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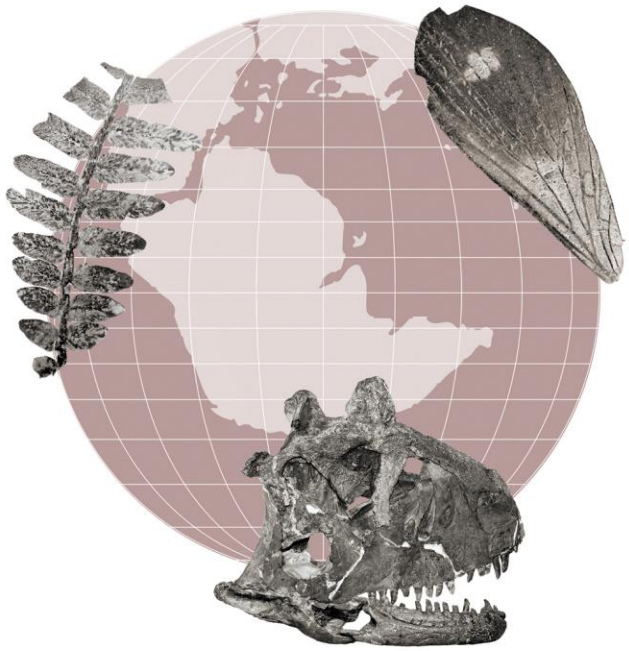

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PODOCARPACEAE FROM THE LATE PLEISTOCENE EL PALMAR FORMATION IN THE MIDDLE BASIN OF THE URUGUAY RIVER, ARGENTINA: WOOD ANATOMY, NEW TAXON AND PALEODENDROLOGY

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Short Description: New species for the Upper Pleistocene in Argentina related to *Podocarpus lambertii*; its biogeography in the Quaternary is discussed

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Abstract. Seven fossil woods recovered from the fossiliferous localities of Concordia and Santa Ana (Entre Ríos Province, Argentina), corresponding to the El Palmar Formation (Late Pleistocene), were analysed. This unit is an important source of information on the climatic and ecological events that occurred towards the end of the Quaternary (MIS5 and MIS7) in the middle basin of the Uruguay River, Southeastern South America. The features of the tracheids and their pits in the radial walls, the cross-fields with cupressoid-type pits, and axial parenchyma allow their assignment to *Podocarpoxylon* Gothan 1905. However, detailed observations such as the amount of diffuse axial parenchyma with smooth transverse end walls, uniseriate contiguous and non-contiguous intertracheal pits in the radial walls, and cross-fields with one or two pits, allow it to be related to the modern species *Podocarpus lambertii* Klotzsh (ex Eichler). This species grows in the Atlantic forests of South America. Based on the preservation of fossil material and direct observations of modern specimens, we erected, *Podocarpoxylon paralambertii* sp. nov. Paleodendrochronological analysis shows that the fossils had an evergreen habit, with an estimated trunk diameter greater than 50 cm. The growth-ring type D (sensu Creber & Chaloner 1984) suggests that the specimens grew in a non-seasonal or weakly seasonal environment. The presence of the Podocarpaceae fossils in the El Palmar Formation indicates that the distribution of this family was more widespread in South America in the past.

Keywords. *Podocarpoxylon*. Growth-rings. Paleoecology. Paleoclimatology. Quaternary. South America.

Resumen. PODOCARPACEAE DEL PLEISTOCENO TARDÍO DE LA FORMACIÓN EL PALMAR EN LA CUENCA MEDIA DEL RÍO URUGUAY, ARGENTINA: ANATOMÍA DE LA MADERA, NUEVO TAXÓN Y PALEODENDROLOGÍA. Se analizaron siete maderas fósiles recuperadas en las localidades fosilíferas de Concordia y Santa Ana (provincia de Entre Ríos, Argentina) provenientes de la Formación El Palmar (Pleistoceno Tardío). Esta unidad constituye una importante fuente de información sobre los eventos climáticos y ecológicos ocurridos hacia fines del Cuaternario (MIS5 y MIS7) en la cuenca media del río Uruguay, Sudeste de Sudamérica. Las características de las traqueidas y sus punteaduras en las paredes radiales, los campos de cruzamiento con punteaduras de tipo cupressoid y el tipo de parénquima axial permiten su asignación a *Podocarpoxylon* Gothan 1905. Aunque observaciones minuciosas como cantidad de parénquima axial difuso con pared transversal terminal lisa, punteaduras uniseriadas contiguas y no contiguas en las paredes radiales de las traqueidas, campos de cruzamiento con una-dos punteaduras permite relacionarlo con la especie actual *Podocarpus lambertii* Klotzsh (ex Eichler). Esta especie crece en los bosques atlánticos de Sudamérica. Sobre la base de la preservación del material fósil, junto a observaciones directas de material actual creamos una nueva especie, *Podocarpoxylon paralambertii* sp. nov. El análisis paleodendrocronológico muestra que los fósiles tenían un hábito perennifolio, con troncos con diámetros estimados superiores a 50 cm. La presencia de anillos de crecimiento de tipo D (*sensu* Creber & Chaloner 1984) sugiere que los especímenes crecieron en un ambiente sin estacionalidad o poco demarcada. La presencia de fósiles de Podocarpaceae en la Formación El Palmar indica que la distribución de esta familia estuvo más extendida en Sudamérica en el pasado.

Palabras claves. *Podocarpoxylon*. Anillos de crecimiento. Paleoecología. Paleoclimatología. Cuaternario. América del Sur.

EXTANT conifers represent the most diverse clade among gymnosperms, or naked-seeded plants (Farjon & Filer, 2013). They originated approximately 320 Ma on the supercontinent Pangea and subsequently diversified as Pangea began to fragment into Laurasia (north) and Gondwana (south) during the Late Mesozoic. Around 150 Ma, angiosperms appeared and rapidly diversified, dominating favourable terrestrial habitats during periods of global warming (Brodribb & Hill, 1999; Specht & Bartlett, 2009; Augusto et al., 2014). Since that time, conifer diversity has undergone a progressive decline and modification, with numerous species becoming extinct. Today, the surviving conifer species are continuously and widely distributed in the Northern Hemisphere; whereas in the Southern Hemisphere the distribution of these species is disjunct and less extensive (Miller, 1988; Brodribb & Hill, 1999; Quiroga et al., 2016; Andruchow-Colombo et al., 2023).

The Podocarpaceae are a morphologically diverse family of conifers with a cryptic fossil record reported since the Permian, the earliest reliable Podocarpaceae occurrences are from the Jurassic of both hemispheres, and the most extant genera appear in the fossil record between the Late Cretaceous and the Early Cenozoic (Andruchow-Colombo et al., 2023). The Podocarpaceae family comprises 19 extant genera and about 180 species, distributed mainly across tropical and subtropical-temperate regions of both hemispheres, including Africa, China, Japan, Mexico, Central, and South America, and the Caribbean (Novara, 1993; Conran et al., 2000; Farjon & Filer, 2013). In addition, Podocarpaceae is widely distributed throughout the Southern Hemisphere (New Caledonia, New Zealand, Madagascar, Tasmania, and South America) with ca.

156 species (Eckenwalder, 2009; Adie & Lawes, 2011). In the neotropical forests of the Americas, the family is represented by five genera: *Podocarpus*, *Prumnopitys*, *Retrophyllum, Lepidothamnus,* and *Saxegothaea*; while in the Neotropical region of Argentina, the family is represented by two *Podocarpus* species—*P. lambertii* and *P. parlatorei*— (Novara, 1993). The species *Podocarpus brasiliensis*, *Podocarpus lambertii*, *Podocarpus salignus*, *Podocarpus sellowii* var. *sellowii* and *Podocarpus sellow*ii var. *angustifoli*a thrive in the warm and humid environments of north-eastern Argentina and southern Brazil (Souza, 2013). In South America, *Prumnopitys* has three species (Fra et al., 2007). The southernmost species, *Prumnopitys andina*, is primarily restricted to Chilean territory, occurring between the Maule River and the Aysén River (35°30′–43°23′ S). Reports from near the Aluminé River, Neuquén Province (Argentina), have been mentioned in the literature but remain unconfirmed (Covas, 1939: 24; Tortorelli, 1956: 215). Recently, based on vegetative characters such as of leaf type, spacing, insertion, and arrangement, Page (2019) circumscribed *Pectinopitys* as a new genus from the alliance of *Prumnopitys* s.l. The native range of *Pectinopitys* is NE Australia, New Caledonia, New Zealand, Costa Rica to NW Venezuela, and Bolivia (POWO, 2025).

In northern Argentina, the fossil record of conifers includes fossil pollen of Araucariaceae and Podocarpaceae identified in the Miocene sediments of the Paraná Formation (Anzótegui, 1990) as well as fossil pollen of Podocarpaceae recorded in the Mio-Pliocene Ituzaingó Formation in Corrientes Province (Anzótegui, 1975; Anzótegui & Lutz, 1987). More recently, fossil wood assigned to *Prumnopityoxylon gnaedingerae* Franco and Brea, which is related to the extant genus *Prumnopitys*, has been described from the Late Miocene Ituzaingó Formation in Entre Ríos Province (Franco & Brea, 2015).

The aim of this work is to present the first fossil record of conifers belonging to the family Podocarpaceae, discovered in gravelly-sandy fluvial deposits of the Late Pleistocene El Palmar Formation, located in a large tropical/subtropical fluvial basin in South-eastern South America (Entre Ríos Province, Argentina).

In addition to analysing the eco-anatomical characteristics of the fossil wood, this study also discusses the palaeoenvironmental conditions under which these plants grew.

GEOLOGICAL SETTING

The El Palmar Formation (Iriondo, 1980; Iriondo & Kröhling, 2008) is the main Late Pleistocene fluvial unit of the Uruguay River valley in its middle basin (North-eastern Argentina). The formation composes the upper fluvial terrace, generated by a gravelly-sandy river, which reaches widths of 4–20 km on both present fluvial margins. High-energy channel deposits characterise the unit, which outcrops with typical thicknesses of 10–15 m. Those are formed by sandy strata with interbedded gravels, red to yellowish brown due to silica and iron oxides cements. The El Palmar Formation overlies Cretaceous and Late Paleogene units, and it is locally covered by Holocene fluvial/paludal and aeolian deposits (Iriondo, 1980; Iriondo & Kröhling, 2008; Kröhling, 2009). According to Iriondo & Kröhling (2008), the El Palmar Formation is correlated with the Salto Formation, defined in Uruguay by Goso & Bossi (1966) and Bossi (1969). This unit is a member of the Salto depositional sequence, represented by a bedload (braided) fluvial system (Veroslavsky & Ubilla, 2007).

Two sedimentary samples taken from outcropping profiles of the El Palmar Formation, and dated by thermoluminescence (TL), yielded ages between ca. 80 ka. BP (Federación locality; Argentina), and ca. 88 ka. BP (Salto locality; Uruguay), and corresponding to the MIS5a warm interstadial (MIS: Marine Isotope Stage; Iriondo & Kröhling (2008)).

An optically stimulated luminescence (OSL) dating of a sample from the upper part of the unit in the type area (Ramos et al., 2017) yielded an age of ca. 184 ka. BP (El Palmar National Park locality, Argentina), extending the age of the El Palmar Formation to the penultimate interglacial (MIS 7; Middle Pleistocene).

According to the biogeographic classification of Morrone et al. (2022), the Uruguay River Basin is included in the Paraná dominion. The Upper Uruguay River Basin is characterised by a humid subtropical/tropical climate, with rainfall of 1500-2000 mm/year, covering the Southeast of Brazil and the Northeastern Argentina.

Today, the middle basin of the Uruguay River is influenced by a transitional subtropical climate in the north and a temperate climate to the south. The average rainfall is 1200 mm/year, and the average annual temperature ranges between 19 and 21 ◦C in the north and 17 ◦C in the south (Bianchi & Cravero, 2010). These conditions favour the presence of a continuous gallery forest along the river, composed of tropical and subtropical trees, shrubs and epiphytes (Rodríguez et al., 2018; Arana et al., 2021). In the southernmost area, this diverse subtropical forest contrasts with the herbaceous vegetation of the adjacent spurs (Batista et al., 2014).

The analysed material comes from two fossiliferous localities (FL) of the El Palmar Formation (Argentina): Santa Ana FL (30◦54′S, 57◦55′W) and Concordia FL (31◦19′S, 57◦59′W) (Fig. 1B), both located in the middle basin of the Uruguay River, in the eastern part of Entre Ríos province, Argentina (Fig. 1). The outcropping stratigraphic profile of the El Palmar Formation at Santa Ana FL is ca. 4.0 m thick. The lower section (1.05 m) consists of a medium sandy bed (very poorly sorted quartz sands, reddish in colour), covered by a thick lenticular bed composed of massive grey clays showing evidence of gleying. The middle section of the profile (1.30 m) is composed of very poorly sorted quartz sands, red to yellowish red, with massive to medium/thick strata,

dominantly formed by matrix-supported graded gravels to gravelly sands and fining upward to a thin bed formed by massive silty clays (representing an abandoned channel). The upper section (1.40 m) is formed by strata of massive to crudely stratified matrix-supported sandy siliceous gravels and gravelly sands in an imbricated and a fining upward pattern, crowned by a lag gravelly deposit (0.50–0.80 m); the fossil woods CIDPALBO-MEG 111, 112, 113, 115 and 116, were found in this section of the profile (Fig. 1). The sedimentary facies association of the profile represents a high-energy fluvial channel with longitudinal sandy gravel and gravelly sand bedforms (Patterer et al., 2020; Ramos et al., 2024).

The outcropping profile of the El Palmar Formation at the Concordia FL, and near the Yuquerí river mouth, is ca. 2.40 m thick. The lower section (0.8 m) is composed of olive brown sandy clays, with Fe-oxides concretions; the middle section (0.60 m) is formed by yellowish red sandy beds (coarsening upwards from fine to medium quartz sands), massive to horizontally stratified; in erosive discordance, the upper section (1.00 m) is formed by medium beds formed by sandy matrix supported poorly sorted gravels/pebbles and cobbles (dominantly siliceous and rounded clasts), massive or with horizontal bedding, red in colour. The sedimentary facies interpretation indicates overbank fine deposits covered by sands representing shallow flow deposits. These are overlain by very poorly sorted materials representing a longitudinal bar (Ramos et al., 2024). The specimens CIDPALBO MEG 108 and 109 were collected in the upper section (Fig. 1).

Figure 1

MATERIALS AND METHODS

Two fossil wood specimens from the Concordia FL were studied, with measurements ranging from 5 to 6 cm in length and 4 to 5 cm in width and five fossil wood specimens were collected from the Santa Ana FL, measuring between 3 to 6 cm in length and 4 to 8 cm in diameter (Fig. 1). The overall preservation of the specimens is relatively good and, the specimens are permineralised.

Standard petrographic sections (ca. 20–40 μm thick) were prepared in transverse (TS), tangential longitudinal (TLS), and radial longitudinal (RLS) orientations for each specimen studied. Quantitative characteristics are based on at least 35 measurements of each xylem element. Average values are given, and minimum and maximum values are indicated in parentheses. The material was examined with a Nikon Eclipse E200 optical microscope, and photomicrographs were taken with a Nikon Coolpix S4 digital camera. Anatomical terminology follows the recommendations of the IAWA List of Microscopic Features for modern Softwood Identification (IAWA *Committee*, 2004). Comparative analysis with extant species, supported by bibliographic references and data from the InsideWood database, indicates a close affinity with *Podocarpus lambertii* (Tortorelli, 1956; de Paula et al., 2000; Correa et al., 2010; Siegloch & Cardoso Marchiori, 2015, among others). Consequently, thin sections of wood from the extant species were prepared to allow for a more detailed comparison. The modern material corresponds to mature specimens (trees > 10 m in height) from the botanical garden of the Facultad de Ciencias Forestales, Universidad Nacional de Misiones, El Dorado (Arg.). The wood was macerated according to Jeffrey's method (Johansen, 1940). Mature wood samples were fixed in 70% alcohol. Transverse, radial, and tangential sections (15 μm to 20 μm thick) were cut using a sliding microtome. Sections were double-stained with 1% fuchs in and astra blue (Roeser, 1972).

For systematic assignment, the proposals and classifications of Philippe & Bamford (2008), Pujana & Ruiz (2017), and Boura et al. (2021) were also considered. For the classification of growth-rings, we follow the scheme of Creber & Chaloner (1984) and Brison et al. (2001). Creber & Chaloner (1984) classified early-wood and late-wood development or growth rings into six types. Type A: rings with little early-wood; pronounced transitions at the early-wood to late-wood boundary. Type B: rings with a broad band of late-wood; the transition to late-wood is more gradual. Type C: Rings with a very gradual transition between early-wood and late-wood; rings indicate growth in an environment with only gradual changes during the growing season. Type D: Rings with a thin band of late-wood; the boundary between early-wood and late-wood is well marked. Type E: Rings similar to type D, but the transition to late-wood is not as pronounced. Type O: Rings resulting from a situation where all growth requirements are constantly present; no noticeable change in tracheid diameter. The minimum estimated diameters (MED) of the woods were assessed based on the curvature of the growth rings; when they presented almost straight growth ring boundaries, they are assigned a diameter of 50 cm (Creber & Chaloner, 1984).

The preservation of growth-rings allowed the use of the Falcon-Lang (2000a, b) Method CSDM curve (cumulative algebraic sum of each cell's deviation from the mean), which defined the species habit and inferred leaf longevity in the plant. By measuring the diameter of the tracheids that constitute the growth-rings, it is possible to calculate the growth-ring markedness index, which provides an ecological parameter of the plant (Falcon-Lang, 2000b). The ring markedness index is stated as the percentage product between the percentage of late-wood and the percentage of ring decrease (see Creber & Chaloner, 1984).

For the analysis, we used the transverse section of the wood and we identified: **a.** the ring boundary (RB) from the discontinuity between late-wood cells of a ring and the cells of the early-wood; **b.** the ring increment (RI) which corresponds to the section between the two adjacent ring boundaries. We examined RI greater than 30 cells in amplitude. Along each RI, the radial diameters of the successive tracheids of five adjacent radial rows are measured and averaged to obtain the final figures. These values are used to calculate the *cumulative algebraic sum of the deviation of each cell from the mean* of the radial diameters, and are plotted as a zero-trending curve (CSDM curve) (according to Creber & Chaloner, 1984). That is, for each RI, we calculate the percentage deviation of the zenith of the CSDM curve from the centre of the figure. Perfectly symmetric CSDM curves have percentage biases of zero magnitude. Deciduous conifer species have predominantly symmetric or left-skewed CSDM curves, while evergreen conifer species have predominantly right-skewed CSDM curves (positive percentage skews). The 'percentage skew' takes the point where the CSDM curve becomes zero for the last time as the early-wood to late-wood boundary.

SYSTEMATIC PALEONTOLOGY

Division PINOPHYTA Cronquist, Takht., Zimmerm. Ex Reveal 1996

Orden CONIFERALES Engler 1897

Family PODOCARPACEAE Endlicher 1847

Genus ***Podocarpoxylon*** Gothan 1905

Type species. *Podocarpoxylon juniperoides* Gothan 1905

Podocarpoxylon paralambertii sp. nov. Ramos, Brea et Kröhling

Figures 2. A – 5. F

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Derivation of name or Etymology. Podocarpaceae, has a strong affinity with the modern species *Podocarpus lambertii* Klotzsch ex Endl. The prefix "para" refers to something similar to. The term "lambertii" honors the English botanist Aylmer Bourke Lambert (1761–1842), who studied conifers.

Type material. CIDPALBO-MEG 108, CIDPALBO-MIC 1365 (three microscopic slides).

Referred material. (4): -CIDPALBO-MEG 113, CIDPALBO-MIC 1370-, -CIDPALBO-MEG 114, CIDPALBO-MIC 1371-, -CIDPALBO-MEG 115, CIDPALBO-MIC 1372-, -CIDPALBO-MEG 112, CIDPALBO-MIC 1369

Geographic occurrence. Concordia department, Entre Ríos Province, Argentina.

Referred material. (2): -CIDPALBO-MEG 109, CIDPALBO-MIC 1366-, -CIDPALBO-MEG 116, CIDPALBO-MIC 1373-.

Geographic occurrence. Santa Ana, Federación departament, Entre Ríos Province, Argentina.

Stratigraphic occurrence. El Palmar Formation (Late Pleistocene, MIS5/7).

Diagnosis. Growth rings distinct. Intertracheary pitting bordered, uniseriate, contiguous and non-contiguous and rounded outline on the radial walls of the tracheids. Axial parenchyma diffuse with smooth (unpitted) transverse end wall. Cross-field pits of cupressoid type, bordered, normally two (or one) half-bordered (= oculipore) pointed pits per cross-field with oblique included aperture. Rays uniseriate and medium-height. End and horizontal walls of ray parenchyma cells smooth.

Description.

In cross-section, the growth rings in samples CIDPALBO-MEG 109, 112, 114, and 116 are distinguished by a slight, gradual transition from late-wood to early-wood, marked by radial compression of the tracheids (Fig. 2. A-C). According to the classification of Creber & Chaloner (1984), these are of type D. Tracheids oval to polygonal and angular in outline, radial to slightly and irregularly arranged with 2-6 rows of tracheids between rays. Tangential diameter 52 (18—84) μm and radial diameter 46 (25—79) μm. Walls 9 (5—17) μm thick (Fig. 2. E, G; Fig. 5. C, D). Only in sample CIDPALBO-MEG 109, 113, and 116 are intercellular spaces observed (Fig 2. F). The rays are separated by 3 to 6 rows of tracheids. Five (4—8) rays per linear mm (Fig. 2. A, B, D). Both rays and tracheids inside show dark contents (Fig. 3. A-F). Axial parenchyma has diffuse (Fig. 2. C, F)

In radial longitudinal section, the tracheids have radial pitting uniseriate, contiguous and non-contiguous, generally spaced without contact, and, less frequently, contiguous in contact, with a rounded outline (Fig. 4. B, C; Fig. 5 D), with a tangential diameter of 17 (15—20) μm and radial diameter of 13 (10—15) μm (Fig. 4. B, C). Cp = 62% and Si = 1. Rays are homocellular, composed of parenchyma cells. Their horizontal and vertical walls are smooth, with pointed ends (Fig. 5. A, B, F). The average height of the parenchyma ray cells is 28 (25—30) μm. The rays have two or one pits per cross-field circular to oval, separated or arranged in pairs, are of the cupressoid type (sensu IAWA Committee, 2004) or podocarpoid type (sensu Boura et al., 2021), and have a diameter of 6 (3-10) μm (Fig. 4. D, E).

Tracheid pits in the tangential longitudinal section (TS) are uniseriate, contiguous or non-contiguous, rounded or circular, with equal size and shape to the pits in radial section, circular openings of 3 (2-5) μm in diameter (Fig. 5. D). Axial parenchyma has smooth transverse end walls (Fig. 4. A). The rays are uniseriate (Fig. 3 A, B, C; Fig. 5

D), only the CIDPALBO-MEG 115 sample showed sectors where the uniseriate rays have aggregated cells (Fig. 3. E). On average, the rays of the specimens are of medium-height, consisting of 11 (2–30) cells in height, measuring 182 (55–931) μm in height and 38 (20–50) μm in width (Fig. 3. A-F).

Observations: The sample CIDPALBO-MEG 109 showed sectors of exaggerated irregular growth, with radially compressed tracheids (Fig. 2 B; Fig. 5. C, D). According to Schweingruber (2006), the collapse of thin-walled cells and radial compression of xylem elements are the consequence of a sudden drop in water pressure, in some cases caused by pollarding (pruning), within the fully differentiated but not lignified tissue of the cambial area. It is most probable that the fossilized specimen had a period of recovery of xylem tissue after undergoing a process of damage. Such damage could be a sudden fall of a branch due to wind, renewed xylem growth after the tree was struck by lightning, or another natural event.

Figures 2, 3, 4, 5

DISCUSSION

Comparisons with current species

Conducting and supporting elements consisting exclusively of tracheids, interconnected by circular or flattened pits arranged in uniseriate or more rows (multiseriate) on the radial walls of the tracheids, and the presence of narrow rays, place these fossil woods within the Coniferales (Greguss, 1955; Miller, 1988; Cevallos-Ferriz, 1992; Siegloch & Cardoso Marchiori, 2015).

Conifers are classified into eight families: Sciadopityaceae, Pinaceae, Araucariaceae, Taxodiaceae, Cupressaceae, Cephalotaxaceae, Taxaceae, and Podocarpaceae (Mabberley, 2000; Jiang et al., 2010), and generally all have a homogeneous wood anatomical structure. However, species of Cupressaceae are characterised by abundant axial parenchyma, often tangentially zonate, and by growth-rings in which the transition from early-wood to late-wood may be abrupt or gradual (Greguss, 1955; Jiang et al., 2010). Uniseriate intertracheary pitting and cupressoid cross-field pits are not diagnostic features of Araucariaceae (Greguss, 1955; IAWA, 2004). The presence of traumatic canals (axial or radial) and window-like cross-field pits in Sciadopityaceae and Pinaceae differ from the woods under analysis (Marchiori 2005; Siegloch & Cardoso Marchiori, 2015). The presence of helical thickenings in longitudinal tracheids in Cephalotaxaceae and Taxaceae species, plus the absence of axial parenchyma in Taxaceae, refute any link with the fossils of the El Palmar Formation (Greguss, 1955; Marchiori, 2005). The presence of diffuse axial parenchyma, cupressoid cross-fields pits, and the arrangement and type of pits on the radial walls of the tracheids suggests assigning the fossil from the El Palmar Formation to the family Podocarpaceae (Phillips, 1941; Greguss, 1955; Tortorelli, 1956; Del Fueyo, 1989; García Esteban et al., 2002; IAWA *Committee*, 2004; Siegloch & Cardoso Marchiori, 2015).

The extant Podocarpaceae show significant wood anatomical variability among their species, both between genera and within species (Correa et al., 2010). Comparative analysis of the wood anatomy of Podocarpaceae, including American and African species, suggests a close affinity between the fossils and neotropical species of the genus *Podocarpus* (Correa et al., 2010; de Paula et al., 2000; Siegloch & Cardoso Marchiori, 2015).

370 *Podocarpus* is characterised by uniseriate, circular intertracheary pitting on the radial
371 walls, exceptionally biseriate and opposite (i.e., arranged in two rows); cross-fields are
372 cupressoid to taxodioid (sensu IAWA, 2004), with diagonally elliptical apertures
373 enclosed within the pit border. Each cross-field may display either a single large pit or
374 up to four smaller pits. Axial parenchyma is scarce to predominant. Rays are 1–40 cells
375 high, although rays ≤ 15 cells predominate; they are uniseriate and have smooth walls
376 (Phillips, 1941; Tortorelli, 1956; de Paula et al., 2000; IAWA *Committee*, 2004;
377 Maranho et al., 2006; Correa et al., 2010; Siegloch & Cardoso Marchiori, 2015).
378 The type and number of pits in the cross-fields, as well as the intertracheary pitting on
379 the radial walls, were partly decisive in determining the genus of the analysed material.
380 As noted above, the anatomy of the fossil specimens studied here is closely related to
381 that of *Podocarpus lambertii*. To support this interpretation, we include microscopic
382 wood sections of the extant species (Fig. 6). Extant and fossil woods have one and two
383 pits per cross-field as the most common, although between one to four pits, all of the
384 same size of the cupressoid type (Fig. 6. E-G), axial parenchyma diffuse (Fig. 6. A, C).
385 Rare intercellular spaces, uniseriate and contiguous and non-contiguous tracheid radial
386 pitting (Fig. 6. B, C), and uniseriate rays of medium height (Fig. 6. B). We also present
387 Table 1, which summarizes South American and African species whose wood anatomy
388 shows the closest affinity with the fossils analysed here.
389 As detailed in Table 1, the wood anatomy of *Prumnopitys andina* (Poepp. Ex Endlicher),
390 *Podocarpus parlatorei* Pilg., *Podocarpus nubigenus* Lindl., *Podocarpus brasiliensis*,
391 and *Podocarpus lambertii*, agrees with the fossil anatomy in the uniseriate and bordered
392 pits of the radial walls of the tracheids, and the homocellular and uniseriate rays.
393 *Prumnopitys andina* and *Podocarpus parlatorei* have one large pit per cross-field,

394 which excludes these species from the comparative analysis (Del Fueyo, 1989; Berrios,
395 2017).
396 *Podocarpus nubigenus* differs in having very small taxodioid pits in the cross-fields.
397 Another distinguishing feature is the height of the rays, which do not exceed 15 cells.
398 Although this character may vary with the age of the individual, the study by Díaz Van
399 (1986) on *Podocarpus nubigenus* showed that even the longest-lived trees low rays (≤
400 15 cells), making this a consistent diagnostic character.
401 We observed that *Podocarpus* species (*Podocarpus henkelii, Podocarpus milanjianus,*
402 and *Podocarpus latifolius*) growing in tropical Africa and Madagascar are comparable
403 to the fossil material in having rays up to 30 cells high and the presence of axial
404 parenchyma, abundant in *Podocarpus madagascariensis*, but they differ in the type of
405 cross-field pits, which vary between pinoid, taxodioid, or with a torus present.
406 The combination of these latter features, which are incompatible with fossil woods, is
407 also observed in South American species such as *Podocarpus glomeratus, Podocarpus*
408 *oleifolius,* and *Podocarpus sprucei* (Phillips, 1941; Greguss, 1955, 1972; Marguerier &
409 Woltz, 1977). The Atlantic Forest species of southern Brazil, *Podocarpus brasiliensis*
410 and *Podocarpus lambertii,* share a greater number of characters with the fossil woods
411 studied here; the only observed difference is the slightly variable ray height in
412 *Podocarpus brasiliensis*, with rays fewer than 15 cells high (de Paula et al., 2000;
413 Maranho et al., 2006; this work).
414 Regarding the anatomy of *Podocarpus lambertii* described by Maranho et al. (2006) in
415 relation to that described in this work, there is one observation to be highlighted.
416 Maranho et al. (2006) observed numerous pits in the cross-fields closely spaced and
417 piceoid type. Siegloch & Cardoso Marchiori (2015) observed in their analysed
418 specimens one or rarely two pits per cross-field of the cupressoid type and abundant

axial parenchyma. In the *Podocarpus lambertii* wood examined in this study (Fig. 6), moderate to predominant axial parenchyma, cross-fields with one or two pits predominate, whereas cross-fields with up to four pits are only rarely observed. All pits are of the cupressoid type according to the IAWA descriptions, and also correspond to the podocarpoid type (with border>aperture) following Boura et al. (2021).

Figure 6

Table 1

Comparison with fossil taxa

A large number of fossils have been assigned to the family Podocarpaceae, including the genera *Podocarpoxylon* Gothan, *Protopodocarpoxylon* Eckhold, *Phyllocladoxylon* Gothan, *Metapodocarpoxylon* Dupéron-Laudoueneix & Pons, *Protophyllocladoxylon* Kräusel, *Circoporoxylon* Kräusel, and *Cupressinoxylon* Göppert (Torres et al., 1994; Philippe & Bamford, 2008; Pujana & Ruiz, 2017; Ruiz et al., 2017). The specimens analysed here are closely related to *Podocarpoxylon*, a genus established by Gothan (1905), and later validated by Philippe & Bamford (2008). The features of the genus include contiguous and non-contiguous pits, which are uniseriate on the radial walls of the tracheids; uniseriate and homocellular rays; diffuse axial parenchyma; and cross-field with pits, generally of the cupressoid type (Gothan, 1905). Although the anatomical differences between *Podocarpoxylon* and *Cupressinoxylon* are minimal, the fossils analysed here differ from the latter because the walls of the axial parenchyma are smooth, the pits in the cross-fields are between 1 and 2 and rarely reach 4, and the pits in the tangential walls of the tracheids are present and are exclusively uniseriate. These characteristics are not definitively confirmed in *Cupressinoxylon* (Göppert enmend. Gothan, 1905).

The list of fossils exhibiting *Podocarpoxylon*-type wood anatomy available in the literature formed the basis for an extensive comparative analysis, encompassing studies published over the past half century through to the most recent contributions (Bose & Maheshwari, 1974; Cevallos-Ferriz, 1992; Vozenin-Serra & Grant-Mackie, 1996; Del Fueyo, 1998; Gnaedinger, 2007, Philippe & Bamford, 2008; Pujana & Ruiz, 2017; Ruiz et al., 2025; Rombola et al., 2024; Vera et al., 2024; and others).

Based on the combination of characters of the fossil specimens studied here, the most closely related species are compared in Table 2. *Podocarpoxylon garcie* Del Fueyo, from Upper Cretaceous Allen Formation (Río Negro, Argentina), is characterised by relatively low rays, consisting of up to 15 cells, and cross-fields pits with large apertures and thin, weakly defined borders; these features differentiate it from *Podocarpoxylon paralambertii* sp. nov. (Del Fueyo, 1998). *Podocarpoxylon austroamericanum* Gnaedinger, from the Middle Jurassic La Matilde Formation (Santa Cruz, Argentina), is characterised by completely opposite, or rarely alternate, biseriate pits on the radial walls of the tracheids and an equal proportion of one to four pits per cross-field. These features do not correspond to the characters observed in the studied fossils; therefore, *Podocarpoxylon austroamericanum* was discarded from the comparisons (Gnaedinger 2007). *Podocarpoxylon* sp. Cevallos-Ferriz, from the Upper Cretaceous Olmos Formation (northern Mexico), differs from *Podocarpoxylon paralambertii* sp. nov. in the type of cross-field pits and predominance of opposite biseriate pits in the radial walls of tracheids (Cevallos-Ferriz, 1992). The presence of Sanio's bar in the structure of *Podocarpoxylon umzambense* Schultze-Motel (1966) and the ray height of up to 35 cells in *Podocarpoxylon* cf. *woburnense* Seward (1919) exclude these species from the comparative analysis. *Podocarpoxylon paralatifolium* Vozenin-Serra & Grant-Mackie 1996, *Podocarpoxylon* sp. Cevallos-Ferriz and *Podocarpoxylon sarmai* Varmai are

similar to the studied specimens in having circular, contiguous, uniseriate tracheid tips, diffuse axial parenchyma, and homogeneous, uniseriate rays. However, *Podocarpoxylon paralatifolium* differs in having predominantly biseriate pits on the radial walls of the tracheids, *Podocarpoxylon sarmai* differs in having numerous pits (four) in the cross-fields, and *Podocarpoxylon* sp. of Cevallos-Ferriz (1992) has very tall rays with up to 56 cells high.

Podocarpoxylon mazzonii (Petriella) Müller-Stoll & Schultze-Motel (1990) is common in the fossil record of Patagonia (Argentina and Chile). There are records from Upper Cretaceous Cardiel, Puntudo Chico, Allen, and Dorotea formations (Del Fueyo, 1998; Vera et al., 2019, 2024; Martínez et al., 2023; Rombola et al., 2024; Passalia et al., 2023; Villegas et al., 2024). There are also records in the Paleocene Salamanca and Bororó formations (Petriella, 1972; Brea et al., 2011; Ruiz et al., 2025), but there are currently some doubts about the age of these sediments in the fossil localities where these specimens were found (Ruiz et al., 2025). This species differs from *Podocarpoxylon paralambertii* sp. nov. in having biseriate rays and numerous pits per cross-field.

Podocarpoxylon paradoxi (Upper Cretaceous, Dorotea Formation) recovered in south-central Chile (Martinez et al., 2023) is characterised by having radial pitting bordered mostly non contiguous, occasional opposite biseriate pits, cross-fields with 1–3 pits of taxodioid type. These characters are not compatible with *Podocarpoxylon paralambertii.*

The fossil wood shares anatomical characteristics with Podocarpaceae fossil species already known. However, its combination of diagnostic characteristics allows the recognition of a new species from the Late Pleistocene of Argentina: *Podocarpoxylon paralambertii* sp. nov. The new fossil species shows a clear affinity with the wood anatomy of extant *Podocarpus lambertii*, particularly in the characters and number of

494 the pits in the cross-fields, uniseriate radial tracheid pitting, and the presence of diffuse
495 axial parenchyma (Fig. 6. E-G).
496
497 Table 2
498
499 **Palaeodendrological and palaeoecological inferences**
500 Baas & Wheeler (2011) through extensive analysis of wood anatomy, pointed out the
501 influence of climate on the structure, morphology, and anatomy of plants. Wood is
502 made up of regularly formed cells, but the sizes and shapes of these cells are coded
503 according to the ecological/climatic conditions of the environments in which the tree
504 grows. Hence, the analysis of annual growth rings in fossil wood provides valuable
505 information on palaeoclimate. In woody species, cells are generally larger and develop
506 thin walls early in the growing season (early-wood), then gradually decrease in diameter
507 while increasing in wall thickness during late-wood formation (Creber & Chaloner,
508 1984). These characteristics can be analysed with dendrological techniques in
509 permineralised woods, because the thickness of the growth rings is not modified during
510 fossilization process (Schweingruber, 1988).
511 Ring boundaries and ring increments were detected in the transverse section of five
512 growth rings in three specimens of *Podocarpoxylon paralambertii* sp. nov.
513 (CIDPALBO-MEG 109, 112, 116) and plotted on the main axis of the CSDM curve
514 (Fig. 7). From the obtained data, the percentage values of the four parameters were
515 calculated: 1. percentage deviation from the curve; 2. late-wood; 3. cell decline; 4. ring
516 markedness index (Table 3).
517
518 Table 3
519 The amplitude of the five ring increments analysed ranged from 31 to 57 cells.

Following Falcon-Lang (2000b), the CSDM curves obtained from the specimens of *Podocarpoxylon paralambertii* nov. sp. shows a rightward skew (percentage of curve deviation +35.6%) (Table 3), demonstrating its evergreen habit (Fig. 7).

The percentage of late-wood of the material under study has an average of 33.17% and varies in a range of 11.75% and 45%. The percentage of cell diminution has an average value of 29.8% (25%-35.16%). The average ring-markedness index of the five increments is 8.35% with extreme values between 2.18% and 13.64% (Table 3).

On the other hand, Falcon-Lang (2000a) found in a study with extant gymnosperm species a linear and inverse relationship between leaf retention time on the plant and the parameters percentage of late-wood, percentage of cell diminution, and ring markedness index of the CSDM curves. The author observed that species with lower values for the percentage of late-wood and ring markedness index retain leaves longer on the plant (greater leaf longevity), thus *Araucaria araucana* (Mol.) Koch has a leaf longevity of up to 15 years, while the highest values of those percentages correspond to the lowest leaf retentions, as is the case with *Larix decidua* Miller, a typically deciduous species. According to the values obtained for *Podocarpoxylon paralambertii* sp. nov. (Table 4), we estimate that the leaf turnover or retention time was between 2 and 6 years. These values are close to those obtained for *Podocarpus totara* by Falcon-Lang (2000a).

Figure 7

Table 4

The family Podocarpaceae is monophyletic (Conran et al., 2000; Quinn & Price, 2003) and in Argentina has a disjunct distribution in three biogeographical provinces: Valdivian Forest, Yungas Forest, and Paranaense-Atlantic Forest (Cabrera & Willink, 1973; Arana et al., 2021), represented by 5 species (*Podocarpus parlatorei*, *Podocarpus*

lambertii, *Podocarpus nubigenus*, *Lepidothamnus fonkii* Phil., and *Saxegothaea conspicua* Lindl sensu Novara, 1993).

Conifers are considered xerophytic plants, typically bearing leaves adapted to withstand drought conditions or freezing temperatures. However, some species within the group are native to tropical and subtropical regions, such as *Podocarpus brasiliensis*, *Podocarpus lambertii*, and *Araucaria angustifolia* (Novara, 1993; Lauterjung et al., 2018). *Podocarpus* species in particular share a common pattern: they thrive only in humid environments (Novara, 1993; Tortorelli, 1956). They can grow in seasonal environments with sub-zero temperatures, but always in areas with a good water supply. From wood anatomy, we have observed that species from neotropical forests, such as *Podocarpus lambertii*, but especially *Podocarpus brasiliensis*, have scarce to rare axial parenchyma compared to *Podocarpus* species from Patagonia. Del Fueyo (1992), in her analysis of the leaf characteristics of three *Podocarpus* species, observed that *Podocarpus nubigenus* (Patagonian species) has a lower density of stomata compared to *Podocarpus lambertii* species, and a higher concentration of axial parenchyma and sclereids. These acquired characteristics of *Podocarpus nubigenus* are strategic from an ecological point of view: the Valdivian Forest, although relatively humid, has long periods of low temperatures (Arana et al., 2021).

Podocarpoxylon paralambertii in the middle-lower Uruguay River basin- Late Pleistocene (MIS 5a / MIS 7)

Colinvaux et al. (1996) in a study of pollen spectra in an Amazonian lowland lake showed that rainforest occupied the region continuously during the Last Glacial

570 Maximum. This suggest that in equatorial areas, glacial stages were not deadly to
571 species.
572 Further south, Pinaya et al. (2024) conducted a study to understand the distribution of
573 species of some genera in both Andean and Atlantic Forests. They interpreted that
574 populations of species such as *Podocarpus* remained in areas less affected or with
575 microclimates suitable for their survival during the glacial climates of the Quaternary.
576 Later, when the climate was more favourable, they extended their distribution.
577 A very interesting study by Bernardi et al. (2020), integrating phylogeography and
578 distribution models for *Podocarpus lambertii* analyses, discusses the disjunction of its
579 populations in South America. During the Pleistocene, the species had a more extensive
580 distribution than in the present (Behling, 1996; De Oliveira et al., 1999; Parolin et al.,
581 2006; Ledru et al., 2007). Bernardi et al. (2020) argue that the current disjunction of the
582 species possibly occurred because of a presumed barrier to gene flow and reveal
583 possible glacial refuges for Quaternary events. One is the southern region of the Atlantic
584 Forest, which provided better climatic conditions for the expansion of the species and
585 the *Araucaria angustifolia* forest to more southerly areas. Piraquive-Bermúdez et al.
586 (2024) also mention the establishment and gradual expansion of the *Araucaria*
587 *angustifolia* during the Holocene. This species, together with *Podocarpus lambertii*,
588 currently have a comparable distribution, partly due to their ecological requirements,
589 but also due to anthropogenic activity in their natural areas.
590 These results are related to the interpretations obtained by Ramos et al. (2024) for the
591 ancient distribution of the species *Aspidosperma polyneuron* Mull Arg. and
592 *Aspidosperma australe* Mull Arg. These Apocynaceae species had a wider distribution
593 during the Last Interglacial and subsequently diverged until they moved back and
594 settled definitively in the Atlantic Forests of South America.

In an analysis of climatic parameters of coexistence in the Santa Ana FL (El Palmar Formation), we observed that the set of recorded species would have coexisted in an environment with an average temperature between 18-24°C and an average rainfall of 1200-1500 mm/yr (Ramos & Brea, 2023). On average, the mesomorphic index of the floristic assemblage was 5149, while the vulnerability index was around 14 (Carlquist, 2001; Ramos, 2015; Ramos et al., 2022; Ramos & Brea, 2023). According to Carlquist (2001), the higher the value of the mesomorphic index, the more mesomorphic the species are, and when the value of the vulnerability index is higher than one, the more vulnerable the species are to water stress events. The species association analysed by Ramos & Brea (2023) was composed of neotropical species of Apocynaceae, Combretaceae, Fabaceae, and Anacardiaceae. Currently, these species, together with *Podocarpus lambertii*, form part of the forests that configure the Atlantic biogeographical province and the Araucaria Forest (ca 26° S), sensu Morrone et al. (2022), which are also areas with similar temperature and precipitation values to those previously mentioned. Although, according to its ecology, *Podocarpus lambertii* could grow at sea level, it is currently found in low mountain ranges of Northeastern Argentina, reaching elevations of up 800 m a.s.l., and is sometimes associated with *Araucaria angustifolia*. As the landscape in the middle-lower basin of the Uruguay River would not have undergone major changes in topography during the Upper Quaternary; it is probably that the dispersion and retreat of *Podocarpus lambertii* populations occurred along the left bank of the Uruguay River, that is, along the hills of what is now the territory of the Republic of Uruguay (Behling, 2002; Iriarte, 2006). Indeed, the northward retreat of *Podocarpus lambertii* populations towards mountainous areas is not only related to recent climatic changes, but also to

anthropogenic activities that have restricted the species to the areas where it currently occurs (Iriarte, 2006; Bonachea et al., 2010; Sobral-Souza et al., 2015).

CONCLUSIONS

The palaeoflora recovered from the fluvial deposits of the El Palmar Formation (Middle Uruguay River Basin, ca. 32°S) represent one of the most diverse subtropical/tropical forest assemblages of the Late Pleistocene in South America.

In this study, we describe seven fossil specimens and propose a new species: *Podocarpoxylon paralambertii* sp. nov. Anatomical wood features place these fossils within the Podocarpaceae familiy, showing a strong affinity with the extant *Podocarpus*. The availability of comparative material —modern wood of *Podocarpus lambertii* — provided greater confidence in this taxonomic assignment.

Podocarpoxylon paralambertii sp. nov. represents the southernmost record of a Neotropical *Podocarpus* species to date. Growth-ring analysis indicates that *Podocarpoxylon paralambertii* sp. nov. had an evergreen habit with a moderate Leaf Retention Time of 4-6 years. The ring type (D, sensu Creber & Chaloner) showed that the species grew in a non-seasonal or low-seasonal environment. Additionally, the degree of curvature in the growth rings suggests that the fossil trees analysed here had a minimum trunk diameter of ca. 50 cm.

Considering the associated fossil plants identified at the San Ana fossil locality, this assemblage closely resembles the present-day flora of the Atlantic Province and/or the Araucaria Forest of South America, located near 27°S.

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Figure captions

Figure 1. Study area and geographical distribution of *Podocarpus lambertii* (A), lithostratigraphic section of El Palmar Formation at Concordia locality and Santa Ana locality (B).

Figure 2. *Podocarpoxylon paralambertii* sp. nov. A, (**CIDPALBO-MEG 116)** general view cross section and ring grown; B, **(CIDPALBO-MEG 109)** showed sectors of exaggerated irregular growth, with radially compressed tracheids; C, (**CIDPALBO-MEG 112)** detail of axial parenchyma (arrow); **D, (CIDPALBO-MEG 114)** detail of growth ring distinct by flattening and thickening of tracheid walls (arrow); E, Holotype **(CIDPALBO-MEG 108)** & G, **CIDPALBO-MEG 115)** detail of thin-walled tracheids; F, **(CIDPALBO-MEG 112)** detail of axial parenchyma. Scale bar: D, E, G = 100 μm, A, B, C = 200 μm, F = 20 μm.

Figure 3. *Podocarpoxylon paralambertii* sp. nov. detail of uniseriate rays A, **(CIDPALBO-MEG 109)** (arrow); B, (**CIDPALBO-MEG 116);** C, **(CIDPALBO-MEG 112);** D, **CIDPALBO-MEG 114);** E, **(CIDPALBO-MEG 109)**. Scale bar: D, E = 20 μm, A, B, C = 100 μm.

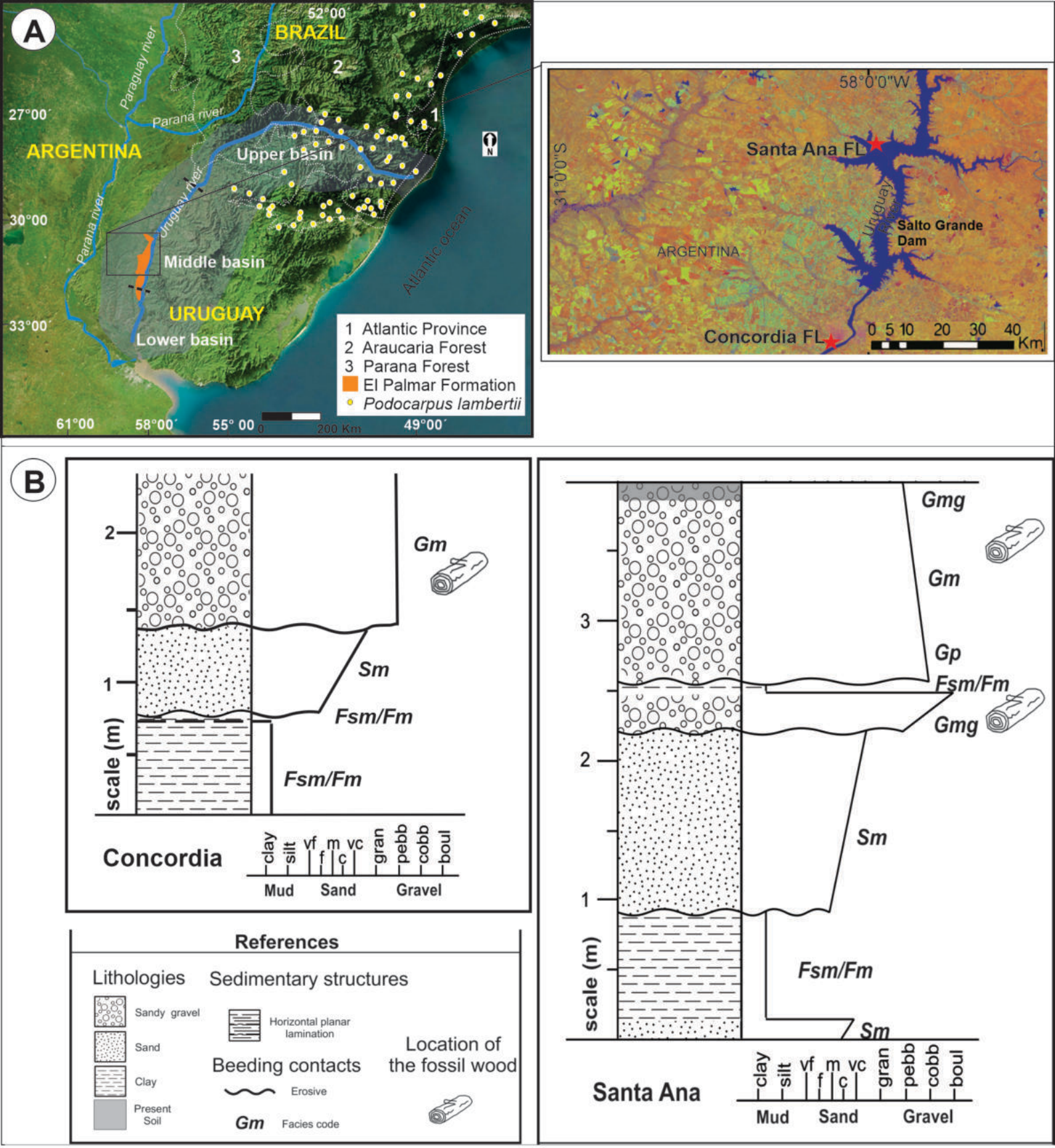
Figure 4. *Podocarpoxylon paralambertii* sp. nov, A, **(CIDPALBO-MEG 114)** detail of axial parenchyma; B, **(CIDPALBO-MEG 114)** & C, Holotype **(CIDPALBO-MEG 108)** detail of tracheid's pitting in radial wall uniseriate bordered, spaced and

contiguous; D, Holotype **(CIDPALBO-MEG 108)** detail of two to- one pits per cross-field and cupressoid (sensu IAWA), podocarpoid type (sensu Boura et al. 2021); E, Diagram of the characteristics and arrangement of the pits in the cross-fields in *Podocarpoxylon paralambertii.* Scale bar: A, B, C, D = 20 μm.

Figure 5. A, (**CIDPALBO-MEG 116)** general view of ray parenchyma cells 100 μm; B, (**CIDPALBO-MEG 114**) general view of section longitudinal radial, tracheids (arrow black), axial parenchyma (arrow grey) and ray parenchyma cells; C & D, **(CIDPALBO-MEG 109)** showed sectors of exaggerated irregular growth, with radially compressed tracheids; E, MEB view of tracheids with contiguous and spaced pits in section tangential longitudinal; F, MEB detail of parenchyma cells and rays with smooth walls (arrow). Scale bar: A, B, E = 100 μm, C, D = 20 μm, F = 50 μm.

Figure 6. RSR N°65 *Podocarpus lambertii,* A, View general of tracheid's, axial parenchyma (black arrow) and growth rings; B, uniseriate and homogeneous rays and axial parenchyma (arrow); C, detail of axial parenchyma (arrows); D, detail of bordered pits present on the radial walls of tracheids; E & F, detail of pits per cross-field and cupressoid (sensu IAWA), and podocarpoid type sensu Boura et al. 2021 (arrows); G, two and-one pit per cross-field. Scale bar: A, B = 100 μm, C = 30 μm, D-G = 20 μm.

Figure 7. Right-skewed CSDM curves of five growth rings and cell diameters of growth ring increment. For each ring increment, the percentage of skew for CSDM curves was calculated using Falcon-Lang method (2000a). The distance where CSDM curve reaches the zenith represents the percentage of skew in relation with the total distance between the center of the CSDM curve to the right of the plot. Growth-ring sequences of *Podocarpoxylon paralambertii* sp. nov. A, Specimen CIDPALBO-MEG 109; B, Specimen CIDPALBO-MEG 109; C, Specimen CIDPALBO-MEG 112; D, CIDPALBO-MEG 116; E, Specimen CIDPALBO-MEG 116.


A
52°00
BRAZIL
3
2
1
Paraguay river
Parana river
27°00´
ARGENTINA
Upper basin
Uruguay river
Parana river
30°00
Middle basin
Atlantic ocean
URUGUAY
33°00´
Lower basin
1 Atlantic Province
2 Araucaria Forest
3 Parana Forest
El Palmar Formation
Podocarpus lambertii
61°00
58°00´
55° 00
0
200 Km
49°00´
58°0'0"W
31°0'0"S
Santa Ana FL
Uruguay River
Salto Grande Dam
ARGENTINA
Concordia FL
0 5 10 20 30 40
Km
B
2
1
scale (m)
Gm
Sm
Fsm/Fm
Fsm/Fm
Concordia
clay
silt
vf
f
m
c
vc
gran
pebb
cobb
boul
Mud
Sand
Gravel
References
Lithologies
Sandy gravel
Sand
Clay
Present Soil
Sedimentary structures
Horizontal planar lamination
Beeding contacts
Erosive
Gm
Facies code
Location of the fossil wood
Gmg
Gm
Gp
Fsm/Fm
Gmg
3
2
1
scale (m)
Sm
Fsm/Fm
Sm
Santa Ana
clay
silt
vf
f
m
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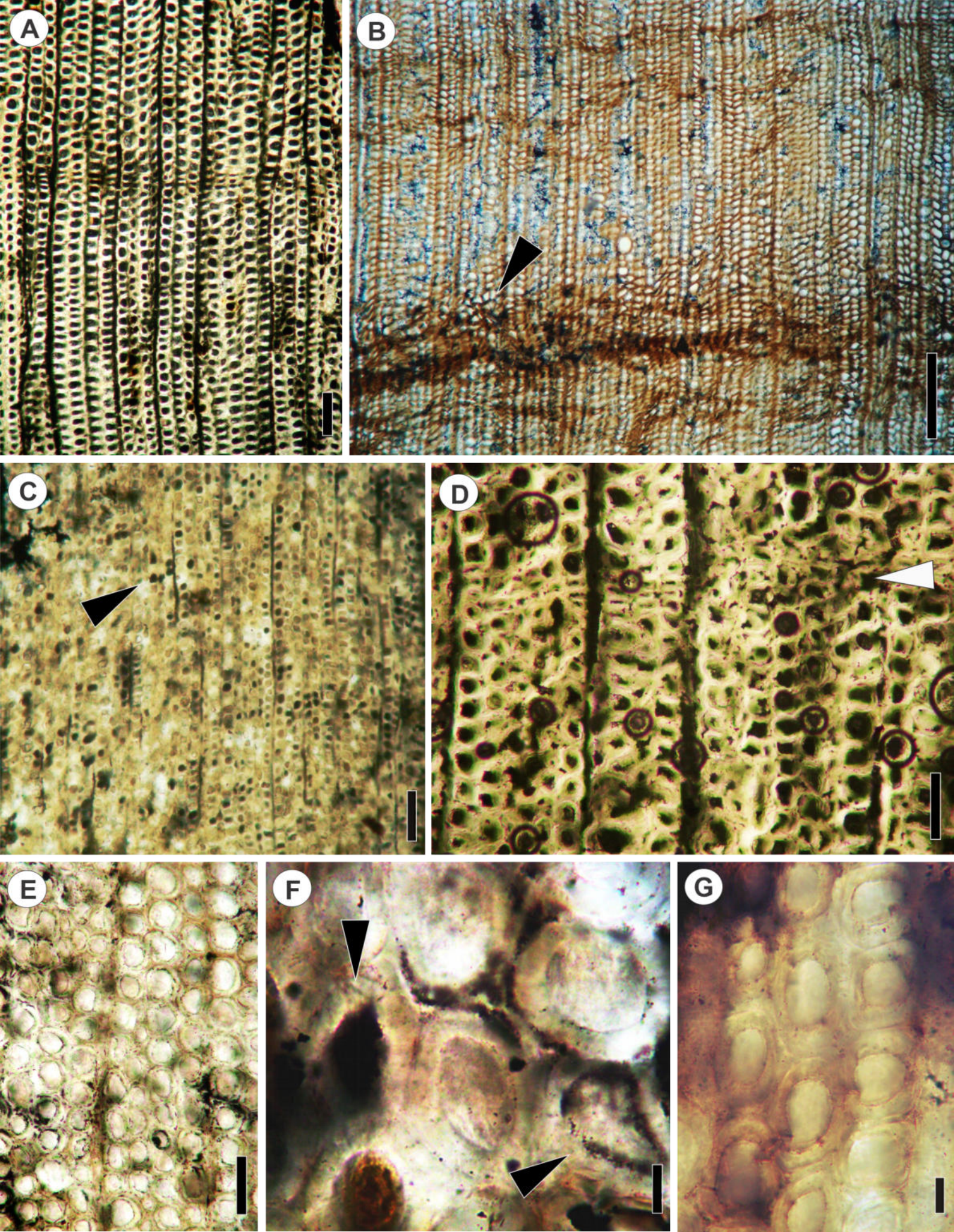
vc
gran
pebb
cobb
boul
Mud
Sand
Gravel


A
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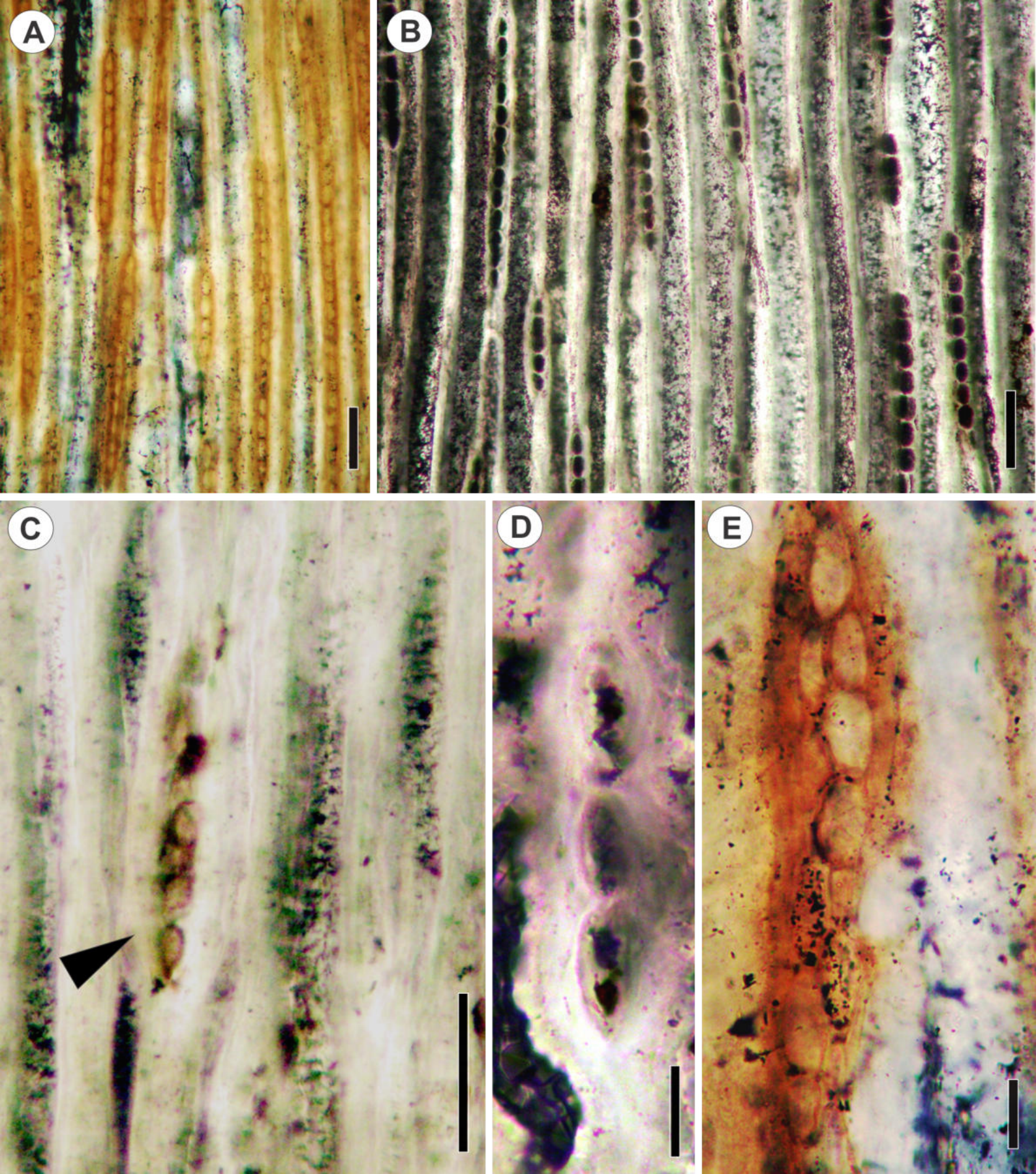
G


A
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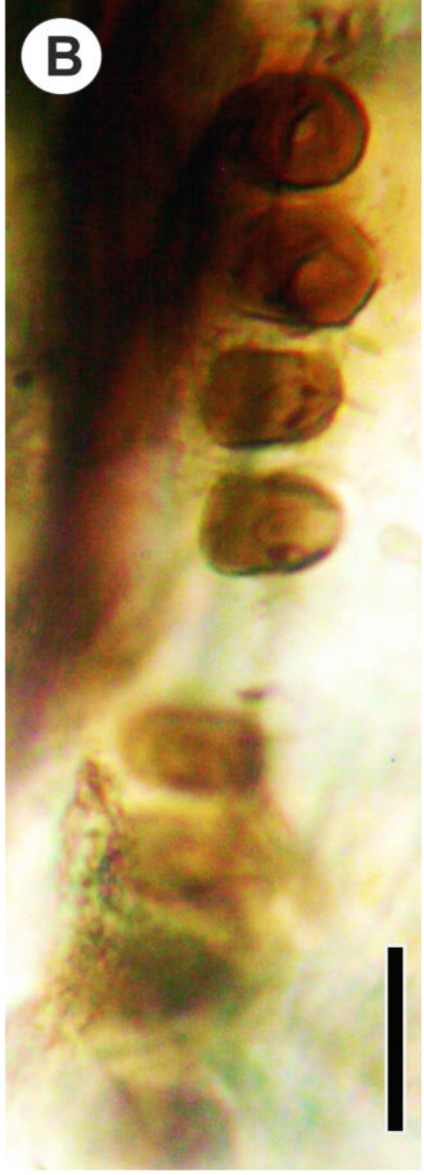
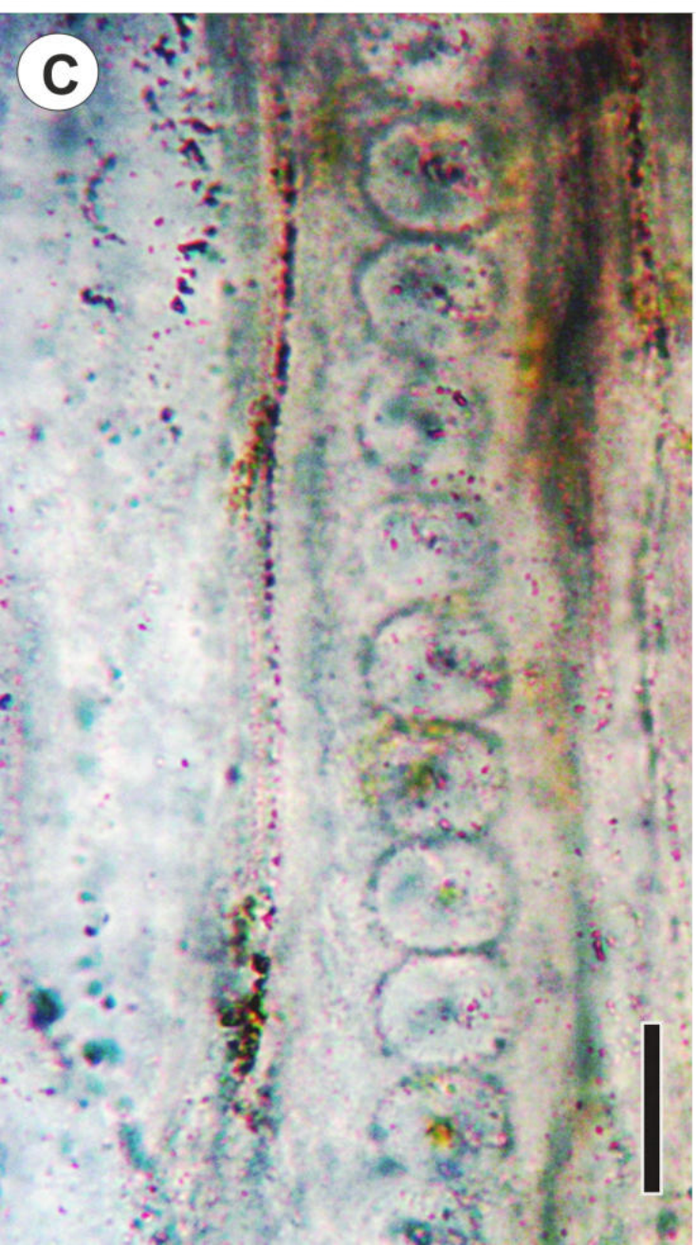
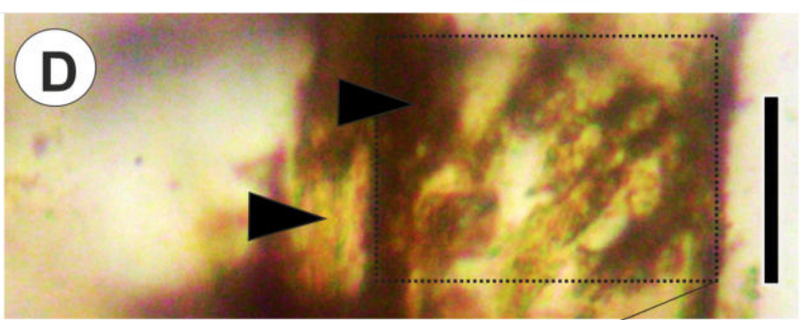
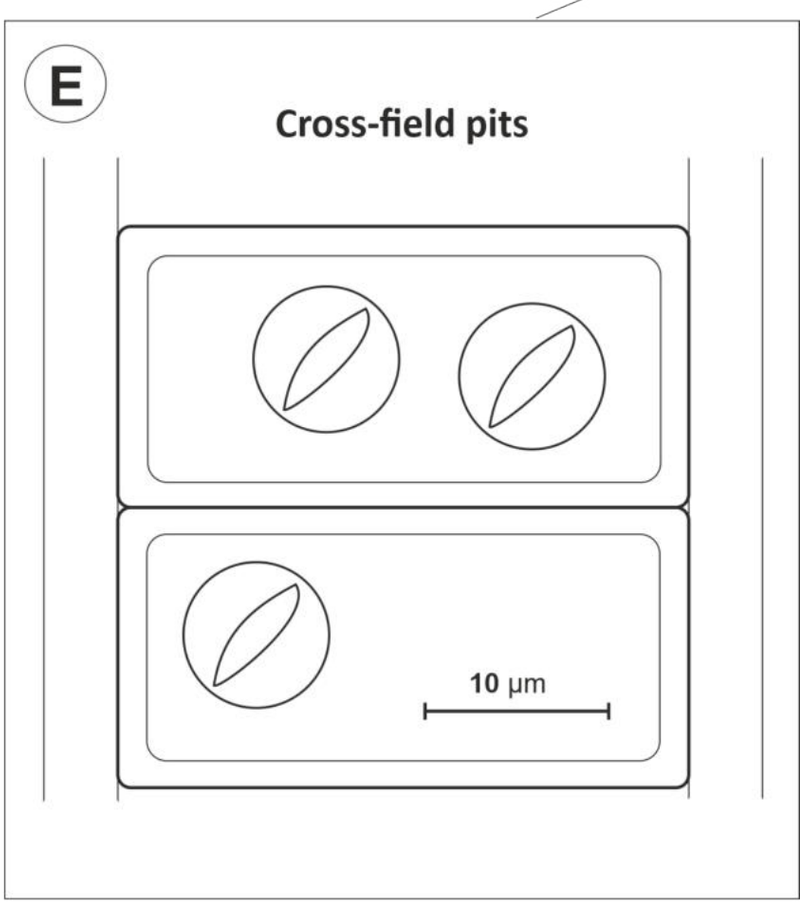
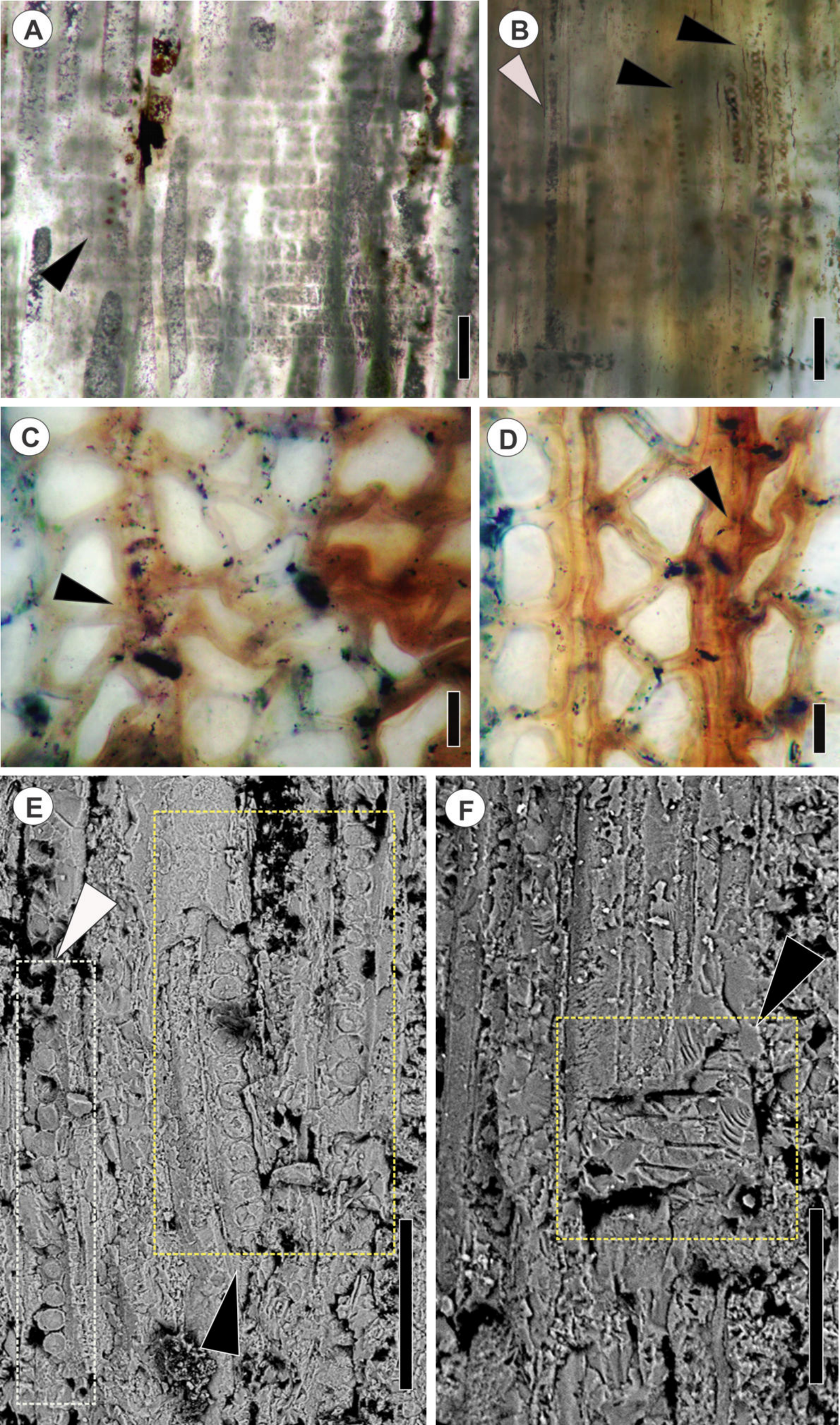
A


B


C


D


E
Cross-field pits
10 µm


A
B
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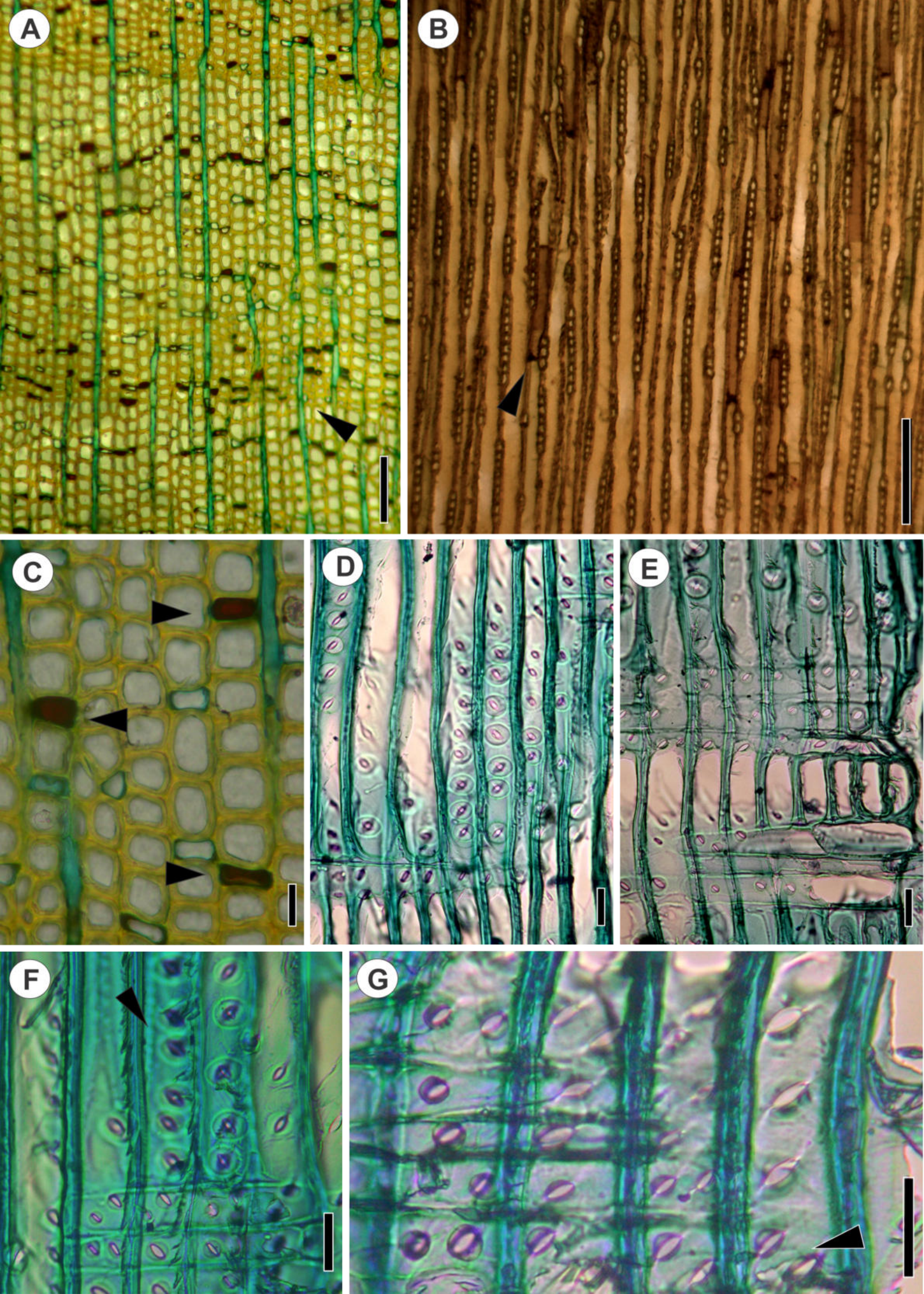
A
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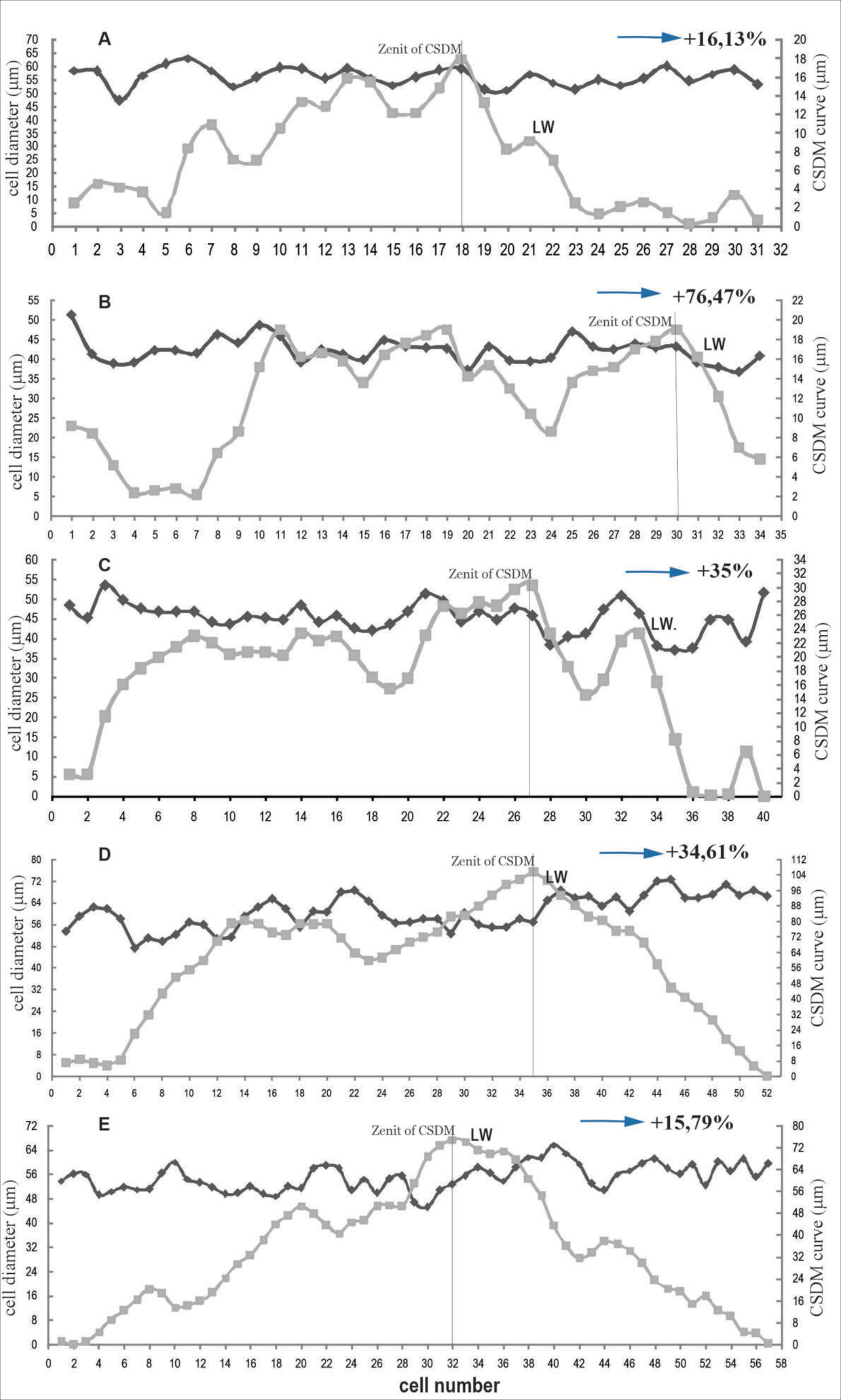
A
Zenit of CSDM
+16,13%
LW
cell diameter (µm)
CSDM curve (µm)
B
+76,47%
Zenit of CSDM
LW
C
Zenit of CSDM
+35%
LW.
D
Zenit of CSDM
+34,61%
LW
E
Zenit of CSDM
LW
+15,79%
cell number

Table 1. Comparison of *Podocarpoxylon paralambertii* sp. nov. with more closely related extant species. references T.D. = tangential diameter, R.D. = radial diameter, D = distinct, LD = slightly distinct, I = indistinct.

Species fossil	**Grown ring**	**Axial parenchyma**	**Radial pits (tracheid pitting in radial wall)**	**Tracheid**	**rays (high cells)**	**Cross-field pits, type**	**Age / location**	**References**
***Podocarpoxylon paralambertii* sp nov.**	LD	Present	uniseriate	TD 52 (18-84) µm, RD 46 (25-79) µm	11 (3 to-30)	1-2 (1-4) pits with aperture diagonal semi-border, cupressoid	Pleistocene / Entre Ríos	this work
Podocarpus parlatorei	D	Present	uniseriate	TD 19 (11-22) µm, RD 26 (16-34) µm	2 to-7	1, pits with borded or window-like, cupressoid	Neotropics and temperate Brazil	Gasson et al. (2011), Tortorelli (1956)
Podocarpus neriifolius	D	Present	uniseriate	TD 28-37 µm	1 to-5, low	1 to-3, pits with aperture diagonal semi-border, cupressoid/taxodoid	Southeast Asia and Pacific	Nishina (1984); Gasson et al. (2011)
Podocarpus milanjianus	D	present	uniseriate	TD 25-25 µm	5 to 15	1-3 pits cupressoid/taxodoid	tropical Africa	Correa et al. (2010)
Podocarpus henkelii		present	uniseriate	TD 20-40 µm	1 to-15	1-2 pits cupressoid/taxodoid	Tropical Africa	Phillips (1948)
Podocarpus latifolius	D	present	uniseriate	TD 27-35 µm	4 to-15	1-2 cupressoid	Tropical Africa	Richter & Dallwitz (2000)
Podocarpus madagascariensis		Present abundant	uniseriate	TD 9-50 RD 14-30	1 to-10	1-2, taxodioid, cupressoid	Madagascar	Margerier & Woltz (1977)
Podocarpus brasiliensis	D	Rare/absent	uni-biseriate	TD 39,6	1 to-15	1-2, pits with reduced borded or window-like	Southern Brazil	De Paula et al. (2000)
Podocarpus lambertii	LD	Present	uniseriate	TD 23 (5-40) µm, RD 25 (12-31) µm	1 to-23	2 (1-4) pits with lenticular borded, cupressoid	Southern Brazil, Neotropics and temperate Brazil	Maranho et al. (2006), Tortorelli (1956), Siegloch & Cardoso Marchiori (2015), This work
Podocarpus nubigenus	D	present	uniseriate	TD 12-24 µm	8 (1-15)	taxodioid	Southern Argentina, Chile	Díaz Van (1986)
Prumnopitys andina	D	Absent	uniseriate	TD 25 (15-37)	1 to-14	1, window-like	Provincia de Cautín, Región de La Araucanía (Chile)	Berrios (2017)

Table 2. Comparison of *Podocarpoxylon paralambertii* sp. nov. with *Podocarpoxylon* species of Godwanic/Cenozoic origin. References Growth rings D = distinct, LD = slightly distinct.

Species fossil	**Grown ring**	**Axial parenchyma**	**Radial pits (tracheid pitting in radial section)**	**Rays width (cells)**	**rays (high cells)**	**Cross-field pits**	**Age / location**	**References**
***Podocarpoxylon paralambertii* sp nov**	LD	present	uniseriate, contiguous and non-contiguous	1	11 (2 to-30)	2, pits with aperture diagonal semi-border	Pleistocene / Entre Ríos	this work
Podocarpoxylon palaeoandinum	I	present	uniseriate	1	6 (1-13)	1, pits simple, large, ovoid	Eocene/Patagonia	Nishina (1984)
Podocarpoxylon palaeosalignum	I	present	uni-biseriate	1	5 (1-10)	1-2 elliptical or thick lenticular pit apertures	Eocene/Patagonia	Nishina (1984)
Podocarpoxylon multiparenchymatosum	I	present	uniseriate	1	8 (2-24)	1-2, pits with reduced borded and oblique to vertical aperture	Eocene/Patagonia	Pujana & Ruiz (2017)
Podocarpoxylon mazzonii	I	rare	uni-biseriate	1 to-3	3 to-21	1-2, pits with reduced borded or window-like	Paleocene/Patagonia	Petriella (1972); Raigemborn et al., (2009); Brea et al., (2011)
Podocarpoxylon dusenii	D	absent	uniseriate	1 to-2	1 to-20	1, rare 2	Cenozoico/ Patagonia	Kräusel (1924)
Podocarpoxylon aparenchymatosum	D	absent	uni-biseriate, rare triseriate	1	1 to-17	2 (1-5), pits with reduced borders and diagonal aperture, mostly near vertical	Paleocene/ Antarctica	Gothan (1908); Pujana et al. (2014)
Podocarpoxylon fildesense	D	absent	uniseriate	1	1 to-16	1-2 (4), pits with narrow border and vertical aperture inclination	Paleocene/Antarctica	Zhang & Wang (1994)
Podocarpoxylon welkitii	D	present	uniseriate	1	1 to-18	1 to-3	Cenozoico /África	Lemoigne & Beauchamp (1972)
Podocarpoxylon garcie			uni-biseriata bietinean type		6 (2-17)	1 to-2, cupressoid type	Cretaceous/ Rio Negro Argentina	Del Fueyo (1998)

Podocarpoxylon paradoxi	**D**	present	Uni-biseriate abietinean type	1	6 (1-13)	1 to-3 taxodioid type	Upper Cretaceous, South Chile	Martinez et al. (2023)
Podocarpoxylon austroamericanum		present	uni-biseriate, abietinean type	1	3 (1-14), low	1 to-4 podocarpoid type	Middle Jurassic/Santa Cruz, Argentina	Gnaedinger (2007)
Podocarpoxylon cf. umzambense		rare	uniseriate, separate		3-18	1 - resin plates	Cretaceous/Namaqual and, South Africa	Bamford & Corbett, (1994)

Table 3. Results of the quantification of ring markedness parameters for *Podocarpoxylon paralambertii* sp. nov.

	% of curve deviation	**% of cell diminution**	**% of late wood**	**ring markedness index**
Growth ring A	16.13	25	45	11.25
Growth ring B	76.47	27	11.75	3.2
Growth ring C	35	31	32.5	2.18
Growth ring D	34.61	35.16	32.7	11.5
Growth ring E	15.79	31	43.9	13.64
Average (%)	35.6	29.83	33.17	8.354

Table 4. Quantification of ring markedness parameters for *Larix decidua, Picea obies, Araucaria araucana* and *Podocarpus totara* taken from data in Falcon-Lang (2000a, 2000b). LRTs: Leaf Retention Times.

	% of curve deviation	**% of cell shrinkage**	**% of late wood**	**ring marking index**
Larix decidua -deciduous-	(-40)–7.7 (-6.8)	71.55–85.91	50–54.83	35.77–44.46 (42.95)
Picea abies (**Evergreen conifers LRTs in** 3-5 **years**)	0–38.2 (12)	72.02–84.03 (76.77)	25.93–45.83	19.9–35.42
Araucaria araucana **(3-15 years)**	55–80 (66.7)	28.67–51.79	10–22.5	3.17–10.35
Podocarpus totara **(2-6 years)**	30.8–40 (35.44)	26±40 (33)		
Podocarpoxylon paralambertii (this work)	15.79–76.47 (35.6)	25–35.16 (29.83)	11.75–45 (33.17)	2.18–13.64 (8.35)