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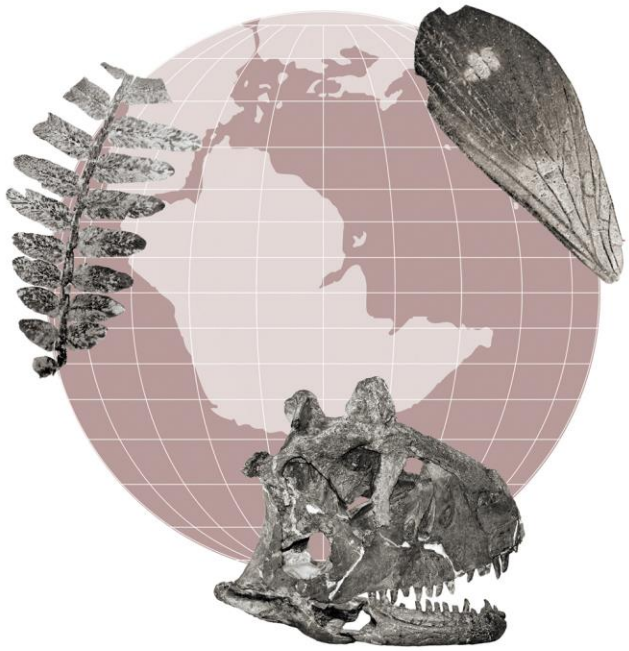

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A reappraisal of *Palmoxylon* (Arecaceae) species from the uppermost Cretaceous Allen Formation, Río Negro Province, Argentinian Patagonia

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Running Header: Vera: Cretaceous *Palmoxylon* species from Allen Formation

Short Description: Three species of *Palmoxylon* described from the uppermost Cretaceous Allen Formation are restudied and new information is provided.

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Abstract

Three species of *Palmoxylon* Schenk, namely *P. santarosense, P. rionegrense* and *P. valchetense*, were described by Ancibor in 1995 for the uppermost Cretaceous (Campanian to Maastrichtian) Allen Formation at the Bajo de Santa Rosa locality, in northern Patagonia, Argentina. A revision of the original specimens, as well as previously unpublished remains, is carried out in light of modern descriptive procedures for palm stems. The diagnoses of the three species are emended to include new characters, as well as modifications on states of characters originally described. Epitypes for *P. santarosense* and *P. valchetense* are defined, to include more complete stems that allow a better characterization of these taxa. *P. rionegrense* is found referable to the subfamily Coryphoideae, with probable affinities to the tribe Caryoteae, while *P. valchetense* is referred to the tribe Trachycarpeae. *P. santarosense* is not referred to any subfamilial category due to inconclusive affinities. Affinities of these taxa provide wide climatic inferences, as they support tropical and non-tropical climates. The presence of Trachycarpeae in the latest Cretaceous of Patagonia challenges postulated divergence time estimations and biogeographic routes for this tribe.

Keywords. Trachycarpeae. Coryphoideae. Campanian. Maastrichtian. Palms. *Stipitichnus.*

Resumen

Reevaluación de especies de *Palmoxylon* (Arecaceae) del Cretácico Superior de la Formación Allen, provincia de Río Negro, Patagonia Argentina. Tres especies de *Palmoxylon* Schenk, *P. santarosense, P. rionegrense* y *P. valchetense*, fueron descriptas por Ancibor en 1995 para la Formación Allen del Cretácico Superior (Campaniano–Maastrichtiano) en la localidad de Bajo de Santa Rosa, en el norte de la Patagonia, Argentina. Se lleva a cabo una revisión de

los ejemplares originales, así como de restos inéditos, teniendo en cuenta procedimientos descriptivos modernos para estípites de palmeras. Se enmiendan las diagnosis de las tres especies para incluir nuevos caracteres, así como modificaciones en los estados de los caracteres originalmente descriptos. Se definen epitipos para *P. santarosense* y *P. valchetense*, con el fin de incluir materiales más completos que permitan una mejor caracterización de estos taxones. *P. rionegrense* es interpretada como referible a la subfamilia Coryphoideae, con probables afinidades con la tribu Caryoteae, mientras que *P. valchetense* se asigna a la tribu Trachycarpeae. *P. santarosense* no es referida a ninguna categoria subfamiliar debido a que presenta afinidades no concluyentes. Las afinidades de estos taxones producen amplias inferencias climáticas, ya que son registradas tanto en climas tropicales como no tropicales. La presencia de Trachycarpeae en el Cretácico Tardío de Patagonia contrasta con las estimaciones postuladas de tiempos de divergencia y de rutas biogeográficas para esta tribu.

Palabras clave. Trachycarpeae. Coryphoideae. Campaniano. Maastrichtiano. Palmeras. *Stipitichnus.*

Introduction

The Allen Formation is an uppermost Cretaceous unit cropping out in Northern Argentinian Patagonia, and is well known by its paleontological content, first preliminarily reported by Andreis et al. (1991) who, since its discovery, pointed out its importance. Numerous vertebrate remains come from its strata, and include fishes (*e.g.*, Agnolín, 2010b; Bogan *et al.*, 2011), frogs (*e.g.*, Agnolín, 2012; Gómez, 2016; Suazo Lara & Gómez, 2022), turtles (*e.g.*, Agnolín *et al.*, 2025; Sterli *et al.*, 2013), lizards (*e.g.*, Garberoglio *et al.*, 2025), plesiosaurs (O'Gorman, 2011), mammals (*e.g.*, Rougier *et al.*, 2009; Connelly *et al.*, 2024), pterosaurs (Novas *et al.*, 2012), birds (*e.g.*, Clarke & Chiappe, 2001; Agnolín, 2010a), and several non-avian dinosaurs (*e.g.*, Salgado & Coria, 1993; Novas *et al.*, 2009; García & Salgado, 2011; Agnolín *et al.*, 2012; Cruzado Caballero & Powell, 2017; Aranciaga Rolando *et al.*, 2021; Riguetti *et al.*, 2022; Rozadilla *et al.*, 2021; Álvarez Nogueira *et al.*, 2025). Contrasting, the fossil plant record of this unit is scarce, and consist of cycad stems (Artabe *et al.*, 2004, 2005; Martínez *et al.*, 2012), conifer woods (Del Fueyo, 1998; Passalia *et al.*, 2023), palm stems and fruits (Ancibor, 1995), and few palynological assemblages (Vallati, 2010; Pérez Pincheira & Garrido, 2024). Several insect and fungal traces have also been reported from the unit, most of them associated with plant stems and fruits (Genise, 1995; Genise *et al*., 2012).

Understanding ecosystem dynamics during the latest Cretaceous is critical for evaluating the effects of the end-Cretaceous extinction and reconstructing ecosystem characteristics prior to this event. In this context, making precise comparisons between fossil-bearing units across different time intervals or sedimentary basins with strata close to the K-Pg requires equally precise and comparable taxonomic data. The three *Palmoxylon* species described by Ancibor (1995) are significant because they were the first Mesozoic species for

the genus reported from South America. Unfortunately, the descriptions and species diagnoses provided by the author were rather brief and many key characters were missing. Furthermore, some images are not clear enough to show the non-described characters. Since these descriptions have been widely used for comparative purposes, a revision of these *Palmoxylon* species was needed, focused on describing and properly illustrating the characters currently used in anatomical descriptions of Arecaceae stems (*e.g.*, Thomas & De Franceschi, 2013), while also incorporating previously undescribed specimens. Such revision allows not only improving the knowledge of fossil palm species that were present prior to the end-Cretaceous mass extinction in Patagonia, but also adjusting their descriptions, which will provide information regarding their botanical affinities within the Arecaceae and, consequently, will allow their use as paleoclimatic proxies.

Anatomical abbreviations. TS, transverse section; LS, longitudinal section; CT, cortex; SZ, subcortical zone; CZ, central zone; TZ, transition zone; fvb, fibrovascular bundle; dcap, fibrous part adjacent to the phloem; vcap, fibrous part adjacent to the xylem; f/v, average ratio between the fibrous part and the vascular part of the fvbs; FCI, fibrous covering index, the ratio between the surface area of the fibrous part of all the fvbs in an examined transverse section and the whole surface area of the examined transverse section.

Materials and Methods

Studied specimens were originally collected during a field trip in the 90's by Drs. Sergio Archangelsky, Renato Andreis, Gerardo Cladera, Jorge Genise, Georgina del Fueyo and Luis Lezama, and offered to Dr. Elena Ancibor for study. They were obtained at Estancia "El Palenque" (39°58'33.88"S, 66°45'2.91"W; Genise pers. comm.), 10 km west of Santa Rosa locality and 60 km northwestern to Nahuel Niyen, Río Negro Province, Argentina, at a site

named “Cañadón de Marcelo” (located at the north of the Estancia “El Palenque”). Information accompanying the fossil palms mention the reference “Bosque 2, Río Negro, Bajo Santa Rosa”. Salgado *et al*. (2007) presented stratigraphic logs for the Salitral de Santa Rosa (=Bajo Santa Rosa) locality, highlighting the presence of fossil trunks in a fossiliferous level approximately at the half of the unit (Salgado *et al*., 2007; fig. 2). The fossils palms collected at this locality, including the ones here studied, can be referred to this fossiliferous level (Salgado, pers. comm.). For a geological characterization of the unit at the Bajo Santa Rosa, see Salgado *et al*. (2007).

All specimens studied by Ancibor (1995) are housed in the Colección Nacional de Paleobotánica of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” under BA Pb (hand specimens) and BA Pb Pm (microscope slides) numbers. Corresponding numbers of these specimens are 862, 879, 880, 884 (BA Pb Pm 263, 264, 265), 887 (BA Pb Pm 266, 267, 268), 888, 889, 890 (BA Pb Pm 257, 258, 259, 260, 261, 262) and 944. The specimen mentioned by Ancibor (1995) as BA Pb 878, as well as microscope slides obtained from specimens different than the holotypes of the three species, are currently not present in the Colección Nacional de Paleobotánica of the MACN, as informed by the Curatorial Technician of the collection (Lezama, pers. comm.), and its current location is unknown.

Specimens BA Pb 881 and 967, not included in the original publication by Ancibor (1995), were revised in this contribution. In addition, the specimen MACN-Icn 123, housed in the Colección Nacional de Icnología of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (originally housed in the Colección Nacional de Entomología of the same institution, under number 53816) was revised, as it was published as an Arecaceae stem containing the holotype of the ichnospecies *Stipitichnus koppae* Genise 1995, traces interpreted as insect borings, from the Bajo de Santa Rosa locality (Genise, 1995).

The fossil palm remains were originally thin-sectioned in TS and LS. Study was carried out using light Microscopy (Olympus BX-51 and Nikon SMZ-2 t Microscopes with attached cameras) on thin sections and polished and non-polished stems. Preservation quality varies between specimens, and some features are not observed. In particular, available longitudinal sections were scarcely informative due to preservation quality, and only few characters are described from them. Measurements were made using ImageJ free software. At least 25 measurements were made for each character, when possible. For descriptions based on several specimens, weighted mean is presented (along with total size range).

Descriptive terminology used here follows the proposal of Thomas and De Franceschi (2013). For clarity's sake, some abbreviations used in the text are included below. The classification scheme follows Dransfield *et al.* (2008). For comparative purposes, the specimens referred to *Palmoxylon* specimens described by Vera *et al.* (2024) from the Campanian to lowermost Maastrichtian Puntudo Chico Formation were revised. Additionally, the Palm-ID online database (Thomas, 2011a), Thomas (2011b) doctoral thesis, and Thomas and De Franceschi (2013) were primarily consulted for comparisons with extant taxa.

Systematic Paleontology

Order Arecales Bromhead 1840

Family Arecaceae C.H. Berchtold et J. Presl, nom. cons. 1820

Fossil genus *Palmoxylon* Schenk 1882

Type species. *Palmoxylon angulare* (Cotta) Schenk 1882, from the Cenozoic of India. Originally published as *Perfossus angularis* Cotta.

Palmoxylon santarosense Ancibor 1995 *emend*. Vera

Figures 1–3

1995. *Palmoxylon santarosense* Ancibor. Ameghiniana 32(3): 298, Plate II

Holotype. BA Pb 887 (BA Pb Pm 266, 267, 268)

Epitype here designed. BA Pb 862

Additional specimens. BA Pb 879, 880, 944, MACN-Icn 123

Geographic occurrence. Estancia El Palenque, 10 km west of Santa Rosa locality and 60 km northwestern to Nahuel Niyeu, Río Negro Province, Argentina, at a site named "Cañadón de Marcelo" (Bosque 2).

Stratigraphic occurrence. Allen Formation; Upper Cretaceous (upper Campanian to Maastrichtian).

Original diagnosis (translated from Ancibor (1995), originally in Spanish). Radially extended fibrovascular bundles; 1–2 metaxylem vessels per fibrovascular bundle; small-lumen fibers forming a bulky cap on the phloem side; phloem generally in a single, highly lobulated strand; interfascicular parenchyma with thin walls and no particular arrangement; siliceous corpuscles are spherical and slightly spiculated.

Emended diagnosis. Stem atactostelic, divided in CZ, SZ and developed CT. Ground tissue composed of isodiametric parenchymatous cells without lacunae in the outer region of the CZ and SZ, and isodiametric and elongate cells in the center of the CZ, with interspersed fibrous bundles in the outer region of the CZ and in the SZ and the CT; growth pattern *Corypha*-type; density of fvbs in the center of the stem c. 113–132 per cm^2 and in the subcortical zone is c. 505–529 per cm^2; f/v ratio c. 1–1.6 in the most internal zone of the CZ and c. 4.3–7.7 in the most external region of the SZ; CT developed; fvbs with dcap Lunaria to Vaginata in the most internal fibrovascular bundles, Reniforma towards the outer region of the CZ, and Reniforma to Sagittata in the SZ, with rounded median sinus; vcap present, tabular parenchyma present, radiating parenchyma absent; phloem undivided; xylem part presenting wide metaxylem vessels, mostly 2 in the CZ and 1 in the SZ, excluded in the outer region of the CZ and in the SZ; end walls of metaxylem elements with long scalariform plates; slope of end walls extremely to very oblique; presence of globular echinate phytoliths in axial series of stegmata at the margins of the fibrous bundles and fibrous part of the fvbs.

Description. The description is partially based on the holotype specimen BA Pb 887, consisting of a fragment of stem c. 9.2 cm in maximum width and 5.7 cm tall (Fig. 1A). The fossil preserves a portion of the internal zone of the stem. Internally, it consists of parenchymatous ground tissue and scattered fvbs, arranged in an atactostele. Other specimens, referred by Ancibor (1995) to this species, as well as others not included in the original work, were studied and complementary information was derived from them. In particular, specimen BA Pb 862 preserves a more complete transverse section of the stem, showing the distribution of fvbs in the central and outer zones (Fig. 1B). Specimens BA Pb 879 and 880 preserve adventitious roots, but preservation is not good.

Stem. In the holotype (BA Pb 887), the density of fvbs in the most internal zone of the CZ is 216–245 per cm^2. Density in the most external preserved region of the CZ is 291 per cm^2 (Fig. 1A). Measured f/v ratio for fvbs is 2.1–4.3 in the most internal zone and 5–8.5 in the most external zone preserved. In the specimen BA Pb 862 (Fig. 1B, C) a more extensive portion of the stem is present, preserving from the most internal region of the CZ towards the SZ, even showing a small portion of the CT. This specimen exhibits changing density and morphology of fvbs from the most internal zone towards the periphery (Fig. 1C), and thus the ratios calculated above are measured for this specimen as well. The density of fvbs in the center of CZ is 113–132 per cm^2. Density in the most external region of the SZ is 505–529 per cm^2. (Fig. 1C). Ratio of density of fvbs in the most external zone (SZ) vs density in the most internal zone (CZ) c. 4.26. Measured f/v for fvbs is 1–1.6 in the most internal zone (f/v_{in}) and 4.3–7.7 in the most external region of the SZ (f/v_{out}). Ratio between f/v_{out} / f/v_{in} c. 4.6. Fibrous covering index is 0.07–0.12 in the most internal region of the CZ (FCI_{in}) and 0.41–0.47 in the subcortical zone (FCI_{out}). Ratio between FCI_{out} and FCI_{in} is 4.63. All these parameters, along with the absence of tangential differentiation of the fibrous part of the fvbs, are in agreement with a *Corypha*-type growth pattern (von Mohl, 1823–1850; Thomas & De Franceschi, 2013).

Fibrovascular bundles. Fibrovascular bundles vary in morphology across the stem, from the center of the CZ to the SZ (Fig. 1C–E, Fig. 2A–H). Proportionally, most of the fvbs in the stem show the morphology of the outer CZ, which are observed in the holotype, and are described first. These fvbs are 530–751 (650±58) μm tall and 318–567 (462±67) μm wide. Tabular parenchyma present, consisting of 2 layers of elongate cells. Radiating parenchyma absent. Fibrous part Reniforma in shape (Stenzel, 1904), with absent auricular sinuses (Fig. 2A–D). Fibrous part centrifugal differentiation not observed. Median sinus rounded (Fig. 2D–E). Dorsal cap 291–480 (376±48) μm high, composed of a dense mass of fibers (Fig.2D–E).

Fibers 12.5–25.6 (19.7±4) μm in diameter, with thick walls. Ventral cap present (Fig.2B–E), crescentiform, composed of cells 10.4–22.4 (14±3.2) μm in diameter, thick walled, sometimes connecting with dcap. The xylem part of the fibrovascular bundles consist of typically 2 (rarely 1) excluded, adjacent (touching) wide metaxylem elements (Fig. 2A–E) 65.6–175.6 (132.6±17.7) μm in diameter, with end walls exhibiting long scalariform plates (Fig. 2O), with many closely spaced bars; metaxylem end wall slope extremely oblique to very oblique (Fig. 2O) (measured on 3 perforation plates, with values of 12, 8 and 5); paravascular parenchyma poorly developed. Small vessels (protoxylem?) observed in some fibrovascular bundles, located adjacent to the contact between wide metaxylem elements (Fig. 2E). Phloem region is located in the zone between the xylem and the dcap. Its shape is triangular with rounded apices to reniform (Fig. 2C–E), often appearing with irregular forms, and sometimes showing a small interruption as a result of a projection of the dcap (Fig. 2C). Sieve cells 11.4–24.2 (17.1±4.3) μm in diameter; smaller elements of the phloem (companion cells?) 5.1–7.8 (6.8±1) μm in diameter (Fig. 2E). Metaphloem sieve plate not observed.

Fibrovascular bundles in the SZ are 639–733 (677±31) μm tall and 156–265 (223±43) μm wide (Fig. 2F–G). Anatomically, they share the features of the ones present in the CZ, but differ in having typically a single (rarely two) wide metaxylem element 74.7–108.3 (92.1±11.3) μm in diameter (Fig. 2F–G). Most distal fvbs exhibit slightly elongate fibrous portions of the fvbs (Fig. 2F), with a ratio between the height of the dcap - height of the vascular portion of the fvb) / width of the fvb of ranging from 1.1–2.1, thus not considered as having radial elongation of the fibrous part (in the SZ), as proposed for Descriptor 8 in Thomas and De Franceschi (2013). Fibrovascular bundles with most elongate portions showing a morphology of the dcap close to Sagittata in shape (Fig. 2F).

Fibrovascular bundles in the most internal part of the CZ are smaller than the previously described from the SZ and the outer region of the CZ, 374–694 (598±102) μm tall and 379–539 (452±61) μm wide (Fig. 1D–E). The dcap is Lunaria to Vaginata in shape, and the vascular portion exhibits 2 large metaxylem vessels, 196–236 (219±13) μm wide (Fig. 1D–E).

Ground tissue. In the Holotype BA Pb 887, ground tissue is essentially parenchymatous, mostly composed of isodiametric, spheroidal to slightly elongate, thin-walled cells, 17.4–55.1 (30.7±10.7) μm in diameter, constituting a compact tissue without lacunae or intercellular spaces (Fig. 2J). The more complete specimen BA Pb 862, ground tissue exhibits the same features in the outer region of the CZ and in the SC, but the inner region of the CZ also shows elongate cells 76.4–139.6 (114.4±26.2) μm in long and 23.7–39.5 (34.6±6.5) μm wide (Fig. 2I). It is unclear if sparse lacunae are present between elongate cells.

Interspersed in the parenchymatous tissue of the most external region of the CZ, in the SZ and in the CT, fibrous bundles are present. These bundles are circular to oval in cross section. 48–73.3 (59.5±8.5) μm in diameter (Fig. 2F, H, K). In addition, the cortical zone exhibits larger fibrous bundles, 112–171 (140±22) μm in diameter (Fig. 2H, K).

Phytoliths. In the longitudinal section of the holotype, globular granulate phytoliths 8–15.2 (12.4±3) μm in diameter are present in stegmata in the marginal region of the fibrous part of the fvbs (Fig. 2P).

Leaf traces. Several bundles with fibrous and vascular components differ in their structure and size from the typical fvbs, and are interpreted as leaf traces. They are 568–845 (732±92) μm tall and 341–627 (496±102) μm wide (Fig. 2L–M). They contain two xylem regions. The central one consists of 2 (rarely 3) separate wide metaxylem elements 69.5–122.5 (98±17.1) μm wide; while the ventral group is composed of several smaller elements, 19.5–51

(31.2±9.8) μm wide (Fig. 2M). Phloem region in these structures appears typically as composed of 2– 3 interconnected lobes. Towards the SZ/CT, leaf traces often show a higher number of smaller metaxylem elements in the central group.

Vascular bridges. Several small bundles are present in the ground tissue, often adjacent (and opposite oriented) to leaf traces. They are 202–380 (297±73) μm tall and 167–346 (288±74) μm wide. They show an anatomy comparable to the one observed in the fvbs of the CZ, but have a dcap similar or smaller in size than the vascular part (Fig. 2L, N).

Cortical zone. A small portion of this region is preserved in BA Pb 862. The maximum measured thickness is approximately 1 mm, but the externalmost limit is unpreserved. It exhibits parenchymatic ground tissue with interspersed small and large fibrous bundles, and scarce vascular bundles (Fig. 2H, K), but is unclear if it corresponds to fvbs or leaf traces due to preservation quality,

Remarks. The holotype specimen (BA Pb 887) selected by Ancibor (1995) preserves a portion of the most external region of the CZ of the stem. Among the rest of the specimens available of this species, BA Pb 862 preserves a complete transverse section of CZ and SZ, as well as a small portion of the CT. Given its informative value, which was used for providing an emended diagnosis for the species, it is here designated as an epitype of *Palmoxylon santarosense* (ICN Art. 9.9).

Ancibor (1995) listed specimen BA Pb 826 among the referred to this species (Ancibor, 1995; p. 298), but it does not correspond with a *Palmoxylon* stem (Lezama & Del Fueyo, pers. comm.). It is clear that it was an involuntary error, as the author lists in the same work the specimen BA Pb 862 (and not 826) as belonging to the “Grupo I” (Ancibor, 1995; p. 292), which is equivalent to *Palmoxylon santarosense*.

The specimen MACN-Icn 123, containing the holotype of the ichnospecies *Stipitichnus koppae* Genise 1995 (traces interpreted as insect borings) has an anatomy comparable with *Palmoxylon santarosense* (Fig. 3), and comparisons with available specimens of this latter taxon allowed the recognition of BA Pb 944 as a slide of the stem containing the ichnofossils MACN-Icn 123.

Comparisons with fossil forms from South America. Several species of *Palmoxylon* have been recorded in South America (Table 1), but no one shares with *Palmoxylon santarosense* the presence of fvbs with typically 2 wide metaxylem elements in the CZ and 1 in the SZ (Fig. 2A–C, F, G). Fragmentary taxa that are completely unknown that have a single (or 1–2) wide metaxylem vessels per fvb include *Palmoxylon* sp. 3 in Vera *et al.* (2024), and *Palmoxylon* sp. 4 in Vera *et al.* (2024), and *Palmoxylon chilense* (Torres & Godoy, 1982). *Palmoxylon* sp. 3 in Vera *et al.* (2024) and *Palmoxylon* sp. 4 in Vera *et al*. (2024) exhibit fvbs from the SZ having Reniforma shape of the dcap (Table 1), different from the typical Sagittata form observed in *P. santarosense* (Fig. 2F, G). On the other hand, *P. chilense* has fvbs with a single wide metaxylem element in the CZ and SZ (Table 1), while in *P. santarosense* the fvbs of the CZ typically have 2 wide metaxylem elements, and 1 only in the outer region of the SZ (Fig. 2A–C, F, G). In addition, *P. chilense* has radiating parenchyma (Table 1), absent in the specimens here studied.

Comparisons with extant taxa and affinities. Extant Arecaceae exhibiting fvbs with two wide metaxylem vessels in the CZ and one in the SZ are present in the genera *Caryota* L. and *Arenga* Labill. of the Coryphoideae tribe Caryoteae, *Eugeissona* Griff., *Mauritia* L. and *Raphia* P. Beauv. of the Calamoideae, and in the Arecoideae (Thomas, 2011a, b; Thomas & De Franceschi, 2013). Thomas and Boura (2015) suggested that the fvbs having a single wide metaxylem element (or having two in the CZ but changing to one in the SZ) were probably

an apomorphic condition, whereas two vessels were plesiomorphic.

Thomas and De Franceschi (2013) state that *Caryota* and *Arenga* of the Caryoteae have typically *Mauritia*-type of stem organization, with a tendency towards *Corypha*-type (the latter state present in *P. santarosense*). Nevertheless, this tribe exhibits radial differentiation of the fibrous part, and trapeziform and combined phytoliths (Thomas & De Franceschi, 2013), both absent in *P. santarosense*.

Phylogenetic studies of the genera of the Calamoideae show disparate results (*e.g.*, Thomas & De Franceschi, 2013; Thomas & Boura, 2015; Baker *et al*., 2009; Kuhnhäuser *et al*., 2021), and thus it is unclear if the presence of two vessels in the fvbs of the CZ and one in the SZ is a plesiomorphic condition of the clade (or some of the tribes within), or if it is sparsely widespread. The genera *Eugeissona*, *Mauritia* and *Raphia* have phytoliths restricted to the subcortical zone near the cortical region, while *Corypha*-type stems as *Palmoxylon santarosense* have phytholiths also in the CZ (Thomas & De Franceschi, 2013). Also, these genera also exhibit radial differentiation of the fibrous part (Thomas & De Franceschi, 2013), absent in the fossil taxon.

Among Arecoideae, the presence of two wide metaxylem elements in the fvbs of the CZ and one in the SZ is distributed across the phylogeny of the clade (see Thomas & Boura, 2015), probably reflecting multiple origins of the character. While most of the characters observed in the studied specimens are present in the clade, no genera have been reported exhibiting a *Corypha*-type stem (Thomas, 2011b). Nevertheless, it is worth mentioning that Arecoideae are a highly diverse family with unknown information regarding the anatomy of the stem of many of its representatives (Thomas, 2011b), and thus comparisons are difficult to make.

In summary, characters present in *Palmoxylon santarosense* are not exclusively present in any modern representative of the Arecaceae. As a result, it is here considered as an Arecaceae *incertae sedis*.

Palmoxylon rionegrense Ancibor 1995 *emend*. Vera

Figures 4–5

1995. *Palmoxylon rionegrense* Ancibor, *pro parte*. Ameghiniana 32(3): 298, Plate III A, D, H

Type specimen. BA Pb 884 (BA Pb Pm 263, 264, 265)

Geographic occurrence. Estancia El Palenque, 10 km west of Santa Rosa locality and 60 km northwestern to Nahuel Niyeu, Río Negro Province, Argentina, at a site named "Cañadón de Marcelo" (Bosque 2).

Stratigraphic occurrence. Allen Formation; Upper Cretaceous (upper Campanian to Maastrichtian).

Original diagnosis (translated from Ancibor (1995), originally in spanish). Radially extended fibrovascular bundles; 4–6 metaxylem vessels per fibrovascular bundle; large-lumen fibers with dark contents forming a cap only on the phloem side; phloem in 3–4 strands; interfascicular parenchyma with thickened walls and no particular arrangement; Siliceous corpuscles are irregular and subspherical with marked spicules.

Emended diagnosis. Stem atactostelic. Central zone with ground tissue composed of slightly elongate to rod-like, thin walled cells constituting a compact tissue with few lacunae; fibrous bundles absent; growth pattern *Corypha*-type; density of fvbs in the CZ c. 190–240 per cm^2;

f/v ratio c. 6–12 in the CZ; fvbs with dcap Reniforma in shape, with rounded median sinus; vcap present, exhibiting 1–2 layers of radially elongate fibers, tabular parenchyma present, radiating parenchyma absent; xylem part excluded, presenting 2 (range 2 to 4) wide metaxylem vessels and paravascular parenchyma poorly developed; presence of globular echinate and conical phytoliths in axial series of stegmata at the margins of the fibrous part of the fvbs.

Description. The description is based on the holotype specimen BA Pb 884, consisting of a sectioned fragment of stem c. 7.6 cm in maximum width and c. 1 cm tall (Fig. 4A). fvbs tend to have variable orientation, although there is some tendency to show a general arrangement with the dcap pointing to one of the margins of the stem in the region which was not sectioned (Fig. 4B–E), and a more irregular distribution towards the center/sectioned portion. As such, it is here interpreted as representing the central region of the CZ, with the portion where fvbs are more irregularly distributed as the most central region of CZ. Subcortical or CT are not preserved (Fig. 4C). Internally, it consists of parenchymatous ground tissue and scattered fvbs, arranged in an atactostele.

Stem. The density of fvbs in the most internal zone is 190–240 per cm^2. Density in the most external zone preserved is 225–235 per cm^2. Measured f/v ratio for fvbs is 6–12 in the most internal zone and 7–11 in the most external zone (Fig. 4C).

Organization and distribution of fvbs is regular throughout the preserved regions of the transverse section. The absence of preserved SZ or TZ zones, the similar values of density of fvbs and f/v ratio in the central and periphery of the preserved portion suggest that all the preserved portion represents the CZ of the stem. Presence of highly elongated parenchyma cells conforming the ground tissue is interpreted as evidence of ground parenchyma sustained growth (Fig. 4K), present in *Corypha*-type and *Mauritia*-type stems (Thomas & De

Franceschi, 2013). *Mauritia*-type stems have highly reduced fibrous portions of the fvbs in the CZ (Thomas & De Franceschi, 2013). As the dcaps are highly developed in this central portion of the studied fossil (with f/v values between 6 and 12), the stem is interpreted as having a *Corypha*-type growth pattern.

Fibrovascular bundles. Fibrovascular bundles typically exhibit the vascular portion with different grades of deformation (Fig. 4D–G), interpreted as the result of the elongation of parenchyma cells of the ground tissue. Description of the fvbs is based on the ones that show less deformation.

Fibrovascular bundles are 685–915 (794±79) μm tall and 488–937 (654±135) μm wide, being the ones located in the most central region slightly wider than the ones located at the periphery (Fig. 4D–G). Tabular parenchyma present, consisting of apparently 2 layers of elongate cells (Fig. 4F, G, K). Radiating parenchyma absent. Fibrous part Reniforma in shape (Stenzel, 1904), with absent to slightly rounded auricular sinuses. Median sinus rounded. Dorsal cap 343–625 (510±65) μm high, composed of a dense mass of fibers (Fig. 4D–G). Fibers 16.2–50.6 (34±9.3) μm in diameter, with thick walls, and showing a tendency of radial elongation towards the margin of the dcap, not observed in the marginal row of fibres (Fig. 4F, G). Ventral cap present, crescentiform, composed of cells 11–21.1 (15.2±3.2) μm in diameter, thick walled, often connecting with dcap (Fig. 4F–J). The xylem part of the fibrovascular bundles consist of typically 2 (rarely 1–4) included wide metaxylem elements 51.7–111 (77.4±16.1) μm in diameter (Fig. 4E–J); paravascular parenchyma poorly developed. Protoxylem and phloem regions are difficult to describe due to compression of the fvbs and preservation quality (Fig. 4H–J).

Ground tissue. Ground tissue is essentially parenchymatous, mostly composed of elongate to rod-like, thin walled cells (Fig. 4K), 32.8–111.9 (75.6±26.6) μm in the longest axis and 18.7–

37.4 (27.6±6.7) μm in the shortest axis (length/width ratio 0.9–5.4), constituting a compact tissue with few lacunae, identified in longitudinal section (Fig. 5E). Fibrous bundles are not present in the ground tissue.

Phytoliths. In the longitudinal section, globular phytoliths 8.2–13.2 (10.8±2.1) μm in diameter (Fig. 5E), along with conical phytoliths 13.1–26.1 (18.8±4.3) μm tall and 10.8–18.4 (15.3±2.6) μm wide (Fig. 5F, G), are present in stegmata in the marginal region of the fibrous part of the fvbs.

Leaf traces. Some bundles with fibrous and vascular components differ in their structure and size from the typical fvbs, and are interpreted as leaf traces. They are 865–1024 (945±111) μm tall and 999–1032 (1015±23) μm wide (Fig. 5A, B). Leaf traces are two-parted. The largest unit consists of a fibrous dcap similar to a Complanata to Reniforma shape, but with rounded auricular sinuses, and a central region exhibiting several (7–9) adjacent metaxylem vessels and probably unpreserved phloem (Fig. 5A–C). The second unit, separated from the first one by ground tissue, is a circular structure exhibiting numerous (20?) isolated metaxylem vessels arranged in an apparent circle (Fig. 5A–C).

Vascular bridges. Small fvbs are present in the ground tissue, adjacent (and opposite oriented) to leaf traces. They are c. 368 μm tall and 328.4 μm wide. They show an anatomy comparable to the one observed in the fvbs of the CZ, but have a dcap similar or smaller in size than the vascular part (Fig. 5A, D).

Cortical zone. Not preserved.

Remarks. Specimen BA Pb 898, originally included by Ancibor (1995) in this species is here referred to *P. valchetense* (see below).

Comparisons with fossil forms from South America. *Palmoxylon rionegrense* differs from *P. santarosense* by presenting ground tissue composed of highly elongate cells (Fig. 4K), fvbs in the central zone having a Reniforma type of fibrous part (Fig. 4D–G), and higher values of f/v ratio, resulting in fvbs with a fibrous part proportionally more developed than in the taxon described above. Additionally, only globular phytolits were identified in *P. santarosense*, while *P. rionegrense* also exhibits conical phytolits (Fig. 5F, G). To date, the Danian *P. patagonicum* is the only other *Palmoxylon* species reported from South America containing conical phytoliths (Table 1), but the Danian species has radiating parenchyma (absent in *P. rionegrense*) and contrasting low density of fvbs in the central zone, 14.5 per cm^2 vs 190–240 per cm^2 (Romero, 1968).

Among other *Palmoxylon* recorded from South America, several species exhibit values close to 2(2–4) wide metaxylem elements in the fvbs and ground parenchyma with elongate to rod-like cells (Table 1). *Palmoxylon garridoi* and *Palmoxylon* sp. 1 in Vera *et al*. (2024) differ from *P. rionegrense* by having fvbs without a developed vcap (Martínez, 2012; Vera *et al*., 2024). The remaining one, *P. subantarcticae*, is closely comparable to the specimen here studied. Martínez *et al*. (2023) reported fibrous bundles commonly present in the central zone of the stems of this species, and could be a difference from *P. rionegrense*, which lacks these structures. Other comparative characters, such as density of fvbs in different regions of the stem, and f/v values are not reported for *P. subantarcticae*, and may be a potentially relevant source of information to evaluate the similarities between these two taxa. In any case, conical phytoliths were unreported in *P. subantarcticae* (Martínez *et al*., 2023, Table 1).

Comparisons with extant taxa and affinities. Few extant Arecaceae exhibit phytoliths that are not exclusively globose, and are included in the Arecoidea, the genus *Nypa* Steck, and the Caryoteae tribe of the Coryphoidea (Thomas, 2011a, b; Thomas & De Franceschi, 2013).

Arecoid palms typically exhibit 2 wide metaxylem elements in the CZ, changing to 1 in the SZ (Thomas, 2011a, b). While the SZ and the CT are unknown for *P. rionegrense*, it is noteworthy that fvbs have typically 2 or more wide metaxylem elements, and even in the outermost preserved regions of the stem fvbs with a single wide metaxylem element are not present. *Nypa*, sole extant representative of the Nypoidea, has a very reduced fibrous portion of the fvbs, with f/v ratio close to 1 (Thomas, 2011b), while the studied specimen exhibits f/v values of 6–12. The number of wide metaxylem elements in *P. rionegrense* is more comparable to the typical configuration of many Coryphoideae (Thomas, 2011b; Thomas & De Franceschi, 2013). Noteworthy, taxa exhibiting non-globular phytoliths among Coryphoidea have a comparable number of wide metaxylem elements per fvb to Arecoideae, i.e. 2 in CZ and 1 in SZ ((Thomas, 2011a, b; Thomas & De Franceschi, 2013). Nevertheless, phylogenetic studies on Coryphoideae suggest that this character state is a synapomorphy of the Caryoteae, while the plesiomorphic condition is fvbs with typically 2 wide metaxylem elements (see phylogeny in Kadam *et al*., 2023, and character mapping in Thomas & Boura, 2015). As a result, *P. rionegrense* may represent a stem of tribe Caryoteae, or a Coryphoid taxon related to the lineage that gave origin to the Caryoteae.

Palmoxylon valchetense Ancibor 1995 *emend*. Vera

Figures 6–7

1995. *Palmoxylon rionegrense* Ancibor, *pro parte*. Ameghiniana 32(3): 298, Plate III B, E, I

1995. *Palmoxylon valchetense* Ancibor. Ameghiniana 32(3): 298, Plate IV A-F

Holotype. BA Pb 890 (BA Pb Pm 257, 258, 259, 260, 261, 262)

Epitype here designed. BA Pb 967

Additional specimens. BA Pb 888, 889

Geographic occurrence. Estancia El Palenque, 10 km west of Santa Rosa locality and 60 km northwestern to Nahuel Niyeu, Río Negro Province, Argentina, at a site named "Cañadón de Marcelo" (Bosque 2).

Stratigraphic occurrence. Allen Formation; Upper Cretaceous (upper Campanian to Maastrichtian).

Original diagnosis (translated from Ancibor (1995), originally in Spanish). Skull-shaped slightly elongate fibrovascular bundles; 1–3 metaxylem vessels per fibrovascular bundle; Fibers with large lumina and variable size, forming a voluminous cap on the phloem side and arranged radially on the xylem side. Interfascicular parenchyma arranged perpendicular to the fibrovascular bundles in the longitudinal section. Phloem in two strands. Siliceous corpuscles sub-spherical to oval, eventually spiculated.

Emended diagnosis. Stem atactostelic, divided in CZ, SZ and CT. Ground tissue composed of isodiametric parenchymatous cells without lacunae, and sparse interspersed fibrous bundles in the CZ, and more abundant towards the periphery of the stem; growth pattern *Cocos*-type; density of fvbs in the CZ c. 14–17 per cm^2 and in the SZ is c. 77–84 per cm^2; f/v ratio c. 3–4 in the most internal zone of CZ and c. 3.3–7.7 in the most external region of the SZ; fvbs with dcap Reniforma in shape, with rounded median sinus; vcap present, exhibiting 1–2 layers of radially elongate fibers, tabular parenchyma present, radiating parenchyma absent; phloem undivided to presenting a partition resulting from ventral projection of the dcap; xylem part excluded, presenting 2 (range 1 to 4) wide metaxylem vessels and

developed paravascular parenchyma; presence of globular echinate phytoliths in axial series of stegmata at the margins of the fibrous bundles and fibrous part of the fvbs.

Description. The description is based on four specimens. The holotype BA Pb 890 is a narrow sectioned fragment of stem, c. 7.6 cm in maximum width and c. 1 cm tall (Fig. 6A). The specimen exhibits only a small transverse section, containing less than 50 vascular bundles (between fvbs and leaf traces). The second specimen referred to Ancibor (1995), BA Pb 888 agrees in the anatomy of the fvbs of the holotype, but shows a small portion with smaller fvbs (Fig. 6B). A third specimen, BA Pb 967 is a large stem showing variable changing density and size of the fvbs in cross section (Fig. 6D), and is referred to this species, allowing the recognition of BA Pb 890 as portion of the CZ, and BA Pb 888 as part of the region between the CZ and TZ. Finally, BA Pb 898 (Fig. 6C) was originally referred to *P. rionegrense* by Ancibor (1995), but is here interpreted as a portion of the TZ of the stem of *P. valchetense*, due to overlapping features with BA Pb 967 of the size, shape and anatomy of the fvbs (Fig. 6F–J).

Stem. The density of fvbs in the center of the CZ is 14–17 per cm^2. Density in the most external preserved region of the SZ is 77–84 per cm^2 (Fig. 6D. E). Ratio of density of fvbs in the SZ vs density in the CZ c. 5.1. Measured f/v for fvbs is 3–4 in the most internal zone of the CZ (f/v_{in}) and 3.7–7.7 in the most external region of the SZ (f/v_{out}). Ratio between f/v_{out} / f/v_{in} c. 1.6. Fibrous covering index is 0.17–0.18 in the most internal zone of the CZ (FCI_{in}) and 0.38–0.44 in the SZ (FCI_{out}). Ratio between FCI_{out} and FCI_{in} is 2.35. All these parameters, along with the absence of tangential differentiation of the fibrous part of the fvbs, are in agreement with a *Cocos*-type growth pattern (von Mohl, 1823–1850; Thomas & De Franceschi, 2013).

Fibrovascular bundles. Fibrovascular bundles of the CZ are 1574.4–2129.3 (1840.6±182.5) μm tall and 1654.4–2025.7 (1794.8±139.8) μm wide (Fig. 6F–H). Tabular parenchyma present, consisting of 2-3 layers of elongate cells (Fig. 6L). Radiating parenchyma absent. Fibrous part Reniforma in shape (Stenzel, 1904) (Fig. 6F–H), with absent to angular auricular sinuses. Median sinus slightly rounded to rounded. Dorsal cap 886–1162.5 (1006.8±117.7) μm high, composed of a dense mass of fibers. Fibers 16.1–75.2 (37.5±18.4) μm in diameter, polygonal to slightly elongate (towards the margin of the dcap) with thick walls (Fig. 6L). Ventral cap present, crescentiform, connecting with the dcap, often exhibiting a projection towards the xylem (Fig. 6F–H, 7A–D). Ventral cap composed of 1–3 layers of isodiametric to polygonal cells 11.1–34.2 (23.2±6.3) μm in diameter, adjacent to the xylem portion, and a single (rarely two), layers of rectangular radiating cells, 26.8–80 (55.8±15.6) μm long and 19–29.4 (24.7±3.9) μm wide (Fig. 7A–D), similar to radiating parenchyma. The xylem part of the fibrovascular bundles consist of typically 2 (range 2–4) excluded wide metaxylem elements 65.3–191.1 (137.2±39.2) μm in diameter (Fig. 6F–H, 7A–D); paravascular parenchyma highly developed (Fig. 7A–D). Protoxylem elements (and small metaxylem elements?) interspersed in the paravascular parenchyma between larger metaxylem vessels, 32.3–70.2 (49.1±13.8) μm in diameter, typically present in fvbs with 2 wide metaxylem elements (Fig. 7D). Phloem typically consists of a single strand, although several fvbs show a partition produced by a ventral projection of the dcap, dividing the phloem in two strands. Sieve cells 15.2–47.8 (28.9±9.4) μm in diameter (Fig. 7A, C); metaphloem sieve plate not observed.

Towards the SZ, fvbs become smaller, 795.3–995.4 (901.5±85.5) μm tall and 981.6–1140.2 (1058.7±57.6) μm wide, retaining the characteristics of the ones present in the CZ. This change in size is somewhat abrupt, having 1 or 2 “transitional fvbs” between the larger ones of the CZ and the smaller of the SZ (Fig. 6I–K; 7E–G).

Ground tissue. Ground tissue is essentially parenchymatous, mostly composed of isodiametric, spheroidal to slightly elongate parenchymatous cells, 17.4–55.1 (30.7±10.7) μm in diameter, constituting a compact tissue without lacunae or intercellular spaces (Fig. 7I–K). Parenchymatous cells of the ground tissue in the holotype (BA Pb 890) exhibit thickened walls (Fig. 7I).

Fibrous bundles in the CZ are typically sparse and small, 66.8–91.8 (75.9±9.6) μm in diameter (Fig. 7J). In the SZ and the CT, larger fibrous bundles are also present, being more abundant than the ones in the CZ (Fig. 7G, H, J, K) . These bundles are circular to oval in cross section, 63.6–196.5 (158.4±31.3) μm in diameter.

Phytoliths. In the longitudinal section, globular granulate phytoliths 8.6–15.3 (11.5±1.8) μm in diameter are present in stegmata in the marginal region of the fibrous part of the fvbs (Fig. 7O).

Leaf traces. Interspersed between fvbs are some slightly larger bundles exhibiting a vascular portion proportionally smaller and slightly rounded to absent median sinus, but otherwise comparable to fvbs, interpreted as leaf traces (Fig. 7L). Leaf traces are 1368–1730 (1539±160) tall and 1795–2080 (1908±151) wide (Fig. 7L–M).

Vascular bridges. Several small bundles are present in the ground tissue, typically adjacent (and opposite oriented) to leaf traces (Fig. 7L). They are 257–539 (413±116.) μm tall and 288–446 (348±68) μm wide, exhibiting an anatomy comparable to the one observed in the fvbs, but having a proportionally smaller dcap, morphologically close to Lunaria in shape (Fig. 7N).

Cortical zone. Only a very small portion interpreted as belonging to the cortex is preserved in BA Pb 967. It differs from the underlying zone by having lower density of fvbs, abundant

fibrous bundles, and fvbs exhibiting slightly elongate dcaps (Fig. 6K, 7H). Measured thickness of the cortical zone is at least 1 mm.

Remarks. The holotype specimen (BA Pb 890) selected by Ancibor (1995) only preserves a small portion of the CZ of the stem, while the specimen BA Pb 888, originally included by the author in the species (Ancibor, 1995), provides more information regarding the structure and distribution of the fvbs in the stem, exhibiting a small portion of the SZ, and would probably have been a better holotype for the species. Nevertheless, the inclusion in this species of BA Pb 967, the most complete specimen available to date of the species (collected after Ancibor's contribution), allows a more comprehensive interpretation of this taxon, as well as the recognition of BA Pb 898 (originally referred to *P. rionegrense*) as another sample belonging to *P. valchetense*. To allow an amendment of the diagnosis of the species and clarify its taxonomic limits, BA Pb 967 is selected as an epitype of *Palmoxylon valchetense* (ICN Art. 9.9).

Thick walled parenchyma cells near composing the ground tissue of the holotype probably reflect a mature condition of the tissue, indicating a provenance of the sample near the base of the stem (Thomas & De Franceschi, 2013).

Comparisons with fossil forms from South America. *Palmoxylon valchetense* can be separated from *P. santarosense* by having 2(1–4) wide metaxylem vessels per fvb (Fig. 6F–K), contrasting with the 2 vessels in the CZ and 1 in the SZ in the latter taxon, as well as by the presence of divided phloem strands in *P. valchetense*, (Fig.7A, C) absent in *P. santarosense*. *Palmoxylon valchetense* differs from *P. rionegrense* by having typically isodiametric to slightly elongate parenchyma ground cells (Fig. 7I), while *P. rionegrense* has elongate to rod-like cells. In the latter species, f/v ratio is 6–12 in the CZ, while in *P.*

588 *valchetense* this value is lower (3–4). *P. rionegrense* also lacks elongate cells forming the
589 vcap.

590 Two species of *Palmoxylon* reported from the region (*P. patagonicum* and *P. vaterum*)
591 exhibit 2(1–4) wide metaxylem elements per fvb and two phloem strands produced by the
592 projection of the dcap (Table 1). *Palmoxylon patagonicum* has abundant fibrous bundles in
593 the central region of the stem (Romero, 1968), contrasting with the scarce number reported in
594 *P. valchetense*. Additionally, *P. patagonicum* has radiating parenchyma and conical phytolits
595 (Table 1), absent in the species here described. On the other hand, *P. vaterum* has fvbs with a
596 dcap exhibiting a Vaginata shape, contrasting with the Reniforma shape observed in *P.*
597 *valchetense* (Fig. 6F–J). A species that has unpreserved phloem but has a similar number of
598 wide metaxylem elements per fvbs is *Palmoxylon bororoense*, but it is also characterized by
599 having fvbs with a dcap Vaginata in shape (Table 1).

600 **Comparisons with extant taxa and affinities.** The presence of fvbs with a sclerotic partition
601 of the phloem as a result of a ventral projection of the dcap, in combination with a vcap, are
602 typically found in the tribe Trachycarpeae of the Coryphoideae (Thomas & De Franceschi,
603 2013). Genera within this tribe also exhibiting a dcap Reniforma in shape and 2(3–4) wide
604 metaxylem elements per fvb include *Serenoa* Hook.f., *Brahea* Mart. ex. Endl., *Copernicia*
605 Mart., *Pritchardia* Seem. et H. Wendl., *Licuala* Thunb. and *Livistona* R. Br. of the
606 Livistoninae, and *Rhaphis* of the Rhaphidinae (Thomas, 2011a, b; Thomas & De Franceschi,
607 2013). Other features recorded in *P. valchetense*, as the *Cocos*-type stem, are also present in
608 some of the trachycarpeoid genera (see Thomas & De Franceschi, 2013), supporting its
609 referral to this tribe.

610

611 **Discussion**

***Palmoxylon* species from the Allen Formation.** The restudy of the *Palmoxylon* species from the Allen Formation allows for a more complete characterization of each taxon and its limits. The inclusion of unpublished remains, together with a reevaluation of the originally described specimens, resulted in the recognition of characters unreported by Ancibor (1995), such as the growth pattern types and other descriptors currently used in modern characterization of living and extinct palm stems (e.g., Thomas & De Franceschi, 2012, 2013; Franco *et al*., 2014; Vera *et al*., 2024; Kumar *et al*., 2025). Consequently, the diagnoses of the three species were emended to incorporate these newly recognized features, and to modify some characters that are interpreted differently in this contribution.

In this study, epitypes for *Palmoxylon santarosense* and *Palmoxylon valchetense* are designated. This procedure was necessary because the selected specimens provide information beyond that obtainable from small stem fragments: they allow a comprehensive interpretation of the growth type and structural changes within the stems. The holotypes selected by Ancibor (1995) consist of limited stem portions where this information was not available. For the remaining species, *Palmoxylon rionegrense*, however, only the holotype is available, and thus no epitype was defined.

The new descriptions presented here show several differences from those of Ancibor (1995), which have been widely used in comparisons with other *Palmoxylon* taxa (*e.g*., Martínez, 2012; Martínez *et al*., 2023; Vera *et al*., 2024); therefore, the revised anatomical data from the Allen Formation palms provide a more robust basis for interspecific and interbasinal comparisons, highlighting the importance of the restudy of previously published taxa. In particular, the incorporation of patterns of distribution of fvbs, as well of the anatomical changes of these structures across the different sections of the stem, were barely mentioned in the original descriptions (Ancibor, 1995), and are currently included in the descriptive traits

that allow characterizing the anatomy of palm stems (*e.g.*, Thomas and De Franceschi, 2013). Moreover, these descriptions offer insights not only into anatomical and taxonomic affinities but also into the broader paleoecological significance of these taxa.

Recognizing the affinities of the Allen Formation *Palmoxylon* species is also critical for evaluating their potential use as paleoclimatic proxies. Among the studied taxa, *Palmoxylon santarosense* proves to be the least informative, as its shows a combination of characters not observed in extant Arecaceae, and thus precluding its referral to any specific subfamily or tribe within Arecaceae. In contrast, *Palmoxylon rionegrense*, although based in a single specimen, has enough anatomical information to warrant its referral to the Coryphoideae, a clade currently restricted to environments with mean annual temperatures (MAT) of 8.9–30 °C (Reichgelt *et al*., 2018). Tentative affinities with the tribe Caryoteae are also suggested, which would imply a narrower MAT range of 15.3–27.4 °C (Reichgelt *et al*., 2018). Finally, *Palmoxylon valchetense* is now interpreted as belonging to the tribe Trachycarpeae, which is associated with MAT values of 8.2–29.4 °C (Reichgelt *et al*., 2018). As discussed below, the record of latest Cretaceous palms with affinities with the Trachycarpeae also provide information regarding the biogeography of the clade. In summary, while tropical conditions for the Allen Formation are not rejected, these results indicate that the three palms described herein are not, at least for the time being, biological proxies supporting (or challenging) these climatic conditions.

Comments on biogeography of Trachycarpeae. The Trachycarpeae has one of the largest geographic distributions among Arecaceae, being present in tropical North and Central America, some regions of central South America, the Mediterranean region, and Australasia (Dransfield *et al*., 2008). Bacon *et al*. (2012) postulated that the origin of the clade

Trachycarpeae occurred during the Coniacian–Santonian in a region spanning southern North America, Central America and the Caribbean, and that crown-Trachycarpeae appeared during the Eocene–Oligocene, diversifying mostly during the Miocene. Baker and Couvreur (2013), while obtaining a similar geographic origin, recovered the divergence of the clade during more recent times (during the Eocene).

Kumar *et al*. (2025) recently described the species *Palmoxylon trachycarpeaeense* Kumar et Khan 2025 from the Maastrichtian–Danian Deccan Intertrappean Beds in India, interpreting it as a representative of the Trachycarpeae. This record, along with younger palm fossils from the region with Trachycarpean affinities, allowed the authors to challenge hypothesis of a Laurasian origin for the tribe made by Bacon *et al*. (2012) and Baker and Couvreur (2013), suggesting that this clade originated in the gondwanan fragment that is India today, after its separation from Antarctica but before its accretion with Laurasia (Kumar *et al*., 2025).

Anatomical characters of *Palmoxylon trachycarpeaeense* show close similarities with *Copernicia* and *Washingtonia* of the Trachycarpeae when included in the Thomas (2011a) Database, highlighting the probable relationship with this tribe. Nevertheless, another taxon is recovered as comparable: the Sabaleae. In fact, anatomical studies focused on descriptive characters carried out by Thomas (2011a, b) and Thomas and De Franceschi (2013) recover the Sabaleae as indistinguishable from these two Trachycarpeoid genera when the defined descriptors are analyzed. Kumar *et al.* (2025) separate *P. trachycarpeaeense* from the Sabaleae indicating that fvbs of both taxa differ in shape and size, without indicating which are these differences in the shape, or which measurements of the fvbs taken into account for the Sabaleae (and its source). However, photographs of fvbs of the species of *Sabal* presented by Thomas (2011b) show, a priori, fvbs similar regarding the morphology and size. It is unclear which morphological differences were recognized by Kumar *et al.* (2025) to segregate the studied *Palmoxylon* species from Sabaleae. As such, while affinities with the

Trachycarpeae cannot be rejected, restricting it to this tribe may be obscuring possible affinities with the Sabaleae.

While the gondwanan record of *Palmoxylon trachycarpeaeense* may or may not challenge the laurasian origin of the clade, the recognized Trachycaepeae affinities of *Palmoxylon valchetense* from the Allen Formation of Patagonia may add a new line of evidence supporting a role of the gondwanan realm in the early history of the Trachycarpeae during the Cretaceous. Interestingly, *Palmoxylon subantarcticae* from the uppermost Cretaceous Dorotea Formation from Chile also shares similarities with the Trachycarpeae and Sabaleae (Martínez *et al*., 2023). In this sense, accepting these Patagonian species as true representatives of the tribe clashes with the molecular divergence estimations carried out by Baker and Couvreur (2013), but may agree with the ones proposed by Bacon *et al*. (2012) for the stem representatives of the clade. In any case, these palm fossils seem to occur earlier in the history of palms than estimated by molecular clocks. Similarly, Chate *et al.* (2019) and Vera *et al.* (2024) reported uppermost Cretaceous to Danian fossils closely comparable to the tribe Phytelepheae of the subfamily Ceroxyloidea from India and Patagonia respectively, predating by more than 20 My the estimated divergence time of the clade (Baker & Couvreur, 2013; Chate *et al*., 2019; Khan *et al*., 2020; Vera *et al*., 2024). It is clear that future studies on Arecaceae, incorporating more fossils with conclusive affinities as calibration points may produce divergence time estimates concordant with what is already known by different fossil specimens, and allow the proposal of new dispersal patterns supported by the already rich known palm fossil record.

Conclusions

The three *Palmoxylon* species originally described by Ancibor (1995) from the Campanian–Maastrichtian Allen Formation (Río Negro Province, Argentina) are restudied here. The new descriptions incorporate additional anatomical data and allowed revised diagnoses. New unpublished material is referred to one of these species, and epitypes are designated for *Palmoxylon santarosense* and *Palmoxylon valchetense*, based on the more comprehensive anatomical information they provide.

This study also establishes new taxonomic affinities for the three taxa. The anatomy of *P. santarosense* is not diagnostic enough to confidently assign it to any subfamily or tribe within Arecaceae and is therefore referred to Arecaceae *incertae sedis*. In contrast, *P. rionegrense* is interpreted as belonging to the subfamily Coryphoideae, with probable affinities to the tribe Caryoteae, while *P. valchetense* is recognized as a member of the tribe Trachycarpeae. Given the broad climatic tolerances of these clades, their occurrence does not provide conclusive support for, nor does it rule out, tropical climatic conditions for the Allen Formation.

The occurrence of Trachycarpeae in the latest Cretaceous of South America has important evolutionary and biogeographic implications. It challenges existing divergence time estimates for the clade and calls into question proposed biogeographic scenarios involving the Laurasian realm or India. These findings highlight the need to incorporate a greater number of fossil records into molecular clock calibrations and analyses of origin and dispersal, which are typically based on modern taxa and include few fossil calibration points.

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Figure legends

Figure 1. *Palmoxylon santarosense* Ancibor *emend*. Vera. A, TS of the holotype (BA Pb 887); B, transverse section of the epitype (BA Pb 862); C, detail of B, showing distribution of fvbs from the center of CZ, through the SZ towards the CT (BA Pb 862); D, distribution of fvbs in the center of the CZ (BA Pb 862); E, detail of D, showing aspect of fvbs. Notice two large metaxylem vessels (white arrows), and developed vcap (black arrow) (BA Pb 862). A, B= 1 cm, C= 3 mm, D=1 mm, and E= 500 μm.

Figure 2. *Palmoxylon santarosense* Ancibor *emend*. Vera. A, distribution of fvbs in the outer region of the CZ (BA Pb 862); B, C, detail of the distribution of fvbs in the outer region of the CZ. Notice small ventral projection of the dcap (arrow) (BA Pb 887); D, detail of a single fvb, showing two wide vessels and phloem region (arrow) (BA Pb 887); E, detail of the vascular zone of a fvb, showing two wide metaxylem vessels (Xi) and preserved phloem cells (arrow) (BA Pb 887); F, distribution of fvbs in the most external region of the CZ towards the SZ. Notice elongate dcap in some fvbs (arrows) (BA Pb 862); G, fvbs in the external region of the SZ towards the CT, showing a single wide vessel per unit (BA Pb 887); H, detail of the SZ and CT, showing abundant fibrous bundles in the latter (arrows) (BA Pb 862); I, detail of the ground tissue in the central region of the CZ, showing isodiametric and elongate parenchyma cells (BA Pb 862); J, detail of the ground tissue in the external region of the CZ,

showing isodiametric parenchyma cells. Notice an ill-preserved fibrous bundle (arrow) (BA Pb 887); K, Detail of the external region of the SZ and the CT, showing small (black arrows) and large (white arrow) fibrous bundles (BA Pb 862); L, leaf trace (lt) and vascular bridge (arrow) (BA Pb 887); M, detail of L, showing a detail of a leaf trace (BA Pb 887); N, detail of L, showing a vascular bridge (BA Pb 887); O, LS showing vessels and perforation plates (BA Pb 887); P, LS showing stegmata with globose phytoliths (arrow) (BA Pb 887). Scale bars: A=1000 μm; B, F, G, H=500 μm; C, I=300 μm; D, K, L, M, O=200 μm; E, J, N, P=100 μm.

Figure 3. *Palmoxylon santarosense* Ancibor *emend.* Vera. A, two TS of the specimen BA Pb 944. Notice the presence of the holotype of *Stipitichnus koppae* Genise, 1995 (MACN-Icn 123), traces interpreted as insect borings, in the upper image (arrows). B, detail of A, showing distribution of fvbs in the outer preserved region of the stem; C, detail of B, showing fvbs; D, detail of A, showing distribution of fvbs in the center of the stem. E, detail of D, showing fvbs. Scale bars: A=2 cm; B, D = 2 mm; C, E=1 mm.

Figure 4. *Palmoxylon rionegrense* Ancibor *emend.* Vera. A, TS of the holotype (BA Pb 884); B, distribution of fvbs towards the center of the stem (BA Pb 884); C, detail of A, showing distribution of fvbs in the fossil (preserving only the CZ), from the center of the stem (CZin) towards the exterior (CZout) (BA Pb 884); D, fvbs in the center of the stem (BA Pb 884); E, fvbs in the outermost preserved region of the stem (BA Pb 884); F, detail of a fvb showing two large vessels (BA Pb 884); G, detail of a fvb showing three large vessels (BA Pb 884); H, detail of the vascular region of a fvb with two large vessels. Notice fibers of the vcap (white arrow) and dcap (black arrow) (Ba Pb 884); I, detail of the vascular region of a fvb with four large vessels (arrows) (Ba Pb 884); J, detail of the vascular region of a fvb with three large vessels (Ba Pb 884); K, ground tissue and interspersed fvbs. Notice elongate parenchymatous

998 cells (white arrows) and tabular parenchyma (black arrows) (BA Pb 884). Scale bars: A= 2
999 cm; B=2 mm; C=3 mm; D, E= 500 μm; F, G, H, K= 200 μm; I, J=100 μm.

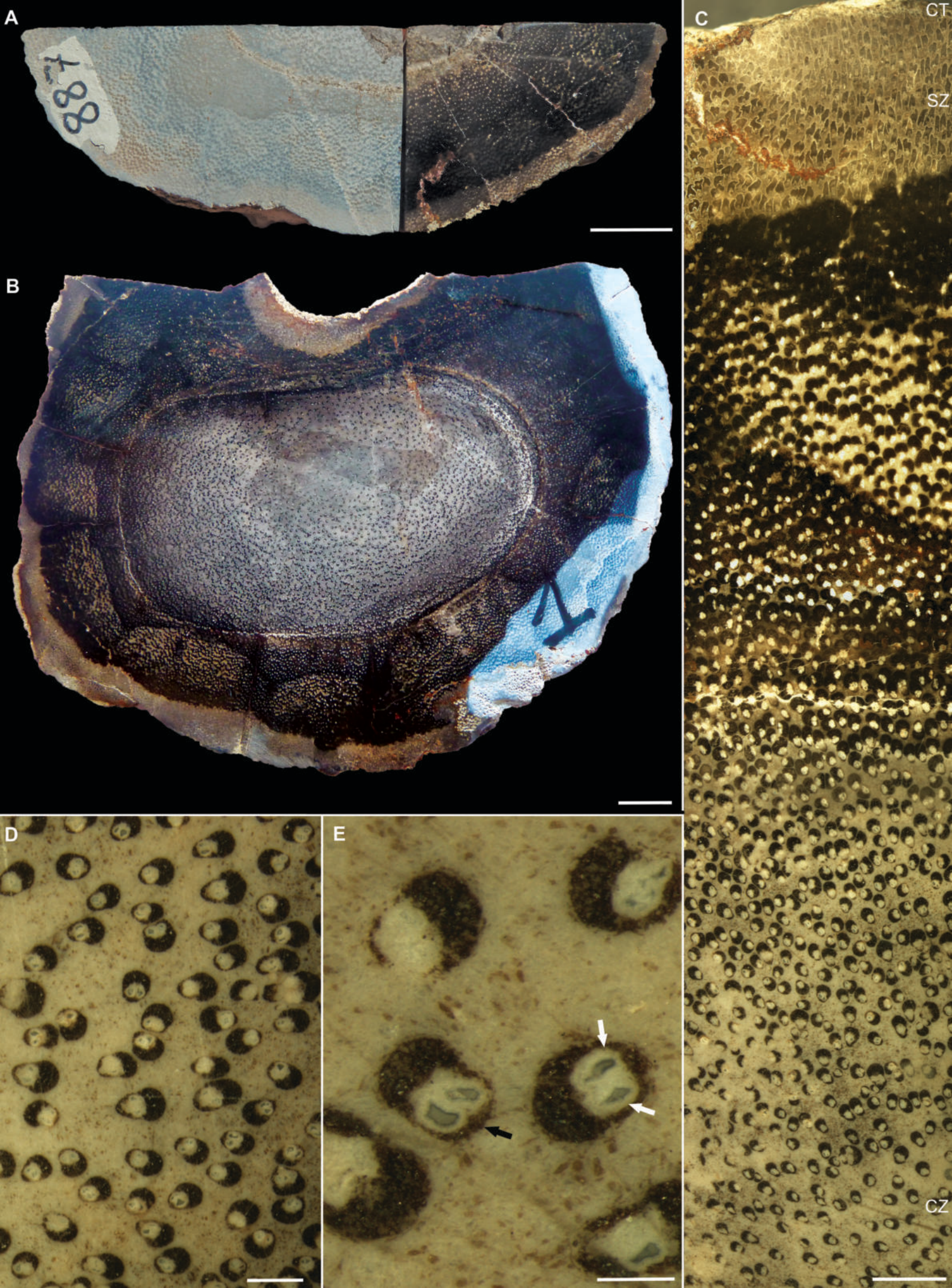
1000 **Figure 5.** *Palmoxylon rionegrense* Ancibor *emend.* Vera. A, B, TS showing a leaf trace with
1001 two vascular units (white arrows). Notice vascular bridge in A (black arrow) (BA Pb 884); C,
1002 detail of the two-parted vascular zone of the leaf trace (white arrows) (BA Pb 884); D, detail
1003 of a vascular bridge (BA Pb 884); E, LS showing stegmata with globose phytoliths (white
1004 arrows) and lacunae in ground tissue (black arrows) (BA Pb 884); F, G, LS showing stegmata
1005 with conical phytoliths (arrows) (BA Pb 884). Scale bars: A, B=300 μm; C, D, E, F, G =100
1006 μm.

1007 **Figure 6.** *Palmoxylon valchetense* Ancibor *emend*. Vera. A, transverse (top) and longitudinal
1008 (bottom) view of the holotype (BA Pb 890); B, transverse section of specimen BA Pb 888; C,
1009 transverse section of specimen BA Pb 889, previously included in *P. rionegrense*; D,
1010 transverse view of the epitype (BA Pb 967); E, detail of D, showing distribution of fvbs from
1011 the CZ to the CT (BA Pb 967); F, detail of a fvb of the CZ in the holotype (BA Pb 890); G,
1012 detail of a fvb of the center CZ (BA Pb 888); H, detail of a fvb of the CZ in the epitype (BA
1013 Pb 967); I, detail of a fvb in the outer region of the CZ/SZ in the epitype (BA Pb 967); J,
1014 detail of a fvb in the outer region of the CZ/SZ in the specimen previously included in *P.*
1015 *rionegrense* (BA Pb 889); K, detail of a fvb with elongated dcap in the SZ of the epitype (BA
1016 Pb 967); L, detail of the fibres of the dcap (white arrow) and tabular parenchyma (black
1017 arrow) (BA Pb 890). Scale bars: A, B= 1 cm; C, E=2 cm; F, G, H, I, J, K=500 μm; L=100
1018 μm.

1019 **Figure 7.** *Palmoxylon valchetense* Ancibor *emend*. Vera. A, detail of the vascular zone of a
1020 fvb, showing two wide metaxylem vessels and developed paravascular parenchyma. Notice
1021 the ventral projection of the dcap into the phloem strand (arrow) (BA Pb 890); B, detail of the

vascular zone of a fvb, showing four wide metaxylem vessels (BA Pb 890); C, detail of the vascular zone of a fvb, showing two wide metaxylem vessels and developed paravascular parenchyma (black arrow). Notice the ventral projection of the dcap into the phloem strand (white arrow) (BA Pb 888). D, detail of a fvb, showing polygonal xylem elements between the two large wide vessels (white arrows), and radially elongate fibers of the vcap (black arrows) (BA Pb 890); E, aspect and distribution of fvbs in the CZ (BA Pb 967); F, aspect and distribution of fvbs in the TZ (BA Pb 967); G, aspect of the SZ. Notice the presence of fibrous bundles (arrows) (BA Pb 967); H, detail of the outer region of the SZ and the preserved portion of the CT, showing abundant fibrous bundles (arrows) (BA Pb 967); I, detail of the ground tissue, showing parenchymatous cells with thickened walls (white arrows). Notice the vcap of a fvb, with elongated cells (black arrow) (BA Pb 890); J, detail of the ground tissue in the SZ, showing fibrous bundles (arrows) (BA Pb 889); K, detail of J, showing a fibrous bundle (BA Pb 889); L, comparison between fvbs and a leaf trace (black arrow). Notice the small vascular bridge (white arrow) (BA Pb 890); M, detail of a leaf trace (BA Pb 890); N, detail of a vascular bridge (BA Pb 890); O, longitudinal section showing stegmata with globose phytoliths (BA Pb 890). Scale bars: A, B, C, J, N=200 μm; D, I, K= 100 μm; E, F, G, H, L= 1 mm; M=500 μm; O=50 μm

Table 1. Comparison between *Palmoxylon* remains of the Allen Formation and other South American taxa. Abbreviations: dcap shape: morphology of the fibrous region adjacent to the phloem in the fibrovascular bundle (*sensu* Stenzel, 1904); vcap: presence of fibrous sheath adjacent to the xylem in the fibrovascular bundles; RP: radial parenchyma; TP: tabular parenchyma. Anatomical data taken from Ancibor (1995), Martínez (2012), Martínez *et al.* (2023), Torres and Godoy (1982), Ottone (2007); Romero (1968); Arguijo (1979, 1981), Franco (2014); Franco *et al.* (2014), Lutz (1980, 1984, 1986), and Vera *et al.* (2024).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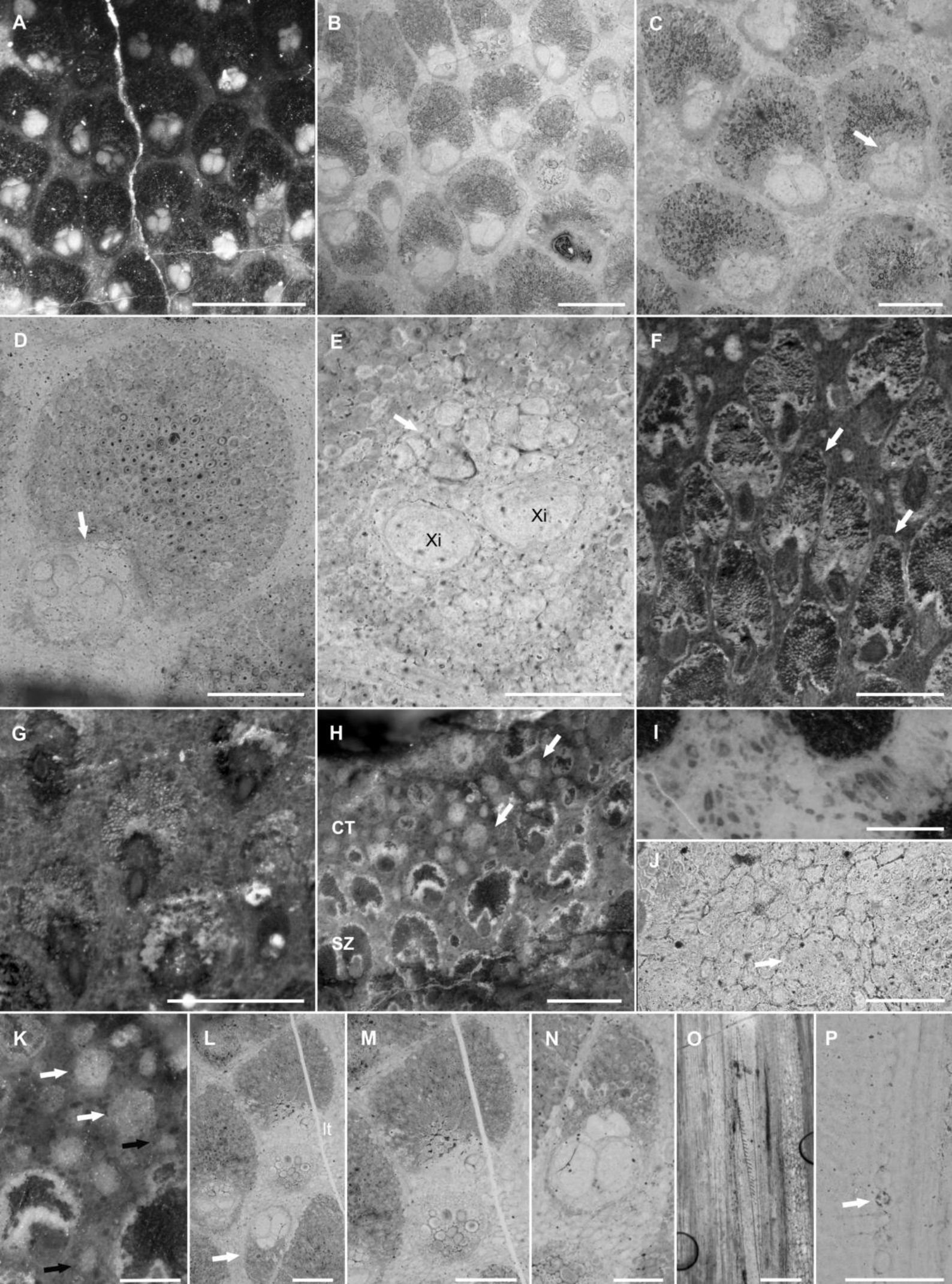
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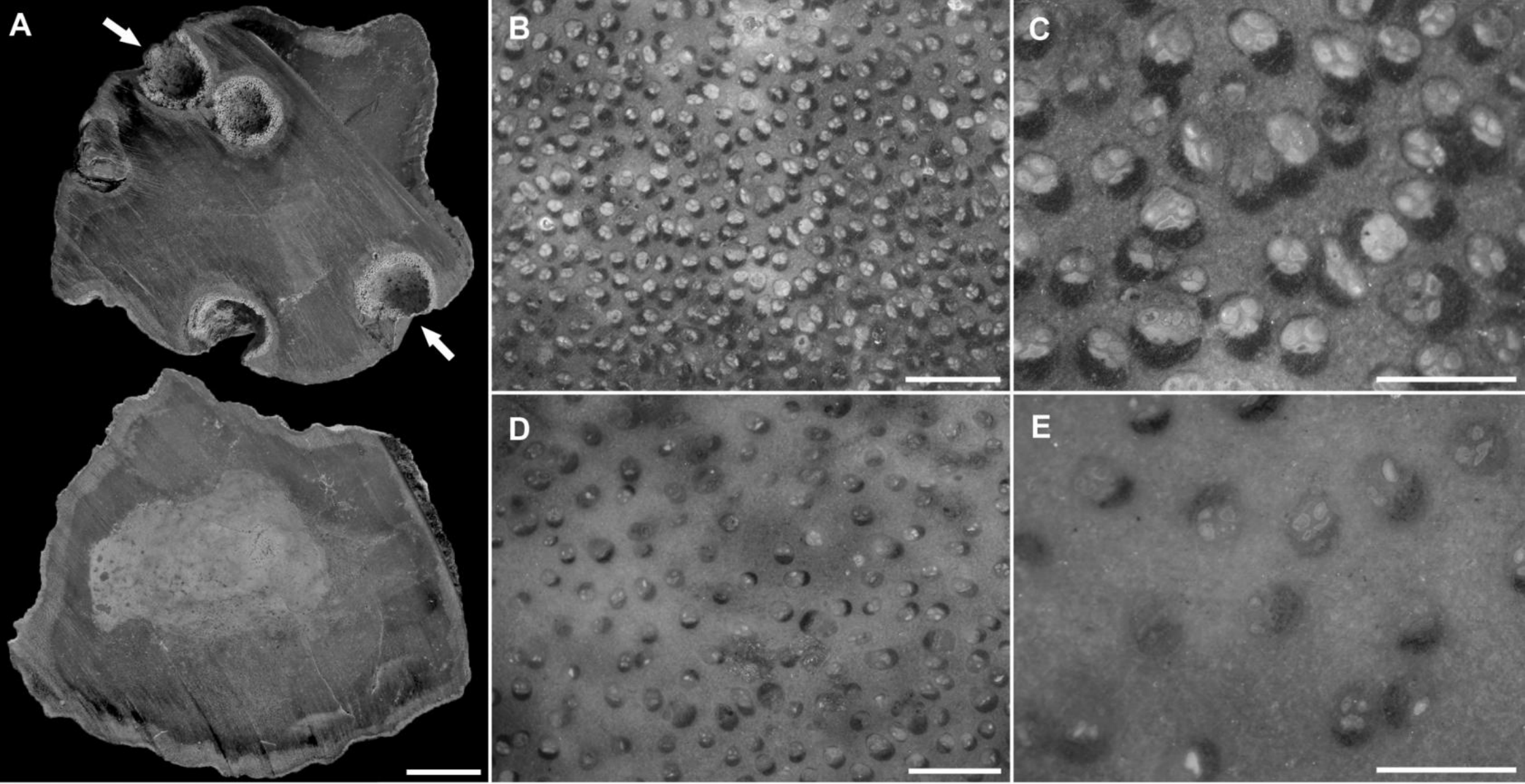
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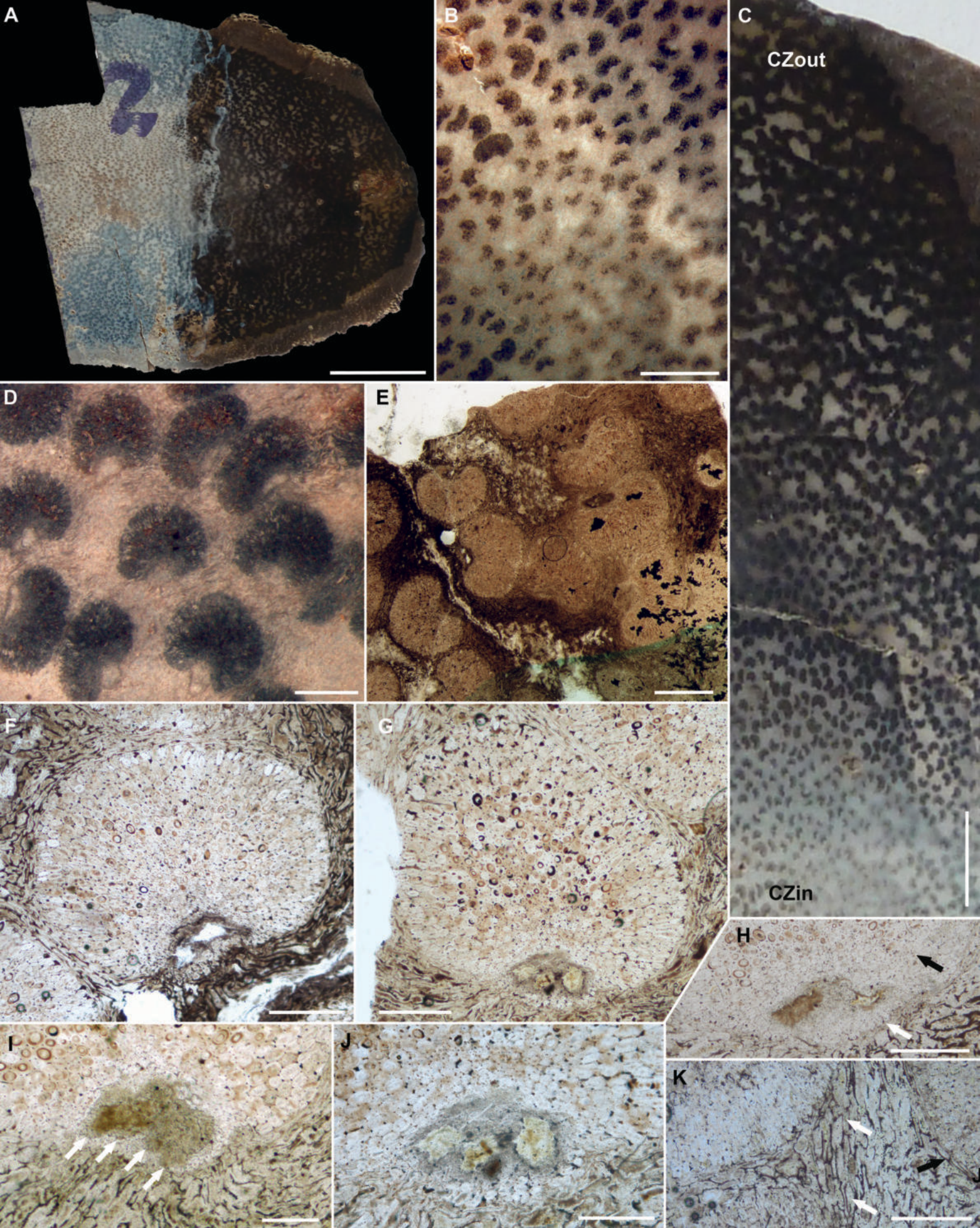
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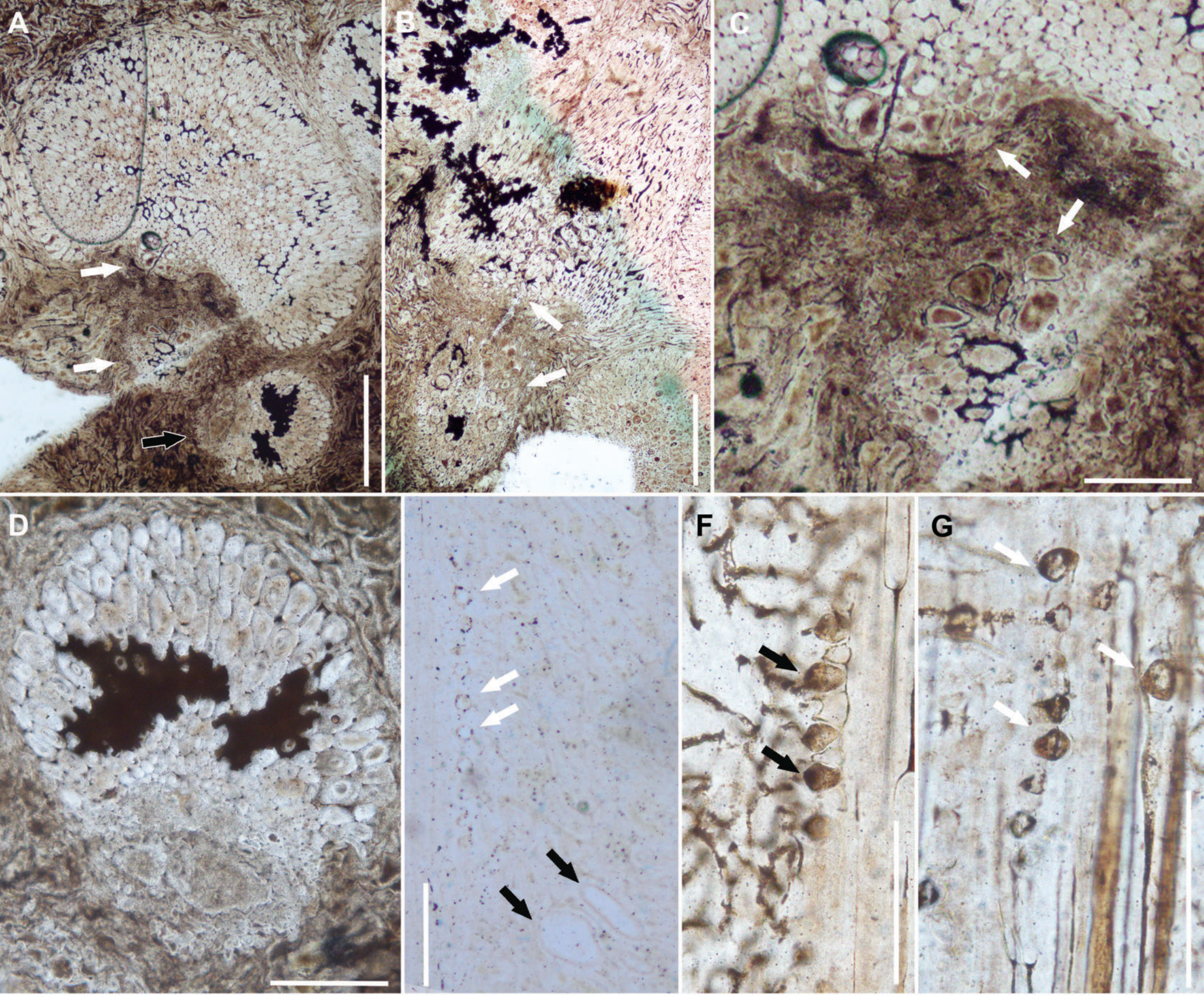
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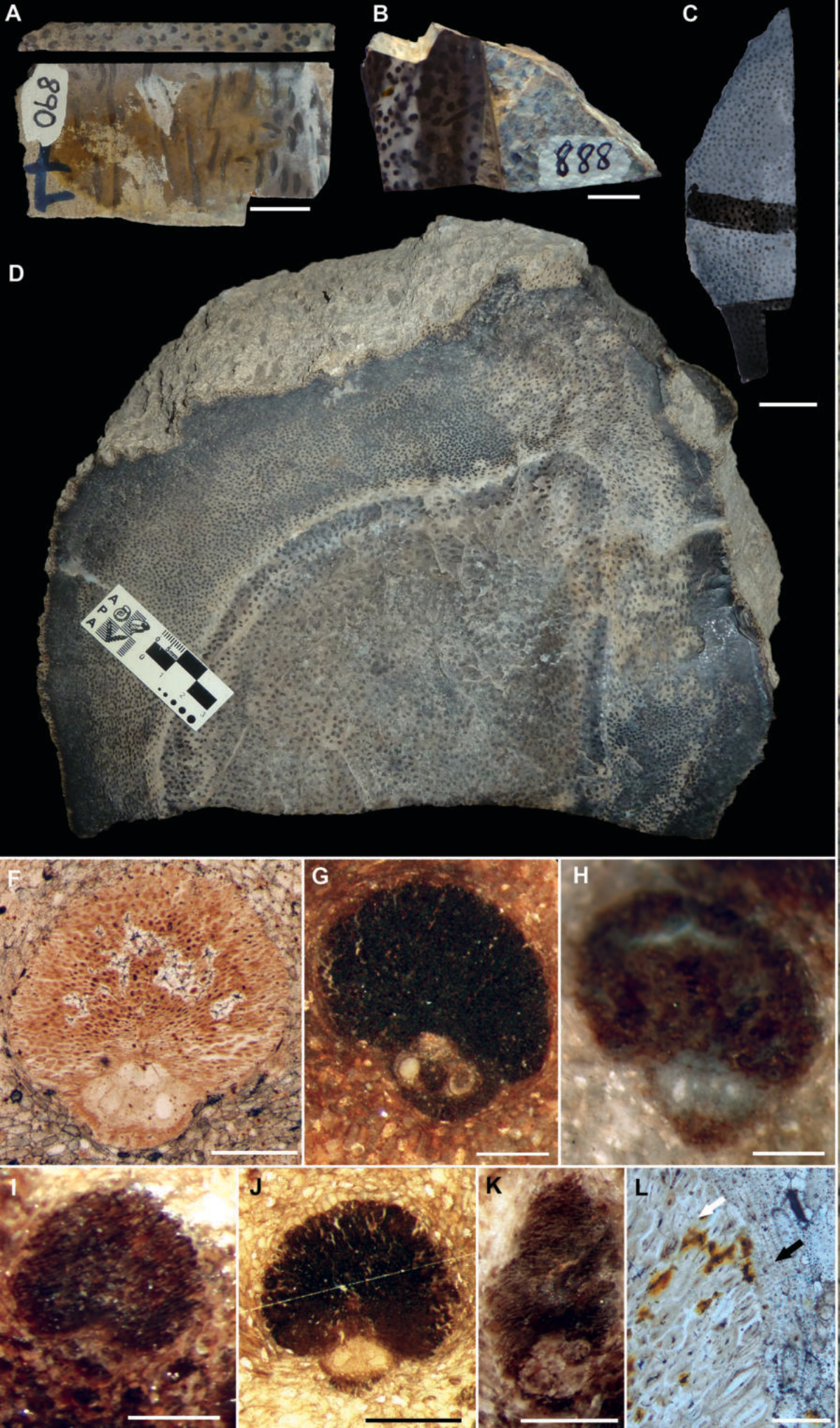
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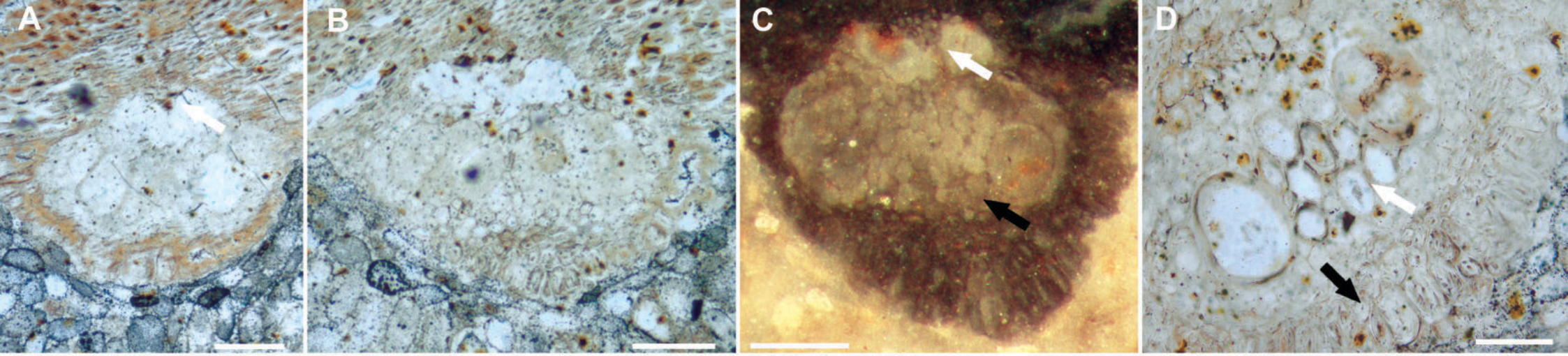
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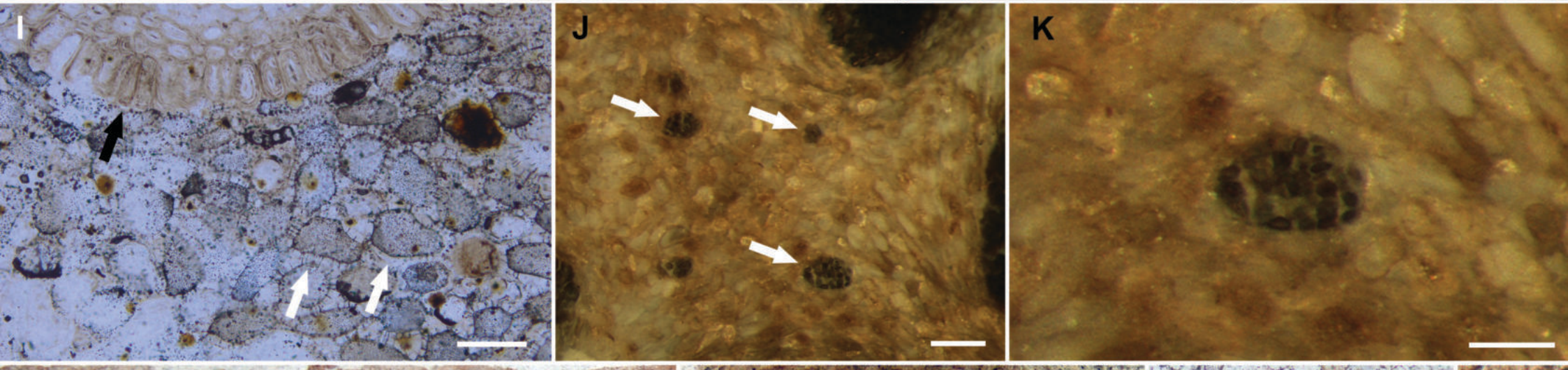
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Taxon	Formation and age	Mx	dcap shape	vcap	Ph	RP	TP	ground tissue cells	fb	Phy
***P. santarosense* Ancíbor emend. Vera**	Allen; uCmp - Maa	1 (CZ), 2 (SZ)	Lu-Va (CZin), Re (CZout), Re/Sa (SZ)	yes	1	no	yes	isodiametric, slightly elongate (CZ /SZ) + elongate (CZ)	in CZout, SZ and CT	GLO
***P. rionegrense* Ancíbor emend. Vera**	Allen; uCmp - Maa	2(2–4)	Re	yes	?	no	yes	highly elongate, with scarce lacunae	No	GLO & CON
***P. valchetense* Ancíbor emend. Vera**	Allen; uCmp - Maa	2(1–4)	Re	yes	1–2	no	yes	isodiametric, elongate	Scarce (CZ), abundant (SC, CT)	GLO
P. garridoi Martínez 2012	Anacleto; Cmp	3 (2–6)	Re/Va	no	1	no	yes	elongate, rhombohedral, sometimes rod-like, constituting an irregular network, delimiting lacunae	No	GLO
P. sp. 1 in Vera *et al*. (2024)	Puntudo Chico; Cmp - lst Maa	2(3–4)	Re	no	1	no	?	isodiametric, elongate, rhombohedral, sometimes rod-like	Yes	?
P. sp. 2 in Vera *et al*. (2024)	Puntudo Chico; Cmp - lst Maa	2(3–4)	Lu/Va	yes	1	no	yes	isodiametric, with elongate cell strands	Yes	?
P. sp. 3 in Vera *et al*. (2024)	Puntudo Chico; Cmp - lst Maa	1	Re	yes	1	no	?	elongate, rhombohedral, sometimes rod-like, constituting an irregular network, delimiting lacunae	No	?
P. sp. 4 in Vera *et al*. (2024)	Puntudo Chico; Cmp - lst Maa	1(2)	Re	no	?	no	yes	isodiametric, with elongate cell strands	yes	?
P. sp. cf. *P. phytelephantoides* Chate et al. 2019 in Vera et al. (2024)	Puntudo Chico; Cmp - lst Maa	more than 10, angular	Co	no	1	no	yes	isodiametric	yes	?
P. subantarcticae Martínez et Leppe, 2023	Dorotea; Maa	3(1–6)	Re	yes	1	no	yes	elongate, rhombohedral, sometimes rod-like, constituting an irregular network, delimiting lacunae	yes	GLO
P. chilensis Torres et Godoy 1982	?; uK? - Pg?	1	Cm	yes	1	yes	yes	isodiametric without lacunae, to lacunate	In CT	?

P. pichaihuensis Ottone 2007	Pichaihue Limestone; Dan	1–5	Re	no	?	?	?	unclear, irregular	no	?
P. patagonicum Romero 1968	Salamanca ; Dan	2(1–4)	Cm/Co	no	1–2	yes	yes	isodiametric to slightly elongate, rarely showing lacunae	yes	GLO & CON
P.bororoense Arguijo 1979	Cerro Bororó; Dan	2–4	Va/Lu	yes	?	no	yes	isodiametric	yes	GLO
P.vaterum Arguijo 1981	Cerro Bororó; Dan	2(3–7)	Va	yes	1–2	yes	yes	isodiametric	yes	GLO
P. romeroi Franco *et al.* 2014	Chiquimil; Mio	3–4(3–5)	Va	yes	1	yes	yes	isodiametric, elongate, undulating	no	GLO
P. concordiense Lutz 1980 emend. Lutz 1986	Salto Chico; Pli	2	Sa/Cm/Co	no	1	yes	yes	isodiametric, elongate	yes	GLO
P. yuqueriense Lutz 1984	Salto Chico / Ituzaingó; Pli	2	Cm/Co/Lu	no	1	yes	yes	isodiametric	no	GLO

Table 1. Comparison between *Palmoxylon* remains of the Allen Formation and other South American taxa. Abbreviations: Mx: number of wide metaxylem elements in fvbs; Ph: number of phloem strands in fvbs; RP: radiating parenchyma; TP: tabular parenchyma; fb: fibrous bundles in ground tissue; Phy: phytoliths Cmp: Campanian; Maa: Maastrichtian; Dan: Danian; K: Cretaceous; Pg: Paleogene; Mio: Miocene; Pli: Pliocene; u: upper/Upper; lst: lowermost; Lu: Lunaria; Va: Vaginata; Co: Cordata; Re: Reniforma; Cm: Complanata; Sa: Sagittata; CZin: inner region of the CZ; CZout: outer region of the CZ; GLO: globular; CON: conical. Anatomical data taken from Ancibor (1995), Martínez (2012), Martínez et al (2023), Torres and Godoy (1982), Ottone (2007); Romero (1968); Arguijo (1979, 1981), Franco (2014); Franco et al. (2014), Lutz (1980, 1984, 1986), and Vera et al. (2024).