

Expanding the diversity of conifer xyloflora from Early Cretaceous Crato Fossil Lagerstätte, Brazil

Domingas Maria da Conceição^{a,*}, William V. Gobo^b, Maria E.P. Batista^{a,c}, Naiara C. Oliveira^a, Alexandra A. Mastroberti^d, Roberto Iannuzzi^b, Marion K. Bamford^e, Lutz Kunzmann^f

^a Universidade Regional do Cariri, Museu de Paleontologia Plácido Cidade Nuvens, R.Plácido Cidade Nuvens, 326, Santana do Cariri, Ceará 63190-000, Brazil

^b Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Departamento de Paleontologia e Estratigrafia, Av. Bento Gonçalves, 9500, Porto Alegre 91501-970, Brazil

^c Universidade Regional do Cariri, Departamento de Biologia, Rua Cel. Antônio Lúiz, 1161, Crato, Ceará 63105-000, Brazil

^d Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Departamento de Botânica, Av. Bento Gonçalves, 9500, Porto Alegre 90650-001, Brazil

^e Evolutionary Studies Institute, University of the Witwatersrand, Jan Smuts Ave, Braamfontein, Johannesburg, South Africa

^f Abteilung Museum für Mineralogie und Geologie, Senckenberg Naturhistorische Sammlungen Dresden, Königsbrücker Landstrasse. 159, D-01109 Dresden, Germany

ARTICLE INFO

Keywords:

Wood anatomy
Bark
Taxonomy
Crato Formation
Araripe Basin

ABSTRACT

Remains of gymnosperms are the most abundant plant macro-fossils in the outcrops of a fossil lagerstätte preserved in lacustrine limestones in the likely lower Aptian Crato Formation of the Araripe Basin in NE Brazil. However, the systematics of most fossil-taxa are mainly based on foliage and reproductive structures, whereas wood anatomy has rarely been used to study fossil plant diversity, despite the abundance of wood fragments. Here we describe a new fossil gymnosperm taxon based on anatomical characters of a well-preserved specimen from this lithostratigraphic unit. The new fossil-genus and fossil-species *Cratoxylon placidoi* gen. nov. et sp. nov. are established using characters of the secondary xylem and the bark, features that are also crucial for their affiliation into conifers. This finding reinforces the already known remarkable preservation potential of organisms in this konservat lagerstätte, since bark tissues are rarely preserved in the fossil record of Mesozoic gymnosperms. The results reveal the great potential of fossil woods for studying diversity of the Crato Formation flora and thus contribute to expand our knowledge on fossil vegetation in equatorial Gondwana during the early diversification of angiosperms.

1. Introduction

Gymnosperms were the predominant floristic component on Earth throughout the Mesozoic era, with conifers forming a considerable part of the global flora (Stewart and Rothwell, 1993; Condamine et al., 2020). Conifers were also important by being one of the major diet resources of giant herbivorous dinosaurs (Gee, 2011). The role of gymnosperms in the vegetation persisted until notable changes in biotic and abiotic factors occurred in the late Mesozoic, such as the emergence and diversification of angiosperms from the mid-Early Cretaceous onwards, and the global cooling after the Cretaceous thermal maximum (Heimhofer et al., 2018; Condamine et al., 2020). These events have triggered the reduction of gymnosperm diversity and abundance (Heimhofer et al., 2018; Condamine et al., 2020). Before they markedly declined, few places in the world have captured the last moments of the

gymnosperm heyday concomitantly with the initial diversification of angiosperms in the Early Cretaceous tropics. One of these rare windows into the paleovegetational history is opened by the *konservat fossil lagerstätte* excavated from the Crato Formation in the Araripe Basin, northeastern Brazil.

The Crato Fossil Lagerstätte (CFL) is considered one of the most important Early Cretaceous paleontological deposits from equatorial Gondwana, primarily due to the abundance, diversity and exceptional preservation of different plant lineages (e.g., angiosperms, conifers, gnetaleans and pteridophytes) as well as several invertebrate and vertebrate groups (Martill et al., 2007; Kunzmann et al., 2021). Fossil gymnosperms are very common in this fossil flora, belonging mainly to conifers (Kunzmann et al., 2006; Mohr et al., 2012; Sucerquia et al., 2015; Batista et al., 2017, 2020, 2021) and gnetophytes (Rydin et al., 2006; Dilcher et al., 2005; Kunzmann et al., 2009, 2011; Lowe et al.,

* Corresponding author.

E-mail address: domingas.paleonto@gmail.com (D.M. da Conceição).

<https://doi.org/10.1016/j.revpalbo.2024.105061>

Received 23 August 2023; Received in revised form 26 December 2023; Accepted 5 January 2024

Available online 11 January 2024

0034-6667/© 2024 Elsevier B.V. All rights reserved.

2013; Ricardi-Branco et al., 2013). Besides, there are a number of gymnospermous plants that still remain enigmatic and of uncertain systematic affinities (Kunzmann et al., 2007; Mohr et al., 2012). In contrast to the number of published gymnosperms from CFL (see Kunzmann et al., 2021, 2023), the number of fossil plants whose wood anatomy is well known is rather limited (e.g., *Brachyphyllum obesum*, Araucariaceae, Sucerquia, 2013; Batista et al., 2017, 2022). Moreover, the number of taxa classified based on their wood anatomy is still low; only *Agathoxylon santanensis* (Santos et al., 2021) and *Duartenia araripeensis* (Mohr et al., 2012) were established primarily using xylotomical features. Features of vascular tissues are additionally described from a few gnetalean, coniferalean and angiosperm fossil-taxa but they were often not diagnostic (e.g., Kunzmann et al., 2009, 2011; Batista et al., 2017; Gobo et al., 2023). In fact, considering the rich paleobotanical record of the Araripe Basin, particularly from the Crato Formation strata, fossil wood has not received sufficient attention, leading to a significant gap in the knowledge of the CFL flora.

Beside the already mentioned fossil-species, some wood anatomical features have been described from additional conifer taxa, represented by sterile vegetative shoots in the Crato Formation, and considered in their taxonomic classification, including *Pseudofrenelopsis* spp. (Sucerquia et al., 2015; Batista et al., 2017); *Brachyphyllum sattlerae* (Batista et al., 2020); and *Araucaria violetae* (Batista et al., 2021). However, almost all of these fossil-species were distinguished based on branching architecture, phyllotaxis and leaf anatomy, while xylotomical features played either no or only a minor rule in the specific diagnosis. Despite the abundance of vegetative shoots of woody coniferous plants, trunks or larger logs are completely unknown from the Crato Formation flora to date (Kunzmann et al., 2021) and only fragmentary remains of stems and branches have been found so far (Mohr et al., 2012; Santos et al., 2021 and reference therein).

It is important to mention that studies focusing on systematics of Mesozoic woods are scarce from other parts of Brazil, particularly from other Cretaceous basins but also from Jurassic deposits. The few papers are merely concentrated on woods from the Triassic deposits of the Paraná Basin (e.g., Crisafulli and Dutra, 2009; Crisafulli et al., 2016, 2018). In the other Cretaceous deposits (e.g., Paraná and Parnaíba Basins), few taxonomic studies have been carried out based on wood anatomy (Oliveira, 1936; Dolianiti, 1948; Mussa, 1974; Duarte, 1989; Araujo et al., 2011). In some of these works, the woods have an

uncertain taxonomic affiliation (Duarte, 1989; Araujo et al., 2011), while in others woods are poorly preserved and putatively linked to the fossil-genera *Cupressinoxylon* (Dolianiti, 1948) or *Palaeopinuxylon* Mussa (Mussa, 1974). More recently, a coniferous wood, i.e., *Brachyoxylon* Hollick et Jeffrey (Hollick and Jeffrey, 1909), has been reported from Cretaceous deposits of the Maceió Formation, Sergipe-Alagoas Basin, Brazil by Santos et al. (2022).

Among the fossil-taxa found in the Brazilian Cretaceous deposits, only *Agathoxylon santanensis* from CFL is described with preserved bark (Santos et al., 2021). However, this fossil-species only exhibits a few bark features, with few identifiable elements preserved, such as dispersed axial resin ducts and sclereids.

Here, we describe a new fossil-genus and fossil-species for conifers based on a specimen encompassing pith, secondary xylem and bark tissues, aiming to fill a gap in the knowledge of CFL flora and encouraging more paleoxylotomical studies on fossil wood from the Crato Formation.

2. Geological setting and paleoenvironment

The Araripe Basin (NE Brazil, Fig. 1.) is renowned for housing one of the most important Cretaceous fossiliferous records in Gondwana, including the Crato Formation deposits of the Santana Group (Assine et al., 2014; Martill et al., 2007). The outcrops in the laminated limestones of the Crato Formation offer a unique insight into an Early Cretaceous paleoecosystems of northern equatorial Gondwana providing fossil remains of a konservat lagerstätte (Martill et al., 2007). Its sedimentary rocks are mainly represented by lacustrine limestones, but bear also strata of deltaic and alluvial siliciclastics (Nascimento Jr. et al., 2022). The laminated limestones are divided into six major units – C1 to C6, representing consecutive phases in the development of the lacustrine paleoenvironment (Neumann et al., 2008). They are interbedded both laterally and vertically with other lithological units such as terrigenous marls, shales, siltstones and sandstones (Neumann et al., 2008; Nascimento Jr. et al., 2022). The lagerstätte deposit is located in the uppermost C6 unit, where the limestones called *Pedra Cariri* are excavated by local miners in several opencast pits between the town Nova Olinda and Santana do Cariri at the northern edge of the Chapada do Araripe, Ceará (Nascimento Jr. et al., 2022; Kunzmann et al., 2021). The ongoing exploitation in opencast pits by these workers constantly

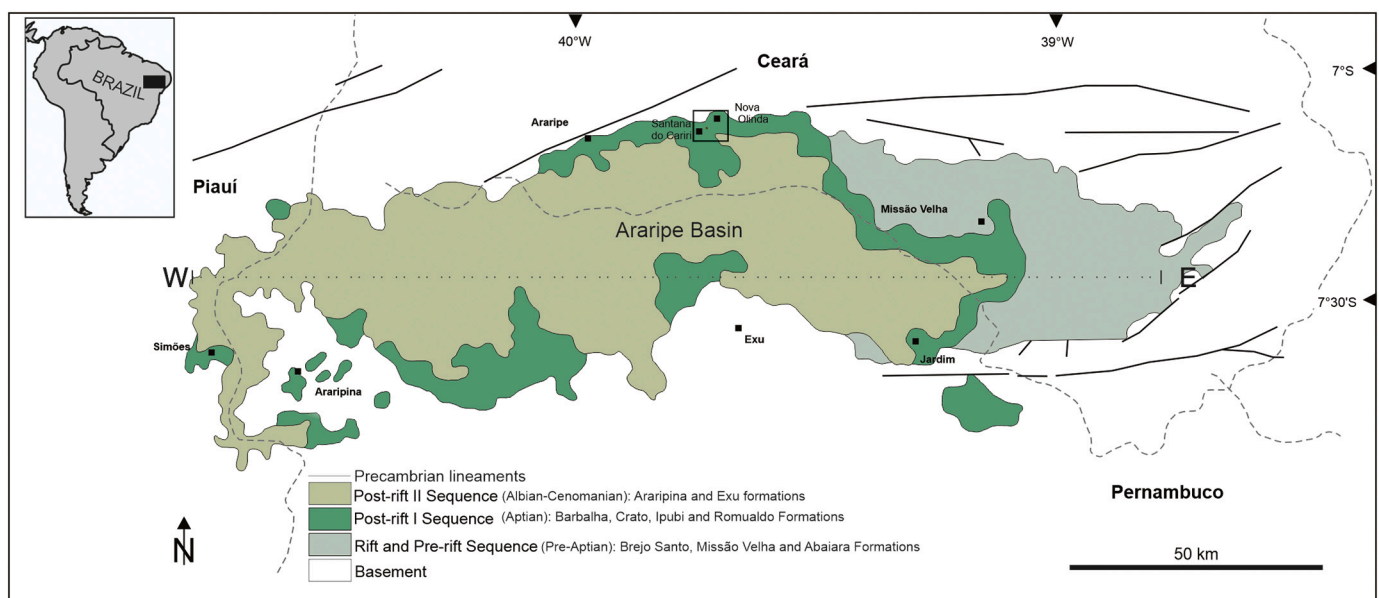


Fig. 1. Geological setting of the studied area. The square indicates the location of the *Três Irmãos* quarry, between the municipalities of Santana do Cariri and Nova Olinda, Ceará State. Modified from Barreto et al. (2022).

reveals new fossil specimens of CFL. The age of Crato Formation and in particular the fossiliferous C6 limestone strata is still controversial and under debate (Nascimento Jr. et al., 2022; Kunzmann et al., 2021; Gobo et al., 2023). Previous estimations based on relative dating suggested a late Aptian/early Albian age for this unit (see Coimbra and Freire, 2021). However, other investigations of the Santana Group formations suggest indirectly a lower Aptian age or even late Barremian age for the Crato Formation (Arai and Assine, 2020; Lúcio et al., 2020; Melo et al., 2020; Barreto et al., 2022). A more comprehensive and updated review of this age estimation is provided by Gobo et al. (2023).

There is multiple evidence from geological observations (e.g., Nascimento Jr. et al., 2022) and paleoecology of CFL biota that the paleoclimate was hot and semiarid and the Crato Lake experienced periods with saline or even hypersaline water conditions. Lithological findings give evidences of seismic activities, flash floods and paleoclimate-driven lake level fluctuations (Nascimento Jr. et al., 2022). So, the paleo-environment from which we describe a new gymnospermous plant was periodically rather harsh and unstable, but the actual course of the history is not sufficiently reconstructed yet.

3. Material and methods

The study material comprises a fragment of fossil gymnosperm axis found in the laminated limestones (C6 unit) of Crato Formation in the

Araripe Basin (Fig. 1). The fossil specimen is preserved by replacement of iron oxide (for detailed information of the fossilization process (see Nascimento Jr. et al., 2022, fig. 7). The fossil consists of a main axis and short fragment of a laterally diverging axis (hereafter called branch and twig, respectively) (Plate I, A–C). It is noteworthy to mention that the fossil was not sampled by controlled scientific excavation but was seized in commercial *Três irmãos* quarry near Nova Olinda, Ceará State, northeast of Brazil, by the Environmental Police and then handed over to the Museu de Paleontologia Plácido Cidade Nuvens – MPPCN (Santana do Cariri, Ceará, Brazil) where it is permanently kept.

The sample was examined using conventional petrographic techniques for preparing thin sections of fossilized wood. Three standard sections (transverse, radial longitudinal, and tangential longitudinal (sensu Jones and Rowe, 1999) were made in the level where both main and minor lateral axes are visible in cross-sectional view (Plate I, A–C). Main and minor lateral axes are called branch and twig hereafter and anatomical descriptions were made from both parts.

Macroscopic images were taken with a Canon EOS T3i camera using a Sigma 70 mm DG Macro lens. Thin sections were examined with two transmitted light microscopes: Leica DM500 and Leica DMR HC and photographs were taken with a Leica MC170 and Zeiss Axiocam HCr digital cameras at the Department of Paleontology and Stratigraphy (Institute of Geosciences), and Laboratory of Plant Anatomy of the Department of Botany (Institute of Biosciences) from Universidade

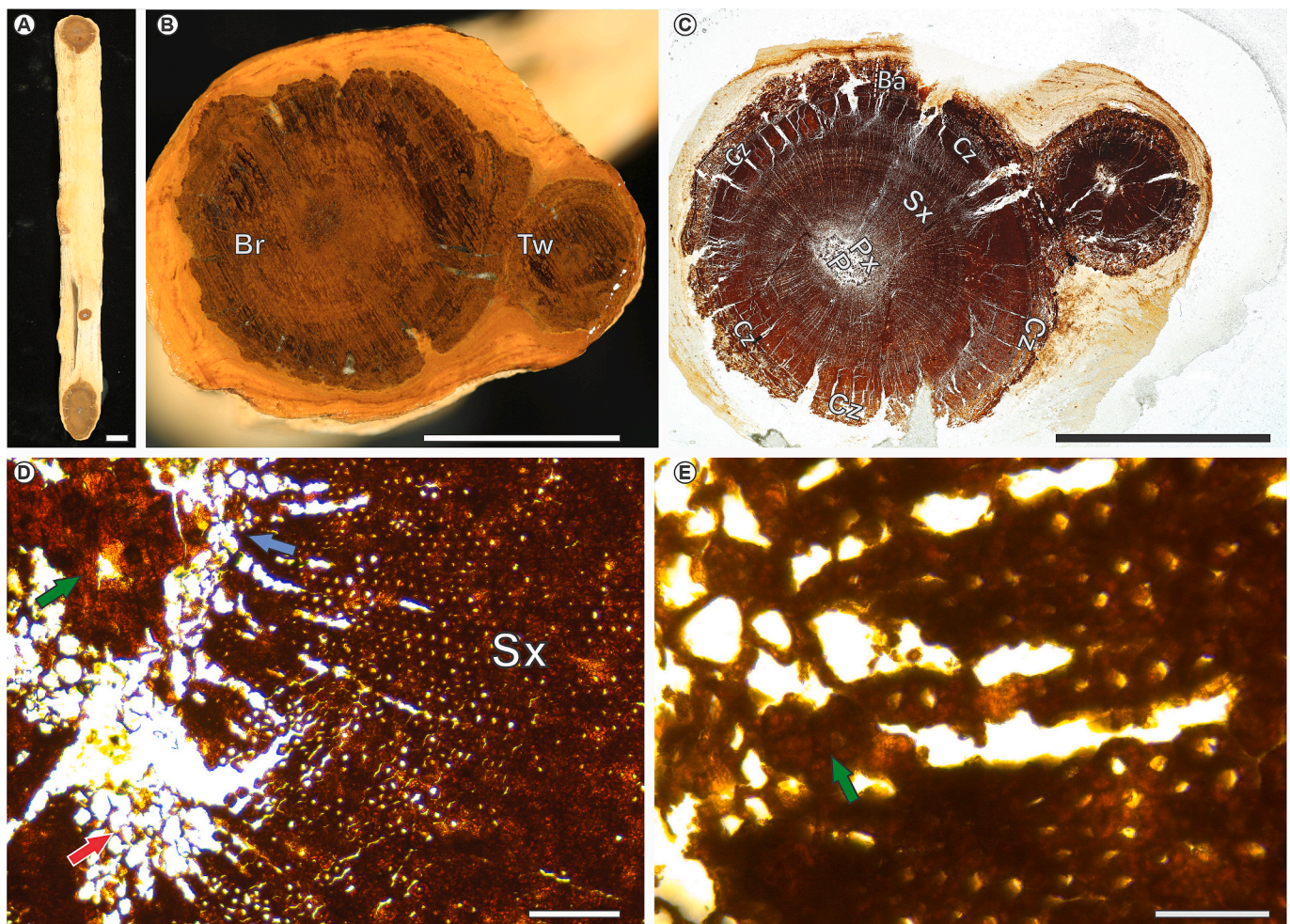


Plate I. *Cratoxylon placidoi* gen. nov. et sp. nov., MPSC PL 5131. Overview of the branch and twig and the primary vascular tissues. (A) Macroscopic views of the specimen. (B) Overview in transverse section of the branch (Br) and twig (Tw). (C) General morphology of the sample showing the pith (P); Primary xylem (PX); secondary xylem (SX) cambial zone (CZ) and bark (Ba). (D) Transverse section showing secondary xylem, strands of primary xylem (blue arrow), parenchyma cells of the pith (red arrow) and clusters of sclerenchyma cells (green arrow). (E) Transverse section with detail of strands of primary xylem (arrow). Scale bars: A, B, C = 10 mm; D = 200 μ m; E = 50 μ m.

Federal do Rio Grande do Sul, Brazil. Additionally, scanning electron microscopy (SEM) analyses were performed under JEOL JSM-6610LV at the Laboratório de Geologia Isotópica (CPGq/IGEO/UFRGS), Porto Alegre, and Hitachi SU3500 SEM at the Universidade Regional do Cariri, Crato. For these analyses, small portions of the sample were removed and mounted directly on stubs with carbon tape. They were then sputter-coated with gold for four minutes and analyzed in high vacuum using the SEI detector (Secondary Electron Imaging).

When possible, average dimensions were calculated from 30 measurements in each of the anatomical characters analyzed. The anatomical terminology used to describe the specimen follows IAWA Committee (2004); Boura et al. (2021) and Esteban et al. (2023). Philippe and Bamford (2008) were followed in the use of classification criteria. As noted by Philippe et al. (2014), in fossil wood taxonomical studies the type of radial pits of the tracheids is determined by three different ways: (i) counting the number of types (uniseriate contiguous, uniseriate spaced, biseriate contiguous alternate, etc.) of radial pitting represented within each tracheid in order to calculate percentages; (ii) assigning each tracheid to a single type of radial pitting, according to its predominant pitting; (iii) assigning each single pit to a type for calculation. We have chosen the second of these methods here. Therefore, we examined over 200 tracheids and assigned each tracheid to a single type of radial pitting, according to its predominant pitting for determining pit percentages.

The term bark is used here to refer to tissues outside the vascular cambium as defined by Evert (2006) and IAWA Committee (2004). Classification of conifers follows Christenhusz et al. (2011).

4. Results

4.1. Systematic paleobotany

Subclass: Pinidae Cronquist, Takht. & Zimmerm. 1966

Order: UNKNOWN

Family: UNKNOWN

Fossil-Genus: **Cratoxylon** Conceição, Gobo, Batista, Mastroberti, Iannuzzi, Bamford et L.Kunzmann **gen. nov.**, [Plates I–V](#).

Type species: **Cratoxylon placidoi** Conceição, Gobo, Batista, Mastroberti, Iannuzzi, Bamford et L.Kunzmann sp. nov., [Plates I–V](#).

Plant Fossil Names Registry Number: PFN 003212

Generic diagnosis: Pith composed of parenchyma cells and clusters of sclerenchyma cells. Pycnoxylic secondary xylem. Bordered pits arranged in abietinean type on radial walls of tracheids. Cross-fields with cupressoid oculipores arranged in araucarioid pattern. Rays homogeneous, exclusively uniseriate and with their horizontal walls unpitted. Secondary phloem composed of tangential layers of fibers, sieve cells, parenchyma cells and dispersed secretory ducts. Cortex parenchymatous with secretory ducts.

Etymology: *Cratoxylon* refers to the geological unit Crato Formation where the fossil specimen was found and the Greek word ξύλον (xylon) meaning wood.

Cratoxylon placidoi Conceição, Gobo, Batista, Mastroberti, Iannuzzi, Bamford et L.Kunzmann sp. nov., [Plates I–V](#).

Plant Fossil Names Registry Number: PFN 003213

Species etymology: the specific epithet *placidoi* is in honor of Plácido Cidade Nuvens, sociologist and professor at URCA, who worked intensively for establishment of Museu de Paleontologia Plácido Cidade Nuvens.

Type locality: Quarry Três irmãos, Nova Olinda, Ceará, Brazil.

Holotype: MPSC-PL5131, figured in [Plates I–V](#).

Stratigraphic horizon: C6 limestone horizon, Crato Formation, Santana Group, Araripe Basin (sensu Assine et al., 2014).

Repository: Museu de Paleontologia Plácido Cidade Nuvens – MPPCN (Ceará, Brazil).

Age: Lower Cretaceous, lowermost Aptian (maximum age range: uppermost Barremian to lowermost Aptian, see International

Chronostratigraphic Chart (2023/06).

Specific diagnosis: Primary xylem with slender strands. Pits on the radial walls of the tracheids exclusively uniseriate, predominantly spaced and rounded with circular apertures. Cross-field, with 4 to 12 oculipores per cross-field, arranged in alternate to opposite rows. Rays parenchymatous, exclusively uniseriate with 1 to 18 cells high. Pits on the tangential walls of the tracheids, uniseriate and sparsely arranged.

4.2. Morphoanatomical description and remarks

General features: The fossil specimen consists of a larger portion of a main axis (most likely a branch) and a short laterally diverging minor axis (twig) ([Plate I](#), A–C). The branch is 20 mm in diameter and 200 mm in length, whereas the twig is about 7 mm in diameter ([Plate I](#), B–C). Both preserve a pith surrounded by wedges of the primary xylem and pycnoxylic secondary xylem, although the pit and primary xylem of the twig are significantly better preserved than those of the branch ([Plate I](#), C–D). Bark tissue is preserved in both parts. If not indicated otherwise, the description combines observations from both axes.

Pith and primary xylem: In transverse section, a small poorly preserved pith is seen ([Plate I](#), C), composed of parenchyma cells and other cells organized in clusters that may belong to sclerenchyma ([Plate I](#), D). The pith is surrounded by slender strands of primary xylem, hardly distinguishable in transverse section ([Plate I](#), D–E), but recognizable in radial section by the scalariform thickenings.

Secondary xylem: The secondary xylem is about 6.1 mm wide in the branch and approximately 2.1 mm in the twig and composed of narrow tracheids and uniseriate parenchyma rays, without growth rings ([Plate II](#), A–B). In cross-section, the tracheids are circular and their lumens are 3.8–10.6 µm (mean: 6.8 µm) in radial diameter and 2.8–11.7 (mean: 6 µm) in tangential diameter, while their walls are 3.9–7.9 (mean: 3.4 µm) thick.

The rays are parenchymatous and exclusively uniseriate, ranging from 1 to 18 cells height (mean: 6 cells). Their density is 29 rays per mm² and their horizontal walls are unpitted ([Plate III](#), D and F). Bordered pits are observed on the tangential walls of tracheids, which are uniseriate and arranged separately ([Plate II](#), D). Traces of branching are seen in the marginal part of the tangential section ([Plate II](#), E).

Bordered pits on the radial walls of tracheids are exclusively uniseriate and predominantly spaced (96%) or contiguous (4%), corresponding to the abietinean type ([Plate II](#), C and [Plate III](#), A–D). These pits are mostly rounded and are 7–14 µm (mean: 11 µm) in diameter, while their elliptical and circular apertures are 1.5–4.6 (mean: 3.2 µm) in diameter ([Plate III](#), D). The cross-fields have 4 to 12 cupressoid oculipores per cross-field, arranged in alternate to opposite rows with a tendency to crowding, which indicates the araucarioid pattern ([Plate III](#), E–H).

Bark

The area outside the secondary xylem is about 2 mm wide and is represented by a thin cambial zone, secondary phloem and periderm cells in the branch ([Plate I](#), C and [Plate IV](#), A). However, due to the poor preservation of the cambial zone, it is not possible to describe its mostly crushed cells in detail.

The secondary phloem, located near the cambial zone, is ca. 0.7 mm thick, and consists of fiber layers, sieve cells and parenchyma cells ([Plate IV](#), B–I). The rays are poorly preserved ([Plate IV](#), C).

The disposition of the phloem cells is difficult to determine because they are mostly crushed, but they appear to be organized in a regular and alternate sequence of fibers, sieve cells and parenchyma cells ([Plate IV](#), B–I). The sieve cells with sieve areas are better seen in the longitudinal radial section, and the parenchyma cells are also best seen in this view ([Plate IV](#), H–I). Resin ducts are usually present and appear scattered throughout the phloem ([Plate IV](#), B).

In transverse section, the fibers are rectangular and their cells are 4–16 µm (mean: 9 µm) in diameter. They are mostly arranged in tangential bands ([Plate IV](#), B–E).

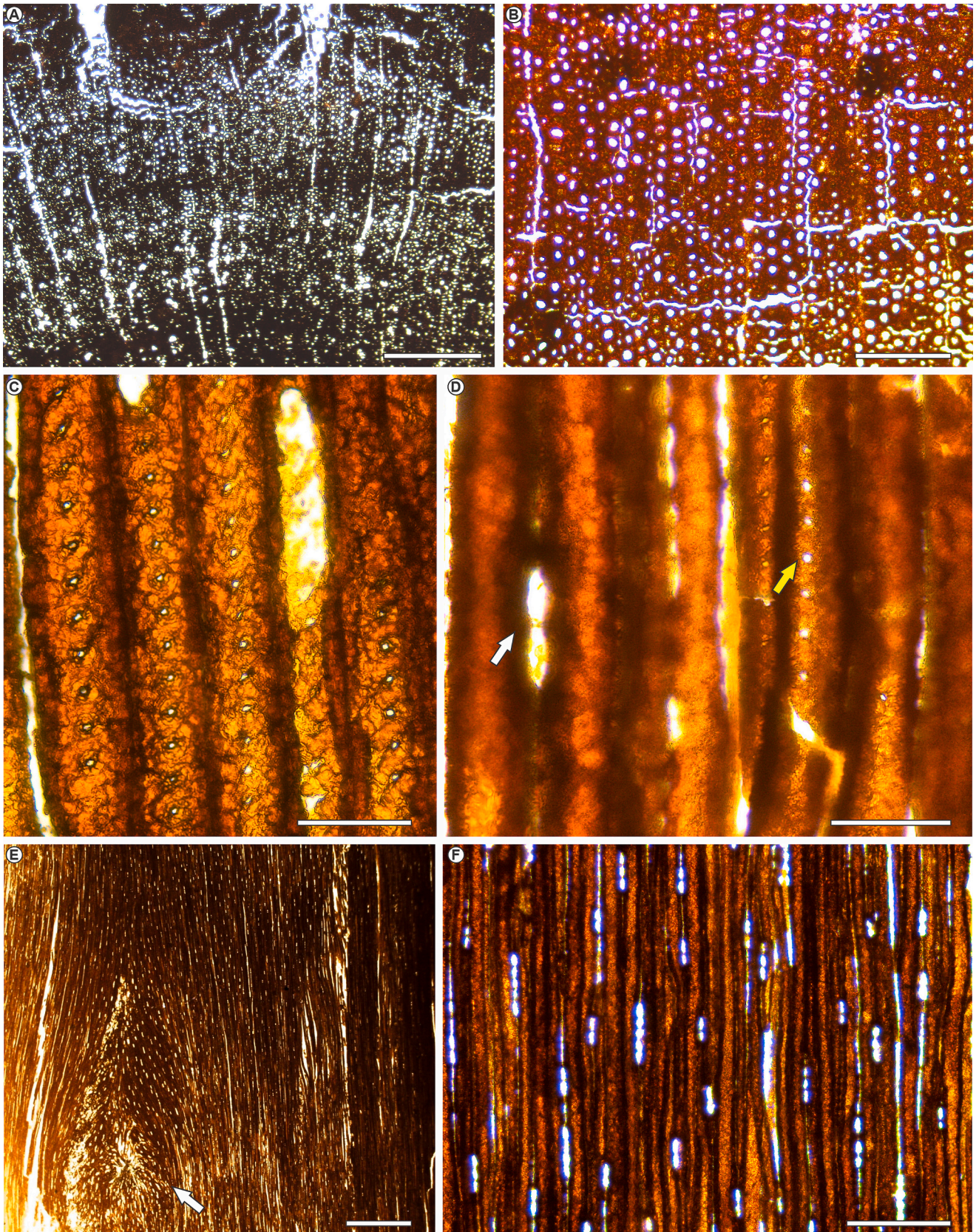


Plate II. *Cratoxylon placidoi* gen. nov. et sp. nov., MPSC PL 5131. Overview of the secondary xylem: (A) Transverse section, showing the overview of secondary xylem without growth rings. (B) Transverse section, details of the secondary xylem (tracheids and rays). (C) Radial section showing the abietinean radial pitting. (D) Tangential pits on the walls of the tracheids and rays. Uniseriate and lower rays with unpitted horizontal walls (white arrow) and pits (yellow arrow). (E) General view of tracheids in tangential section with uniseriate rays and branch trace (arrow). (F) Details of the fig. E showing uniseriate and parenchymatous rays. Scale bars: A = 500 μm ; B, F = 200 μm ; C, D = 50 μm ; E = 2 mm.

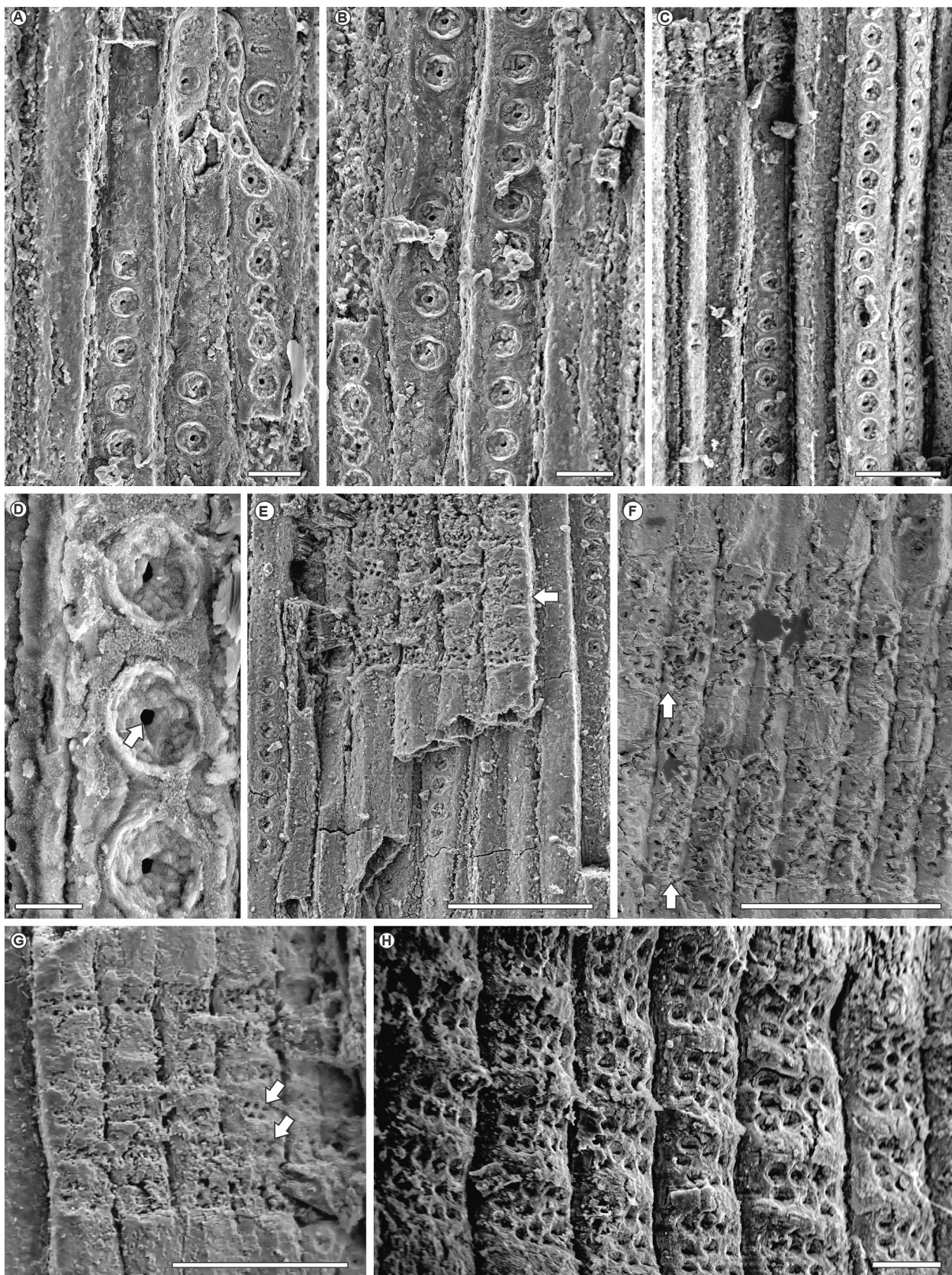


Plate III. *Cratoxylon placidoi* gen. nov. et sp. nov., MPSC PL 5131. Anatomical details under SEM in radial views, showing abietinean radial pitting and cross-fields. (A–D) Uniseriate, rounded and spaced pits, and very occasionally contiguous pits (C). (D) Detail of the pits with circular aperture (arrow). (E) General view of araucarioid cross-fields (arrow). (F–G) Overview of the araucarioid cross-fields (arrows). (H) Detail of cross-fields of the araucarian type. Scale bars: A = 20 μm ; B = 200 μm ; C = 50 μm ; D = 10 μm ; E = 50 μm ; F, G = 100 μm ; H = 20 μm .

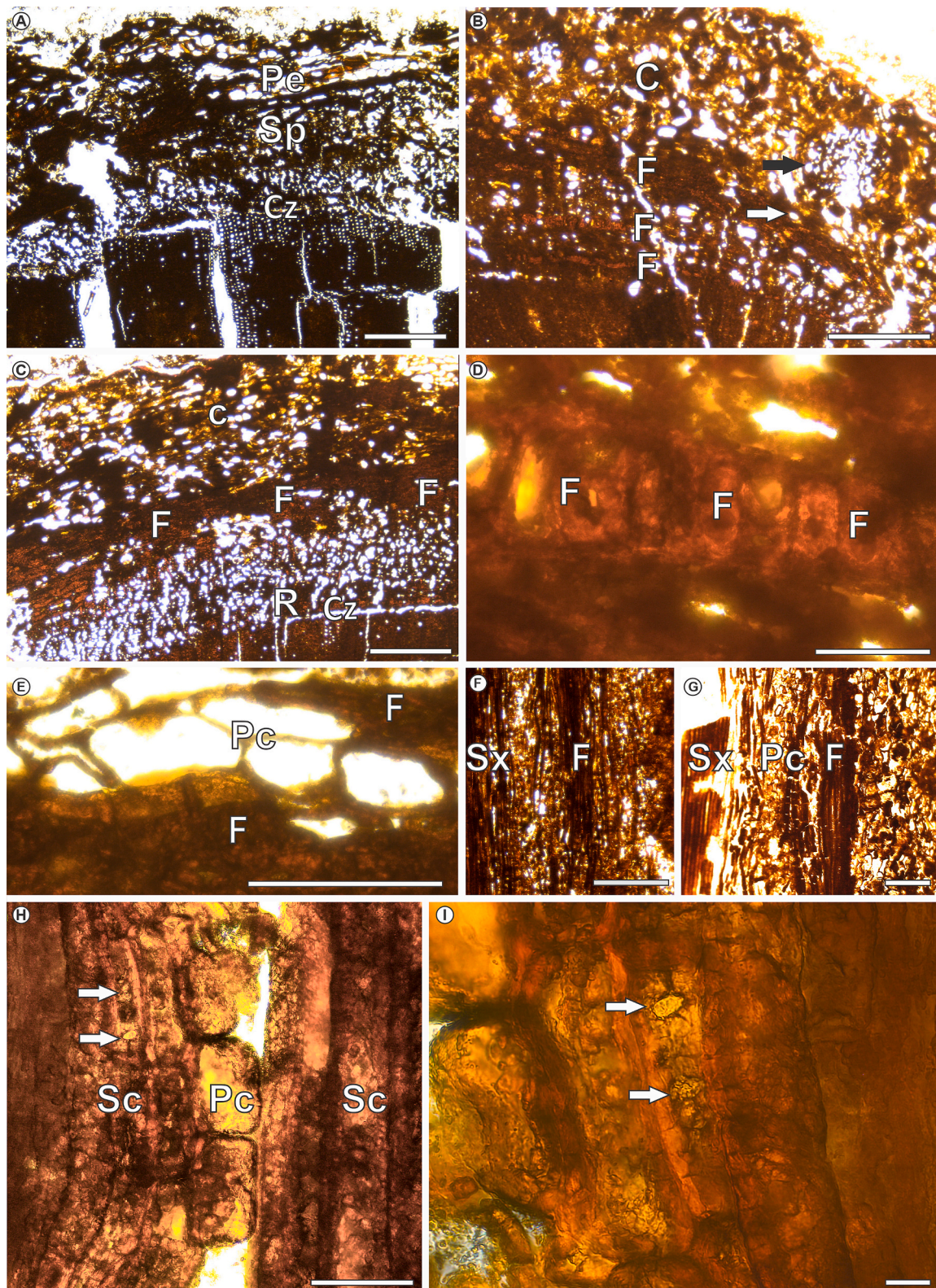


Plate IV. Bark anatomy of *Cratoxylon placidoi* gen. nov. et sp. nov., MPSC PL 5131. Overview of the bark of the branch and Twig in transverse section. (A) overview of the bark in the branch, showing the cambial zone (Cz), secondary phloem (Sp) and periderm (Pe). (B – C) General view of the bark of the twig in transverse section showing the layers of fibers (F), cortex (C); Rays (R) and resiniferous canals (arrow). (D – E) close-up of the layers of fibers (F) and parenchymatic cells (Pc). (F) Tangential section, showing the part of the secondary xylem (Sx) and fibers of the phloem. (G) Radial section, showing part of the secondary xylem, remnant of parenchyma cells (Pc) and fibers. (H) Radial section, showing the organization of phloem cells with alternate layers of sieve cells (Sc) and parenchyma cells (Pc) Arrows indicate the sieve cell areas. (I) Close-up of sieve cell areas (arrows). Scale bars: A, B, C, F = 500 µm; D, E, H = 50 µm; G = 0, 2 mm; I = 10 µm.

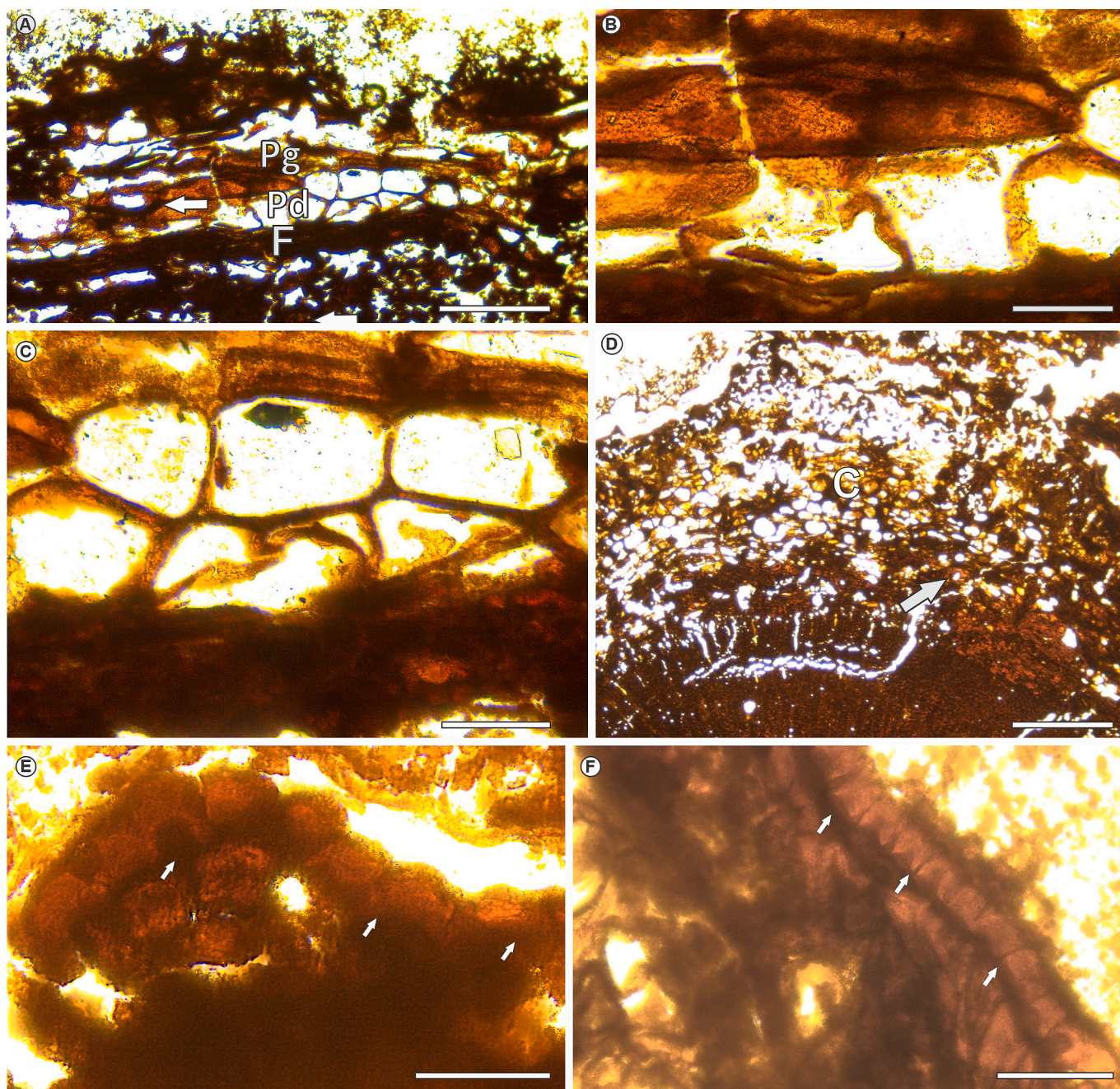


Plate V. *Cratoxylon placidoi* gen. nov. et sp. nov., MPSC PL 5131. Overview of the peridermal region in the branch and remnant of epidermal of the twig (A) Transverse section, overview of the layer of fibers (F); remnant phelloderm cells (Pd) and phellogen cells (Pg). (B) Transverse section, showing phellogen cells. (C) Transverse section, showing phelloderm cells compactly arranged. (D) Twig, overview of the cortex (C) in transverse section. White arrow points to resinous duct in the phloem (E) Twig, remains of epidermal in transverse section. Note the compact cell arrangement. Arrows indicate the layer of cells. (F) Twig, radial section, showing epidermal cells with U-shaped wall thickenings. Arrows indicate the layer of cells. Scale bars: A = 200 μm ; B, C, E, F = 50 μm ; D = 500 μm .

Near the outer limits of the phloem in the branch, there is a poorly preserved peridermal region, which bears two distinct cell types (Plate V, A–C). The first layer extends outward through rectangular cells (up to 47 μm thick), interpreted here as phellogen cells (Plate V, A–B). The second layer extends inward through polygonal cells (up to 53 μm thick), interpreted here as phelloderm cells (Plate V, A and C). These cells are usually compactly arranged. It should be noted that the preservation of these cells layers does not show continuity through the branch, making it difficult to obtain more accurate information about the periderm organization.

The composition of secondary phloem is the same in the branch and twig. On the other hand, the cortical region is more completely

preserved in the twig (Plate V, D). There is no visible development of periderm in the twig, instead there are remnants of an epidermis (Plate V, E–F), probably because it is a rather younger ramification. The cortical cells are polygonal and 47–13 μm (mean: 30 μm) in diameter. Occasional secretory ducts are observed scattered throughout the cortical region; and they are ca. 400 μm in diameter (Plate IV, B). The epidermal cells have a compact arrangement with U-shaped wall thickenings (Plate V, E–F).

5. Discussion

5.1. Conifer affinity

Fossil woods with the combination of anatomical characters as observed in *Cratoxylon placidoi* gen. nov. et sp. nov. have been assigned to the conifer lineage (see [Stewart and Rothwell, 1993](#); [IAWA, 2004](#)). These characters are: (1) homogeneous wood; (2) pycnoxylic secondary xylem with absence of vessels; (3) narrow secondary xylem tracheids; (4) xylem rays exclusively uniseriate.

Among other plant lineages that are also common in Mesozoic deposits, wood produced by Cycadales, pteridosperms and Gnetales is easily distinguishable from coniferous wood. Cycads and pteridosperms have manoxylic secondary xylem and multiseriate rays, while the wood of some Gnetales has conspicuous presence of vessel elements and also multiseriate rays ([Stewart and Rothwell, 1993](#); [Taylor et al., 2009](#); [Martínez et al., 2012](#)).

On the other hand, it is quite difficult distinguishing the wood of Ginkgoales from that of conifers. Ginkgoales exhibit similar features, such as pycnoxylic wood, circular bordered pits in one to two rows on the radial walls, bars of Sanio associated with these pits, and xylem rays that are usually uniseriate ([Stewart and Rothwell, 1993](#)). However, according to [Zheng and Zhang \(2000\)](#); [Feng et al. \(2012\)](#) and [Jiang et al. \(2016\)](#) some diagnostic features of Ginkgoales, which could distinguish them from conifers, are the presence of inflated axial parenchyma cells and intrusive tracheid tips. The latter seems to be curved along the rays in radial sections, like hockey sticks ([Greguss, 1955](#)).

In addition, woods of a few angiosperm families, such as Amborellaceae, Chloranthaceae, Winteraceae and Trochodendraceae are vesselless with secondary xylem composed primarily of tracheids and thus being superficially very similar to coniferous woods. However, they usually have elongated and large rays that distinguish them from conifers ([Suzuki et al., 1991](#); [Evert, 2006](#); [Pipo et al., 2020](#)).

5.2. Comparison with Mesozoic coniferous woods worldwide

The nomenclature and taxonomic treatment of Mesozoic coniferous woods are carried out according to the criteria of the [IAWA Committee \(2004\)](#) and [Philippe and Bamford \(2008\)](#), which are mostly based on anatomical features of the secondary xylem. On the other hand,

characteristics of pith, primary xylem and bark are rarely used to describe Mesozoic axes, since there are still relatively few specimens that preserve these tissues (e.g., [Ramanujam and Stewart, 1969](#); [Meyer-Berthaud and Taylor, 1991](#); [Meyer-Berthaud et al., 1993](#); [Ash and Savidge, 2004](#); [Brink et al., 2009](#)). This contrasts with Paleozoic plants, where several pteridosperms and some basal conifers have been described with preserved bark (e.g., [Pigg et al., 1987](#); [Dunn et al., 2003](#); [Wang et al., 2003](#); [Masselter et al., 2007](#); [Hilton et al., 2009](#); [Decombeix, 2013](#); [Decombeix et al., 2014](#); [Yang et al., 2017](#)).

The present fossil specimen is characterized by having pith and primary xylem, secondary tracheids with abietinean radial pitting, araucarioid cross-fields with cupressoid oculipores, exclusively uniseriate rays, tangential pits, and bark preserved ([Plates I–V](#) and [Table 1](#)). Some of these features of the secondary xylem, especially the abietinean radial pitting, are shared with some well-known Mesozoic conifer woods, such as: *Cupressinoxylon* Göppert ([Göppert, 1850](#)); *Phyllocladoxylon* Gothan and *Podocarpoxylon* Gothan ([Gothan, 1905](#)); *Circoporoxylon* Kräusel ([Kräusel, 1949](#)); *Turkestanioxylon* Khudaiberdyev ([Khudaiberdyev et al., 1971](#)); *Oguraxylon* Nishida ([Nishida, 1974](#)); *Semicircoporoxylon* Süß et Schultka ([Süß and Schultka, 2006](#)) and *Austrocupressinoxylon* Nunes, Bodnar et Escapa ([Nunes et al., 2019](#)). However, all these fossil-genera differ from the specimen described here in having distinct cross-field pits, and some of these fossil-genera have axial parenchyma, e.g., *Austrocupressinoxylon*; *Cupressinoxylon*, *Phyllocladoxylon*, *Podocarpoxylon* ([Table 1](#)). In addition, *Oguraxylon* also differs by its thickenings on the radial walls of the tracheids of the secondary xylem. It is noteworthy that - although *Cupressinoxylon* (Cupressaceae) is known for its isolated tracheidoxyls, as pointed out by [Philippe and Bamford \(2008\)](#) - this fossil-genus was originally established including bark and pith features in the diagnosis, similar to the material described here. Nevertheless, considering that our specimen has araucarioid cross-fields ([Plate III, E–H](#)) it cannot be affiliated in *Cupressinoxylon*, which presents cupressoid cross-field pitting, pitted walls of the ray cells and axial parenchyma ([Philippe and Bamford, 2008](#)).

Cretaceous conifer woods have been also described from Namibia which was paleogeographically adjacent to NE Brazilian basins during the Mesozoic before the opening of the South Atlantic. The woods predominantly belong to the Podocarpaceae and include fossil-species of *Podocarpoxylon*. A poorly preserved sample is determined as

Table 1
Mesozoic taxa with secondary xylem similar to *Cratoxylon* gen. nov.

Genus	Secondary xylem							Occurrence and age
	Radial pits	Cross-field pits	Xylem rays	Axial parenchyma	Tangential pits	Helical thickenings	Crassulae	
<i>Cupressinoxylon</i> Göppert, 1850	Abietinean	Cupressoid	Uniseriate	Present	Present	Absent	Absent	Widespread; Triassic to Cenozoic
<i>Phyllocladoxylon</i> Gothan, 1905	Abietinean	Podocarpoid- oopores	Uniseriate?	Present	Absent	Absent	Absent	Widespread; Jurassic to Cenozoic
<i>Podocarpoxylon</i> Gothan, 1905	Abietinean	Podocarpoid- oculipores	Uniseriate?	Present	Absent	Absent	Absent	Widespread; Permian to Cenozoic
<i>Protocupressinoxylon</i> Eckhold, 1921	Mixed	Cupressoid	Uniseriate	?	Present	Absent	Absent	Widespread; Jurassic to Cretaceous
<i>Brachyoxylon</i> Hollick et Jeffrey, 1909	Mixed	Araucarioid	Uniseriate	Absent	Absent	Absent	Absent	Widespread; Permian to Cretaceous
<i>Circoporoxylon</i> Kräusel, 1949	Araucarian	“Circopores”	Uniseriate	Absent	Absent	Absent	Absent	Widespread; Jurassic to Miocene
<i>Turkestanioxylon</i> Khudaiberdyev et al., 1971	Abietinean	Taxodioid	Uniseriate rarely biseriate	Present	Present	Absent	Present	France; Jurassic
<i>Oguraxylon</i> Nishida, 1974	Abietinean	Taxodioid?	Uniseriate, with pitted cells	Present	Present	Present	Present	Japan; Cretaceous
<i>Palaeopinuxylon</i> Mussa, 1974	Mixed	Pinoid	Uniseriate	Absent	Absent	Absent	Absent	Brazil; Cretaceous
<i>Semicircoporoxylon</i> Süß and Schultka, 2006	Abietinean	“Circoporoid”	Uniseriate?	Absent	Absent	Absent	Absent	Africa; Jurassic
<i>Austrocupressinoxylon</i> Nunes et al., 2019	Abietinean	Araucarioid/ Cupressoid	Uniseriate	Present	Absent	Absent	Absent	Argentina; Cretaceous
<i>Cratoxylon</i> gen. nov.	Abietinean	Araucarioid	Uniseriate	Absent	Present	Absent	Absent	Brazil; Cretaceous

Protocupressinoxylon cf. *purbeckensis* (Bamford and Corbett, 1995) with well-defined growth rings and uniseriate mixed tracheid bordered pitting. The latter feature differs from our sample. Additionally, the Namibian wood differs in having very low uniseriate rays (1–6 cells high) and only 2–7 cupressoid oculipores per cross-field. Although the oculipores of both woods are very similar in size and type, the numbers and crowding of these pits are different.

In addition to the fossil woods recorded in the Crato Formation (see the next section 5.4), other Early Cretaceous woods have been reported from the Paraná Basin in Brazil. Some of them are putatively related to *Cupressinoxylon* (Oliveira, 1936, Dolianiti, 1948); *Palaeopinuxylon* Mussa (Mussa, 1974) and *Brachyoxylon* Hollick et Jeffrey (Hollick and Jeffrey, 1909) while others are poorly preserved and remain undeterminable (see Duarte, 1989).

Palaeopinuxylon has secretory canals in the secondary xylem, a mixed type of radial intertracheary pitting and pinoid cross-fields, thus clearly distinguishable from our sample (Table 1). Furthermore, according to Mussa (1974), the diagnostic characteristics of *Palaeopinuxylon* are not well-preserved, which partly precludes accurate comparisons with other wood samples.

Finally, the recently recorded *Brachyoxylon* by Santos et al. (2022) from rocks of the upper Aptian Maceió Formation of the Sergipe-Alagoas Basin, Brazil has the following diagnostic features: mixed type of radial tracheid pitting and araucarioid cross-field pitting (Philippe and Bamford, 2008). However, *Brachyoxylon* and *Cratoxylon* gen. nov. differ in their types of radial pits, since the former has a mixed type of radial tracheid pits. In addition, *Brachyoxylon* is a fossil-genus classified solely on the basis of tracheidoxyl characteristics, unlike the material described here, which retains wood, pith, primary xylem, and bark (Table 2).

5.3. Comparison with coniferous fossils bearing secondary xylem and bark

Among Mesozoic conifers that are classified by using anatomical features of the secondary xylem and the bark, and that are comparable with the Crato Formation specimen, there are *Taxodioxydon gypsaceum* (Göppert) Kräusel (in Ramanujam and Stewart, 1969) from the Upper Cretaceous of Alberta, Canada; *Notophytum krauselii* Meyer-Berthaud et Taylor from the Triassic of Antarctica (Meyer-Berthaud and Taylor, 1991) and *Cunninghamia hornbyensis* Brink et Stockey (Brink et al., 2009) from the Upper Cretaceous of Columbia, Canada.

Taxodioxydon gypsaceum presents similarly the phloem composed of alternating fibers, sieve cells and parenchyma cells. However, it differs significantly in the characteristics of the secondary xylem, since the aforementioned fossil-species has araucarian pits in the radial tracheid walls and taxodioid cross-field pits. Hence, it is easily distinguishable from our sample that has abietinean pits in the radial tracheid walls and araucarioid cross-field pitting (Table 2).

Notophytum krauselii, despite having phloem composed of fibers, sieve cells, and parenchyma cells, which is similar to the specimen studied here, this fossil-taxon differs significantly in having a mixed type of radial tracheid pitting, as well as cross-fields with a single and large oculipore (Table 2).

Cunninghamia hornbyensis is represented by twigs with attached leaves, which share similar secondary xylem and phloem features with the material described here. However, the description of *C. hornbyensis* lacks information of cross-field pits (Brink et al., 2009). Furthermore, the taxonomic classification of this fossil-species is mainly based on phyllotaxis, leaf architecture and leaf anatomy evidencing affiliation within the genus of Cupressaceae (see Brink et al., 2009 and Table 2).

5.4. Comparisons with fossil-taxa from Crato Formation

In the Crato Formation, there are few conifer taxa with secondary xylem features described and considered in their classifications. These fossil-taxa are *Agathoxylon santanensis* (Santos et al., 2021); *Araucaria violetae* (Batista et al., 2021); *Brachyphyllum obesum* (Sucerquia, 2013; Batista et al., 2022); *Duartenia araripensis* (Mohr et al., 2012) and *Pseudofrenelopsis* sp. (Batista et al., 2017).

The araucarioid cross-field pitting and ray structure are two features shared between the specimen studied and *Agathoxylon santanensis* and *Brachyphyllum obesum*. These fossil species are considered to be related within the Araucariaceae (Batista et al., 2017; Santos et al., 2021). *Agathoxylon santanensis* is a fossil wood taxon (Santos et al., 2021) and *Brachyphyllum obesum* has been taxonomically described based on phyllotaxis, leaf architecture and leaf anatomy (Batista et al., 2017). Wood of both fossil-taxa displays araucarian pitting in the radial walls of their tracheids (Sucerquia, 2013; Santos et al., 2021), which contrast with abietinean radial pitting in our specimen (Table 3, Plate III, A–D). Although bark tissues have been described in *Agathoxylon santanensis*, they are poorly preserved and show only few identifiable elements such as dispersed axial resin ducts and sclereids, making comparisons of bark and phloem structures difficult.

Table 2
Comparison with coniferous fossils bearing secondary xylem and bark.

Genus	Secondary xylem Bark									Occurrence and age
	Radial pits	Cross-field pits	Xylem rays	Axial parenchyma	Tangential pits	Helical thickenings	Crassulae	Phloem	Cortex	
<i>Taxodioxydon gypsaceum</i> Ramanujam and Stewart, 1969	Araucarian	Taxodioid	Uniseriate and biseriate	Present	Absent	Present	Present	Sieve cells, fibers and axial parenchyma	Absent	Canada; Cretaceous
<i>Notophytum krauselii</i> Meyer-Berthaud and Taylor, 1990	Mixed	Podocarpoid	Uniseriate	Present	Absent	Absent	Absent	Sieve cells, fibers and axial parenchyma	Parenchyma cells and secretory canals	Antarctica; Triassic
<i>Cunninghamia hornbyensis</i> Brink and Stockey, 2009	Abietinean	?	Uniseriate	?	?	?	?	Fibers and sieve cells	Parenchyma cells and resin canals,	Canada; Cretaceous
<i>Cratoxylon</i> gen. nov	Abietinean	Araucarioid	Uniseriate	Absent	Present	Absent	Absent	Sieve cells, fibers, axial parenchyma and ducts	Parenchyma cells and secretory canals	Brazil; Cretaceous

Table 3
Taxa from the Crato Formation with secondary xylem comparable with *Cratoxylon* gen. nov.

Genus	Secondary xylem							Occurrence and age
	Radial pits	Cross-field pits	Xylem rays	Axial parenchyma	Tangential pits	Helical thickenings	Crassulae	
<i>Araucaria violetae</i> Batista et al., 2021	Araucarian	?	?	Absent	Absent	Absent	Absent	Brazil; Cretaceous
<i>Agathoxylon santanensis</i> Santos et al., 2021	Araucarian	Araucarioid	Uniseriate	Absent	Absent	Absent	Absent	Brazil; Cretaceous
<i>Brachyphyllum obesum</i> Heer, 1881	Araucarian	Araucarioid	Uniseriate?	Absent	Absent	Absent	Absent	Portugal, Brazil, Japan; Cretaceous
<i>Duartenia araripensis</i> Morh et al., 2015	Abietinean	Podocarpoid	Uniseriate	Absent	Absent	Absent	Absent	Brazil, Cretaceous
<i>Pseudofrenelopsis</i> sp. Batista et al., 2017	Abietinean	Araucarioid/Cuoresoid?	Uniseriate?	Absent	Absent	Absent	Absent	Brazil; Cretaceous
<i>Cratoxylon</i> gen. nov	Abietinean	Araucarioid	Uniseriate	Absent	Present	Absent	Absent	Brazil; Cretaceous

Another representative of Araucariaceae, *Araucaria violetae*, is based on (pen-) ultimate whiplike foliage shoots with few characters of stem anatomy preserved. Despite sharing resin ducts in the cortical region with the sample here described, its radial pitting is different (Table 3). Furthermore, *Araucaria violetae* lacks essential anatomical attributes of the secondary xylem for an effective comparison, such as cross-field pits (see Batista et al., 2021).

Duartenia araripensis is an enigmatic conifer with anisotomous branching mode and scale-like leaves assumed to be affiliated with Cheirolepidiaceae. This fossil-species shares abietinean radial pitting as well as its narrow and lower rays with the specimen described here, but differs in having distinct podocarpoid cross-field pitting (Mohr et al., 2012, Table 3).

Pseudofrenelopsis sp. is a leafy twig and its wood anatomy is quite similar to that of our specimen by sharing its abietinean radial pitting, cross-field pitting and secretory ducts in the cortical region (Batista et al., 2017). However, the description of *Pseudofrenelopsis* sp. (Batista et al., 2017) lacks information on xylem rays, which precludes direct comparison with some features of the secondary xylem of the specimen considered. Thereby, additional *Pseudofrenelopsis* spp. material from Crato Formation is needed to provide more complete data on secondary xylem anatomy, particularly regarding the type of radial pitting and ray features. Curiously, *Pseudofrenelopsis* spp. from other localities (see Thévenard et al., 2022) have mixed pitting and thus differ from *Pseudofrenelopsis* sp. from Crato Formation. It is also worth noting that the phyllotaxis and cuticular characters are important taxonomic features in the description of *Pseudofrenelopsis*, all of which are absent in our material. Despite this, *Pseudofrenelopsis* is clearly a frenelopsid taxon within the extinct Cheirolepidiaceae (Batista et al., 2017).

Eventually it should be noted that some gymnosperms from the CFL flora lack information of wood anatomy to date, e.g., the conifer *Lindleycladus* sp. (Kunzmann et al., 2004) and the erdtmanithecalean taxon *Araripestrobus resinus* (Seyfullah et al., 2020). Therefore, our new fossil-taxon cannot provisionally be compared with these fossil-taxa.

Given the above, we can clearly demonstrate that our study specimen is distinct and is therefore classified as *Cratoxylon placidoi* gen. nov. et sp. nov.

5.5. Family affinities based on secondary xylem and phloem

Botanical identifications at family level based on only isolated pieces of wood are often challenging, as already noted by Miller Jr (1977) and Wheeler and Lehman (2005), but frequently possible. Consequently, several fossil-taxa have been linked to extinct and living conifer families based on isolated wood pieces (e.g., Bodnar et al., 2013; Tian et al., 2018; Nunes et al., 2019; Greppi et al., 2020, 2021; Bodnar et al., 2022; Santos et al., 2022). These systematic affinities are often performed considering the associated presence of foliage and/or reproductive organs in the same geological stratum where the conifer wood fragments

are disconnectedly found (e.g., Bodnar et al., 2013; Tian et al., 2018; Santos et al., 2022).

Extant conifer families that were distributed widely throughout the Mesozoic are, for instance, Cupressaceae, Araucariaceae and Podocarpaceae, while Pinaceae became more abundant and widespread in the Cretaceous and other families such as Cephalotaxaceae, Sciadopityaceae and Taxaceae occurred only subordinately in the Cretaceous (Farjon, 2008; Kunzmann et al., 2004). However, one of the most widespread and diverse Mesozoic conifer families is the extinct Cheirolepidiaceae (also known as Hirmeriellaceae) (Thévenard et al., 2022; Doweld, 2020). Cheirolepidiaceae occurred in middle and low latitudes in both hemispheres and became extinct at the end of the Cretaceous. Other extinct families, which were present in the Cretaceous, are Doliostrubaceae, Geinitziaceae, Miroviaceae and “Podozamitaceae (e.g., Farjon, 2008; Taylor et al., 2009). In this respect, it is obvious that when dealing with extinct conifer families, the systematic affinities of isolated wood pieces can be considerably more complex and classifications have to be handled with caution, otherwise ambiguous systematic links can be made.

It is well known that the types of radial pits of tracheids and cross-field pits are important sources of taxonomic information and systematic affinities in wood of both living and fossil conifers (see Philippe and Bamford, 2008; IAWA Committee, 2004). However, botanical identifications based solely on the radial pits of tracheids and types of cross-fields pits are weakly supported, because sometimes the same type of radial pitting occurs in more than one family. A similar situation also occurs with cross-field pits, where cupressoid cross-field pits are common in members of the Cupressaceae, but are also found in Podocarpaceae (IAWA Committee, 2004).

Furthermore, it has to be stated that anatomical characters of wood can vary between stems, branches and roots and it is often challenging to affiliate isolated pieces of stem, branch and root wood to the same fossil plant. This is more complicated when dealing with wood of extinct conifer families based on fragmented fossils. Additionally, knowledge on wood anatomy of extinct conifer families and some Mesozoic genera of extant conifer families is still incomplete.

Cratoxylon placidoi gen. nov. et sp. nov. does not exhibit anatomical features that can be restricted to a particular conifer family. On the contrary, it shares some anatomical characters with more than one family. In the secondary xylem, our fossil-species exhibits pits on the radial walls of the tracheids, which are circular, bordered, uniseriate and spaced with an araucarioid cross-field pitting. In the fossil record, this type of radial pitting is recognized as an abietinean type (sensu Eckhold, 1921; Philippe and Bamford, 2008), and is commonly found in several conifer families, e.g., Cupressaceae and Podocarpaceae, (Kräusel, 1949; Bamford and Philippe, 2001; Nunes et al., 2019). Additionally, in some extant conifers, for example, in *Dacrydium* (Podocarpaceae) and *Calocedrus* (Cupressaceae), the pits on the radial walls of the tracheids are circular, bordered, uniseriate and spaced (IAWA Committee, 2004;

Esteban et al., 2023). The araucarioid cross-field pitting currently appears to be restricted to Araucariaceae (see IAWA Committee, 2004; Esteban et al., 2023), but in the geological past this type of cross-field pits is also recorded doubtlessly in wood of Cheirolepidiaceae, e.g., from *Pseudofrenelopsis* sp. (Batista et al., 2017; Thévenard et al., 2022).

Regarding the phloem tissue, the composition and organization of its cells in conifers, e.g., the presence and arrangement of fibers, can be of great taxonomic importance and are very useful for characterizing conifer families (Chang, 1954; Ramanujam and Stewart, 1969; Taylor et al., 2009). The fibers of the secondary phloem of *Cratoxylon placidoi* gen. nov. et sp. nov. are arranged in regular tangential rows and appear to exhibit a pattern along the phloem with an alternating sequence of fiber layers, sieve cells, and parenchyma cells. According to Evert (2006) and Den Outer (1967), this type of phloem organization occurs in modern conifers such as Taxaceae, Cupressaceae, and some Podocarpaceae. Among these, assignment of *Cratoxylon placidoi* gen. nov. et sp. nov. to the Taxaceae or taxodioid clades of Cupressaceae is unlikely because they have helical thickenings in the secondary-xylem tracheids as a conspicuous feature, and distinct cross-field pitting (IAWA Committee, 2004; Esteban et al., 2023). It is also be inappropriate to assign *Cratoxylon placidoi* gen. nov. et sp. nov. to Cupressaceae s. str. or Podocarpaceae only based on similarities of the secondary xylem shared between them, already mentioned above. Additionally, both families have different cross-fields from those of our material.

Although *Cratoxylon placidoi* gen. nov. et sp. nov. shares several anatomical features of the secondary xylem with a member of the family Cheirolepidiaceae, i.e., *Pseudofrenelopsis* sp. (see Batista et al., 2017; Thévenard et al., 2022 and Table 3), little is still known about the phloem tissues of Cheirolepidiaceae (according to Miller Jr, 1977), clearly preventing affiliation to this family at the moment.

All-in-all, *Cratoxylon placidoi* gen. nov. et sp. nov. is unambiguously placed within the conifer lineage. Unfortunately, a more specific systematic positioning is impossible at the moment since the new fossil-species bears anatomical features shared by more than one conifer family.

6. Conclusions

Despite the high diversity of woody gymnosperms in the Cretaceous deposits of the Araripe Basin, there is still relatively limited knowledge about their wood anatomy. Here, a portion of fossil conifer wood is described and a new fossil-taxon is erected, i.e. *Cratoxylon placidoi* gen nov. et sp. nov. The secondary xylem is characterized by abietinean pitting on the radial walls of the tracheids, araucarioid cross-fields, tangential pits and ray cells with smooth walls. In the bark, features of the secondary phloem, periderm and remains of cortex and epidermis are recognized. Fibers of the secondary phloem are arranged in regular tangential rows, exhibiting an alternating sequence of fiber layers, sieve cells and parenchyma cells along the tissue.

This discovery demonstrates the potential of gymnospermous fossils from the Crato Formation for paleoecological research. Plenty of fossil wood fragments from CFL need to be investigated by wood anatomical approaches as a premise for complete capture of plant diversity in CFL. Systematic studies of these fossil woods can contribute to better understand the paleobiology of conifers and other gymnosperms from an ancient tropical paleoenvironment.

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

Data will be made available on request.

Acknowledgments

DMC, MEPB and NCO thanks the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP processes: PV-00424072/2022, BP5-0197-00135.01.00/22 and PV1-0187-00060.01.00/21, respectively). We would also like to thank the Brazilian National Council of Technological and Scientific Development (CNPq) for grants to RI (Process PQ313946/2021–3). The authors are indebted with Luiz F. Lopez for the excellent macroscopic photos taken from the material. Thanks also to Laboratory of Plant Anatomy at the Institute of Biosciences (Universidade Federal do Rio Grande do Sul) for providing access to the transmitted light microscope: Leica DMR HC. We are grateful to the Museu de Paleontologia Plácido Cidade Nuvens and J. L. Silva for providing the fossil specimens studied here. We are also very grateful to Daniel Triboli Vieira for the help with sample analyzed on the Scanning Electronic Microscope. We would also like to thank the Environmental Police and the Federal Police for their excellent work against the illegal fossil trade in the Araripe Basin. The authors would also like to thank Zhuo Feng and the anonymous reviewers for their substantial help in improving the manuscript.

References

- Arai, M., Assine, M.L., 2020. Chronostratigraphic constraints and palaeoenvironmental interpretation of the Romualdo Formation (Santana Group, Araripe Basin, Northeastern Brazil) based on palynology. *Cretac. Res.* 116, 104610 <https://doi.org/10.1016/j.cretres.2020.104610>.
- Araújo, K.C.O., Guerra Sommer, M., Medeiros, M.A., Girnos, E.C., Schmidt, I.D., 2011. Lenhas de coníferas do Mesocretáceo do Norte do Maranhão, Brasil. *Rev. Brasil. Paleontol.* 14, 29–38.
- Ash, R.S., Savidge, R.A., 2004. The bark of the Late Triassic *Araucarioxylon arizonicum* tree from Petrified Forest National Park, Arizona. *Int. Assoc. Wood Anat.* 25 (3), 349–368.
- Assine, M.L., Perinotto, J.A.J., Neumann, V.H., Custódio, M.A., Varejão, F.G., Mescolotti, P.C., 2014. Sequências Depositionais do Andar Alagoas (Aptiano superior) da Bacia do Araripe, Nordeste do Brasil. *Boletim de Geociências da Petrobras* 22 (1), 3–28.
- Bamford, M.K., Corbett, I.B., 1995. More fossil wood from the Namaqualand coast, South Africa; onshore material. *Palaeontol. Afric.* 32, 67–74.
- Bamford, M.K., Philippe, M., 2001. Jurassic - Early Cretaceous Gondwanan homoxylous woods: a nomenclatural revision of the genera with taxonomic notes. *Rev. Palaeobot. Palynol.* 113, 287–297.
- Barreto, A.M.F., Bertotti, A.L., Sylvester, P.J., Prado, L.A.C., Araripe, R.C., Oliveira, D.H., Tomé, M.E.T.R., Lemos, F.A.P., Nascimento, L.R.L., Pereira, P.A., Albayrak, A.I., 2022. U/Pb geochronology of fossil fish dentine from Romualdo Formation, Araripe Basin, northeast of Brazil. *J. South Am. Earth Sci.* 116, 103774 <https://doi.org/10.1016/j.cretres.2020.104610>.
- Batista, M.E.P., Silva, D.C., Sales, M.A.F., Sá, 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, e0173090. <https://doi.org/10.1371/journal.pone.0173090>.
- Batista, M.E.P., Kunzmann, L., Sá, A.A., Saraiva, A.A.F., Loiola, M.I.B., 2020. A new species of *Brachyphyllum* from the Crato Formation (Lower Cretaceous), Araripe Basin, Brazil. *Ameghiniana* 57 (6), 519–533. <https://doi.org/10.5710/AMGH.23.06.2020.3333>.
- Batista, M.E.P., Martine, A.M., Saraiva, A.A.F., Lima, F.J., Barros, O.A., Sá, A.A.A., Loiola, M.I.B., 2021. *Brachyphyllum*: state of the art and new data regarding *B. obesum*, the most representative fossil plant in the Araripe Basin, Brazil. *J. South Am. Earth Sci.* 110, 103405 <https://doi.org/10.1016/j.jsames.2021.103405>.
- Batista, M.E.P., Loiola, M.I.B., Soares, A.A., Mastroberti, A.A., Sá, A.A., Nascimento Jr., D.R., Silva Filho, W.F., Kunzmann, L., 2022. New insights into the evolution of mucilage cells in Araucariaceae: *Araucaria violetae* sp. nov. from the Early Cretaceous Araripe Basin (Northeast Brazil). *Int. J. Plant Sci.* 183 (1), 43–60. <https://doi.org/10.1086/717104>.
- Bodnar, J., Escapa, I.H., Cúneo, R., Gnaedinger, S., 2013. First record of conifer wood from the Canadón Asfalto Formation (Early-Middle Jurassic), Chubut province, Argentina. *Ameghiniana* 50, 227–239.
- Bodnar, J., Sagasti, A.J., Correa, A.G., Miranda, V., Medina, F., 2022. Araucariaceous fossil woods from the Upper Triassic Ischigualasto Formation (San Juan Province, Argentina): paleofloristic and paleoclimatic implications. *J. Paleol.* 1–25. <https://doi.org/10.1017/jpa.2022.45>.
- Boura, A., Bamford, M., Philippe, M., 2021. Promoting a standardized description of fossil tracheidoxyls. *Rev. Palaeobot. Palynol.* 295, 104525 <https://doi.org/10.1016/j.revpalbo.2021.104525>.
- Brink, K.S., Stockey, R.A., Beard, G., Wesley, C.W., 2009. *Cunninghamia hornbyensis* sp. nov. permineralized twigs and leaves from the Upper Cretaceous of Hornby Island, British Columbia, Canada. *Rev. Palaeobot. Palynol.* 155 (1–2), 89–98.

- Chang, Y.P., 1954. Bark structure of North American conifers. In: Technical Bulletin. Department of Agriculture, U.S 1095, pp. 1–91.
- Christenhusz, M., Reveal, J., Farjon, A., Gardner, M., Mill, R., Chase, M., 2011. A new classification and linear sequence of extant gymnosperms. *Phytotaxa* 19, 55–70.
- Coimbra, J.C., Freire, T.M., 2021. Age of the Post-rift Sequence I from the Araripe Basin, Lower Cretaceous, NE Brazil: implications for spatio-temporal correlation. *Rev. Brasil. Paleontol.* 24, 375–46.
- Condamine, F.L., Silvestro, D., Koppellus, E.B., Antonelli, A., 2020. The rise of angiosperms pushed conifers to decline during global cooling. *Proc. Natl. Acad. Sci. USA* 117, 28867–28875. <https://doi.org/10.1073/pnas.2005571117>.
- Crisafulli, A., Dutra, T.L., 2009. *Kaokoxydon zalesskyi* (Sahni) Maheswari in los niveles superiores de la Secuencia Santa Maria 2 (Formacion Caturrita). *Cuenca de Paraná. Brasil. Gaea* 5, 61–69.
- Crisafulli, A., Dutra, T.L., Herbst, R., 2016. *In-situ* Late Triassic fossil woods from the fluvial channel deposits of the Caturrita Formation, Faxinal do Soturno, Rio Grande do Sul, Brazil. *Gaea* 9, 37–46.
- Crisafulli, A., Herbst, R., Dutra, T.L., 2018. New gymnosperm wood fossil, a seed-ovule structure, and a new generic affinity to *Cedroxylon canoasense* Rau from the Permian and Triassic–Jurassic of southern Brazil. *Rev. Brasil. Paleontol.* 21, 47–62. <https://doi.org/10.4072/rbp.2018.1.03>.
- Decombeix, A.L., 2013. Bark anatomy of an Early Carboniferous tree from Australia. *Int. Assoc. Wood Anat.* 34 (2), 183–186. <https://doi.org/10.1163/22941932-00000016>.
- Decombeix, A.L., Galtier, J., Meyer-Berthaud, B., 2014. Secondary phloem in Early Carboniferous seed plants: anatomical diversity and evolutionary implications. *Int. J. Plant Sci.* 175 (8), 891–910. <https://doi.org/10.1086/677650>.
- Den Outer, R.W., 1967. Histological investigations of the 27 phloem in gymnosperms. 1. Introduction. *Meded Landbouwhoges Wagening* 67, 1–119.
- Dilcher, D.L., Bernardes-de-Oliveira, M.E., Pons, D., Lott, T.A., 2005. Welwitschiaceae from the lower Cretaceous of northeastern Brazil. *Am. J. Bot.* 92, 1294–1310. <https://doi.org/10.3732/ajb.92.8.1294>.
- Dolaniiti, E., 1948. A paleobotânica no Brasil. *Boim. Div. Geol. Miner. Bras.* 123, 1–87.
- Doweld, A.B., 2020. The controversial nomenclature of the fossil plant names *Cheirolepis*, *Cheirolepidium* and *Hirmeriella* (Cheirolepidaceae/Cheirolepidiaceae/Hirmeriaceae). *Taxon* 69 (5), 1092–1098. <https://doi.org/10.1002/tax.12287>.
- Duarte, L., 1989. Remains of the Lower Cretaceous plants from North-East of Brazil. In: *Anais do XI Congresso Brasileiro de Paleontologia*, pp. 219–233.
- Dunn, M.T., Krings, M., Mapes, G., Rothwell, G.W., Mapes, R.H., Keqin, S., 2003. *Medullosa steinii* sp. nov., a seed fern vine from the Upper Mississippian. *Rev. Palaeobot. Palynol.* 124, 307–324.
- Eckhold, W., 1921. Die Hoftüpfel bei rezenten und fossilen Koniferen. *Hochschulverlag, Breslau* 4.
- Esteban, L.G., de Palacios, P., Heinz, I., Gasson, P., García Ruela, A., García-Fernández, F., 2023. Softwood anatomy: a review. *Forests* 14, 323. <https://doi.org/10.3390/f14020323>.
- Evert, R.F., 2006. *Esau's Plant Anatomy: Meristems, Cells, and Tissues of the Plant Body: Their Structure, Function, and Development*, 3rd edn. John Wiley and Sons, Hoboken, NJ, USA.
- Farjon, A., 2008. *The Natural History of Conifers*. Timber Press, New York.
- Feng, Z., Wang, J., Liu, L.J., Rößler, R., 2012. A novel coniferous tree trunk with septate pith from the Guadalupian (Permian) of China: ecological and evolutionary significance. *Int. J. Plant Sci.* 173 (7), 835–848. <https://doi.org/10.1086/666660>.
- Gee, C.T., 2011. Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective. In: Klein, N., Remes, K., Gee, C.T., Sander, P.M. (Eds.), *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*. Indiana University Press, Bloomington, pp. 34–56.
- Gobo, W.V., Kunzmann, L., Iannuzzi, R., Dos Santos, T.B., Conceição, D.M., Nascimento Jr., D.R., Silva Filho, W.F., Bachelier, J.B.B., Coiffard, C., 2023. A new remarkable Early Cretaceous nelumbonaceous fossil bridges the gap between herbaceous aquatic and woody protealeans. *Sci. Rep.* 13, 8978. <https://doi.org/10.1038/s41598-023-33356-z>.
- Göppert, H.R., 1850. Monographie der fossilen Coniferen. *Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Harlem* vol. 12.
- Gothan, W., 1905. Zur Anatomie lebender und fossiler Gymnospermen-Hölzer. *Abhandlungen zur preussischen geologische Landesanstalt* 44, 1–108.
- Greguss, P., 1955. Identification of Living Gymnosperms on the Basis of Xylotomy. *Akademiai kiado, Budapest*.
- 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. <https://doi.org/10.1016/j.cretres.2019.104322>.
- Greppi, C.D., Pujana, R.R., Umazano, A.M., Bellosi, E.S., 2021. Early Cretaceous *Brachyoxylon* woods from Argentinean Patagonia and comments on the Cheirolepidiaceae distribution. *J. South Am. Earth Sci.* 106, 103050. <https://doi.org/10.1016/j.jsames.2020.103050>.
- Heimhofer, U., Wucherpfennig, N., Adatte, T., Schouten, S., Schneebeli-Hermann, E., Gardin, S., Keller, G., Kentsch, S., Kujau, A., 2018. Vegetation response to exceptional global warmth during Oceanic Anoxic Event 2. *Nat. Commun.* 9 (1), 3832.
- Hilton, J., Wang, S.J., Galtier, J., Bateman, R.M., 2009. Cordaitalean seed plants from the Early Permian of North China. II. Reconstruction of *Cordaixylon tianii*. *Int. J. Plant Sci.* 170 (3), 400–418. <https://doi.org/10.1086/595287>.
- IAWA Committee, 2004. IAWA list of microscopic features for softwood identification. *IAWA* 25, 1–70.
- International Commission on Stratigraphy (ICS) – International Chronostratigraphic Chart – Version: 2023/06. <http://www.stratigraphy.org/ICSChart/ChronostratChart2023-06.pdf>.
- Jiang, Z.K., Wang, Y.D., Philippe, M., Zhang, W., Tian, N., Zheng, S.L., 2016. A Jurassic wood providing insights into the earliest step in Ginkgo wood evolution. *Sci. Rep.* 6 (1), 38191. <https://doi.org/10.1038/srep38191>.
- Jones, T.P., Rowe, N.P., 1999. Fossil plants and spores: modern techniques. *J. Geol. Soc. Lond.* 396p.
- Khudaiberdyev, R., Gomolitzky, N.P., Lobanova, A.V., 1971. Matériaux pour la flore jurassique du Fergana méridional. *Paleobot. Uzbekistana* 2, 3–61.
- Kräusel, R., 1949. Die fossilen Koniferen-Hölzer (Unter Ausschluss von *Araucarioxylon* Kraus) II. Teil. Kritische Untersuchungen zur Diagnostik lebender und fossiler Koniferen Hölzer. *Palaeontogr. B* 89, 83–203.
- Kunzmann, L., Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Wilde, V., 2006. Gymnosperms from the Early Cretaceous Crato Formation (Brazil). II. Cheirolepidiaceae. *Fossil Record* 9 (2), 213–225. <https://doi.org/10.1002/mmng.200600009>.
- Kunzmann, L., Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., 2004. Gymnosperms from the Lower Cretaceous Crato Formation (Brazil). I. Araucariaceae and Lindleycladus (incertae sedis), 7. Mitteilungen des Museums für Naturkunde Berlin, Geowissenschaftliche Reihe, pp. 155–174.
- Kunzmann, L., Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., 2007. *Novaalindia dubia* gen. et sp. nov., an enigmatic seed plant from the Early Cretaceous of northern Gondwana. *Rev. Palaeobot. Palynol.* 147 (1–4), 94–105.
- Kunzmann, L., Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., 2009. *Cearania heterophylla* gen. nov. et sp. nov., a fossil gymnosperm with affinities to the Gnetales from the Early Cretaceous of northern Gondwana. *Rev. Palaeobot. Palynol.* 158, 193–212. <https://doi.org/10.1016/j.revpalbo.2009.09.001>.
- Kunzmann, L., Mohr, B.A.R., Wilde, V., Bernardes-de-Oliveira, M.E.C., 2011. A putative gnetalean gymnosperm *Cariria orbiculiconiformis* gen. nov. et spec. nov. from the Early Cretaceous of northern Gondwana. *Rev. Palaeobot. Palynol.* 165, 75–95. <https://doi.org/10.1016/j.revpalbo.2011.02.005>.
- Kunzmann, L., Coiffard, C., Westerkamp, A.P.A.O., Batista, M.E.P., Uhl, D., Solórzano-Kraemer, M.M., Mendes, M., Nascimento Jr., D.R., Iannuzzi, R., Silva Filho, W.F., 2021. The Crato flora, a 115 million years old window into the Cretaceous world of Brazil. In: Iannuzzi, R., Rößler, R., Kunzmann, L. (Eds.), *Brazilian Paleofloras: From Paleozoic to Holocene*. Springer Nature, Cham, Switzerland, pp. 1–40. https://doi.org/10.1007/978-3-319-90913-4_27-1.
- Kunzmann, L., Westerkamp, A.P.A.O., Batista, M.E.P., Rydin, C., 2023. Gymnosperms from the Early Cretaceous Crato Flora – competitors for the nascent flowering plants. In: Iannuzzi, R., Rößler, R., Kunzmann, L. (Eds.), *Brazilian Paleofloras: from Paleozoic to Holocene*. Springer Nature, Cham, Switzerland xxx.
- Lowe, S.A., Mohr, B.A.R., Coiffard, C., Bernardes de Oliveira, M.E.C., 2013. *Friedsellowia gracilifolia* gen. nov. et sp. nov. a new gnetophyte from the Lower Cretaceous Crato Formation (Brazil). *Palaeontogr. Abt. B* 289, 139–177.
- Lúcio, T., Neto, J.A.S., Selby, D., 2020. Late Barremian/Early Aptian Re–Os age of the Ipubi Formation black shales: stratigraphic and paleoenvironmental implications for Araripe Basin, northeastern Brazil. *J. South Am. Earth Sci.* 102, 102699. <https://doi.org/10.1016/j.jsames.2020.102699>.
- Martill, D.M., Bechly, G., Loveridge, R.F., 2007. *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge University Press, Cambridge.
- Martínez, L.C.A., Artabe, A.E., Bodnar, J., 2012. A new cycad stem from the Cretaceous in Argentina and its phylogenetic relationships with other Cycadales. *Bot. J. Linn. Soc.* 170, 436–458.
- Masselter, T., Rowe, N.P., Speck, T., 2007. Biomechanical reconstruction of the Carboniferous seed fern *Lyginopteris oldhamia*: implications for growth form reconstruction and habit. *Int. J. Plant Sci.* 168 (8), 1177–1189.
- Melo, R.M., Guzmán, J., Débora, A.-L., Piovesan, E.K., Neumann, V.H.M.L., Sousa, A.J., 2020. New marine data and age accuracy of the Romualdo Formation, Araripe Basin, Brazil. *Scient. Rep.* 10, 15779. <https://doi.org/10.1038/s41598-020-72789-8>.
- Meyer-Berthaud, B., Taylor, T.N., 1991. A probable conifer with podocarpacean affinities from the Triassic of Antarctica. *Rev. Palaeobot. Palynol.* 67, 179–198. [https://doi.org/10.1016/0034-6667\(91\)90041-Z](https://doi.org/10.1016/0034-6667(91)90041-Z).
- Meyer-Berthaud, B., Taylor, T.N., Taylor, E.L., 1993. Petrified stems bearing *Dicroidium* leaves from the Triassic of Antarctica. *Palaeontographica* 36, 337–356.
- Miller Jr., C.N., 1977. Mesozoic conifers. *Bot. Rev.* 43, 217–280.
- Mohr, B.A.R., Schultka, S., Süß, H., Bernardes-de-Oliveira, M.E.C., 2012. A new drought resistant gymnosperm taxon *Duarteria araripensis* n. gen. et sp. (Cheirolepidiaceae?) from the Early Cretaceous of Northern Gondwana. *Palaeontogr. Abt. B* 289, 1–25. <https://doi.org/10.1127/palb/289/2012/1>.
- Mussa, D., 1974. Paleoxilomatia Brasileira: I. Protopinaceae da Formação Botucatu, Minas Gerais, Brasil. *An. Acad. Bras. Cienc.* 3 (4), 497–513.
- Nascimento Jr., D.R., da Silva Filho, W.F., Erthal, F., 2022. Crato Lake Deposits. Rocks to preserve an extraordinary Fossil Lagerstätte. In: Iannuzzi, R., Rößler, R., Kunzmann, L. (Eds.), *Brazilian Paleofloras*. Springer, Cham, pp. 2–54.
- Neumann, V.H.M.L., Aragão, M.A.N.F., Valença, L.M.M., Lea, J.P., 2008. Ambientes Lacustres. In: Silva, A.J.C.L.P., Aragão, M.A.N.F., Magalhães, A.J.C. (Eds.), *Ambientes de Sedimentação Siliciclástica do Brasil 1*. Beca-BALL Edições, São Paulo, pp. 132–136.
- Nishida, M., 1974. *Oguraxylon*, a new genus belonging to the family Taxodiaceae, from the Cretaceous of Hokkaidō. *Bot. Magaz.* 87, 113–121. <https://doi.org/10.1007/BF02489063>.
- Nunes, C.I., Bodnar, J., Escapa, I.H., Gandolfo, M.A., Cuneo, N.R., 2019. A new cupressaceous wood from the Lower Cretaceous of central Patagonia reveals possible clonal growth habit. *Cretac. Res.* 99, 133–148. <https://doi.org/10.1016/j.cretres.2019.02.013>.
- Oliveira, E.P., 1936. Madeira petrificadas do planalto dos Parecis. *Notas Preliminares e Estudos. Divisão de Geologia e Mineralogia. DNPM* 3, 2–14.

- Philippe, M., Bamford, M.K., 2008. A key to morphogenera used for Mesozoic conifer-like woods. *Rev. Palaeobot. Palynol.* 148, 184–207. <https://doi.org/10.1016/j.revpalbo.2007.09.004>.
- Philippe, M., Boura, A., Oh, C., Pons, D., 2014. *Shimakuroxylon* a new homoxylous Mesozoic wood genus from Asia, with palaeogeographical and palaeoecological implications. *Rev. Palaeobot. Palynol.* 204, 18–26.
- Pigg, K.B., Taylor, T.N., Stockey, R.A., 1987. Paleozoic seed ferns: *Heterangium kentuckyensis* sp. nov., from the Upper Carboniferous of North America. *Am. J. Bot.* 74, 1184–1204.
- Pipo, M.L., Iglesias, A., Bodnar, J., 2020. A new vesselless angiosperm stem with a cambial variant from the Upper Cretaceous of Antarctica. *Acta Palaeontol. Polon.* 65, 261–272. <https://doi.org/10.4202/app.00697.2019>.
- Ramanujam, C.G.K., Stewart, W.N., 1969. Taxodiaceous Bark from the Upper Cretaceous of Alberta. *Am. J. Bot.* 56 (1), 101–107. <https://doi.org/10.2307/2440400>.
- Ricardi-Branco, F., Torres, M., Tavares, S.S., de Souza Carvalho, I., Tavares, P.G.E., Campos, A.C.A., 2013. *Itajuba yansanae* gen. and sp. nov. of Gnetales, Araripe Basin (Albian Aptian) in Northeast Brazil. In: Zhang, Y., Ray, P. (Eds.), *Climate Change and Regional/Local Responses*. Rijeka, InTech, pp. 187–205.
- Rydin, C., Pedersen, K.R., Crane, P.R., Friis, E.M., 2006. Former diversity of *Ephedra* (Gnetales): evidence from Early Cretaceous seeds from Portugal and North America. *Ann. Bot.* 98, 123–140. <https://doi.org/10.1093/aob/mcl078>.
- Santos, A.C.S., Sieglösch, A.M., Guerra-Sommer, M., Degani-Schmidt, I., Carvalho, I.S., 2021. *Agathoxylon santanensis* sp. nov. from the Aptian Crato fossil Lagerstätte, Santana Formation, Araripe Basin, Brazil. *J. South Am. Earth Sci.* 112, 103633. <https://doi.org/10.1016/j.jsames.2021.103633>.
- Santos, A.C.S., Guerra-Sommer, M., Degani-Schmidt, I., Sieglösch, A.M., Carvalho, I.S., 2022. Record of *Brachyoxylon patagonicum*, a Cheirolepidiaceae wood preserved by gelification in the Aptian Maceió Formation, Sergipe-Alagoas Basin, NE Brazil. *J. South Am. Earth Sci.* 118, 103950. <https://doi.org/10.1016/j.jsames.2022.103950>.
- Seyfullah, L., Roberts, E.A., Schmidt, A.R., Agazzi, E., Anderson, K., Nascimento Junior, D.R., Silva Filho, W.F., Kunzmann, L., 2020. Revealing the diversity of amber source plants from the Early Cretaceous Crato Formation, Brazil. *Evol. Biol.* 20 (107), 2–22.
- Stewart, W.N., Rothwell, G.W., 1993. *Paleobotany and the Evolution of Plants*. Cambridge University Press, Cambridge.
- Sucerquia, P.A., 2013. Taxonomia, modos de preservação e fitogeografia de coníferas aptianas da região paleoequatorial da América do Sul. PhD Thesis. Instituto de Geociências da Universidade de São Paulo, São Paulo, 86 p.
- Sucerquia, P.A., Bernardes-de-Oliveira, M.E., Mohr, B.A., 2015. Phytogeographic, stratigraphic, and paleoclimatic significance of *Pseudofrenelopsis capillata* sp. nov. from the Lower Cretaceous Crato Formation, Brazil. *Rev. Palaeobot. Palynol.* 222, 116–128. <https://doi.org/10.1016/j.revpalbo.2015.07.012>.
- Süß, H., Schultka, S., 2006. Koniferenhölzer (Fusite) aus dem Oberjura vom Tendaguru (Tasania, Ostafrika). *Palaeontogr. Abt. B* 275, 133–165.
- Suzuki, M., Joshi, L., Noshiro, S., 1991. *Tetracentron* wood from the Miocene of Noto Peninsula, Central Japan, with a short revision of homoxylous fossil woods. *Bot. Mag.* 104, 37–48.
- Taylor, T.N., Taylor, E.L., Krings, M., 2009. *Palaeobotany, the Biology and Evolution of Fossil Plants*, second ed. Elsevier, Burlington.
- Thévenard, F., Chernomoretz, O., Moreau, J.D., Neraudeau, D., Philippe, M., 2022. A review of the Hirmeriaceae (Cheirolepidiaceae) wood. *IAWA J.* 43 (4), 428–447. <https://doi.org/10.1163/22941932-bja10099>.
- Tian, N., Zhu, Z.-P., Wang, Y.-D., Wang, S.-C., 2018. Occurrence of *Brachyoxylon* Hollick et Jeffrey from the Lower Cretaceous of Zhejiang Province, southeastern China. *J. Palaeogeogr.* 7, 1–10. <https://doi.org/10.1186/s42501-018-0008-0>.
- Wang, S.J., Hilton, J., Tian, B.L., Galtier, J., 2003. Cordaitalean seed plants from the Early Permian of North China. I. Delimitation and reconstruction of the *Shanxiioxylon sinense* plant. *Int. J. Plant Sci.* 164 (1), 89–112.
- Wheeler, E.A., Lehman, T.M., 2005. Upper Cretaceous–Paleocene conifer woods from Big Bend National Park, Texas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 226, 233–258. <https://doi.org/10.1016/j.palaeo.2005.05.014>.
- Yang, J.Y., Shen, J.J., Xu, X., Chen, Y.X., Wei, H.B., Kerp, H., Feng, Z., 2017. The bark anatomy of *Ningxiaites specialis* from the Permian of China. *Rev. Palaeobot. Palynol.* 240, 11–21. <https://doi.org/10.1016/j.revpalbo.2017.01.001>.
- Zheng, S.L., Zhang, W., 2000. Late Paleozoic ginkgoalean woods from northern China. *Acta Palaeontol. Sin.* 39, 119–126.