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Seasonally dry tropical forests in the late Pleistocene of Mesopotamia, Argentina and their relationship to environmental changes during the Last Interglacial

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ABSTRACT: The concept of seasonal forests groups structural types of vegetation that are related to climatic seasonality in the tropics of South America. Consequently, this determines the physiognomy of the vegetation, from semi-deciduous to strongly deciduous. The strongest link between seasonally dry tropical forests (SDTFs) is their floristic composition, where Leguminosae and Anacardiaceae dominate the woody flora. The fossil records of the Neogene of northwestern Argentina reveal a list of species found in various locations and formations of the Miocene–Lower Pleistocene obtained from studies of pollen, woods (logs), cuticles, impressions of leaves and fruits. The analysis of sediments and woody structures from the Tapebicuá, Toropí/Yupoí and El Palmar Formations (Upper Pleistocene) of the Mesopotamia region allowed us to identify several pollen taxa and silicified wood fragments (mineralized). The woody and shrubby association whose current relatives characterize the SDTF is composed of the 16 fossil species described here belonging to seven families. In our samples, *Anadenanthera colubrina* and *Myracrodruon balansae* are the most significant members of the families Leguminosae and Anacardiaceae, which are dominant in the SDTF. The paleobotanical species described in this study confirm the extension of the SDTF to the province of Corrientes, coinciding with various climatic events (dry subtropical, semi-desert and warm-humid climate) that would have favored the development of these forests during the Pleistocene in this region. The absolute dates obtained for the Toropí/Yupoí and Tapebicuá Formations confirm their synchronicity and correlation to Marine Isotope Stage 5. The palynological analysis, the presence of *Menendoxylon* and the sedimentological data allow us to infer the existence of a seasonally dry humid paleoclimate in northeastern Argentina during the Late Pleistocene favorable to the development of the SDTF. © 2024 John Wiley & Sons, Ltd.

KEYWORDS: Argentina; Late Pleistocene; Mesopotamia; MIS5; seasonally dry tropical forests

Introduction

To date, no sufficiently in-depth studies have been carried out to allow us to understand the complexity of how seasonally dry tropical forests (SDTFs) developed and have persisted over time.

The concept of seasonal forests as used here derives mainly from Beard's (1944, 1955) 'seasonal formation series', which groups structural types of vegetation related to climatic seasonality in the tropics of South America. Consequently, this determines the physiognomy of the vegetation types involved, from semi-deciduous to strongly deciduous (Prado, 2000).

The scientific study of seasonally dry forests has been largely neglected until recently, due to the overwhelming interest in species-rich tropical rainforests. In contrast to the humid forests, SDTF covers a type of woody vegetation, with a strong climatic seasonality, the product of a dry season of variable duration (Banda-R et al., 2016). These are arboreal and shrubby ecosystems, with a relatively continuous and deciduous canopy, with annual rainfall ranging from 350 to 1000 mm and a notable dry season of 3–6 months (Gentry 1995; Graham and Dilcher 1995).

These forests have an shorter stature and lower basal area than tropical rainforests (Murphy and Lugo, 1986), and spiny species are often abundant. Net primary productivity is lower than in tropical rainforests because growth only takes place in the rainy season. Leaf litter accumulates in the dry season because the vegetation is mostly deciduous and sunlight penetrates the forest floor and reduces decomposition by lowering the relative humidity. The wettest forests are semi-deciduous and deciduousness tends to increase as rainfall decreases (Mooney et al., 1995).

A horseshoe-shaped distribution pattern of various woody tree species can be observed in the seasonally dry forests of South America. This pattern crosses the continent, starting from the Caatingas region in northeastern Brazil and extending through the old Jesuit missions of Brazil, Paraguay and Argentina, the Bolivian Chiquitanía, the Subandean Pedemontane Forest of southwest Bolivia and northwest Argentina, and some inter-Andean dry valleys of Bolivia and Peru. It has been proposed that this fragmentary and disjunct distribution of SDTF represents a new Phytogeographic Domain, with the 'cebil' *Anadenanthera colubrina* (Vell.) Brenan (Mimosoideae, Leguminosae) as its most emblematic species (Prado, 2000) (Fig. 1).

The strongest link between different SDTF areas is their floristic composition, which has been demonstrated both by analyzing the biogeographical distribution patterns of their

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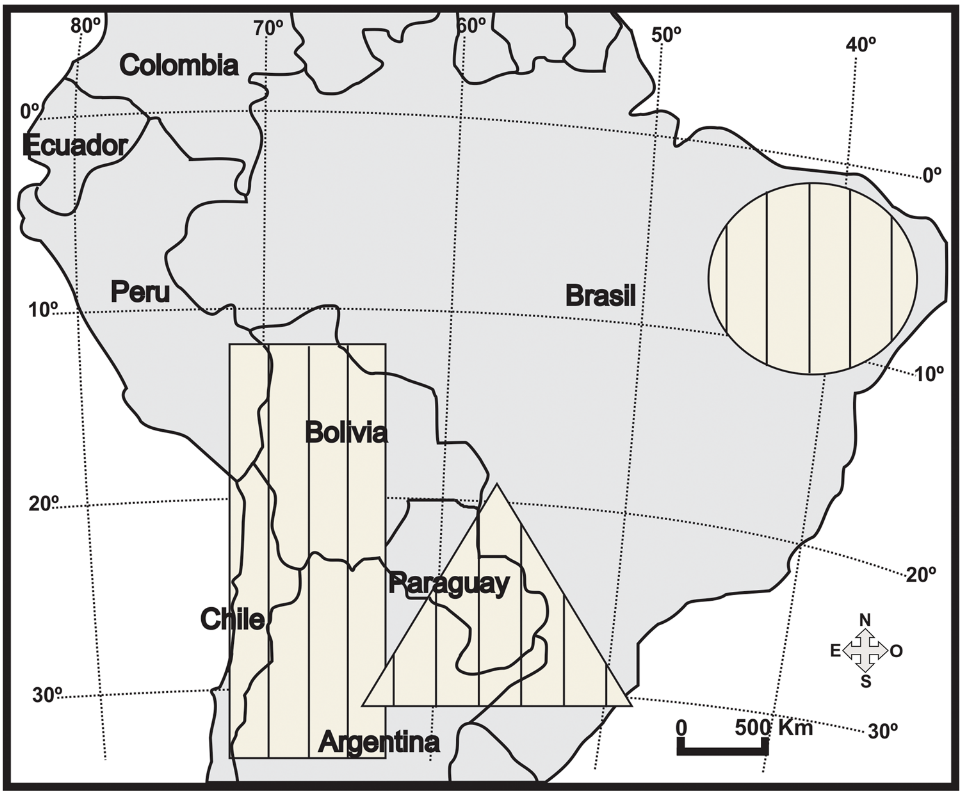

Figure 1. Current distribution centers of SDTFs. Oval, Caatingas Center; triangle, Misiones Center; rectangle, Pedemontane Subandinean Center. [Color figure can be viewed at wileyonlinelibrary.com]

most important woody species and by comparing their vegetation (using classical phytosociological analysis and numerical analysis). In areas dominated by Leguminosae (The Catalogue of Life Partnership, 2017) and Anacardiaceae, the woody flora consists mostly of Burseraceae, Myrtaceae, Rubiaceae, Sapindaceae, Euphorbiaceae, Flacourtiaceae and Sapotaceae, but their proportion is low (Gentry, 1995).

The fossil records of the Neogene of northwestern Argentina reveal a list of species found in various locations and formations. They come from a database made up of 438 fossil species of the Miocene–Lower Pleistocene obtained from studies of pollen, woods (logs), cuticles, impressions of leaves and fruits (Garralla et al., 2016; Baez et al. 2018; Martínez and Crisafulli, 2019; Baez and Crisafulli, 2021; Baez, 2021) typical of tropical and subtropical habitats, indicating the coexistence of warm and cold intervals. On the other hand, in northeastern Argentina (Entre Ríos province), the phytolith associations described by Patterer and Frezzia (2022) indicate the presence of a paleoflora composed of a continuous herbaceous stratum of meso-megathermic grasses accompanied by isolated trees and palms in an open savanna physiognomy, probably with a temperate/warm climate with low rainfall and medium to high temperatures. The records of taxa from the Miocene–Pleistocene of northeastern Argentina (Entre Ríos province) mentioned in Brea and Franco (2013), Brea, and Zucol, and Franco (2013), Franco and Brea (2008, 2009, 2010, 2013), Franco (2009, 2017) and Franco, Brea, Orfeo, et al. (2013) and the paleoflora of northwestern Argentina documented by Anzótegui and Horn (2011), Mautino and Anzótegui (2014), Garralla et al. (2016) and Anzótegui et al. (2017) were used to identify possible members of the current SDTF. We aim to determine the fossil woody flora (trees and shrubs), by means of palynological and xylological analysis of sediments and woody structures from the Tapebicuá, Toropí/Yupoí and El Palmar Formations (Upper Pleistocene) of Corrientes province, and to relate it to the characteristic flora of the current SDTF, in order to establish its extension in northeastern Argentina during the Late Quaternary.

Geological and environmental framework

The Quaternary of Corrientes province is represented in different geological formations throughout the territory, most of them related to the dynamics of the Paraná and Uruguay rivers. Some of the units of greatest interest for their paleoenvironmental implications, and therefore most studied, are the Toropí/Yupoí, Tapebicuá and El Palmar Formations. The Toropí/Yupoí Formation extends in the western region of Corrientes province, and in this area it was defined by Santa Cruz et al. (2020) as the Old Upper Paraná Fluvial System. The Tapebicuá Formation is distributed in a wide portion of the area referred to by Herbst and Santa Cruz (1985) as the Eastern Erosion Plain. The El Palmar Formation is distributed along the fluvial plains and terraces of the Uruguay River, all of them deposited during the Late Pleistocene Marine Isotope Stahe 5 (MIS5) (Ernesto et al., 2015).

The Toropí/Yupoí Formation is one of the best known units due to its extensive distribution and wide paleontological content, mainly composed of fossil vertebrates (Zurita et al., 2014, Francia et al., 2015, 2019) as well as microfossils (Erra et al., 2013; Fernandez Pacella et al., 2020; Contreras et al., 2019). This formation was initially recognized by Herbst and Alvarez (1977) as two different formations (Toropí Formation and Yupoí Formation). Subsequently, Iriondo (1996) considered that they do not correspond to different formational units and grouped them within the Toropí/Yupoí Formation, and two stratigraphic sections informally named as 'units' were recognized by Scillato-Yané et al. (1998) or, more recently, as 'members' by Francia et al. (2015) and Erra et al. (2016). These two sections are separated by a silcrete with abundant rhizolites corresponding to a paleosol. From a paleoenvironmental perspective, Iriondo (2010) interpreted this formation as a filling of wetland environments, accumulated in strips abandoned by the Paraná River. In the Arroyo Toropí area, datings of this unit yielding ages of 98.4–127 kaBP were obtained (Francia, 2014; Prevosti et al., 2021).

The stratigraphic section analyzed here work is 3.3 m thick (Fig. 2, section A), and it is located in the upper part of the ravines of the Paraná River, north of the city of Empedrado (27°56′42″S, 58°48′41″W). It consists mainly of deposits of clayey sands and silty sands with ferruginous and manganese concretions dispersed in the matrix. These characteristics allow us to refer it to the 'upper member' of the Toropí/Yupoí Formation (Fig. 3A).

In the eastern sector of the province, there are outcrops of the Tapebicuá Formation, which according to Iriondo and Kröhling (2008), who formally define this unit, corresponds to marsh and alluvial deposits accumulated by the Paraná River when it joined the Uruguay River. Stratigraphically, this formation presents high-energy channel facies covered by alluvial plain facies, which evolve into swamp deposits. The top of this unit was affected by pedogenesis. Iriondo (2010) considers this formation as a clear example of sandy wetlands or pantanal. According to absolute dating by Iriondo and Kröhling (2008) of a sample of the palustrine facies, the age of this formation is between 93.8 ± 11 and 126.5 ± 14 kaBP, which indicates that it is contemporary with the Toropí/Yupoí Formation. It should be noted that Herbst and Santa Cruz (1985) considered that both units corresponded to the same formation. However, unlike the Toropí/Yupoí Formation, the Tapebicuá Formation has not yet provided fossil vertebrates.

The analyzed section is 2.2 m thick (Fig. 2, section B) and is exposed on Route 14, 2 km north of the town of Tapebicuá (29°28′53″ S 56°58′34″ W). It is mainly composed of silty and clayey sand layers, mainly massive, with abundant ferruginous and manganese concretions. In the upper part, there are remarkable prismatic structures and rhizolites related to the development of pedogenetic processes. These features allow us to refer it to the upper section of the formation, which was interpreted by Iriondo and Kröhling (2008) as alluvial plain facies (Fig. 3B).

Finally, the El Palmar Formation (Iriondo, 1980) corresponds to fluvial deposits accumulated by the Uruguay River, where channel fill, floodplain and levee facies can be recognized (Iriondo, 2010). Important records of fossil vertebrates (Ferrero et al., 2007) and silicified woods (Ramos et al., 2017) are documented. According to Iriondo (2010), in different localities this formation dates to between of 80 670 ± 13 420 and 88 370 ± 35 680 BC.

The stratigraphic section analyzed is 1 m thick (Fig. 2, section C) and is exposed on the margins of the Uruguay River, 1 km northeast of the town of La Cruz (29°10′14″ S, 56°37′30″ W). The base of the stratigraphic column begins with a 0.5-m deposit of massive medium sands with a clayey matrix, which may correspond to levee facies, which is covered by a conglomerate deposit with predominantly siliceous clasts among which fragments of silicified wood were found, which is interpreted as a channel fills facies of the El Palmar Formation (Fig. 3C).

Materials and methods

The sediments used for palynological analysis come from the upper member of the Tapebicuá Formation at the town of Tapebicuá, and the upper member of the Toropí/Yupoí Formation at the town of Empedrado in Corrientes province (see Fig. 2). Thirteen samples were collected from the Tapebicuá Formation and ten samples from the Toropí/Yupoí Formations. The samples were collected in three columns separated by 50 cm and every 5 cm from the base of the upper

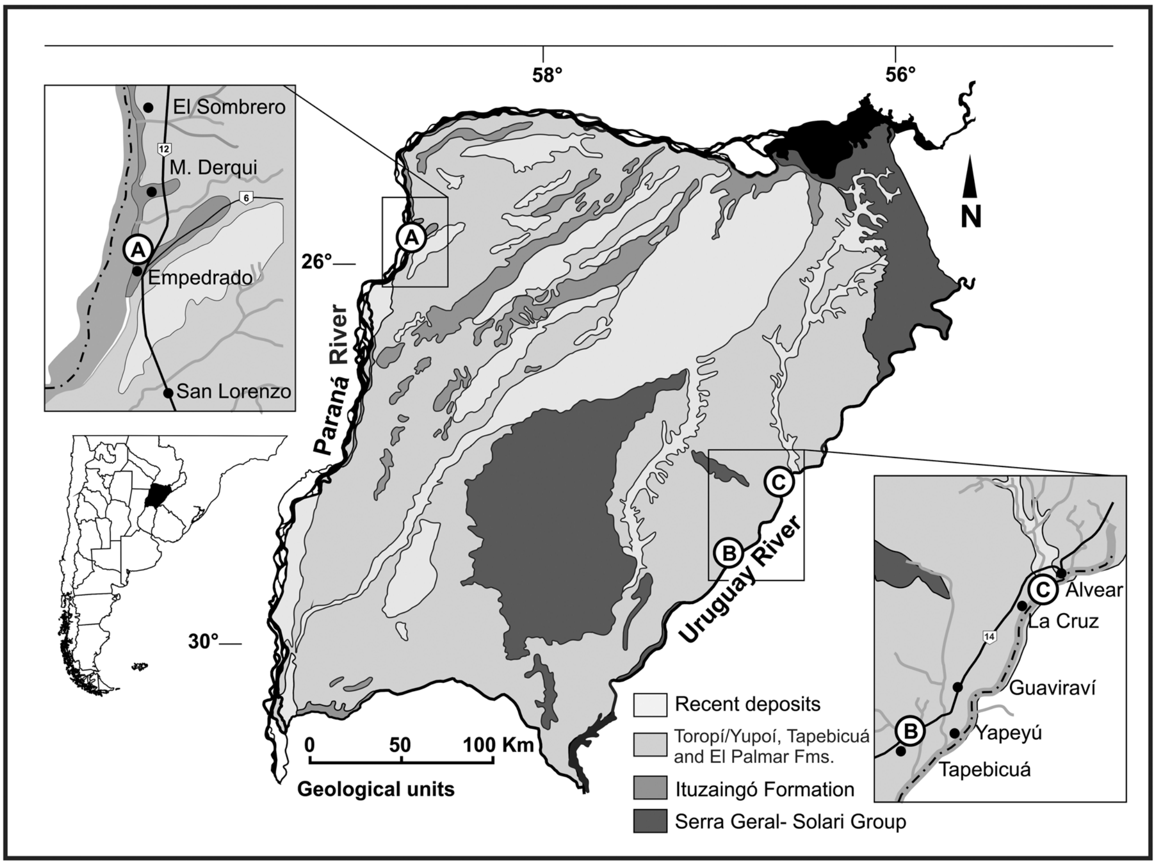

Figure 2. Geographic map of Corrientes province; arrow indicates the fossiliferous locality. A, Toropí/Yupoí Fm; B, Tapebicuá Fm; C, El Palmar Fm.

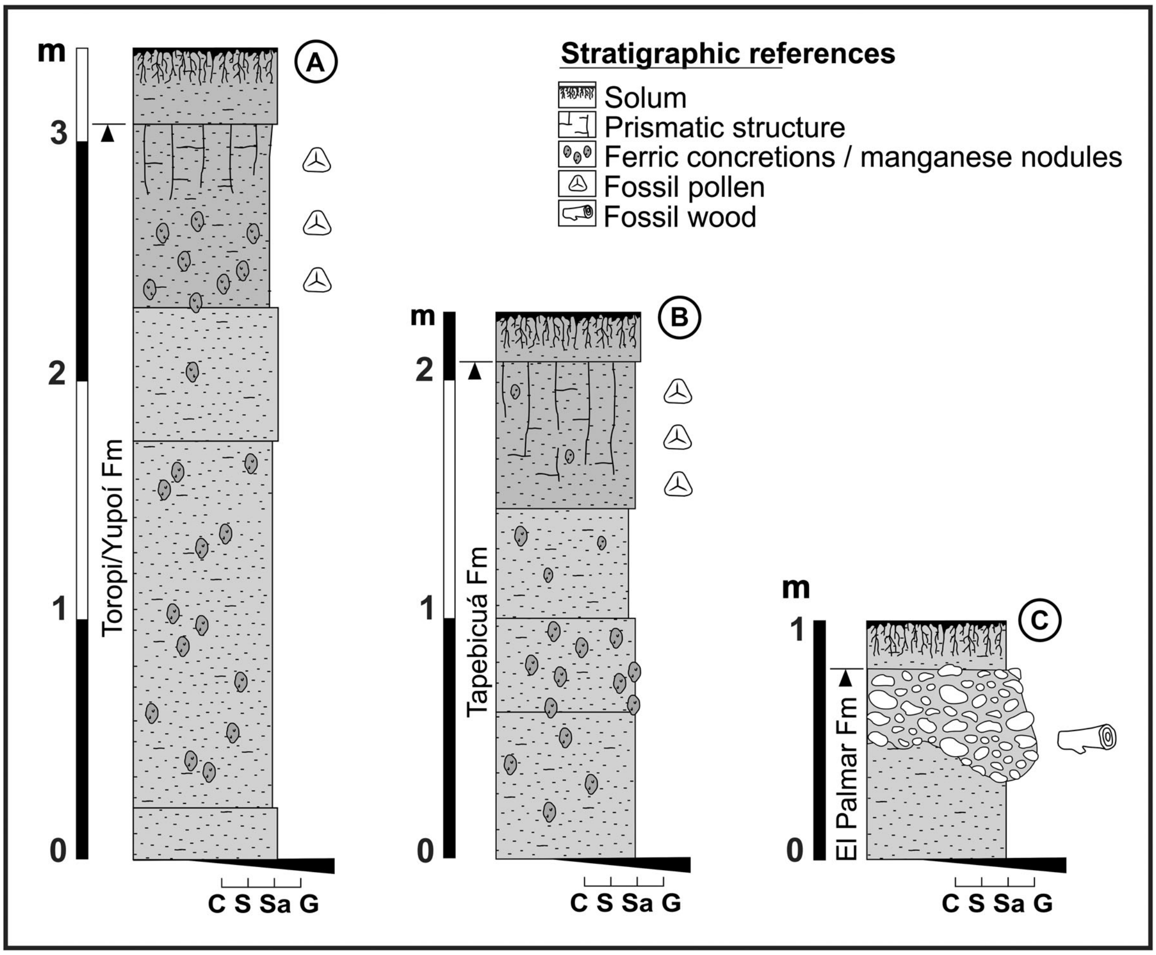

Figure 3. Stratigraphic profile. A, Toropí/Yupoí Fm; B, Tapebicuá Fm; C, El Palmar Fm.

layer of both formations. They were processed for palynology at the laboratory of CECOAL (Centro de Ecología Aplicada del Litoral)-CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas)-UNNE (Universidad Nacional del Nordeste), where they are housed in the collection 'Dr. Rafael Herbst'-PMP-CTES. The chemical techniques used to concentrate the pollen content of the samples are those used by Heusser and Stock (1984), and consisted on the elimination of carbonates, silica and silicates by means of acids (HCl and HF), partial oxidation of the organic matter with nitric acid and potassium chlorate, and removal of humates with KOH. After each stage, successive washings, filtrations and centrifugations were performed. Residues were mounted in slides using jelly-glycerin.

The morphological description of palynomorphs was carried out under a Nikon Eclipse E200 optical microscope and illustrations with a AmScope MU1803 18-mp video camera (40× and 100× magnification), and England Finder coordinates are provided. We followed the classification of Curtis et al. (2001) and Raven et al. (1991) for pollen grains, and the APG IV Classification System (The Catalogue of Life Partnership, 2017). The terminology used for descriptions of pollen grains is after Punt et al. (2007) and contributions of Sáenz Laín (2004). For the identification of pollen grains, the reference collection PMP-CTES of the UNNE and specialized literature were consulted (e.g. Acevedo and Anzótegui, 1998; Anzótegui and Ferrucci, 1998; Cuadrado, 1998; Anzótegui, 2001; Anzótegui and Caccavari, 2001; Anzótegui and Mautino, 2001a, b; Garralla and Cuadrado, 2001; Caccavari and Dome, 2001, 2006; Fernandez Pacella et al., 2014a, b). Pollen data are presented as the relative frequency of pollen of each taxon in pollen diagrams using the TILIA-TILIA GRAPH and TGView v.2.0.2 computer programs (Grimm, 2004).

The woody samples come from the upper member of the El Palmar Formation at La Cruz (San Martín Department) in Corrientes province (see Fig. 2).

Silicified wood fragments (mineralized) with well-preserved tissues were selected for our analysis. Thin sections (transverse, radial longitudinal and tangential longitudinal) were observed under a DL500 microscope and illustrations were made via a Leica ICC50 video camera, and a Leica M50 stereoscope with Leica EC3 digital video camera.

Cell dimensions of the wood fragments were based on at least 25 measurements, the average value being in all cases cited first and the minimum and maximum values given in parentheses. The terminology used in the present study was taken from IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989; Carlquist, 2001; Kribs, 1935; Boureau, 1957; Tortorelli, 2009; Cozzo, 1964), and the standard classifications of Chattaway (1932) and Avise and Johns (1999). The catalogue of Gregory et al. (2009) on the genera and fossil species of magnoliopsids was used. The APG IV system of flowering plant classification (Chase et al., 2016) were followed.

The study examined the anatomical features of wood fragments in detail to determine the climatic and ecological conditions to which they were exposed. The analysis focused on water transport-related characteristics such as porosity, density of vessels (no. mm^{-2}), vessel length, vessel type, axial parenchyma type, drilling plate type, pit type, presence of crystals and tylosis (Wheeler and Baas, 1991; Lindorf, 1994; Moglia and Giménez, 1998). The Vulnerability Index (VI) and

Mesomorphy Index (MI) were also calculated (Carlquist, 1977) where VI = mean vessel diameter/vessel diameter per mm^2, and MI = VI × length of vessel elements.

Results

Palynological analysis allowed us to identify 15 pollen taxa given below in alphabetical order by family and genera. The results of the palynological analyses are presented in percentage palynological diagrams (Figs. 4 and 5).

Pollen grains

Family ANACARDIACEAE

Myracrodruon balansae (Engl.) Santin (Plate 1A, B)

Description: Tricolporate pollen grain, radial symmetry. [Polar Axis (PA)] 21–28 μm, subprolates (Ecuatorial Axis) 16–24 μm. Isopolar. Colpi 2.5 μm wide, lalongate endoapertures 1.4–2.1 × 7–10 μm (height × width). Exine 1.4 μm thick. Sexine semi-tectate. Surface striate, short and wide striations less than 2.5 μm in length, and greater than 1.7 μm in width, walls 0.5 μm wide and from 0.2 to 0.3 μm high.

Comparisons: The specimens were compared to *Myracrodruon* (=*Astronium*) *balansae* (Anzótegui, 2001), present in the flora of Corrientes. The main distinguishing morphological characters are exine with a tendency to being striated in the polar area and striated in the mesocolpi; short and wide stretch marks.

Schinopsis balansae Engl. (Plate 1C–F)

Description: Tricolporate pollen grain, radial symmetry. (PA) 27–30 μm, (EA) 26–28 μm. Isopolar. Colpi 1–2.5 μm in maximum equatorial width, acute or blunt apices. Lalongate endoapertures 3–4 × 7–8 μm (height × width). Exine 0.7–2 μm thick. Surface striate, long striations, longer than 2.5 μm and 1 μm or less in width, wall slightly greater than 0.5 μm in height.

Comparisons: The specimens were compared to *Schinopsis balansae* (Anzótegui, 2001), present in the flora of Corrientes. The main morphological characters that allowed this identification are: longer and narrow stretch marks; equatorial axis size and endoapertures.

Schinus longifolia Speg. and Girola (Plate 1 G, H)

Description: Tricolporate pollen grain, radial symmetry. (PA) 25–30 μm, (EA) 20–22 μm. Isopolar. Colpi from 1 to 2.5 μm wide, with ribs 1.4–3.5 μm thick at the equator limited by a small psilate margin 2 μm wide. Lalongate endoapertures 1 × 10 μm. Exine 0.7–2.5 μm thick. Surface striate, long striations (more than ~2.5 μm long).

Comparisons: The morphology of our specimens agrees with *Schinus longifolia* described by Anzótegui (2001) present in the flora of Corrientes. The main distinguishing morphological characters are longer and narrow stretch marks; equatorial axis size and endoapertures.

Family CELTIDACEAE

Celtis iguanaea (Jacq.) Sarg. (Plate 1I, J)

Description: Triporate pollen grain, radial symmetry. (PA) 25–28 μm, (EA) 23–30 μm. Isopolar. Pores slightly sunken, circular 1–2 μm in diameter, limited by a ring 0.5–2 μm thick. Exine 0.5–1.4 μm thick. Scabrate.

Comparisons: The specimens were compared to *Celtis iguanaea* (Anzótegui and Mautino, 2001a) present in the flora of Corrientes. The main morphological characters that allowed

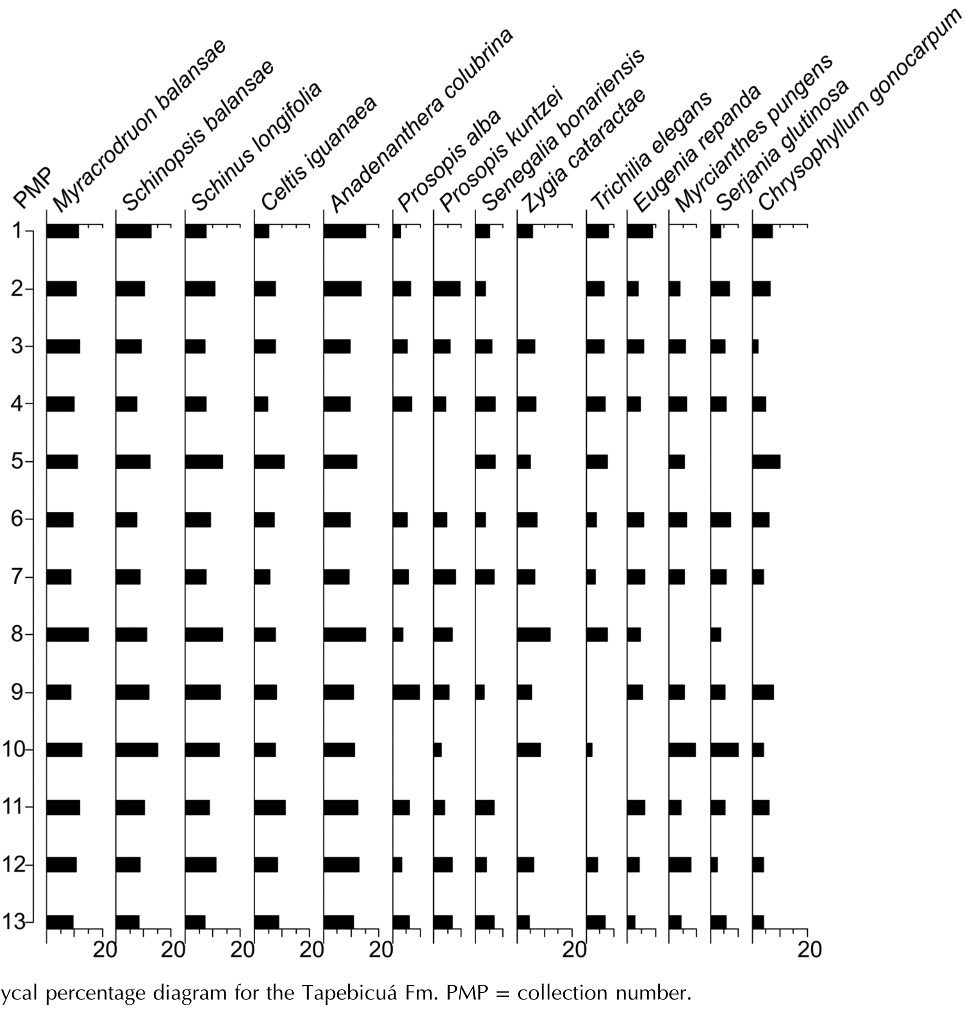

Figure 4. Palynologycal percentage diagram for the Tapebicuá Fm. PMP = collection number.

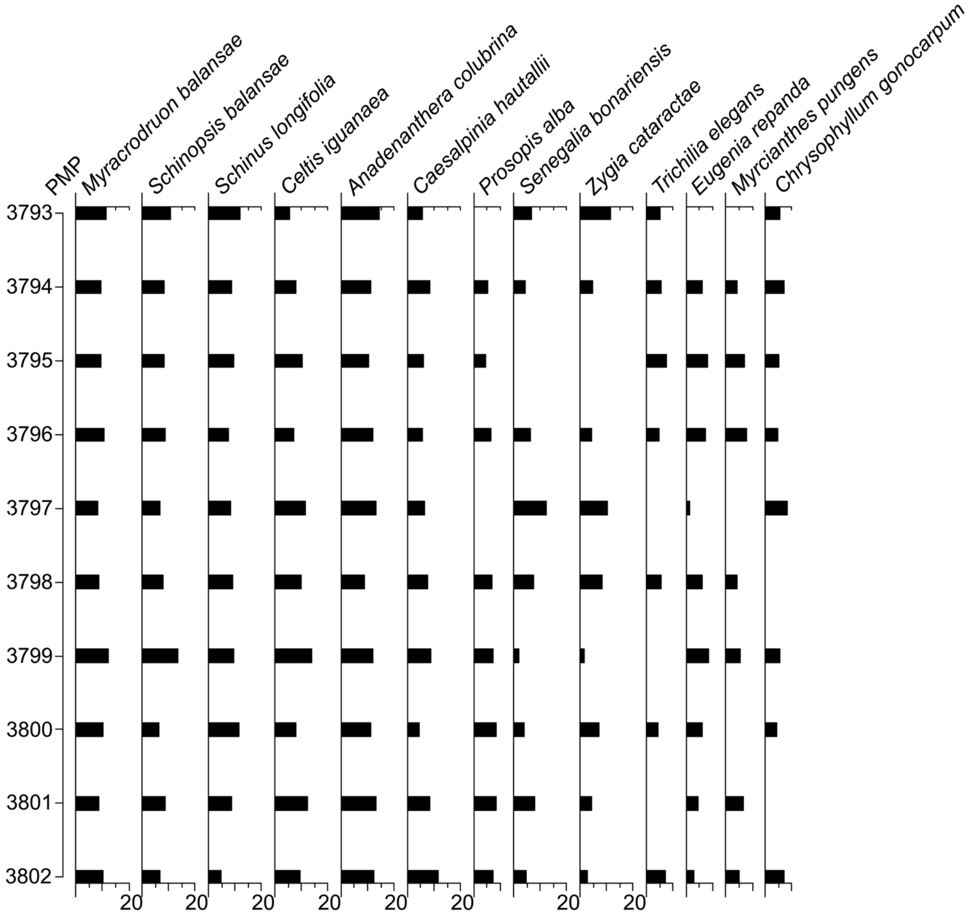

Figure 5. Palynologycal percentage diagram for the Toropí/Yupoí Fm. PMP = collection number.

identification are: number of endoapertures, thickness of the exine and sculpture type.

Family LEGUMINOSAE

Anadenanthera colubrina (Vell.) Brenan (Plate 1 K, L)

Description: Polyads spheroidal to ellipsoidal formed by 16 pollen grains regularly arranged, 33–37 × 34–40 μm in size. Exine 1.3 μm thick. Verrucate, warts 1 μm in diameter.

Comparisons: The specimens were compared to *Anadenanthera colubrina* (Caccavari and Dome, 2006) present in the flora of Corrientes. The main distinguishing morphological characters are number and arrangement of pollen grains in the polyad and sculpture type.

Caesalpinia hautallii Harms. (Plate 1 M, N)

Description: Tricolporate pollen grain of radial symmetry. Medium in size, isopolar, subspheroidal (PA) 47–55 μm, (EA) 47–52 μm. Colpi width 14–17 μm, with aperture zone limited by an exine ridge. Exine 2–3 μm thick, semi-tectate reticulate.

Comparisons: The specimens were compared to *Caesalpinia hautallii* (Fernandez Pacella et al., 2014b) present in the flora of Corrientes. The main morphological characters that allowed identification are: aperture zone limited by an exine ridge and sculpture type.

Prosopis alba Griseb. (Plate 1 O, P)

Description: Tricolporate pollen grain of radial symmetry. Small to medium in size, subtriangular–spheroidal (PA) 22–36 μm, prolate (EA) 18.5–33 μm. Isopolar. Long colpi and small endoapertures (2.5–5.6 μm in diameter). Exine 1–2 μm thick, sexine semi-tectate, scabrate.

Comparisons: The specimens were compared to *Prosopis alba* (Fernandez Pacella et al., 2014b) present in the flora of Corrientes. The main morphological characters are size of pollen grains and sculpture type.

Prosopis kuntzei Harms. (Plate 2 A, B)

Description: Tricolporate pollen grain of radial symmetry. Small to medium size, subtriangular–spheroidal (PA) 22–33 μm, (EA) 21–30 μm. Isopolar. Long colpi and small pores (3–4 μm in diameter). Exine 1–2 μm thick, sexine tectate, psilate.

Comparisons: The specimens were compared to *Prosopis kuntzei* (Fernandez Pacella et al., 2014) present in the flora of Corrientes. The main morphological characters that allowed identification are: size of pollen grains and sculpture type.

Senegalia bonariensis (Gillies ex Hook. and Arn.) Seigler and Ebinger (Plate 2 C, D)

Description: Polyads formed by 16 monads with regular arrangement, size 32 (33) 34 × 32 (33.5) 35 μm. Exine 1–1.9 μm thick. Sexine tectate, granulate.

Comparisons: The morphology of our specimens agrees with *Senegalia (=Acacia) bonariensis* Gill. ex Hook. et Arn. described by Caccavari and Dome (2001). The main morphological characters that allowed identification are: size of the polyads and slightly granulated exine.

Zygia cataractae (Kunth) L. Rico (Plate 2E, F)

Description: Polyads spheroidal formed by 16 pollen grains regularly arranged. Diameter 69–79 μm. The contour of pollen grains is quadrangular. Exine 1.85 μm thick, psilate.

Comparisons: The specimens were compared to *Pithecellobium cauliflorum* (Roxb.) Benth. (Home et al., 2012), as the main morphological characters are similar. Currently *Zygia cataractae* is the synonym of *Pithecellobium cauliflorum* (Anton and Zuloaga, 2021).

Family MELIACEAE

Trichilia elegans A. Juss. (Plate 2 G, H)

Description: Tetracolporate pollen grain with radial symmetry. Small in size, (PA) 24–29 μm, (EA) 22–25 μm. Isopolar.

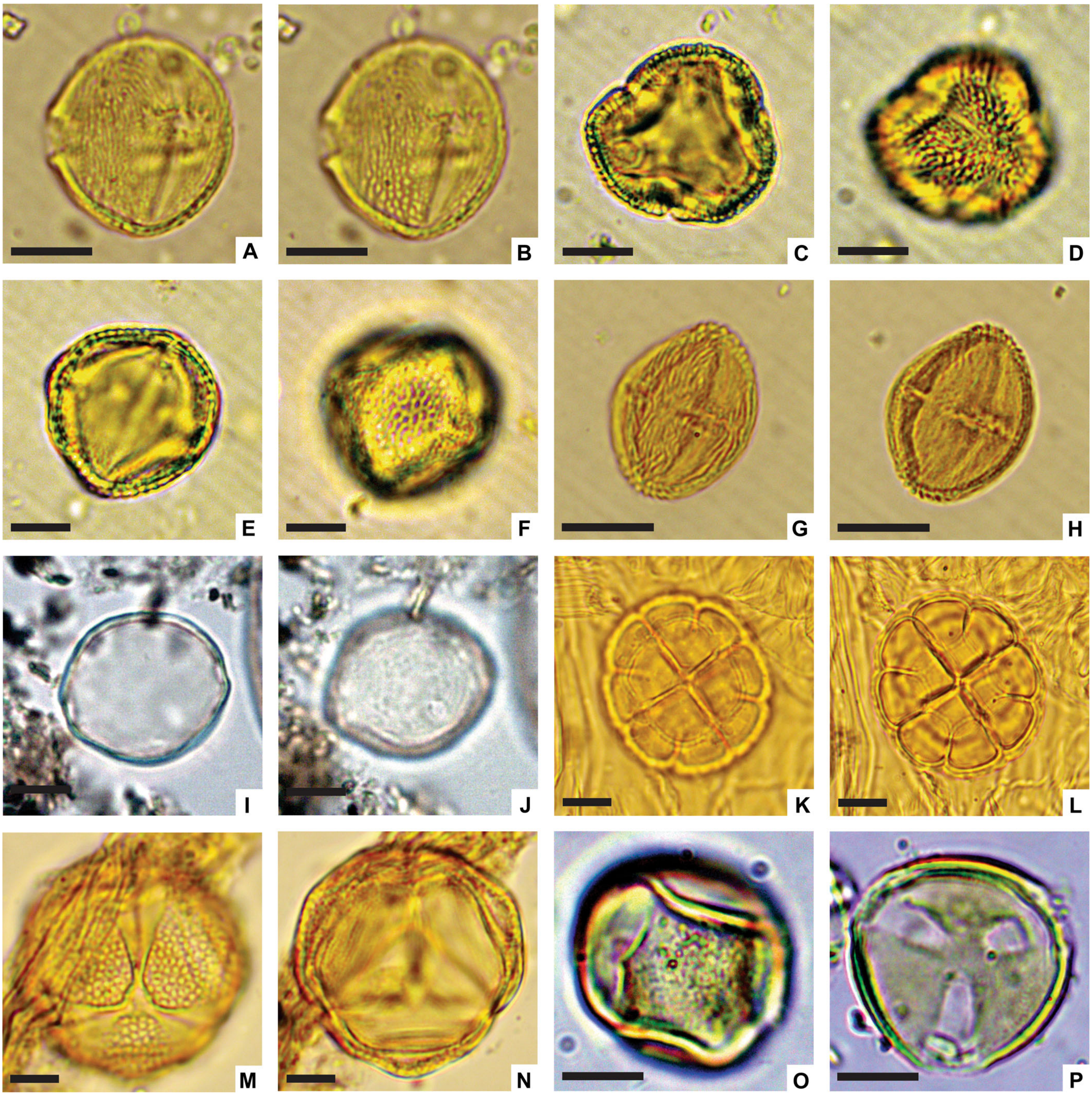

Plate 1. *Myracrodruon balansae*. A: equatorial view in optical section (100×). B: equatorial view in upper focus (100×). *Schinopsis balansae*. C: polar view in optical section (100×). D: polar view in upper focus (100×). E: equatorial view in optical section (100×). F: equatorial view in upper focus (100×). *Schinus longifolius*. G: equatorial view in upper focus (100×). H: equatorial view in optical section (100×). *Celtis iguanaea*. I: equatorial view in optical section (100×). J: equatorial view in upper focus (100×). *Anadenanthera colubrina*. K: poliade in upper focus (100×). L: poliade in optical section (100×). *Caesalpinia hautallii*. M: polar view in upper focus (100×). N: polar view in optical section (100×). *Prosopis alba*. O: equatorial view in upper focus (100×). P: polar view in optical section (100×). Scale bars: 10 μm. [Color figure can be viewed at wileyonlinelibrary.com]

Colpi 15–17 μm long, lalongate endoapertures 2 × 6 μm, with ring thickening of 1.4–3 μm. Exine 1.4 μm thick, perforate.

Comparisons: The specimens were compared to *Trichilia elegans* (Garralla and Cuadrado, 2001) documented in the flora of Corrientes. The main morphological characters that allowed identification are: prolate to subprolate pollen grains and perforated exine.

Family MYRTACEAE

Eugenia repanda Berg. (Plate 2I, J)

Description: Tricolporate grains, radial symmetry, small (PA) 15–17 μm, (EA) 14–18 μm, triangular to subtriangular amb, anguloaperturates. Linear colpi. Endoapertures 2.1 × 3.5 μm. Exine 1.4-2 μm thick. Perforate.

Comparisons: The morphology agrees with *Eugenia repanda* described by Acevedo and Anzótegui (1998), present in the flora of Corrientes. The main morphological characters are similar, such as free colpis at both poles, size of pollen grains and sculpture type.

Myrcianthes pungens (O. Berg) D. Legrand (Plate 2 K, L)

Description: Tricolporate pollen grain, radial symmetry. Small in size, (PA) 11–15 μm, (EA) 9–13 μm. Isopolar. Linear or wide colpi. The apocolpium fields can have well-defined or diffuse edges and are of different sizes in both poles. Pores 1.4–2 μm. Exine 0.7–3 μm thick, sexine tectate, psilate.

Comparisons: The specimens were compared to *Myrcianthes pungens* (Acevedo and Anzótegui, 1998) present in

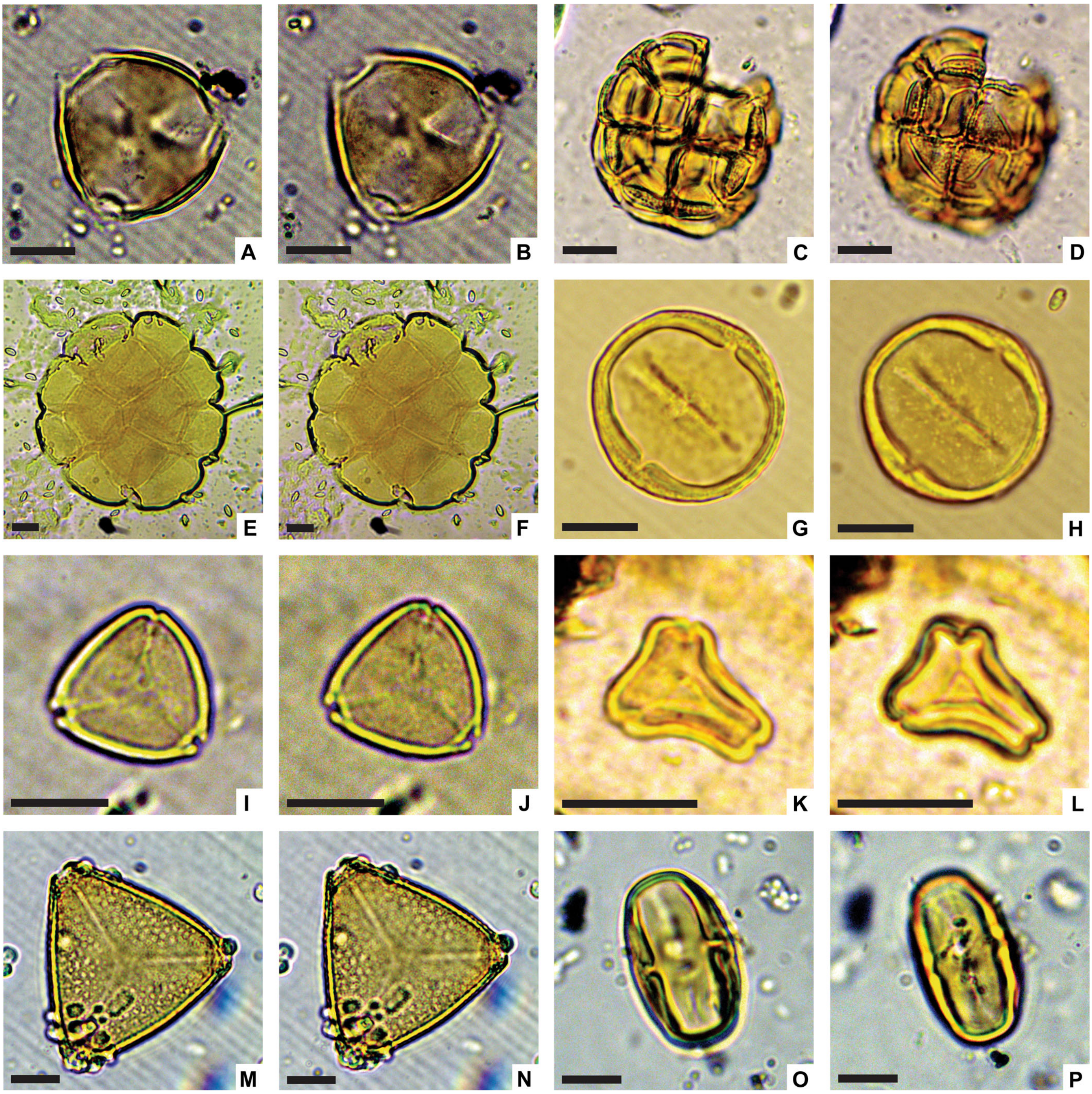

Plate 2. *Prosopis kuntzei*. A: polar view in optical section (100×). B: polar view in upper focus (100×). *Senegalia bonariensis*. C: polyad in optical section (100×). D: polyad in upper focus (100×). *Zygia cataractae*. E: polyad in upper focus (100×). F: polyad in optical section (100×). *Trichilia elegans*. G: equatorial view in optical section (100×). H: equatorial view in upper focus (100×). *Eugenia repanda*. I: polar view in upper focus (100×). J: polar view in optical section (100×). *Myrcianthes pungens*. K: polar view in optical section (100×). L: polar view in upper focus (100×). *Serjania perulacea*. M: polar view in upper focus (100×). N: polar view in optical section (100×). *Chrysophyllum marginatum*. O: equatorial view in optical section (100×). P: equatorial view in upper focus (100×). Scale bars: 10 μm. [Color figure can be viewed at wileyonlinelibrary.com]

the flora of Corrientes. The main morphological characters that allowed identification are: colpis with forked ends delimiting apocolpium fields and size of pollen grains.

Family SAPINDACEAE

Serjania glutinosa Radlk. (Plate 2M, N)

Description: Tricolporate pollen grain, radial symmetry. (PA) 15–28 μm, (EA) 28–44 μm. Heteropolar. Linear colpi joined at the apertural pole, wide (1–2 μm), reaching the equator, bulging pore. Exine 1–2.5 μm thick, reticulate. Circular to polygonal lumens, 1–3.7 μm in diameter.

Comparisons: The morphology agrees with *Serjania glutinosa* described by Anzótegui and Ferrucci (1998), present in the flora of Corrientes. The main morphological characters are similar, such as colpis fused into a single pole and sculpture type.

Family SAPOTACEAE

Chrysophyllum gonocarpum (Mart. et Eich.) Engler (Plate 2 O, P)

Description: Tetracolporate pollen grain with radial symmetry. Colpi 13 μm long, lalongate endoaperture, protruding, 4 × 2.5 μm with annular thickening 1.4 μm. (PA) 26–30 μm, (EA) 20–23 μm. Exine 2 μm thick at polar level and 3.5 μm at the equatorial level, psilate. No supratectal sculpture observed.

Comparisons: The specimens were compared to *Chrysophyllum gonocarpum* (Cuadrado, 1998) present in the flora of Corrientes. The main morphological characters that allowed identification are: length of colpis, thickness of exine and sculpture type.

Main features of the assemblages

The quantitative composition of the 13 samples of the marsh facies of the Tapebicuá Formation indicated the presence of *Myracrodruon aff. balansae* (11%), *Schinopsis aff. balansae* (12%), *Schinus aff. longifolia* (7%), *Celtis aff. iguanaea* (5%), *Anadenanthera aff. colubrina* (15%), *Prosopis aff. alba* (9%), *Prosopis aff. kuntzei* (5%), *Senegalia aff. bonariensis* (5%), *Zygia aff. cataractae* (6%), *Trichilia aff. elegans* (6%), *Eugenia aff. repanda* (5%), *Myrcianthes aff. pungens* (5%), *Serjania aff. glutinosa* (4%) and *Chrysophyllum aff. gonocarpum* (7%) (Fig. 4).

The quantitative composition of the ten samples of the marsh facies of the Toropí/Yupoí Formation indicated the presence of *Myracrodruon aff. balansae* (9%), *Schinopsis aff. balansae* (6%), *Schinus aff. longifolia* (9%), *Celtis aff. iguanaea* (7%), *Anadenanthera aff. colubrina* (11%), *Caesalpinia aff. hautallii* (6%), *Prosopis aff. alba* (5%), *Senegalia aff. bonariensis* (7%), *Zygia aff. cataractae* (7%), *Trichilia aff. elegans* (5%), *Eugenia aff. repanda* (5%), *Myrcianthes aff. pungens* (6%) and *Chrysophyllum aff. gonocarpum* (7%) (Fig. 5).

Mineralizaed wood fragments

Family LEGUMINOSAE

Type species: *Menendoxylon vasallensis* Lutz, 1979

Menendoxylon lutzi Baez and Crisafulli 2021 (Plate 3)

Description: Silicified wood fragment. Preservation of scarce tissue. Growth rings are marked in the cross-section. Diffuse porosity. The vessels are mostly solitary (52%) and radial multiples of 2–3 (48%). They have a tangential diameter of 126 (100–170) µm and radial diameter of 190 (110–260) µm. Vessel density is 17 mm^{-2}. The vessels have an oval to circular contour. Fibers are not visible due to poor preservation. Presence of either gums or resins. The axial parenchyma is aliform and vasicentric paratracheal. The rays have a straight disposition. In radial longitudinal section, the vessel elements are on average 621 (388–1033) µm in length. Rays are composed of procumbent cells. In longitudinal tangential section, intervessel pits are vestured and alternate and perforation plates are simple. Presence of crystalliferous parenchyma. Wood rays are uniseriate (45%), biseriate/partially uniseriate (30%) and triseriate (25%). Ray height (expressed as the cell number) is 11 (5–17) µm.

Comparisons: This is a new record of Leguminosae wood and the morphoanatomical characters are similar to those of *Menendoxylon lutzi* Baez and Crisafulli recorded in the Miocene sediments of the Chiquimil Formation in Catamarca province. These main features are diffuse porosity, solitary and multiple radial 2- and 3-element vessels, vasicentric and aliform paratracheal parenchyma, homogeneous rays of procumbent, uniseriate, partially biseriate and triseriate cells, vessels with ornate and alternate pits, simple perforation plates and presence of crystalliferous parenchyma. Although the holotype has biseriate rays and confluent parenchyma, these are minor differences with our specimen that do not justify the creation of a new species.

The finding of this Leguminosae in the sediments of the La Cruz locality provides a new record of this family in the Mesopotamia region since the first records were described by Lutz (1979), from the Salto Chico and Ituzaingó Formations (Pliocene–Pleistocene) in the province of Entre Ríos. Lutz erected the genus *Menendoxylon* with three morphospecies *M. vasallensis*, *M. mesopotamiensis* and *M. areniensis*. The last of these was reassigned to *Mangroveoxylon areniensis* Moya and Brea in the Ituizangó Formation. *M. vasallensis* was found in this unit by Lutz (1979) and Franco and Brea (2013), and in the Chiquimil Formation (Catamarca) by Baez et al. (2018). *M. mesopotamiensis* was found in the Ituzaingó Formation (Lutz, 1979) and Las Cañas Formation (Martínez and Crisafulli, 2019) in Santiago del Estero.

This occurrence extends the *Menendoxylon* biochron to the Late Pleistocene and extends the (bio)stratigraphic record to the El Palmar Formation, again confirming the evolutionary success of this family in South America.

The vulnerability (VI = 7.41) and mesomorphic (MI = 4602) indices obtained indicate that the fossil specimen analysed is mesomorphic, vulnerable to cavitation and efficient in water transport, with good adaptability of the wood to humidity, especially for seasonally dry humid ecosystems.

Discussion

The woody and shrubby association whose current relatives characterize the SDTF is composed of the 16 fossil species described here belonging to seven families. It is of note that, in the Middle Miocene *Myracrodruon balansae*, *Zygia cataractae* and *Anadenanthera colubrina* were already installed in the northwestern region (Anzótegui et al., 2017). *Anadenanthera colubrina* stands out in having a longer temporal and areal distribution, since Barreda and Caccavari (1992) found it in Lower Miocene sediments in Argentine Patagonia, whereas in the northwest region it is recorded from the Middle Miocene to the Present. The presence of these families reflects the same current trend suggested by Prado (2000), Prado and Gibbs (1993), Pennington et al., (2000, 2004), Caetano et al. (2008), Mogni et al. (2015) and Banda-R et al. (2016) for current SDTF associations in Argentina.

In our samples, *Anadenanthera colubrina* and *Myracrodruon balansae* are the most significant members of the families Leguminosae and Anacardiaceae, which are dominant in the SDTF (Prado and Gibbs, 1993; Prado, 1995, 2000; Pennington et al., 2000, 2004; Mayle, 2004; Mayle et al., 2004; Gosling et al., 2005; Caetano et al., 2008; Mogni et al., 2015).

The debate regarding when neotropical species arose and how climatic changes have affected their evolution has focused mainly on tropical rainforests, and especially those in the Amazon basin. According to Pennington et al. (2004), evolutionary rate analysis indicates that the diversification of species in the SDTF with high levels of endemism occurred during the Late Miocene and Pliocene. Therefore, the paleovegetation of the Neogene of northern Argentina, which was described by Anzótegui and Horn (2011) and Mautino and Anzótegui (2014), can be considered the predecessor of the current SDTF.

During the Middle Miocene, *Anadenanthera* integrated the floras of northwestern Argentina (Santa María Valley) constituting paleocommunities of hygrophilous forest in which Myrtaceae predominated (*Myrtipites* sp., *Myrtipites annulatus* Cookson, *Syncolporites minimus* Leffingwell, *Myrtaceidites parvus* Cookson and Pike), Ulmaceae (*Ulmipollenites undulosus* Wolf) and other Leguminosae (*Rhoipites exiguous* Pocknall) (Mautino, 2009). This evidence, together with the records of leaves and fruits, confirms the existence of warm climatic conditions, seasonally dry and locally humid, with development of water bodies that allowed the existence of these forests and hygrophilous vegetation during this period in northwestern Argentina (Anzótegui, 2006). Since the Middle–Late Miocene, the genus formed part of the vegetation of northeastern Argentina (Santa Fe and Entre Ríos provinces), and together with *Astronium* Jacq., *Celtis* L., *Schinus* L. and *Janusia* A. Juss., characterizes dry semi-deciduous forests (Brea & Zucol, & Franco, 2013).

After the Miocene Climatic Optimum, there was a decrease in temperature and rainfall, which led to an increase in temperatures extremes. Towards the end of the Neogene, from

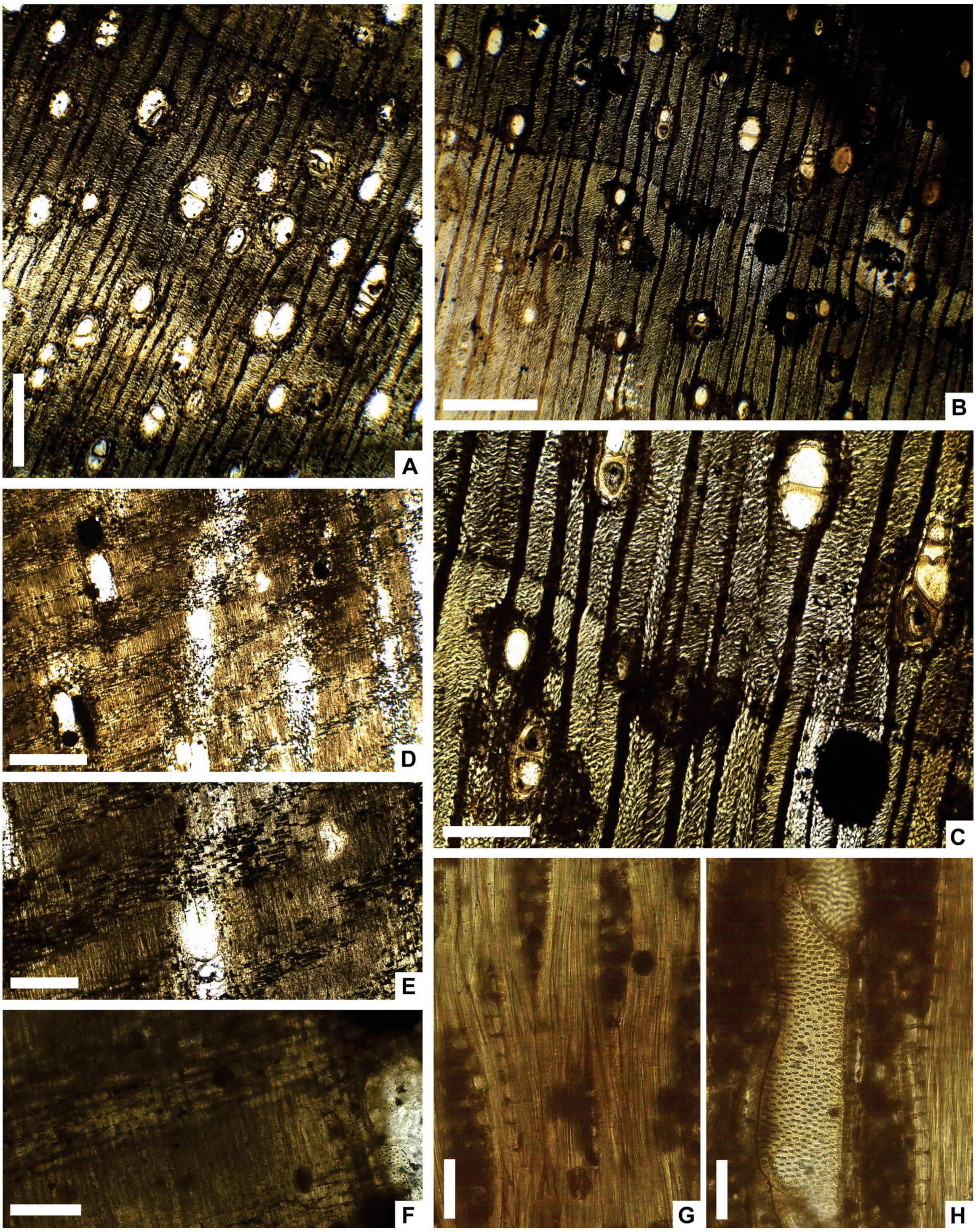

Plate 3. *Menendoxylon lutzi.* (A–C) Cross-sections of wood. A: growth rings are marked (arrow); diffuse porosity and vessels oval to circular in shape. B: vessels with dark content and vasicentric paratracheal parenchyma. C: detail of photo B. (D–F) Radial longitudinal sections. D: appearance of the short vessel elements and rays formed by procumbent cells. E–F: detail of procumbent cells. G–H: tangential longitudinal sections. G: appearance and seriation of rays. H: vessel with alternate and ornate intervessel pits. Scale bars: A, B, E, F = 200 μm; C = 100 μm; D = 500 μm; G, H = 50 μm. [Color figure can be viewed at wileyonlinelibrary.com]

the Middle Miocene to Pliocene, several factors contributed to an increase in aridity in the subtropical regions of South America (Hinojosa and Villagrán, 197; Latorre et al., 1997; Villagrán and Hinojosa, 1997). During the Pliocene, the separation of South America from Antarctica, the establishment of the Circumpolar and Humboldt Currents, and the glaciation of western Antarctica played a significant role in the expansion of dry semi-deciduous floras. Additionally, the rain shadow effect caused by uplift of the Andes Mountains also contributed to this expansion. Evidence for this is given by Reguero et al. (2014) and Reguero and Goin (2021). The climate in which these paleocommunities developed would have been warm with conditions that ranged from humid to semi-arid since the flora of southwest Argentine Mesopotamia demonstrates the existence of a heterogeneity of environments and different types of plant communities (Brea & Zucol, & Franco, 2013).

Some very interesting distribution patterns emerged in South America, which have led to speculation regarding the influence of past wet–dry climatic fluctuations in the region (Prado and Gibbs, 1993). One of these is the 'Arc of Residual Pleistocene Seasonal Formations' or Pleistocene Arch (Prado and

Gibbs, 1993), which comprises a remarkable group of woody vegetation types, here considered as seasonal forests. These vegetation units are remarkable when they are compared with other formations across the continent (Prado, 2000).

Study of the current distribution of SDTFs supports the idea that these formations were more widespread in the cooler, drier periods of the Pleistocene (Prado and Gibbs, 1993; Toby Pennington et al., 2000). This is supported in part by the vegetation modeling of Mayle et al. (2004), showing that broadleaf deciduous forests covered the southern half of Amazonia during the Last Glacial Maximum. The distribution pattern of the woody species of the seasonal forests of South America is very significant in the map of what has been called the Pleistocene Arc (Prado and Gibbs, 1993). Therein, three concentrations or 'cores' can be clearly distinguished: (i) 'Caatingas core' in northeastern Brazil; (ii) 'Misiones core' in the Paraguay–Paraná fluvial system in northeastern Argentina, eastern Paraguay and southwestern Mato Grosso do Sul; and (iii) 'core of the Sub-Andean Pedemontane' of the Sub-Andean Pedemontane Forests in southwestern Bolivia and northwestern Argentina (see Fig. 1). The distribution of SDTF in Corrientes province during the Late Pleistocene (Fig. 6) is represented by three formations: Toropí/Yupoí to the northwest, El Palmar to the east and Tapebicuá to the southeast. The species identified in this study support the presence of these formations within the 'Misiones core', and, in turn, the characteristics of seasonal forests related to humid to semi-arid climates of the plant species present and that would favor the development of the SDTF during the Pleistocene in this region ratify the extension of the Pleistocene Arch to Corrientes province.

The Caatingas core is connected to the Misiones core through a 'track', which extends along the São Francisco and Jequitinhonha rivers (northeastern Brazil) to northeastern Argentina (Prado and Gibbs, 1993). The latter region is reported to have been subject to intense wet–dry climatic fluctuations during the Pleistocene (Cailleux and Tricart, 1959; Tricart, 1961). The Upper Pleistocene of southern South America experienced a repeated alternation of dry and warm/humid events. This alternating connection of the area with environments characteristic of the Pampas plains and tropical regions occurred at certain times. This situation is widely accepted and is compatible with the Quaternary period (Zurita and Lutz, 2002; Carlini et al., 2008; Ubilla et al., 2004; Zacarías et al., 2014; Fernandez Pacella et al., 2020; Prevosti et al., 2021; Alvarez-Herrera et al., 2022). On the other hand, high concentrations of montmorillonite, illite and kaolinite clays may indicate complex climatic conditions with semi-arid periods with well-defined seasons and periods of humid and temperate climate (Iriondo, 2007).

The pollen records described here together with the available mastozoological evidence indicate that the climatic scenario in which the formations analyzed were deposited was quite complex. The dates obtained for the Toropí/Yupoí and Tapebicuá Formations indicate that they are contemporaneous and would correspond to MIS5. The faunal records recovered from levels of the Toropi/Yupoí Formation indicate a alternation of warm and cold intervals based on the presence of species such as *Leopardus pardalis* (Prevosti et al., 2021) typical of tropical and subtropical habitats, with mammals and birds typical of cool temperate regions such as *Dolichotis patagonum* (Zurita et al., 2014; Francia et al., 2019) and *Choelophaga* (Alvarez-Herrera et al., 2022) indicating different climatic conditions during the deposition of this formation. By contrast, phytolith analysis by Contreras et al. (2019) in the Toropí/Yupoí Formation indicates a seasonal subtropical climate. With regard to the El Palmar Formation, ages also place it within MIS5, and based on geological and micro-paleobotanical records Patterer et al. (2020) inferred warm and humid conditions during most of the deposition of this formation. On the other hand, phytolith analysis in the Toropí/Yupoí Formation indicates a seasonal

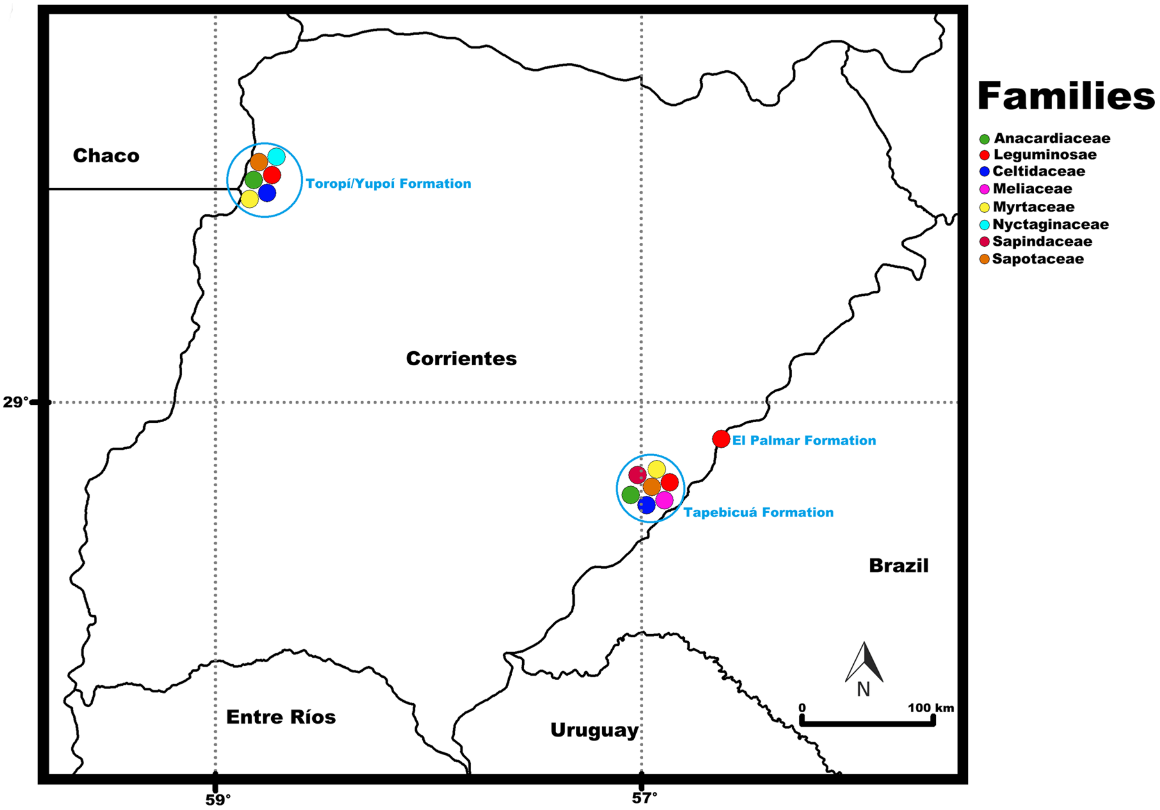

Figure 6. Map of the province of Corrientes, Argentina, indicating the presence of plant families in three formations: Toropí/Yupoí, Tapebicuá and El Palmar. [Color figure can be viewed at wileyonlinelibrary.com]

subtropical climate (Contreras et al., 2019). Patterer et al. (2020) studied the geological and micro-paleobotanical record of the El Palmar Formation and inferred that its deposition occurred in warm and humid conditions for the most part within the MIS5 period. Similarly, Ernesto et al. (2015) also recorded sequences in southern Entre Ríos province assigned to the same period. Patterer and Frezzia (2022) interpreted a paleoflora composed of a continuous herbaceous layer of meso-megathermic grasses accompanied by isolated trees and palms based on the phytolith associations described in this area. The landscape was mostly open savanna with low rainfall and high temperatures, suggesting a temperate/warm climate.

Conclusion

The woody and shrubby association described here, whose current relatives characterize the SDTF, allows us to assume the existence of SDTF (see Fig. 6) in Corrientes province (of which there is no record so far) during the Late Pleistocene, thus allowing us to infer the extension of the SDTF in northeastern Argentina during the late Quaternary. This confirms the 'Pleistocene Arch' theory on the influence of past wet and dry climate fluctuations in South America on patterns of seasonal forest distribution.

It is noteworthy that the spatial and temporal succession of the SDTF in Argentina would have been closely associated with the tectonic and climatic events that occurred during the Neogene and Quaternary, coexisting, in the Mesopotamia Region (provinces of Corrientes, Entre Ríos, Misiones and Santa Fe), with two different types of climate: warm-humid and temperate-dry.

Likewise, information obtained based on the vulnerability and mesomorphy indices from *Menendoxylon* agrees with the paleoclimatic inferences presented in this work and provides further understanding of the climate and environment in the region during the period studied.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Abbreviations. CTES-PMP, Colecciones Paleontológicas de la Universidad Nacional del Nordeste 'Dr. Rafael Herbst' – Preparados Micropaleontológicos, Corrientes; EA, equatorial axis; MI, Mesomorphy Index; PA, polar axis; SDTF, seasonally dry tropical forest; VI, Vulnerability Index.

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