representation of an atypical cross-field pitting of a wood described as *Agathoxylon* by Batista et al. (2017) for the Crato Member preclude comparison with typical *Agathoxylon* diagnostic features. The present record amplifies the paleobiogeographic distribution of this morphogenus for the Jurassic–Cretaceous interval in the Western Gondwana, which was so far recorded from coeval Warm to Cool-Temperate belts (Del Fueyo et al., 2021).

While in the Mesozoic *Agathoxylon* has been linked with *Araucaria*-like fossil woods (Rößler et al., 2014), Peralta-Medina and Falcon-Lang (2012) affirmed that Mesozoic fossil woods that resemble extant Araucariaceae cannot be definitively placed into this family. This statement is based on distinct systematic affiliations that have been attributed to the morphogenus by its association with axes of Cordaitales, Pentoxylales, Glossopteridales, Cheirolepidiaceae and Pteridospermermales
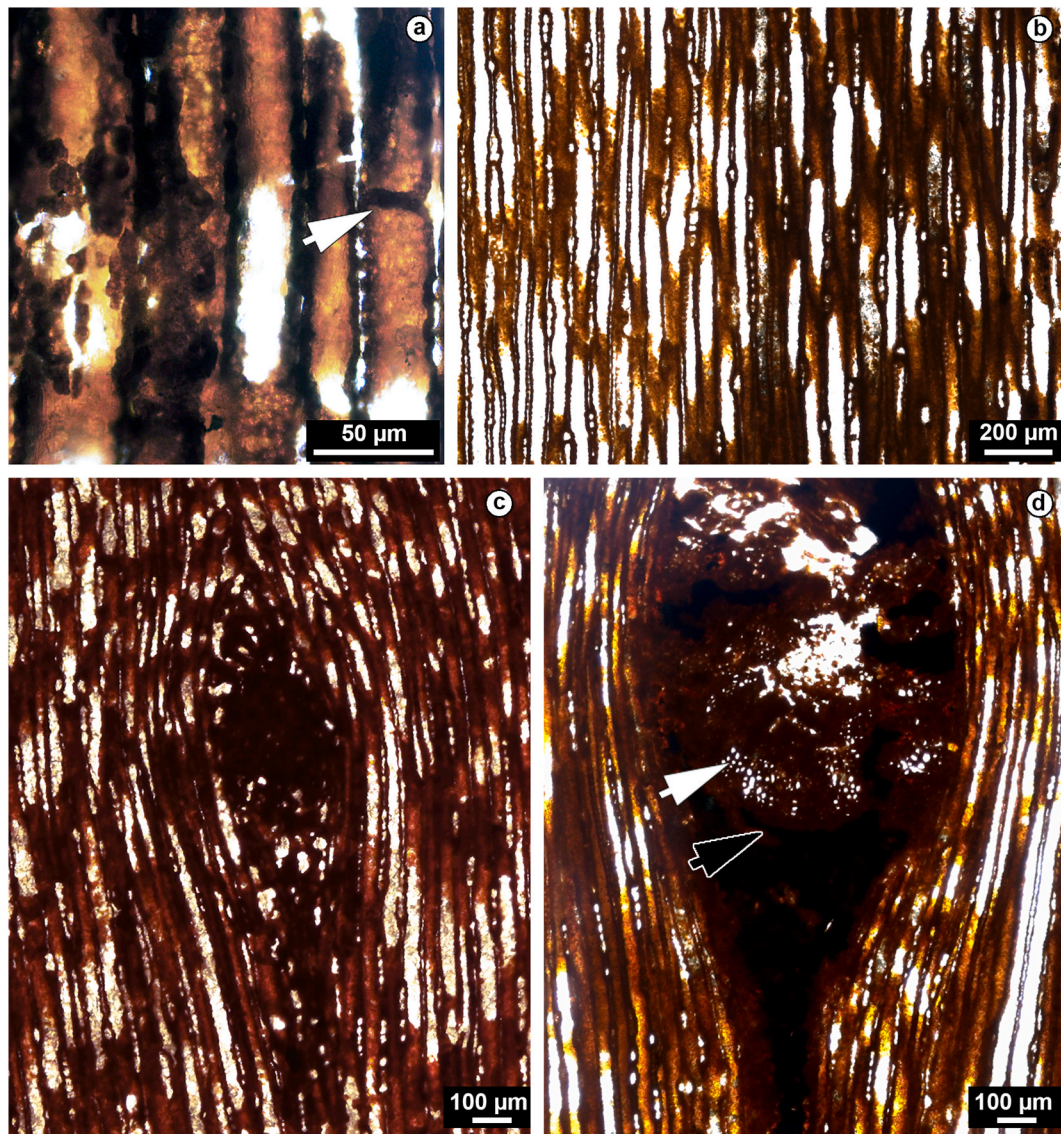
Fig. 4. Main anatomical wood pattern in radial and tangential sections. a) Resin plug in tracheid in radial section (arrow); b) uniseriate, homogenous rays (slide 2443 Pb-22); c) ellipsoid branch trace cross-cutting the xylem tissue (slide 2443 Pb-01); d) detail of a branch trace showing a central pith with parenchymatous (white arrow) and sclerenchymatous cells (black arrow) (slide 2443 Pb-08).

(Peralta-Medina and Falcon-Lang, 2012).

The affinity of *Agathoxylon* wood-types from the Mezosoic of Western Gondwana with Araucariaceae has been strongly suggested by different authors (García-Massini et al., 2012; Gnaedinger and Herbst, 2009; Gnaedinger et al., 2015; Greppi et al., 2020; Kloster and Gnaedinger, 2018; Panti et al., 2012; Vera and Césari, 2012; Zamuner and Falaschi, 2005). However, the Araucariaceae affinity has mainly been supported indirectly by the abundance of megafloral and microfloral Araucariaceae remains occurring in the same strata as *Agathoxylon* woods. According to Vera and Césari (2012) and Ignacio and Perez-Loinaze (2021), *Agathoxylon antarcticus,* from the late Aptian Punta del Barco Formation (Baqueró Group) of Patagonia (Argentina) shares anatomical features with the leafy shoots of *Araucaria grandifolia* (Feruglio) Del Fueyo and Archangelsky, 2002 found in the same lithostratigraphic unit. Del Fueyo and Archangelsky (2002) also suggested the same biological identity for these two genera.

In the petrified wood from the Crato Lagerstätte, in addition to the *Agathoxylon*-type xylem (present in extant Araucariaceae), axial resin ducts found in the phloem (Agueda-Castro, 2009; Agueda-Castro et al., 2006) as well as in the cortex (Chan, 1986), associated with a tangential

belt of sclereids, are similar to those in the bark of the extant Araucariaceae. The presence of a sclereid belt and numerous resin ducts in the bark associated with *Agathoxylon*-type xylem in a single wood specimen led Sagasti et al. (2019) to speculate that the parent plant of a Jurassic wood sample from Argentina was comparable to the extant Argentinian species of *Araucaria* (Agueda-Castro, 2009).

In the material studied here the preservation process partially obscured the epidermal characters of an organically associated leaf, but there are similarities with the araucarian leaves belonging to most Araucariaceae sections – except for section Eutacta – namely the sessile insertion, stomata with four subsidiary cells and orientation parallel with the leaf axis (Andruchow-Colombo et al., 2018).

The sessile leaf connected to the axis showing a thick lamina, parallel venation and coriaceous cuticle with deeply sunken stomata encircled by papillae, points to evergreen leaves such as those present in modern podocarp and araucarian conifers (Enright and Hill, 1995).

The Araucariaceae conifer family has been described from the Crato Lagerstätte by means of megafloral remains such as *Araucaria cartellei* leaves (Duarte, 1993), *Araucariostrobus* sp. cones (Kunzmann et al., 2004), branches of *Brachyphyllum obesum* (Duarte, 1985; Kunzmann
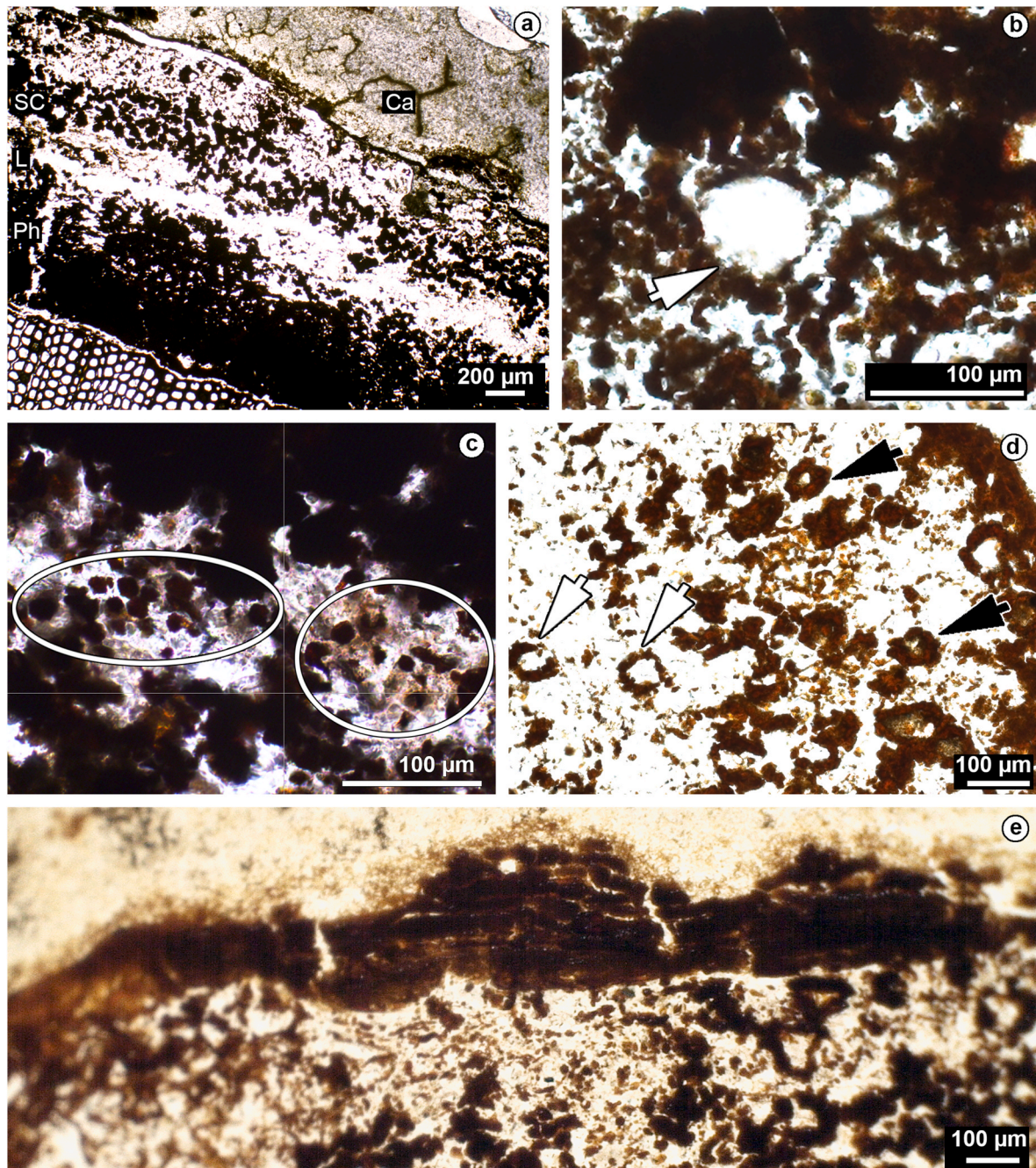
Fig. 5. Bark anatomy in transversal section (slide 2443Pb-3). a) Phloem (Ph), lacuna (L), belt of stone cells (SC), and surrounding carbonate (Ca); b) resin duct within the non-functional phloem (arrow); c) stone cells packed together; d) resin ducts (white arrows) and expanded sclereids (black arrows) within the cortex; e) thin periderm with layered cells.

et al., 2004; Batista et al., 2017) and *Brachyphyllum sattlerae* (Batista et al., 2020). The macroscopic occurrences are also supported by palynological data (Heimhofer and Hochuli, 2010; Souza-Lima and Silva, 2018).

Batista et al. (2017) suggested the occurrence of Araucariaceae wood in the Aptian Crato Lagerstätte by linking external surface patterns of a *Brachyphyllum obesum* branch and anatomical patterns of *Agathoxylon*-type wood. Nevertheless, the poor preservation of the material precludes direct comparison with *Agathoxylon* diagnostic features.

For the Triassic of the Paraná Basin, *Agathoxylon africanum* Crisafulli and Herbst, 2016 has been considered as *incertae sedis* and *A. canoasense* Crisafulli et al., 2018, from the same interval, was assigned to Araucariaceae (Crisafulli and Herbst, 2016; Crisafulli et al., 2018).

It is known that analysis of wood growth patterns can be problematic if the approach is based on a single sample and especially as in the present case, on a branch, which is in general not suited for climatic purposes. However, different authors (Forward and Nolan, 1961; Krause, 1992, Krause and Eckstein, 1992; Schweingruber, 1996, 2007) stated that despite potential local differences in sunlight and water availability, climatic constraints are evident from the anatomy of most branches, allowing for analysis from a dendrochronologic perspective.

Given the scarcity of petrified wood sampling that prevails throughout the depositional interval of the Crato Lagerstätte, analysis of growth pattern was nevertheless carried out in the petrified twig specimen aiming to provide some clues, although still speculative, into the interpretation of the paleoclimate conditions.
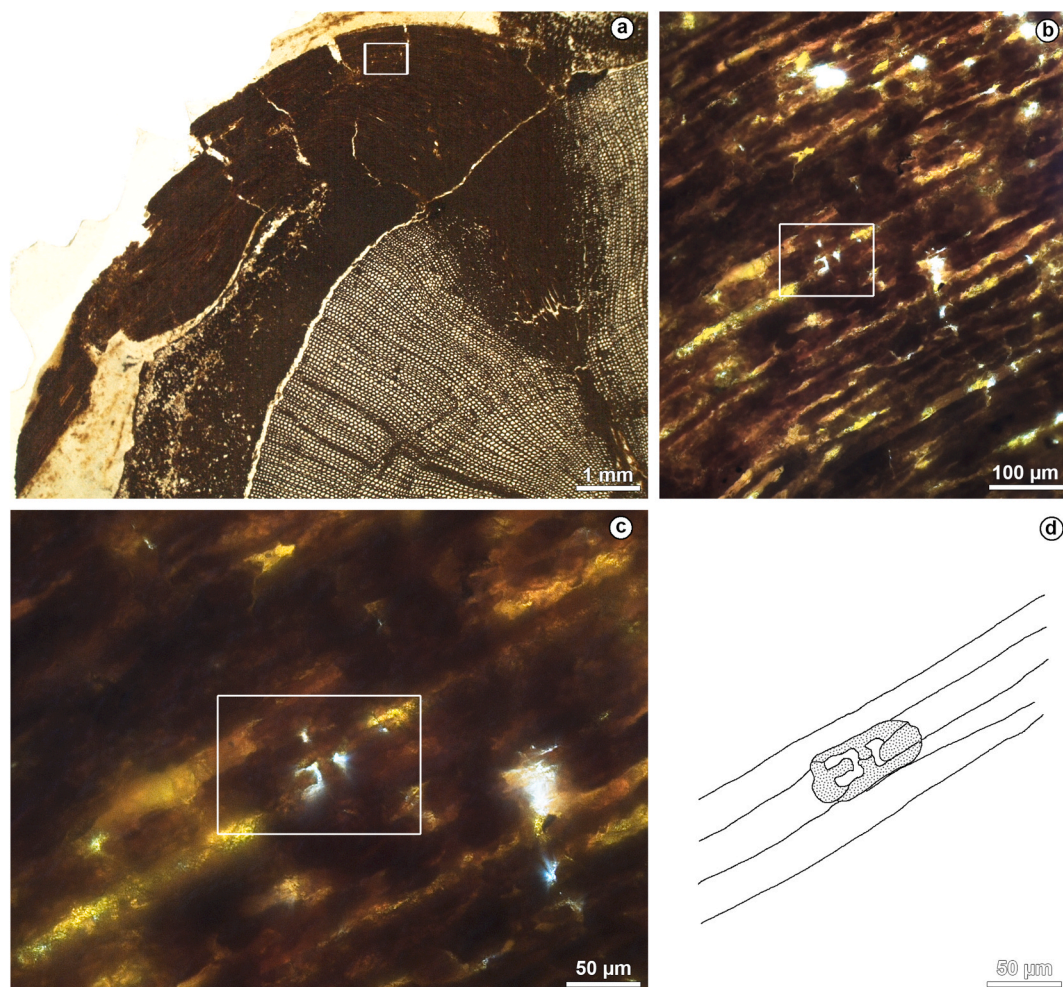
Fig. 6. Leaf surface (slide 2443 Pb-12). a) Sessile leaf with acute apex organically connected to the axis; b) detail of (a) showing parallel venation and stoma; c) detail of (b) showing stoma with two lateral and two polar papillae; d) schematic drawing of the stoma figured in (c).

The non-occurrence of wood eccentricity along the whole twig length (395 mm) ruled out plagiotropism (horizontal growth) and, consequently, pointed to an erect, long branch. This kind of branches, which are not subject to mechanical stress, are more suited for dendroclimatological studies than intensely mechanically stressed branches (Krause, 1992; Schweingruber 1996, 2007).

In addition to wood anatomical data, the sessile leaf connected to the axis points to evergreen leaves. According to Falcon-Lang (2000a, b), leaf longevity must be taken in account in addition to the influence exerted by climate in growth ring boundary markedness. Furthermore, the irregular "wood growth interruption zones" present in our material are attributed to a temporal slowing down, but not switching off of cambial activity, which originates true growth rings (Creber and Chaloner, 1984; Falcon-Lang, 2003; Schweingruber, 1992, 1996).

Wood growth interruption zones are originated by drought, flood, fire, wind damage or unusual low temperature (Ash, 1983; Ash and Creber, 1992; Dechamps, 1984; Fritts, 1976; Schweingruber, 1992, 1996, 2007; Young et al., 1993). In the material studied here, from the periequatorial Aptian arid interval, their presence was interpreted as a qualitative signal of short, abrupt cycles of water shortage, which were the limiting factor for favorable growing (Falcon-Lang, 2005). This wood signature led us to speculate that environmental conditions were available in areas not so distant from the Crato paleolake for the development of conifer trees with *Agathoxylon*-type wood and bark with probable Araucariaceae affinity.

6. Conclusion

The present study provided the taxonomic identification of a gymnospermous wood for late Aptian lacustrine Crato Member of the Santana Formation (Araripe Basin, Brazil) with anatomical characteristics of the xylem that are certainly compatible with *Agathoxylon*-type wood and led to the description of the new species *Agathoxylon santanensis*.

In addition to the common presence of *Agathoxylon* in coeval Warm- and Cool-Temperate belts in the Early Cretaceous of Western Gondwana, its presence in the Tropical-Equatorial Hot arid belt amplifies the paleobiogeographic occurrence of the genus.

The presence of (1) axial resin ducts and a dense band of sclereids (stone cells) in the non-functional phloem, and (2) the characteristics of an attached leaf showing parallel venation and stomata longitudinally oriented between ridges suggest a probable affinity of the specimen with Araucariaceae.

The wood signature led to speculate about the occurrence of growth adaptations induced by fluctuations in the water supply during the deposition of the basal interval of the fossil Crato Lagerstätte.

Author contributions

A.C.S. Santos: Formal Analysis, Investigation, Writing - original draft, Writing - review & editing A.M. Siegloch: Formal Analysis, Investigation, Writing - original draft. M. Guerra-Sommer: Conceptualization, Methodology, Validation, Writing - original draft, Writing -

Table 1

Selected Mesozoic *Agathoxylon* species from Western Gondwana showing triseriate radial pitting (modified from Del Fueyo et al., 2021).

Taxon and references	Age and provenance	Growth rings	Radial pitting	Tangential pitting	Rays	Cross-fields	Axial parenchyma	Resin plugs
Agathoxylon agathiodes (Kräusel and Jain, 1964) Kloster and Gnaedinger (2018)	Middle Jurassic, Argentina	Indistinct	Uniseriate, biseriate, less frequently triseriate alternate; hexagonal	–	Unisseriate, rarely biseriate, 1–22 cells high	2-6 araucarioid or 4–6 cupressoid	–	Present
Agathoxylon (Araucarioxylon) arayaii Torres et al., 1982 (Torres and Lemoigne, 1989; Torres et al., 2000)	Jurassic and Early Cretaceous, Antarctica	Slightly distinct	Uniseriate, biseriate alternate, and rarely biseriate opposite and triseriate alternate; hexagonal	n.a.	Uniseriate, 2–20 cells high	2-5 cupressoid	–	Present
Agathoxylon (Araucarioxylon) chapmanae Poole and Cantrill (2001)	Late Cretaceous, Antarctica	Distinct	Mostly biseriate, alternate, sometimes uniseriate, rarely triseriate; circular to hexagonal	n.a.	1-25 cells high	2–11	–	Present
Agathoxylon (Araucarioxylon) kellerense Lucas and Lacey (1981) (Nishida et al., 1992; Pujana et al., 2017)	Late Cretaceous, Chile; Late Cretaceous Antarctica	Distinct	Uniseriate to triseriate alternate; flattened to hexagonal	n.a.	Uniseriate, 1–11 cells high	1–4	n.a.	n.a.
Agathoxylon (Araucarioxylon) pluriresinosum Torres and Biro-Bagoczky (1986)	Late Cretaceous, Chile	Distinct, 2–5 mm width	Uniseriate to tetraseriate; hexagonal	n.a.	Uniseriate, 1–25 cells high	2-8 cupressoid	Present	Present
Agathoxylon (Araucarioxylon) resinosum Torres and Biro-Bagoczky (1986)	Late Cretaceous, Chile	Distinct, 2–5 mm width	Uniseriate to triseriate alternate; hexagonal	Present	Uniseriate, rarely biseriate, 1–40 cells high	2-3 cupressoid	–	Present
Agathoxylon santacruzense Kloster and Gnaedinger (2018)	Middle Jurassic, Argentina	Distinct, n.a.	Mostly biseriate; rarely uniseriate or triseriate; alternate, hexagonal	–	Uniseriate, 1–16 cells high	2-14 araucarioid	–	–
Agathoxylon termieri (Attims, 1965) Gnaedinger and Herbst (2009) (Kloster and Gnaedinger, 2018)	Middle Jurassic, Argentina	Distinct, n.a.	Uniseriate to biseriate, occasionally triseriate; alternate, circular	n.a.	Uniseriate, 1–12 cells high	1-8 araucarioid	n.a.	n.a.
Agathoxylon santanensis sp. nov.	Early Cretaceous (Aptian) Brazil	Gowth interruption zones	Mostly triseriate (95%), alternate hexagonal	Present	Uniseriate	4-8 araucarioid	n.a.	Present

n.a. = not available; – = absent.

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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.

References

Agueda-Castro, M., 2009. Corteza: Especies Leñosas de los Bosques Andino Patagónicos Argentina, p. 268. L.O.L.A. (Literature of Latin America). Remedios de Escalada, Argentina.

Agueda-Castro, M., Apóstolo, M.N., Navarro, L.E., 2006. Bark anatomy of three indigenous conifers from southern South America. Aust. J. Bot. 54, 73–82.

Andruchow-Colombo, A., Escapa, I.H., Cúneo, N.R., Gandolfo, M.A., 2018. *Araucaria lefipanensis* (Araucariaceae), a new species with dimorphic leaves from the Late Cretaceous of Patagonia, Argentina. Am. J. Bot. 105, 1067–1087.

Ash, J., 1983. Growth rings in *Agathis robusta* and *Araucaria cunninghamii* from tropical Australia. Aust. J. Bot. 31 (3), 269–275.

Ash, S.R., Creber, G.T., 1992. Palaeoclimatic interpretation of the wood structures of the trees in the chinle formation (upper triassic), petrified forest national park, Arizona, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 96 (3–4), 299–317.

Attims, Y., 1965. Etude anatomique et paléogéographique de quelques bois jurassiques du Maroc. Introduction stratigraphique par G. Choubert. Notes Mem. Serv. Geol. 24, 33–52.

Barefoot, A.C., Hankins, F.W., 1982. Identification of Modern and Tertiary Woods. University Press, Oxford, p. 189.

Barling, N., Martill, D.M., Heads, S.W., Gallien, F., 2015. High fidelity preservation of fossil insects from the Crato formation (lower cretaceous) of Brazil. Cretac. Res. 52, 605–622.

Batista, M.E.P., Silva, D.D.C., Sales, M.A., Sa, A.A., Saraiva, A.A., Loiola, M.I.B., 2017. New data on the stem and leaf anatomy of two conifers from the Lower Cretaceous of the Araripe Basin, northeastern Brazil, and their taxonomic and paleoecological implications. PLoS One 12 (3), e0173090.

Batista, M.E.P., Kunzmann, L., Sá, A.A., Saraiva, A.A., Loiola, M.I., 2020. A new species of *Brachyphyllum* from the Crato formation (lower cretaceous), Araripe Basin, Brazil. Ameghiniana 57 (6), 519–533.

Bernardes-de-Oliveira, M.E.C., Sucerquia, P.A., Mohr, B., Dino, R., Antonioli, L., Garcia, M.J., 2014. Indicadores paleoclimáticos na paleoflora do Crato, final do Aptiano do Gondwana Norocidental. In: Carvalho, I.S., Garcia, M.J., Lana, C.C., Strohschoen Jr., O. (Eds.), Paleontologia: Cenários de Vida e Paleoclimas, vol. 5, pp. 101–119. Interciência, Rio de Janeiro.

Carvalho, I.S., Agnolin, F., Rolando, M.A.A., Novas, F.E., Xavier-Neto, J., Freitas, F.I., Andrade, J.A.F.G., 2019. A new genus of pipimorph frog (anura) from the Early Cretaceous Crato Formation (Aptian) and the evolution of South American tongueless frogs. J. S. Am. Earth Sci. 92, 222–233.

Chan, L.L., 1986. The anatomy of the bark of *Agathis* in New Zealand. IAWA J. 7 (3), 229–241.

Chumakov, N.M., Zharkov, M.A., Herman, A.B., Doludenko, M.P., Kalandadze, N.N., Lebedev, E.L., Ponomarenko, A.G., Rautian, A.S., 1995. Climatic belts of the mid-Cretaceous time. Stratigr. Geol. Correl. 33, 42–63.

Creber, G.T., Chaloner, W.G., 1984. Influence of environmental factors on the wood structure of living and fossil trees. Bot. Rev. 50 (4), 357–448.

Crisafulli, A., Herbst, Dutra T.L., 2016. In-situ late Triassic fossil conifer woods from the fluvial channel deposits of the Soturno River (Caturrita Formation, Rio Grande do Sul, Brazil). Gaea-Unisinos 9 (1), 37–46.

Crisafulli, A., Herbst, R., Dutra, T.L., 2018. New gymnosperm wood fossils, a seed-ovule structure, and a new generic affinity to *Cedroxylon canoasesnse* Rau from the Permian and Triassic – Jurassic of southern Brazil. Rev. Bras. Palaontol. 21 (1), 47–62.

Dechamps, R., 1984. Evidence of bush fires during the Plio-Pleistocene of Africa (Omo and Sahabi) with aid of fossil woods. In: Coetzee, J.A., Van Zinderen Bakker, E.M. (Eds.), Palaeoecology of Africa and Surrounding Islands. A.A. Balkema, Rotterdam, pp. 291–294.

Decombeix, A.L., Boura, A., Tomescu, A.M., 2019. Plant hydraulic architecture through time: lessons and questions on the evolution of vascular systems. IAWA J. 40 (3), 387–420.

Del Fueyo, G.M., Archangelsky, A., 2002. *Araucaria grandifolia* feruglio from the lower cretaceous of Patagonia, Argentina. Cretac. Res. 23 (2), 265–277.

Del Fueyo, G.M., Carrizo, M.A., Poire, D.G., Lafuente Diaz, M.A., 2021. Recurrent volcanic activity recorded in araucarian wood from the lower cretaceous springhill formation, Patagonia, Argentina: palaeoenvironmental interpretations. Acta Palaeontol. Pol. 66 (1), 231–253.

Duarte, L., 1985. Vegetais fósseis da Chapada do Araripe, Brasil. Coletânea de Trabalhos Paleontológicos. Ser. Geol. 27, 557–563.

Duarte, L., 1993. Restos de araucariáceas da Formação Santana - formação Crato (Aptiano), NE do Brasil. An Acad. Bras Ciências 65, 357–362.

Enright, N.J., Hill, R.S., 1995. Ecology of the Southern Conifers. Melbourne University Press, Carlton.

Escapa, I.H., Catalano, S.A., 2013. Phylogenetic analysis of Araucariaceae: integrating molecules, morphology, and fossils. Int. J. Plant Sci. 174 (8), 1153–1170.

Falcon-Lang, H.J., 2000b. The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies. Palaeogeogr. Palaeoclimatol. Palaeoecol. 160 (3–4), 317–328.

Falcon-Lang, H.J., 2003. Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: implications for palaeoclimate and dinosaur palaeoecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 199 (3–4), 299–314.

Falcon-Lang, H.J., 2005. Global climate analysis of growth rings in woods, and its implications for deep-time paleoclimate studies. Paleobiology 31 (3), 434–444.

Falcon-Lang, H.J., 2000a. A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of growth ring anatomy: a new palaeoecological tool. Palaeontology 43 (4), 785–793.

Forward, D.F., Nolan, N.J., 1961. Growth and morphogenesis in the Canadian forest species. V. Further studies of wood growth in branches and main axis in *Pinus resinosa* Ait. under conditions of open growth, suppression, and release. Can. J. Bot. 39 (2), 411–436.

Fritts, H., 1976. Tree Rings and Climate. Academic Press, San Franscisco, p. 567.

García-Massini, J.L., Falaschi, P., Zamuner, A.B., 2012. Fungal–arthropod–plant interactions in the jurassic petrified forest monumento natural bosques petrificados, Patagonia, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 329, 37–46.

Gnaedinger, S., Herbst, R., 2009. Primer registro de maderas gimnospérmicas de la Formación Roca Blanca (Jurásico inferior), provincia de Santa Cruz, Argentina. Ameghiniana 46 (1), 59–71.

Gnaedinger, S., García-Massini, J.L., Bechis, F., Zavattieri, A.M., 2015. Coniferous woods and wood-decaying fungi from the el freno formation (lower jurassic), Neuquén basin, Mendoza province, Argentina. Ameghiniana 52 (4), 447–467.

Greppi, C.D., Pujana, R.R., Scasso, R.A., 2020. Fossil woods from the lower cretaceous tres Lagunas formation of central Patagonia (chubut province, Argentina). Cretac. Res. 108, 104322.

Insects from the Santana Formation, lower cretaceous of Brazil. In: Grimaldi, D.A. (Ed.), Bull. Am. Mus. Nat. Hist. 195, 1–191.

Heimhofer, U., Hochuli, P.A., 2010. Early Cretaceous angiosperm pollen from a low-latitude succession (Araripe Basin, NE Brazil). Rev. Palaeobot. Palynol. 161 (3–4), 105–126.

Heimhofer, U., Martill, D.M., 2007. The sedimentology and depositional environment of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. University Press, Cambridge, pp. 44–63.

Hartig, A., 1848. Beiträge zur Geschichte der Pflanzen und zur Kenntnis der norddeutschen Braunkohlen--Flora. Botanische Zeitung 6, 185–190.

Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S.P., Martill, D.M., Rios-Netto, A. M., 2010. Deciphering the depositional environment of the laminated Crato fossil beds (early cretaceous, Araripe Basin, north-eastern Brazil). Sedimentology 57 (2), 677–694.

IAWA Committee, 2004. Iawa list of microscopic features for softwood identification. IAWA J. 25, 1–70.

Ignacio, V. E., Perez-Loinaze, V.S., 2021. Ecological interactions in conifers (*Agathoxylon* and *Protocupressinoxylon*) from the Punta del Barco Formation (Baqueró Group, upper Aptian), Patagonia, Argentina. Cretaceous Research, 105035.

Kloster, A.C., Gnaedinger, S.C., 2018. Coniferous wood of *Agathoxylon* from the La matilde formation (middle jurassic), Santa Cruz, Argentina. J. Paleontol. 92 (4), 546–567.

Krause, C., 1992. Ganzbaumanalyse von Eiche, Buche, Kiefer und Fichte mit dendroökologischen Methoden: unter besonderer Berücksichtigung von Klima-Wachstums-Beziehungen und Weiserjahren. Dissertation. Universität Hamburg.

Krause, C., Eckstein, D., 1992. Holzzuwachs an Ästen Stamm und Wurzeln bei normaler und extremer Witterung. In: Michaelis, W., Bauch, J. (Eds.), Lutverunreinigungen und Waldschäden am Standort "Postturm" Forstamt Farchau/Ratzeburg, vol. 100, pp. 215–242. GKSS-Forschungszent Geesthacht.

Kräusel, R., Jain, K.P., 1964. New fossil woods from the Rajmahal hills, Bihar, India. Palaeobotanist 12 (1), 59–67.

Kunzmann, L., Mohr, B.A., Bernardes-de-Oliveira, M.E., 2004. Gymnosperms from the lower cretaceous Crato formation (Brazil). I. Araucariaceae and *Lindleycladus* (incertae sedis). Fossil Record 7 (1), 155–174.

Leslie, A.B., Beaulieu, J., Holman, G., Campbell, C.S., Mei, W., Raubeson, L.R., Mathews, S., 2018. An overview of extant conifer evolution from the perspective of the fossil record. Am. J. Bot. 105 (9), 1531–1544.

Lucas, R.C., Lacey, W.S., 1981. A permineralized wood flora of probable early tertiary from king George Island, South Shetland Islands. Br. Antarct. Surv. Bull. 53, 147–151.

Martill, D.M., 1993. Fossils of the Santana and Crato Formations, Brazil, vol. 5, p. 159. Palaeontological Association, London, Field Guides to Fossils.

Martill, D.M., 2007. The age of the Cretaceous Santana Formation fossil Konservat Lagerstätte of north-east Brazil: a historical review and an appraisal of the biostratigraphic utility of its palaeobiota. Cretac. Res. 28, 895–920.

Martill, D.M., Bechly, G., 2007. Introduction to the Crato formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. University Press, Cambridge, pp. 3–7.

Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Loveridge, R.F., 2007. The macrophyte flora of the Crato Formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. University Press, Cambridge, pp. 537–565.

Naish, D., 2007. Turtles of the Crato formation. In: Martill, D.M., Bechly, G., Loveridge, R.F. (Eds.), The Crato Fossil Beds of Brazil: Window into an Ancient World. University Press, Cambridge, pp. 452–457.

Nishida, M., Ohsawa, T., Nishida, H., Rancusi, M.H., 1992. Permineralized coniferous woods from the XI region of Chile, central Patagonia. Research Institute of evolutionary biology. Sci. Rep. 7, 47–59.

Panti, C., Pujana, R.R., Zamaloa, M.C., Romero, E.J., 2012. Araucariaceae macrofossil record from South America and Antarctica. Alcheringa 36 (1), 1–22.

Peralta-Medina, E., Falcon-Lang, H.J., 2012. Cretaceous forest composition and productivity inferred from a global fossil wood database. Geology 40 (3), 219–222.

Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. Rev. Palaeobot. Palynol. 148 (2–4), 184–207.

Philippe, M., Bamford, M., McLoughlin, S., Alves, L.S.R., Falcon-Lang, H.J., Gnaedinger, S., Ottone, E.G., Pole, M., Rajanikanth, A., Shoemaker, R.E., Torres, T., 2004. Biogeographic analysis of jurassic–early cretaceous wood assemblages from Gondwana. Rev. Palaeobot. Palynol. 129 (3), 141–173.

Pinheiro, F.L., Horn, B.L., Schultz, C.L., Andrade, J.A., Sucerquia, P.A., 2012. Fossilized bacteria in a Cretaceous pterosaur headcrest. Lethaia 45 (4), 495–499.

Ponte, F.C., Appi, C.J., 1990. Proposta de revisão da coluna litoestratigráfica da Bacia do Araripe. In: Anais Congresso Brasileiro de Geologia. Sociedade Brasileira de Geologia, Natal, pp. 211–226.

Poole, I., Cantrill, D., 2001. Fossil woods from Williams Point beds, Livingston Island, Antarctica: a late Cretaceous southern high latitude flora. Palaeontology 44 (6), 1081–1112.

Pujana, R.R., Raffi, M.E., Olivero, E.B., 2017. Conifer fossil woods from the Santa Marta formation (upper cretaceous), Brandy bay, James Ross Island, Antarctica. Cretac. Res. 77, 28–38.

Regali, M.S.P., Santos, P.S., 1999. Palinoestratigrafia e geocronologia dos sedimentos albo-aptianos das Bacias de Sergipe e Alagoas-Brasil. In: Simpósio sobre o Cretáceo do Brasil, vol. 5, pp. 411–419.

Rios-Netto, A.M., Regali, M.S.P., Carvalho, I.S., Freitas, F.I., 2012. Palinoestratigrafia do intervalo Alagoas da Bacia do Araripe, Nordeste do Brasil. Braz. J. Genet. 42, 331–342.

Rößler, R., Philippe, M., Van Konijnenburg-van Cittert, J.H.A., McLoughlin, S., Sakala, J., Zijlstra, G., Bamford, M., Booi, M., Brea, M., Crisafulli, A., Decombeix, A.L., Dolezych, M., Dutra, T., Esteban, L.G., Falaschi, P., Feng, Z., Gnaedinger, S., Guerra-Sommer, M., Harland, M., Herbst, R., Iamandei, E., Iamandei, S., Jiang, H., Kunzmann, L., Kurzawe, F., Merlotti, S., Naugolnykh, S., Nishida, H., Noll, R., Oh, C., Orlova, O., de Palacios, P.D.P., Poole, I., Pujana, R.R., Rajanikanth, A., Ryberg, P., Terada, K., Thévenard, F., Torres, T., Vera, E., Zhang, W., Zheng, S., 2014. Which Name(s) Should Be Used for Araucaria-like Fossil Wood?—Results of a Poll. Taxon, vol. 63, pp. 177–184.

Sagasti, A.J., García-Massini, J.L., Escapa, I.H., Guido, D.M., 2019. Multitrophic interactions in a geothermal setting: arthropod borings, actinomycetes, fungi and fungal-like microorganisms in a decomposing conifer wood from the Jurassic of Patagonia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 514, 31–44.

Santos, A.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Siegloch, A.M., Carvalho, I.S., Mendonça Filho, J.G., Mendonça, J.O., 2020. Fungus-plant interactions in aptian tropical equatorial Hot arid belt: white rot in araucarian wood from the Crato fossil Lagerstätte (Araripe Basin, Brazil). Cretac. Res. 114, 104525.

Schopf, J.M., 1975. Modes of fossil preservation. Rev. Paleobot. Palynol. 20, 27–53.

Schweingruber, F.H., 1992. Annual growth rings and growth zones in woody plants in southern Australia. IAWA J. 13, 359–379.

Schweingruber, F.H., 1996. Tree Rings and Environment: Dendroecology. Bern, Paul Haupt AG, p. 609.

Schweingruber, F.H., 2007. Wood Structure and Environment. Springer, Berlin, p. 291.

Selden, P., Nudds, J., 2012. Evolution of Fossil Ecosystems. Academic Press, London, p. 288.

Souza-Lima, W., Silva, R.O., 2018. Aptian–Albian paleophytogeography and paleoclimatology from Northeastern Brazil sedimentary basins. Rev. Palaeobot. Palynol. 258, 163–189.

Torres, T., Biro-Bagoczky, L., 1986. Xilotomía de coníferas fósiles de la Isla Quiriquina, Chile. Comunicaciones 37, 65–80.

Torres, T., Lemoigne, Y., 1989. Hallazgos de maderas fósiles de Angio-spermas y Gimnospermas del Cretácico Superior en punta Williams, isla Livingston, islas Shetland del Sur, Antártida. Serie Científica del Instituto Antártico Chileno 39, 9–29.

Torres, T., Valenzuela, E., Gonzalez, I., 1982. Paleoxilología de Península Byers, Isla Livingston, antartica. In: Actas del III Congreso Geológico Chileno, Concepción, vol. 2, pp. 321–342.

Torres, T., Galleguillos, H., Philippe, M., 2000. Maderas fósiles en el Monte Flora, Bahía Esperanza, Península Antartica. In: Actas del IX Congreso Geológico Chileno, Puerto Varas, pp. 386–390.

Vera, E.I., Césari, S.N., 2012. Fossil wood (coniferales) from the Baqueró group (aptian), Santa Cruz province, Argentina. An Acad. Bras Ciências 84, 617–625.

Vogel, K., 1995. Mikroskopische Untersuchung zur Typisierung der Kreuzungsfeldtüpfel bei Nadelhölzern. Diplomarbeit der Forstwissenschaftlichen Fakultät der Ludwig-Maximilians-Universität, München, pp. 1–96.

Young, P.J., Megonigal, J.P., Sharitz, R.R., Dat, F.P., 1993. False ring formation in bald cypress (*Taxodium distichum*) saplings under two flooding regimes. Wetlands 13, 293–298.

Zamuner, A.B., Falaschi, P., 2005. *Agatoxylon matildense* n. sp., leño araucariaceo del Bosque Petrificado del cerro Madre e Hija, Formación La Matilde (Jurásico Medio), provincial de Santa Cruz, Argentina. Ameghiniana 42, 339–346.

Ziegler, A.M., Eshel, G., Rees, P.M., Rothfus, T.A., Rowley, D.B., Sunderlin, D., 2003. Tracing the tropics across land and sea: permian to present. Lethaia 36, 227–254.