# Pollen and spores morphology from the Holocene of the Iberá Wetlands in northeastern Argentina

## Morfología del polen y esporas del Holoceno de los Esteros del Iberá en el noreste de Argentina

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### Summary

**Background and aims**: Taxonomic works of the modern pollen grains from the vegetation of the Iberá Wetlands from northeastern Argentina, and other areas of the Corrientes province, have mostly been carried out in last decade. However, very few of these taxonomic works include illustration of palynomorphs. The objective of this contribution is to provide the first morphological records of palynomorphs of angiosperms, ferns, lycophytes and bryophytes from sediments from the Holocene of the Iberá Wetlands.

**M&M**: Core samples obtained by mean of a Livingston-type sampler from six lakes in their central and deepest parts on the western margin of the Iberá Wetlands were analyzed.

**Results:** Fifty-five types of palynomorphs are described and illustrated: 46 pollen types correspond to 27 families of angiosperms and nine trilete spore-types to ferns, lycophytes and bryophytes. Information to differentiate local (species that form part of the natural vegetation of the Iberá Wetlands) and extra-local taxa (those that do not belong to the Iberá), that achieved to depocenters mostly by means of wind currents coming from farther regional vegetation, was included.

**Conclusions**: Pollen grains and spores identifications up to species level enhances paleoenvironmental reconstructions based on more accurate ecologic information and geographical distribution. This work broadens the knowledge of the palynological flora of northeastern Argentina and it will contribute to differentiate the local vegetation from the extra-local in future paleocological and paleoenvironmental interpretations.

### Keywords

Corrientes Province, hydrographic system Iberá, holocene, palynomoph.

### Resumen

**Introducción y objetivos**: Los trabajos taxonómicos de polen actual de la vegetación de los esteros del Iberá en el noreste de Argentina y otras áreas de la provincia de Corrientes se han llevaron a cabo mayoritariamente en la última década. Sin embargo, muy pocos de estos trabajos incluyen la ilustración de los palinomorfos. El objetivo de esta contribución es proporcionar el primer registro morfológico de palinomorfos de angiospermas, helechos, licofitas y briofitas de sedimentos del Holoceno de los Esteros del Iberá.

**M&M**: Se analizaron muestras de núcleos obtenidos por medio de un muestreador tipo Livingston de seis lagos en sus partes central y más profunda en el margen occidental de los Esteros del Iberá.

**Resultados**: Se describen e ilustran 55 tipos de palinomorfos: 46 tipos de polen corresponden a 27 familias de angiospermas y nueve tipos de esporas triletas a helechos, licofitas y briofitas. Se incluye información para diferenciar taxones locales (que forman parte de la vegetación natural de los Esteros del Iberá) y extra-locales (aquellos que no pertenecen al Iberá) que lograron llegar a los depocentros provenientes de vegetación regional más lejana.

**Conclusiones**: La identificación de granos de polen y esporas hasta el nivel de especie mejora las reconstrucciones paleoambientales basadas sobre información ecológica y distribución geográfica más precisas. Este trabajo amplía el conocimiento de la flora palinológica del noreste de Argentina y contribuirá a diferenciar la vegetación local de la extra-local en futuras interpretaciones paleoecológicas y paleoambientales.

### Palabras clave

Holoceno, palinomorfo, Provincia de Corrientes, sistema hidrográfico Iberá.

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## Introduction

The geological history of the region currently known as Iberá Wetlands in central-eastern South America, currently northeastern Argentina, begins to have its own identity from the tectonic movements that determined the rise of the Andean mountain range (Ramos, 1999). Orogeny unleashed compressive forces from the East that fractured the powerful basaltic lava flows belonging to the Solari-Serra Geral Formation (Cretaceous) accumulated in the study region (Herbst & Santa Cruz, 1985). Thus, large blocks of rock generated and separated by several fault systems with dominant NE-SW and NW-SE strikes. The subsequent epirogenic movements gave rise to the independent adjustment of the megablocks, modeling the topography of the subsoil covered by sedimentary fill (Gentili & Rimoldi, 1979). This generated in northeastern Argentina, province of Corrientes, the extensive depression that crosses it almost entirely in a NE-SW direction, on which important fluvial runoff routes were developed. At the end of the Pliocene, water excesses were concentrated in these depressed lands, initiating its geological activity in the current Paraná River. Later tectonic movements accentuated the vertical displacement of the subsoil blocks, triggering changes in the runoff design of surface waters, and being a consequence in the province of Corrientes, the Paraná River migrated from South to North until it occupied its current position, which evidences a clear structural control (Iriondo, 1994). The central depression of the Corrientes territory disconnected from the Paraná River, in the surrounding of the town of Ituzaingó, where the old river valley transformed into a shallow basin, was inefficient to evacuate excess of water. This gave rise to the development of a complex association of lentic environments fed fundamentally by precipitation and probably by the Paraná River due to subterranean transfluence (Orfeo, 2005).

Therefore a complex association of lentic and lotic environments distributed over large areas of the Iberá Wetlands in eastern Corrientes developed during the Quaternary (Neiff, 1997; Iriondo, 2010), from which taxonomic works of modern pollen grains of floristic biomes carried out mostly in the last decades (e.g. Fernandez Pacella, 2013, 2014). This botanical and ecological information is relevant to construct modern analogs of this region applied in palynological studies of surface and subsurface samples, although very few taxonomic works with illustration of palynomorphs published up to today (Anzótegui & Garralla, 1985). Cuadrado & Neiff (1993) contributed with the first analysis of disperse pollen from samples collected in dammed vegetation ("embalsados") located in eastern region of Iberá Wetlands. These authors established that only upper levels yielded pollen grains representative of the current vegetation. They also found that pollen grains are poorly preserved, even physic and chemical features (e.g. low oxygen, low light, acid pH and high amounts of organic matter) could have favored the preservation of organic matter. Later, Garralla (1998) interpreted that the region was vegetated by xero-halophyte forests at around 3,500 years BP.

*Characteristics of the study area*

Iberá Wetlands is one of the most important tropical wetlands of the biosphere, in terms of its extension and diversity of both animals and plants. The toponymy referred to "waters that shine" (*Y verá* in Guarani language). It comprises a complex water system composed of, marshes, shallow lakes and interconnected river courses (Orfeo & Neiff, 2008).

The lagoons correspond to extensive and shallow plains fed mainly by the rains (1,200 to 1,500 mm year) and they are one of the most important wetlands in Latin America due to its extension with more than 12,000 km$^2$. It is located in the central part of Corrientes with a major axis NE-SW direction (Fig. 1), where a complex association of lentic and lotic environments are vaguely and transitionally delineated (Neiff, 1997). Its extension into the Paraguay Republic "Esteros de Ñeembucú", bearing about 45,000 km$^2$, are developed in its western area and confirms the great influence of the rivers in the maintainance of its fluvial plains such as the large Paraná (Neiff, 2004).

The plant communities of the study area in the Iberá Wetlands are included in the eastern district of the Chaco province. Its humid sandy plains are composed of typical savanna of *Andropogon lateralis* Nees (Poaceae), accompanied by Cyperaceae and other species of Poaceae, developed in more or less elevated sectors well-drained; in depressions with slow permeability, this vegetation is sometimes transformed into marshes (Carnevalli, 1994). Deeper

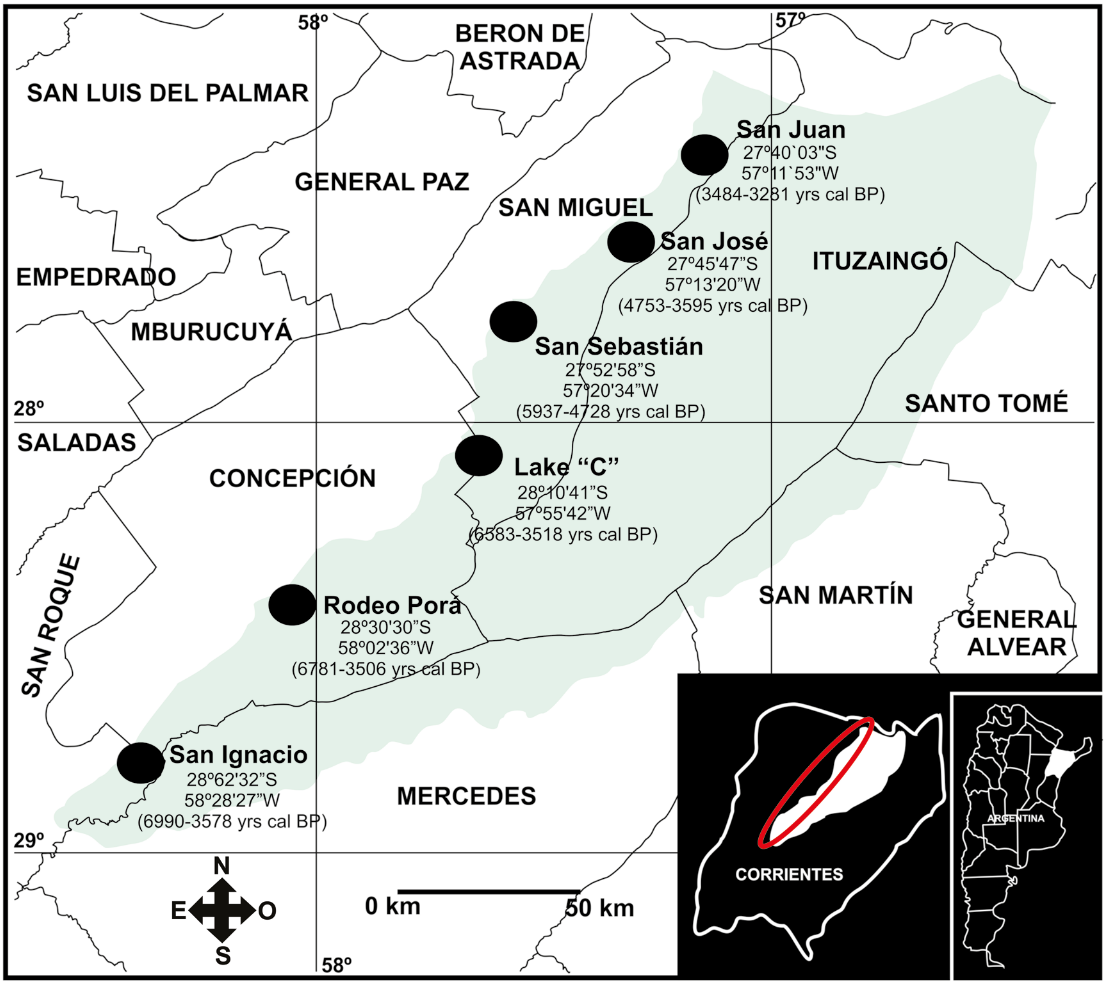


**Fig. 1.** Map of the western margin of the Iberá Wetland showing the sequence of the lakes studied, and cal BP age range for each lake (from Fernandez Pacella & Lara, 2019).

sand areas ("espartillares"), that are well-drained soils of pluvial in origin, are colonized by *Elionurus muticus* (Spreng.) Kuntze (Poaceae), as well as grasslands of *Sorghastrum agrostoides* (Speg.) Hitchc., *Paspalum* sp. and *Spartina* sp. (Poaceae) generally located in floodable soils like streams and marshes. The hygrophilous forest (e.g. Poaceae, Leguminosae) extended over wavy red sands (Carnevalli, 1994).

*Paleoenvironment during the Holocene in the study area*

Palynomorphs were identified in lacustrine sediments of northwestern of the Iberá Wetlands (Fernandez Pacella *et al*., 2011, 2013; Fernandez Pacella & Lara, 2019) which represented mostly marsh-herbaceous vegetation under humid condition between 5968-5000 years cal BP. In agreement with Iriondo (1994), drier conditions were determined from 5000 to 3506 years cal BP with a decrease in the species frequency typical of wet environments and increase of xero-halophyte vegetation. This author pointed out that the influence of template climate in Patagonia would have affected the southern region of Corrientes evidencing changes in landscapes. The clogging of the water body occurred from 3484 years cal BP onwards when herbaceous vegetation dominated.

The appearance of arboreal pollen indicates the beginning of the modern hygrophilous forest. Those paleoenvironmental changes of alternating wetter and drier episodes recorded in this region are supported by fields of eolian dunes in Iberá Wetlands, developed during the drier periods in the late Holocene (Iriondo, 2010).

The objective of this contribution is to provide the first morphological documentation of angiosperms, ferns, lycophytes and bryophytes from core sediments of six lakes of the Holocene western margin of the Iberá Wetlands. Species from local *versus* extra-local vegetation differentiated in the taxonomic description in order to contribute to a better understanding of the floral composition of the Iberá Wetlands and environmental changes yet documented during the Holocene.

## Materials and Methods

The taxonomic analysis of pollen grains and spores presented in this contribution is a new study derived from previous studies carried out by Fernandez Pacella *et al*. (2011), Fernandez Pacella (2013) and Fernandez Pacella & Lara (2019) in which paleoenvironmental interpretations based on main palynologic groups addressed. These works included the study of core samples obtained with a Livingston-type sampler from six lakes in their central and deepest parts on the western margin of the Iberá Wetlands. The interval studied of each core dated by $C^{14}$ spans c. 6000 to 3000 Years BP (Fig. 1). Samples were taken each 5 cm from five lakes (San Juan, 75 cm, 27º 40´ 0´´ S 57º 11´ 53´´ W; San José, 85 cm, 27º 45´ 47´´ S 57º 13´ 20´´ W; Lake "C", 110 cm, 28º 10´ 41´´ S 57º 55´ 42´´ W; Rodeo Porá, 120 cm, 28° 30´ 30´´ S 58° 2´ 3´´ W; San Ignacio, 145 cm, 28° 32´ 32´´ S 58° 28´ 27´´ W). From the San Sebastián lake (24 cm, 27º 52´ 58´´ S 57º 20´ 34´´ W) the interval of sampling used was each 2 cm.

The palynological maceration followed usual techniques of Faegri & Iversen (1989), which consisted on deflocculation of clays with $(NaPO_3)_6$ 10%, elimination of humic acids with NaOH 5%, elimination of carbonates with HCl 10%, separation of organic matter from inorganic material with heavy liquids ($ZnCl_2$) and elimination of silicates with HF.

The material processed and housed in the laboratory at the CECOAL (Centro de Ecología Aplicada del Litoral) of CONICET-UNNE (Universidad Nacional del Nordeste), in the collection "Dr. Rafael Herbst".

The morphological description was based on 30-50 pollen grains for each taxon, and it was done under optical microscope NIKON ECLIPSE E100 illustrated with a camera Nikon 590CU (40x and 100x magnification). We followed the classification of Curtis *et al*. (2001) and Raven *et al*. (1991) for pollen grains, and genera included in the APG VI Classification System (2017) and PPG I (2016). Terminology used for descriptions of pollen grains and spores is based on Kremp (1965), Nilson & Praglowski (1992), Punt *et al*. (2007), and Sáenz Laín (2004). The reference collection PAL-CTES of the UNNE and specialized literature were used to identify pollen grains and spores (Acevedo & Anzótegui, 1998; Anzótegui & Ferrucci, 1998; Anzótegui, 2001; Anzótegui & Caccavari, 2001; Anzótegui & Mautino, 2001a, b; Bhattacharya *et al*., 2009; Caccavari & Dome, 2001, 2006; Cuadrado, 1998a, b, c; Fernandez Pacella & Canteros, 2014; Fernandez Pacella *et al*., 2014a, b; Fuertes & Rodríguez, 2009; Garralla & Cuadrado, 2001; Markgraf & D`Antoni, 1978; Pire *et al*., 2006).

Local taxa refer to those species that are part of the natural vegetation of the Iberá Wetlands (Arbo & Tressens, 2002) whereas the extra-local taxa are those that do not belong to the Iberá. The latter species found in low percentages in the Tilia diagrams of the lakes analyzed by Fernandez Pacella *et al*. (2011) and Fernandez Pacella & Lara (2019). They achieved to depocenters by means of wind currents coming from farther regional vegetation of N, NW and W of Corrientes and E of Chaco (Carnevali, 1994; Fontana, 2018). This is due to the Iberá Wetlands was probably a closed basin made up of an extensive mosaic of lentic bodies fed by rain and without connection with rivers or streams during the Mid-Late Holocene (Neiff, 2004; Orfeo, 2005).

## Results

Fifty-five palynomorphs were recorded in the study area of the Iberá Wetlands. Forty-six of them are pollen types corresponding to 27 families of angiosperms and nine trilete spore-types of ferns, lycophytes, and bryophytes that are described and illustrated (Figs. 2-5). In the taxonomic description, helpful information to differentiate local and extra-local taxa for each site studied is included (Table 1).

The 46 recorded species with pollen are listed alphabetically by family:

*Acanthaceae (Magnoliopsida, Lamiales)*

**Justicia brasiliana** Roth, *Nov. Pl. Sp.*: 17. 1821. Fig. 2A-C.

Morphology: Diporate pollen grain, radial symmetry. Circular amb, (PA) 17-84 µm, prolate (EA) 14-43 µm. Lalongate endoapertures, 2-7 µm diam. Exine 1-5 µm thick, thinner in apertural area, 0.5-1 µm thick, sexine semitectate, reticulated, heterobrocate reticulum, with straight or sinuous walls and circular or polygonal lumens. Surrounding the aperture differentiate and contain 2-6 rows of 4-10 islands (Pire *et al.,* 2006).

Ecological procedence: grass or shrub well represented in forests of *S. balansae* and *M. balansae*, corresponding to extra-local taxa of Corrientes (Fontana, 2018). Native species of Chacoan and Paranaense floristic provinces (Anton & Zuloaga, 2021).

*Amaranthaceae (Magnoliopsida, Caryophyllales)*

**Amaranthus muricatus** (Moq.) Hieron., *Bol. Acad. Nac. Ci.* 4: 421. 1882. Fig. 2D.

Morphology: Pantoporate pollen grain, radial symmetry, spheroidal, small size, diameter 19-22 µm. Apolar. Circular pores, 28-45, with thick margin, distributed all over the grain surface, 1-2 µm in diameter. Exine 1.2 a 1.5 µm thick. Microreticulate (Cuadrado, 1998a).

Ecological procedence: herbaceous species frequent in natural grasslands of the Iberá Wetlands (Arbo & Tressens, 2002) and mainly in North-central Argentina (Anton & Zuloaga, 2021).

**Gomphrena perennis** L., *Sp. Pl.* 1: 224. 1753. Fig. 2E, F.

Morphology: Pantoporate pollen grain, radial symmetry. Spheroidal, 14-22 µm. Apolar. Pores 30-37, 1.2-2.3 µm diam. Exine 1.5-3.5 µm thick, metareticulate, with hexagonal elements (Cuadrado, 1998a).

Ecological procedence: herbaceous species in grasslands of the Iberá Wetlands (Arbo & Tressens, 2002), and North-central region of Argentina (Anton & Zuloaga, 2021).

*Amaryllidaceae (Liliopsida, Asparagales)*

**Crinum americanum** L., *Sp. Pl.* 1: 292. 1753. Fig. 2G.

Morphology: Monosulcate pollen grain, radial symmetry. Small size, suboblate, (PA) 12-15 µm, (EA) 16-18 µm. Heteropolar. Sulcus 2 x 4 µm. Exine 2 µm thick, sexine tectate, microechinate of ca. 1 µm (Medeanic *et al*., 2008).

Ecological procedence: herbaceous local species well represented in marshes of the natural vegetation of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002).

*Anacardiaceae (Magnoliopsida, Sapindales)*

**Myracrodruon balansae** (Engl.) Santin, *Revista Brasil. Bot.* 14: 135. 1991. Fig. 2H, I.

Morphology: Tricolporate pollen grain, radial symmetry. Subtriangular amb, subprolate, (PA) 21-28 µm, (EA) 16-24 µm. Isopolar. Colpi 2.5 µm wide, ribs 1.4-2 µm thick, lalongate endoapertures 1.4-2.1 x 7-10 µm. Exine 1.4 µm thick. Sexine semitectate. Surface striate, short and wide striations lesser than 2.5 µm in length, and larger than 1.7 µm in width, walls 0.5 µm wide and 0.2-0.3 µm high (Anzótegui, 2001).

Ecological procedence: native extra-local tree represented in forests of *S. balansae* and *M. balansae*, of the natural vegetation of Corrientes (Boelcke, 1992; Fontana, 2018) and other region of Chacoan and Paranaense floristic provinces (Anton & Zuloaga, 2021).

**Schinopsis balansae** Engl., *Bot. Jahrb. Syst.* 6: 286. 1885. Fig. 2J.

Morphology: Tricolporate pollen grain, radial symmetry. Prolate, (PA) 32-35 µm, (EA) 24-27 µm. Isopolar. Colpi 1-2.5 µm maximum equatorial in width, acute or blunt apices, ribs 1.4-3.5 µm thick at the equator. Lalongate endoapertures 3-4 x 7-8 µm. Exine 0.7-2 µm thick. Surface striate, long striations, longer than 2.5 µm and 1 µm or less in width, walls slightly taller than 0.5 µm in height (Anzótegui, 2001).

Ecological procedence: native extra-local species of the natural vegetation of Corrientes in forests of *S. balansae* and *M. balansae* (Fontana, 2018) belonging to the Chacoan floristic province (Anton & Zuloaga, 2021).

**Schinus longifolia** (Lindl.) Speg., *Cat. Descr. Maderas*: 413. 1910. Fig. 2K.

Morphology: Tricolporate pollen grain, radial

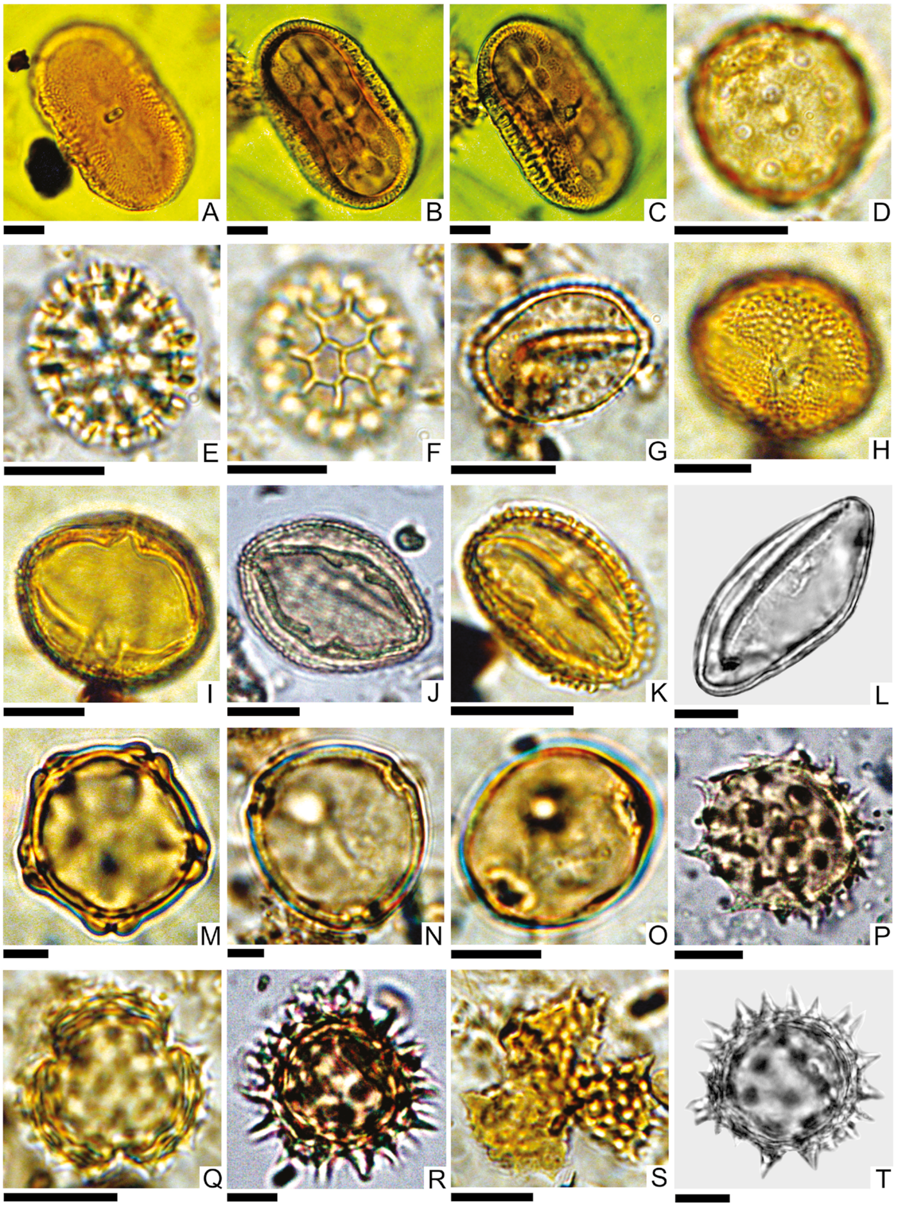


**Fig. 2.** Pollen of *Justicia*, *Amaranthus*, *Gomphrena*, *Crinum*, *Myracrodruon*, *Schinopsis*, *Schinus*, *Syagrus*, *Alnus*, *Tecoma*, *Celtis*, *Anthemis*, *Baccharis*, *Bidens*, *Conyza*, and *Gaillardia*. **A**: *Justicia brasiliana*, equatorial view in superior focus (100x). **B**: Equatorial view in optical section (100x). **C**: Equatorial view in optical section (100x). **D**: *Amaranthus muricatus,* general view in superior focus where endoapertures are appreciated (100x). **E**: *Gomphrena perennis*, general view in optical section (100x). **F**: General view in superior focus (100x). **G**: *Crinum americanum*, polar view in optical section (100x). **H**: *Myracrodruon balansae*, equatorial view in superior focus (100x). **I**: Equatorial view in optical section (100x). **J**: *Schinopsis balansae*, equatorial view in optical section (100x). **K**: *Schinus longifolia*, equatorial view in optical section (100x). **L**: *Syagrus romanzoffiana*, polar view in optical section (100x). **M**: *Alnus acuminata*, polar view in optical section (100x). **N**: *Tecoma stans*, polar view in optical section (100x). **O**: *Celtis iguanaea*, equatorial view (100x). **P**: *Anthemis cotula*, polar view in superior focus (100x). **Q**: *Baccharis trimera*, polar view in optical section (100x). **R**: *Bidens subalternans*, polar view (100x). **S**: *Conyza pampeana*, polar view in superior focus (100x). **T**: *Gaillardia megapotamica*, equatorial view (100x). Scales= 10 µm.

**Table 1.** Pollen and spores procedence for each site studied. Abreviatures= **L**: local taxa; **EL**: extra-local taxa.

| Species or genus | Procedence | San Ignacio | Rodeo Porá | Lake "C" | San Sebastián | San José | San Juan |
|---|---|---|---|---|---|---|---|
| *Alnus acuminata* | L | | X | X | | | |
| *Amaranthus muricatus* | L | X | X | | X | X | |
| *Anadenanthera colubrina* | EL | X | X | X | | | |
| *Anthemis cotula* | L | X | X | X | | X | |
| *Anthoceros* aff. *lamellatus* | L | X | X | | | X | |
| *Baccharis trimera* | L | X | X | X | X | X | |
| *Bidens subalternans* | L | X | X | X | X | X | X |
| *Calliandra parvifolia* | EL | | | X | | X | |
| *Celtis iguanaea* | L | X | X | X | | X | X |
| *Chrysophyllum marginatum* | L | X | | | X | X | X |
| *Cissus verticillata* | L | X | X | | | X | |
| *Conyza pampeana* | L | X | X | X | | X | |
| *Crinum americanum* | L | | X | X | | | X |
| *Cyathea* aff. *atrovirens* | L | | X | X | | X | |
| *Cypella herbertii* | L | X | X | | | X | X |
| *Cyperus rotundus* | L | X | X | X | X | X | X |
| *Echinochloa crus-galli* | L | X | X | X | X | X | X |
| *Echinochloa polystachya* | L | X | X | X | X | X | X |
| *Empetrum* aff. *rubrum* | L | X | X | X | | | |
| *Eryngium elegans* | L | X | X | X | X | X | X |
| *Gaillardia megapotamica* | L | X | X | X | | X | X |
| *Gomphrena perennis* | L | | | | X | | X |
| *Gutierrezia resinosa* | L | X | X | X | | X | |
| *Hymenachne pernambucensis* | L | X | X | X | X | X | X |
| *Imperata brasiliensis* | L | X | X | X | X | X | X |
| *Jamesonia flexuosa* | L | X | X | | | | |
| *Justicia brasiliana* | EL | X | X | | X | X | |
| *Ludwigia peploides* | L | X | X | X | | | |
| *Mikania cordifolia* | L | X | X | X | | X | |
| *Myracrodruon balansae* | EL | | X | X | X | | |
| *Myrcianthes pungens* | EL | X | | X | X | | |
| *Myriophyllum aquaticum* | L | X | X | | | | |
| *Pellaea* sp. | L | X | | | | X | |
| *Phaeoceros bulbiculosus* | L | | X | X | | | |
| *Phaeoceros tenuis* | L | | X | X | | | |
| *Phlegmariurus* aff. *mandiocanus* | L | | X | | | X | |
| *Phyllostylon rhamnoides* | EL | X | X | | X | | |
| *Pisonia aculeata* | EL | | X | X | | X | |

| Species or genus | Procedence | San Ignacio | Rodeo Porá | Lake “C” | San Sebastián | San José | San Juan |
|---|---|---|---|---|---|---|---|
| *Plinia rivularis* | L | | | X | X | X | X |
| *Polygala leptocaulis* | L | X | X | | | | |
| *Polygonum acuminatum* | L | X | X | | | X | |
| *Polygonum convolvulus* | L | X | X | | | X | |
| *Prosopis alba* | EL | | X | | X | X | |
| *Schinopsis balansae* | EL | X | | X | X | X | |
| *Schinus longifolia* | EL | | X | X | | X | |
| *Selaginella* aff. *marginata* | L | | X | X | X | X | |
| *Senecio bonariensis* | L | X | X | X | X | X | |
| *Senegalia bonariensis* | L | | | | | X | X |
| *Serjania perulacea* | EL | X | X | X | | X | |
| *Sphagnum* sp. | L | X | | X | | | |
| *Syagrus romanzoffiana* | EL | | | | X | | |
| *Tecoma stans* | L | | X | | X | | X |
| Thinouia mucronata | L | | | X | | X | X |
| Trichilia elegans | EL | X | | X | X | | |
| *Typha domingensis* | L | X | X | X | | | X |

symmetry. Prolate, (PA) 18-21 µm, (EA) 14-16 µm. Isopolar. Colpi 1-2.5 µm wide, with 1.4-3.5 µm thick ribs at the equator limited by a small psilate margin of 2 µm wide. Endoapertures 1.4 x 4 µm in size. Exine 0.7-2.5 µm thick. Surface striate, long striations, approximately more than 2.5 µm long (Anzótegui, 2001).

Ecological procedence: extra-local shrub or tree well represented in the natural palm grove vegetation of Corrientes (Fontana, 2018) and in Chacoan and Paranaense floral provinces (Anton & Zuloaga, 2021).

*Arecaceae (Liliopsida, Arecales)*

**Syagrus romanzoffiana** (Cham.) Glassman, *Fieldiana, Bot.* 31: 382. 1968. Fig. 2L.

Morphology: Monosulcate pollen grain, bilateral symmetry. Medium size, oblate, (PA) 15-17 µm, (EA) 37-39 µm. Heteropolar. Sulcus 35.4 µm long. The exine is 1.6 µm thick, sexine tectate and psilate (Trigo & Fernández, 1995; Bauermann *et al*., 2010).

Ecological procedence: extra-local arboreal species well represented in small palm stocks and riparian natural vegetation in Corrientes (Boelcke, 1992; Carnevalli, 1994; Cabral & Castro, 2007). Mainly endemic of Pampean and Paranaense floral provinces (Anton & Zuloaga, 2021).

*Betulaceae (Magnoliopsida, Fagales)*

**Alnus acuminata** Kunth, *Nov. Gen. Sp. (quarto ed.)* 2: 20. 1817. Fig. 2M.

Morphology: Pentazonoporate pollen grain of radial symmetry. Medium size, pentagonal amb (EA) 40-43 µm. Isopolar. Pores 3-5 µm, protrudent and vestibular. Exine 2 µm thick, psilate (Markgraf & D`Antoni, 1978).

Ecological procedence: extra-local tree represented in forests of *S. balansae* and *M. balansae* of Corrientes (Boelcke, 1992; Fontana, 2018).

*Bignoniaceae (Magnoliopsida, Lamiales)*

**Tecoma stans** (L.) Juss. ex Kunth, *Nov. Gen. Sp. (quarto ed.)* 3: 144. 1819. Fig. 2N.

Morphology: Brevicolpate pollen grain, radial symmetry. Subtriangular amb, (EA) 48-52 µm. Isopolar. Exine 3 µm thick, sexine semitectate. Microreticulate (Markgraf & D`Antoni, 1978).

Ecological procedence: shrub or small tree represented in the natural vegetation of the Iberá

Wetlands in hygrophilous forests (Fontana, 2018). Native of North-central region of Argentina (Anton & Zuloaga, 2021).

*Celtidaceae (Magnoliopsida, Rosales)*
**Celtis iguanaea** (Jacq.) Sarg., *Silva* 7: 64. 1895. Fig. 2O.

Morphology: Triporate pollen grain, radial symmetry. Subtriangular to circular amb, suboblate, (PA) 9-30 µm, (EA) 11-32 µm. Isopolar. Pores slightly sunken, circular 1-2 µm in diam., limited by a ring 0.5-2 µm thick. Exine 0.5-1.4 µm thick. Sexine tectate. Scabrate (Anzótegui & Mautino, 2001a).

Ecological procedence: shrub (creep) or tree represented in hygrophilous forests of the Iberá Wetlands and extra-local forests of *S. balansae* and *M. balansae* in Corrientes (Arbo & Tressens, 2002; Fontana, 2018). Native of central-northern region of Argentina (Anton & Zuloaga, 2021).

*Compositae (Magnoliopsida, Asterales)*
**Anthemis cotula** L., *Sp. Pl.* 2: 894. 1753. Fig. 2P.

Morphology: Tricolporate pollen grains of radial symmetry. Spheroidal, (PA) 23-24 µm, (EA) 22-23 µm. Isopolar. Exine 4.5 µm thick. Sexine tectate, echinate, spines 4 to 5 µm (Alonso, 2014).

Ecological procedence: herbaceous local taxon in grasslands of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002) in Corrientes and widely present in southern South America (Anton & Zuloaga, 2021).

**Baccharis trimera** (Less.) DC., *Prodr*. 5: 425. 1836. Fig. 2Q.

Morphology: Tricolporate, radial symmetry. Spheroidal, (PA) 15-16 µm, (EA) 14-15 µm. Isopolar. Exine 4 µm thick. Sexine tectate, echinate, spines 2-2.5 µm long (Markgraf & D`Antoni, 1978).

Ecological procedence: this genus is well represented in natural grassland vegetation of the Iberá Wetlands (Arbo & Tressens, 2002) and in North-central region of Argentina (Anton & Zuloaga, 2021).

**Bidens subalternans** DC., *Prodr*. 5: 600. 1836. Fig. 2R.

Morphology: Tricolporate pollen grain, radial symmetry. Oblate-spheroidal, (PA) 26-28 µm, (EA) 27-28 µm. Isopolar. Exine 2.5-3 µm thick, sexine tectate, echinate, spines 7-7.5 µm (Markgraf & D`Antoni, 1978).

Ecological procedence: herbaceous taxon presents in grasslands of the Iberá Wetlands (Arbo & Tressens, 2002).

**Conyza pampeana** (Parodi) Cabrera, *Man. Fl. Al. Buenos Aires*: 481. 1953. Fig. 2S.

Morphology: Tricolporate pollen grain of radial symmetry. Prolate to subcircular, (PA) 25-27 µm, (EA) 21-24 µm. Isopolar. Exine 4 µm thick. Sexine tectate, echinate, spines 2 µm (Medeanic *et al.,* 2008).

Ecological procedence: this genus is well represented in the natural vegetation of the Iberá Wetlands in grasslands (Arbo & Tressens, 2002).

**Gaillardia megapotamica** (Spreng.) Baker, *Fl. Bras.* 6: 276. 1884. Fig. 2T.

Morphology: Tricolporate pollen grains of radial symmetry. Medium, suboblate, (PA) 27-30 µm, (EA) 34-37 µm. Isopolar. Exine 2 µm thick, sexine tectate, echinate, with spines 4 µm long (Markgraf & D`Antoni, 1978).

Ecological procedence: perennial grass or subshrub well represented in grasslands of the Iberá Wetlands (Arbo & Tressens, 2002).

**Gutierrezia resinosa** (Hook. & Arn.) S. F. Blake, *Contr. U.S. Natl. Herb.* 26: 232. 1930. Fig. 3A.

Morphology: Tricolporate pollen grain, radial symmetry. Small size, spheroidal, (PA) 14-18 µm, (EA) 14-18 µm. Isopolar. Exine 2 µm thick. Sexine tectate, echinate, spines 1.5 µm long (Markgraf & D`Antoni, 1978).

Ecological procedence: *Gutierrezia* Lag. is present in natural grasslands of the Iberá Wetlands (Arbo & Tressens, 2002).

**Mikania cordifolia** (L. f.) Willd., *Sp. Pl.* 3: 1746. 1803. Fig. 3B.

Morphology: Tricolporate pollen grains of radial symmetry. Medium size, subprolate (PA) 27-30 µm, (EA) 22-25 µm. Isopolar. Exine 1 µm thick, sexine tectate, echinate, spines 2 µm (Ybert *et al*., 2016).

Ecological procedence: perennial creeper well represented in hygrophilous forest vegetation of Iberá Wetlands (Arbo & Tressens, 2002), as well as in forests, savannas, riparian banks of rivers and streams of South America (Anton & Zuloaga, 2021).

**Senecio bonariensis** Hook. & Arn., *J. Bot. (Hooker)* 3: 340. 1841. Fig. 3C.

Morphology: Tricolporate pollen grain, radial symmetry. Circular in (PA) 28-40 µm, prolate in (EA) 16-35 µm. Isopolar. Exine 2-5 µm thick. Sexine tectate, echinate, spines 2-3 µm (Markgraf & D`Antoni, 1978).

Ecological procedence: *Senecio* L. is well represented in the natural vegetation of the Iberá Wetlands in marsh and grassland, corresponding to local taxa (Arbo & Tressens, 2002) and present in Chacoan, Paranaense and Pampean floristic provinces (Anton & Zuloaga, 2021).

*Cyperaceae (Liliopsida, Poales)*

**Cyperus rotundus** L., *Sp. Pl.* 1: 45. 1753. Fig. 3D.

Morphology: Monoporate pollen grain and radial symmetry. Heteropolar, prolate, (PA) 27-37 µm, (EA) 16-24 µm. Exine 1.5 µm thick, ornamentation granular (Fernandez, 1987).

Ecological procedence: perennial marsh grass well represented in the natural vegetation of the Iberá Wetlands (Arbo & Tressens, 2002).

*Ericaceae (Magnoliopsida, Ericales)*

**Empetrum** aff. **rubrum** Vahl ex Willd., *Sp. Pl.* 4: 713. 1806. Fig. 3E, F.

Morphology: Tetrad with tricolporate pollen grain, radial symmetry. Small, circular-subcircular, (EA) 19-22 µm. Isopolar. Exine 2 µm thick (Markgraf & D`Antoni, 1978).

Ecological procedence: subshrub represented in marshes of the natural vegetation of the Iberá Wetlands (Carnevalli, 1994; Arbo & Tressens, 2002).

*Haloragaceae (Magnoliopsida, Saxifragales)*

**Myriophyllum aquaticum** (Vell.) Verdc., *Kew Bull.* 28: 36. 1973. Fig. 3G.

Morphology: Tetrazonoporate pollen grain with radial symmetry. Subcircular-angular amb, oblate to spheroidal (PA) 29-38 µm, (EA) 34-41 µm. Pores 4-5 µm diam., protrudent, with thickening of the endexine. Exine 1.5 µm thick. Sexine tectate, scabrate (Díez Dapena, 1988).

Ecological procedence: perennial aquatic herb well represented in the natural vegetation of the Iberá Wetlands (Arbo & Tressens, 2002) also present in central-northern region of Argentina (Anton & Zuloaga, 2021).

*Iridaceae (Liliopsida, Asparagales)*

**Cypella herbertii** Herb., *Bot. Mag.* 53: sub t. 2637. 1826. Fig. 3H.

Morphology: Monosulcate pollen grain and bilateral symmetry. Heteropolar, suboblate, (PA) 40-54 µm, (EA) 45-61 µm. Sulcus 35-54 µm long. Exine 1-2.2 µm thick, sexine semitectate and microreticulate (Salgado, 2006).

Ecologic procedence: bulbous herbaceous local species in marsh areas (Boelcke, 1992; Arbo & Tressens, 2002). Endemic of Pampean and Paranaense floral provinces (Anton & Zuloaga, 2021).

*Leguminosae, Mimosoideae (Magnoliopsida, Fabales)*

**Calliandra parvifolia** (Hook. & Arn.) Speg., *Revista Argent. Bot.* 1: 193. 1926. Fig. 3I.

Morphology: Polyads 185 x 112 µm diam. usually of 8 pollen grains. Exine 2 µm thick, rugulate (Markgraf & D`Antoni, 1978).

Ecological procedence: extra-local shrub represented in the natural vegetation of Corrientes province in forests of *S. balansae* and *M. balansae* (Fontana, 2018).

**Anadenanthera colubrina** (Vell.) Brenan, *Kew Bull.* 10: 182. 1955. Fig. 3J.

Morphology: Polyads spheroidal to ellipsoidal of 12 pollen grains irregularly arranged, or of 16 pollen grains regularly arranged. Exine 1.3 µm thick. Verrucate, 1 µm diam. warts (Caccavari & Dome, 2006).

Ecological procedence: extra-local tree represented in forests of *S. balansae* and *M. balansae* of Corrientes province (Fontana, 2018).

**Prosopis alba** Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 19: 131. 1874. Fig. 3K.

Morphology: Tricolporate pollen grain of radial symmetry. Small to medium size, prolate, (PA) 22-36 µm, (EA) 18.5-33 µm. Isopolar. Long colpi 17-30 µm and pores 4-6 µm diam. Exine 1-2 µm thick, sexine tectate, scabrate (Fernandez Pacella *et al.,* 2014b).

Ecological procedence: extra-local tree

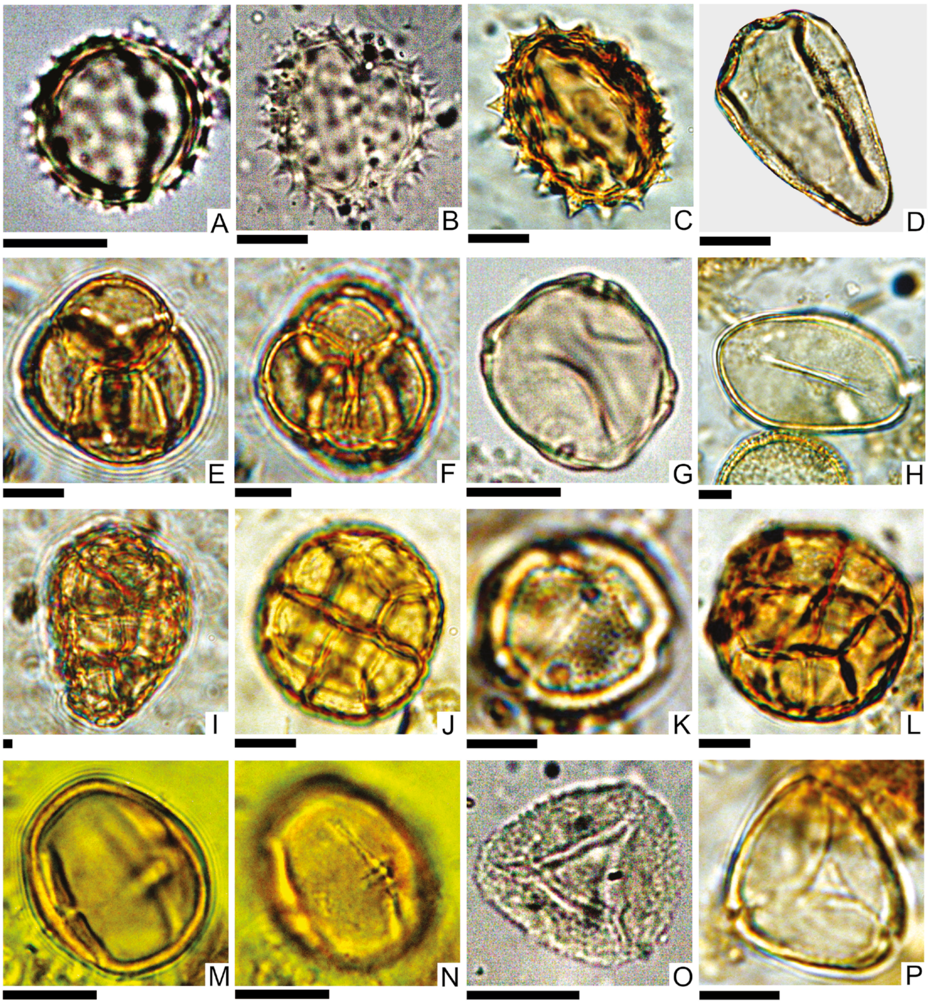


**Fig. 3.** Pollen of *Gutierrezia*, *Mikania*, *Senecio*, *Cyperus*, *Empetrum*, *Myriophyllum*, *Cypella*, *Calliandra*, *Anadenanthera*, *Prosopis*, *Senegalia*, *Trichilia*, *Myrcianthes*, and *Plinia*. **A**: *Gutierrezia resinosa*, equatorial view in optical section (100x). **B**: *Mikania cordifolia*, polar view in optical section (100x). **C**: *Senecio bonariensis*, polar view in optical section (100x). **D**: *Cyperus rotundus*, equatorial view in optical section (100x). **E**: *Empetrum* aff. *Rubrum*, poliade in optical section (100x). **F**: Poliade in superior focus (100x). **G**: *Myriophyllum aquaticum*, polar view in superior focus (100x). **H**: *Cypella herbertii*, polar view in optical section (100x). **I**: *Calliandra parvifolia*, poliade (100x). **J:** *Anadenanthera colubrina*, poliade (100x). **K**: *Prosopis alba*, polar view in superior focus (100x). **L:** *Senegalia bonariensis*, poliade (100x). **M**: *Trichilia elegans*, equatorial view in optical section (100x). **N**: Equatorial view in superior focus (100x). **O**: *Myrcianthes pungens*, polar view in superior focus (100x). **P**: *Plinia rivularis*, polar view in superior focus (100x). Scales= 10 µm.

represented in forests of *S. balansae* and *M. balansae* of Corrientes (Boelcke, 1992; Fontana, 2018).

**Senegalia bonariensis** (Gillies ex Hook. & Arn.) Seigler & Ebinger, *Phytologia* 88: 50. 2006. Fig. 3L.

Morphology: Polyads of 16 pollen grains with regular arrangement, major axis (34-42 µm), minor axis (22-30 µm). Exine 1.55-2.55 µm thick. Sexine tectate. Infratectum with columellae 0.5-0.9 µm long. Ornamentation slightly granulate (Caccavari & Dome, 2001).

Ecological procedence: tree or shrub present in hygrophilous forests of the Iberá Wetlands (Boelcke, 1992; Fontana, 2018).

*Meliaceae (Magnoliopsida, Sapindales)*
**Trichilia elegans** A. Juss., *Fl. Bras. Merid. (quarto ed.)* 2: 79, t. 98. 1829. Fig. 3M, N.

Morphology: Tetracolporate pollen grain, radial symmetry. Small size, quadrangular amb (PA) 17-25 µm, subprolate (EA) 14-21 µm. Isopolar. Colpi 15-22 µm long, lalongate endoapertures with ring thickening 1.4-3 µm thick. Exine 1.4 µm thick and microreticulate ornamentation (Oliveira & Santos, 2014).

Ecological procedence: extra-local tree represented in forests of *S. balansae* and *M. balansae* of the natural vegetation of Corrientes (Fontana, 2018) and noreastern Argentina (Anton & Zuloaga, 2021).

*Myrtaceae (Magnoliopsida, Myrtales)*
**Myrcianthes pungens** (O. Berg) D. Legrand, *Bol. Fac. Agron. Univ. Montevideo* 101: 52. 1968. Fig. 3O.

Morphology: Parasintricolporate pollen grain, radial symmetry. Small size, triangular, oblate, (PA) 9-17 µm, (EA) 12-21 µm. Isopolar. Narrow or wide colpi an apocolpial field or island, of triangular form. Apocolpial fields with edges and are of different sizes in both poles. Endoapertures 1.4-2 µm. Exine 0.7-3 µm thick, sexine semitectate, microreticulate (Acevedo & Anzótegui, 1998).

Ecological procedence: the natural vegetation of Corrientes province in forests of *S. balansae* and *M. balansae* (Boelcke, 1992; Fontana, 2018). Native of North-central region of Argentina (Anton & Zuloaga, 2021).

**Plinia rivularis** (Cambess.) Rotman, *Bol. Soc. Argent. Bot.* 24: 195. 1985. Fig. 3P.

Morphology: Parasyntricolporate pollen grain, radial symmetry. Triangular amb, oblate, (PA) 13-17 µm, (EA) 19-28 µm. Isopolar. Linear colpi, less than 1 µm wide, lalongate endoapertures 1 x 2.3 µm. Exine 0.7-2 µm thick. Sexine tectate. Psilate (Acevedo & Anzótegui, 1998).

Ecological procedence: tree well represented in hygrophilous forests of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002). Exclusive of Entre Ríos, Corrientes and Misiones belonging to the Paranaense floristic province (Anton & Zuloaga, 2021).

*Nyctaginaceae (Magnoliopsida, Caryophyllales)*
**Pisonia aculeata** L., *Sp. Pl.* 2: 1026. 1753. Fig. 4A, B.

Morphology: Tricolporate pollen grain of radial symmetry. Medium size, prolate, (PA) 34-37 µm, (EA) 24-27 µm. Isopolar. Colpi 32-35 µm long. Pores 2-3 µm diam. Exine 1-1.5 µm thick, sexine semitectate, microreticulate (Oliveira & Santos, 2014).

Ecological procedence: shrub or creeper species present in natural forests of *Schinopsis balansae* Engl. and *Myracrodruon balansae* (Engl.) Santin in Corrientes province (extra-local taxon) (Carnevalli, 1994; Fontana, 2018), and northern region of Argentina (Anton & Zuloaga, 2021).

*Onagraceae (Magnoliopsida, Myrtales)*
**Ludwigia peploides** (Kunth) P.H. Raven, *Reinwardtia* 6: 393 1963[1964]. Fig. 4C.

Morphology: Tricolporate pollen grain, radial symmetry. Large size, subtriangular amb, subprolate, (PA) 94-108 µm, (EA) 74-86 µm. Isopolar. Colpi 18 x 4 µm, endoapertures 20 x 16 µm protrudent-vestibuled. Exine 3-4 µm thick. The surface of the ridges is rugulate-striated. The area between the ridges has an uneven coarse rugulate appearance, due to the presence of irregular striae (Cecotti Álvarez *et al.*, 2017).

Ecological procedence: aquatic herbaceous taxon well represented in fresh water bodies of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002). Native of central-northern region of Argentina (Anton & Zuloaga, 2021).

*Poaceae (Liliopsida, Poales)*
**Echinochloa crus-galli** (L.) P. Beauv., *Ess. Agrostogr.* 1: 53, 161, 169, pl. 11, f. 2. 1812. Fig. 4D.

Morphology: Monoporate pollen grain and radial symmetry. Spheroidal amb, (PA) 46-49 µm, (EA) 46-49 µm. Heteropolar. Pore 2 µm in diameter, with annulus 1 µm thick. Exine 2 µm thick. Sexine tectate, psilate to scabrate (Fernandez Pacella & Canteros, 2014).

Ecological procedence: herbaceous species in marsh and grasslands of natural vegetation of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002) and widely distributed in Argentina (Anton & Zuloaga, 2021).

**Echinochloa polystachya** (Kunth) Hitchc., *Contr. U.S. Natl. Herb.* 22: 135. 1920. Fig. 4E.

Morphology: Monoporate pollen grain and radial symmetry. Spheroidal amb, (PA) 53-57 µm, (EA) 60-62 µm. Heteropolar. Pore with annulus 2 µm in diameter. Exine 2 µm thick, sexine tectate, psilate to scabrate (Fernandez Pacella & Canteros, 2014).

Ecological procedence: herbaceous taxon, local of marsh and grasslands in the natural vegetation of the Iberá Wetlands (Arbo & Tressens, 2002). Extra-local species present in Paranense, Chacoan and Pampean floral provinces of Argentina (Anton & Zuloaga, 2021).

**Hymenachne pernambucensis** (Spreng.) Zuloaga, *Amer. J. Bot.* 90: 817. 2003. Fig. 4F.

Morphology: Monoporate pollen grain, radial symmetry. Prolate-spheroidal, (PA) 42-44 µm, (EA) 36-39 µm. Heteropolar. Pore 3 µm in diameter. Exine 2 µm thick. Sexine tectate, psilate to scabrate (Fernandez Pacella & Canteros, 2014).

Ecological procedence: *H. pernambucensis* local genus is well represented in marsh and grasslands (Arbo & Tressens, 2002). Present in Paranense and Chacoan floral provinces of Argentina (Anton & Zuloaga, 2021).

**Imperata brasiliensis** Trin., *Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math.* 2: 331. 1832. Fig. 4G.

Morphology: Monoporate pollen grain, radial symmetry. Spheroidal amb, (PA) 21-37 µm, (EA) 18-33 µm. Heteropolar. Pore 1-4 µm diameter with a ring 1 to 6 µm thick. Exine 1-3 µm thick, tectate, psilate to scabrate (Fernandez Pacella & Canteros, 2014).

Ecological procedence: herbaceous species well represented in marsh and grassland areas of the natural vegetation of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002).

*Polygalaceae (Magnoliopsida, Fabales)*

**Polygala leptocaulis** Torr. & A. Gray, *Fl. N. Amer.* 1: 130. 1838. Fig. 4H.

Morphology: Pantozonocolporate pollen grain with radial symmetry. Subcircular amb (PA) 20-30 µm, subprolate amb (EA) 18-21 µm. Isopolar. Colpi 8-15, 17-25 µm long. Lalongate endoaperture 2 x 4 µm. Exine 0.7-2.5 µm thick. Sexine tectate. Psilate (Cuadrado, 1998c).

Ecological procedence: herbaceous species well represented in marshes and grasslands of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002).

*Polygonaceae (Magnoliopsida, Caryophyllales)*

**Polygonum acuminatum** Kunth, *Nov. Gen. Sp. (quarto ed.)* 2: 178. 1818. Fig. 4I, J.

Morphology: Triporate pollen grain with radial symmetry. Circular amb, (EA) 59-62 µm. Exine 6 µm thick. Sexine 1.5-2 µm thick, reticulate, walls 1.5 µm thick, simplicolumellate, lumen 10 µm wide (Ybert *et al*., 2018).

Ecological procedence: herbaceous species well represented in hygrophilous forests of the Iberá Wetlands (Fontana, 2018).

**Polygonum convolvulus** L., *Sp. Pl.* 1: 364. 1753. Fig. 4K.

Morphology: Triporate pollen grain with radial symmetry. Circular-subcircular amb, (EA) 39-42 µm. Isopolar. Exine 3 µm thick, reticulate, walls 1 µm thick, simplicolumellate, irregular lumen 2 x 2 µm wide (Ybert *et al*., 2018).

Ecological procedence: herbaceous species represented in hygrophilous forests of the Iberá Wetlands (Fontana, 2018).

*Sapindaceae (Magnoliopsida, Sapindales)*

**Serjania perulacea** Radlk., Consp. Sect. Sp. Serjan.: 11. 1874. Fig. 4L, M.

Morphology: Hemisyntricolporate pollen grain, radial symmetry. Subtriangular amb, oblate, (PA) 8-40 µm, (EA) 6-58 µm. Heteropolar. Colpi 1-2 µm wide. Exine 0.7-2.5 µm thick, sexine semitectate, microreticulate (Anzótegui & Ferrucci, 1998).

Ecological procedence: extra-local perennial creeper represented in the forests of *Schinopsis balansae* and *Myracrodruon balansae*, natural vegetation of Corrientes (Fontana, 2018) and other provinces of northern Argentina: Chaco, Formosa, Jujuy, Salta (Anton & Zuloaga, 2021).


**Fig. 4.** Pollen of *Pisonia*, *Ludwigia*, Echinochloa, *Hymenachne*, *Imperata*, *Polygala*, *Polygonum*, *Serjania*, *Thinouia*, *Chrysophyllum*, and *Typha*. **A**: *Pisonia aculeate*, equatorial view in optical section (100x). **B**: Equatorial view in superior focus (100x). **C**: *Ludwigia peploides*, polar view in optical section (100x). **D**: *Echinochloa crus-galli*, equatorial view in superior focus (100x). **E**: *Echinochloa polystachya,* equatorial view in superior focus (100x). **F**: *Hymenachne pernambucensis*, equatorial view in optical section (100x). **G**: *Imperata brasiliensis*, equatorial view in superior focus (100x). **H**: *Polygala leptocaulis*, equatorial view in superior focus (100x). **I**: *Polygonum acuminatum*, polar view in superior focus (100x). **J**: Polar view in optical section (100x). **K**: *Polygonum convolvulus*, polar view in superior focus (100x). **L**: *Serjania perulacea*, polar view in inferior focus (100x). **M**: Polar view in superior focus (100x). **N**: *Thinouia mucronata*, polar view in superior focus (100x). **O**: *Chrysophyllum marginatum*, equatorial view in optical section (100x). **P**: *Typha domingensis*, equatorial view in superior focus (100x). Scales= 10 µm.

**Thinouia mucronata** Radlk., *Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München* 8: 282. 1878. Fig. 4N.

Morphology: Tricolporate pollen grain, radial symmetry. Subtriangular amb, oblate, (PA) 11-27 µm, (EA) 23-27 µm. Sides slightly convex to substraight. Isopolar. Colpi (1.4-4 µm wide). Lalongate endoapertures 1.4 x 4.3 µm. Exine 1.4-2.1 thick. Psilate to slightly scabrate (Anzótegui & Ferrucci, 1998).

Ecological procedence: local perennial creeper well represented in hygrophilous forest vegetation of the Iberá Wetlands (Arbo & Tressens, 2002; Boelcke, 1992) and in northern Argentina (Anton & Zuloaga, 2021).

*Sapotaceae (Magnoliopsida, Ericales)*

***Chrysophyllum marginatum*** (Hook. & Arn.) Radlk., *Act. Occ. Exp. Univ. Anvers Coin. Exp. Int. Hort.*: 170. 1887. Fig. 4O.

Morphology: Tetracolporate pollen grain with radial symmetry. Subtriangular amb, prolate, (PA) 20-24 µm, (EA) 14-16 µm. Isopolar. Narrow colpi ± 14 µm long. Endoapertures 2 x 3 µm with an annular thickening of 2 µm given by protruding endexine. Exine 3 µm thick, columellate infratectal layer observed. At the poles, the exine is 2 µm, the columellae being longer than the thick of the tectum and the nexine 1 µm; at the equator the sexine thins, until approximately 1 µm and the nexine increases its thickness to 2 µm. Surface scabrate (Cuadrado, 1998b).

Ecological procedence: shrub or small tree well represented in forests of the Iberá Wetlands and Norht-central region of Argentina (Arbo & Tressens, 2002; Anton & Zuluoga, 2021).

*Typhaceae (Liliopsida, Poales)*

**Typha domingensis** Pers., *Syn. Pl.* 2: 532. 1807. Fig. 4P.

Morphology: Monoporate pollen grain, radial symmetry. Spheroidal amb, (PA) 17-20 µm, (EA) 17-20 µm. Heteropolar. Exine 2.5 µm thick. Sexine columellate, wall 0.25 µm thick, reticulate (Alonso, 2014).

Ecological precedence: robust emergent aquatic herbaceous local taxon well represented in marshes of natural vegetation of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002).

*Ulmaceae (Magnoliopsida, Rosales)*

**Phyllostylon rhamnoides** (J. Poiss.) Taub., *Oesterr. Bot. Z.* 11: 409. 1890. Fig. 5A, B.

Morphology: Tetra-pentazonoporate pollen grain, radial symmetry. Spheroidal, (PA) 36-39 µm, (EA) 36-39 µm. Isopolar. Circular pores 1-3 µm in diam., some of them arranged in a subequatorial plane. Exine 1 µm thick. Psilate to verrucate (Anzótegui & Mautino, 2001b).

Ecological procedence: extra-local tree well represented in forests of *S. balansae* and *M. balansae* of Corrientes province (Boelcke, 1992; Fontana, 2018). Native of Chacoan and Yungas floristic provinces of Argentina (Anton & Zuloaga, 2021).

*Umbeliferae (Magnoliopsida, Apiales)*

**Eryngium elegans** Cham. & Schltdl., *Linnaea* 1: 348. 1826. Fig. 5C.

Morphology: Tricolporate pollen grain, radial symmetry. Prolate, (PA) 28-36 µm, (EA) 18-23 µm. Isopolar. Narrow and long colpi, relatively large pore. Exine 1 µm thick. Sexine semitectate, perforate, microreticulate (Alonso, 2014).

Ecological procedence: local herb in marshes of the Iberá Wetlands (Boelcke, 1992; Arbo & Tressens, 2002), and elsewhere in Corrientes (Fontana, 2018) and North-central Argentina (Anton & Zuloaga, 2021).

*Vitaceae (Magnoliopsida, Vitales)*

**Cissus verticillata** (L.) Nicolson & C.E. Jarvis, *Taxon* 33: 727. 1984. Fig. 5D-F.

Morphology: Tricolporate pollen grain, radial symmetry. Subtriangular amb, subprolate, (PA) 75-77 µm, (EA) 58-60 µm. Isopolar. Colpi long, maximum width of 4.5 µm and ribs 2.8-4.5 µm thick at the equator. Lalongate endoapertures 5-8 x 3-4 µm to circular 3 µm diam. Exine 2-4 µm thick, reticulate (Anzótegui & Caccavari, 2001).

Ecological procedence: perennial creeper represented in hygrophilous forest of the natural vegetation of the Iberá Wetlands (Fontana, 2018) and in central-northern of Argentina (Anton & Zuloaga, 2021).

The nine recorded species with spores are listed alphabetically by family:

*Anthocerotaceae (Anthocerotopsida, Anthocerotales)*

**Anthoceros** aff**. lamellatus** Steph., *Sp. Hepat. (Stephani)* 5: 1000. 1916. Fig. 5G, H.

Morphology: Trilete spore. Polar view subtriangular. Laesura with straight rays reaching the equator. Exospore 3.5 µm thick, smooth inner proximal surface, bacullate distal surface and equatorial amb. Size: 48-76 µm (Gradstein, 2018).

Ecological procedence: cosmopolitan genus is represented on compact rock surfaces exposed to light (Peñaloza-Bojacá *et al*., 2020).

*Cyatheaceae (Polypodiopsida, Cyatheales)*
**Cyathea** aff. **atrovirens** (Langsd. & Fisch.) Domin, *Rozpr. Kral. Ceske Spolecn. Nauk, Tr. Mat.-Prir.* 2: 262. 1929. Fig. 5I.

Morphology: Trilete spore. Polar view triangular. Laesura 35-40 µm long. Exospore 1.4 µm thick. Psilate or scabrate. Size: 43-53 µm (Contreras-Duarte *et al*., 2006).

Ecological procedence: tree to shrub and herb on soils and rock substrate (rupicolous species) on roadsides, ravines, in abandoned fields, swamps and secondary forests of forests of the Iberá Wetlands (Arbo & Tressens, 2002) and in Corrientes and Misiones provinces (Anton & Zuloaga, 2021).

*Lycopodiaceae (Lycopodiopsida, Lycopodiales)*
**Phlegmariurus** aff. **mandiocanus** (Raddi) B. Øllg., *Rodriguésia* 63: 480. 2012. Fig. 5J.

Morphology: Trilete spore. Polar view subtriangular, with rounded angles. Lesura with straight rays reaching to the equator. Exospore 1.6 µm thick. Psilate on proximal face. Size: 28-38 µm. Illustrations of this taxon by Sersic (1983) and comparison with other species of the genus consulted in Rincón *et al*. (2014).

Ecological procedence: epiphyte present in hygrophilous forests of Yungas and Paranaense floral provinces in Argentina (Anton & Zuloaga, 2021; Windisch *et al*., 2015).

*Notothyladaceae (Anthocerotopsida, Notothyladales)*
**Phaeoceros bulbiculosus** (Brot.) Prosk., *Rapp. Comm., VIII Congr. Int. Bot.*: 69. 1954. Fig. 5K.

Morphology: Trilete spore. Polar view subtriangular. Laesura with straight rays reaching the equator. Exospore 2.3 µm thick. Granular/gemmate sculpture. Size: 32-38 µm. Illustrated from Argentina (Morbelli *et al*., 2010).

Ecological procedence: cosmopolitan genus is represented on compact, moist soil, and on rock in moist environments, exposed or partially shaded microhabitats (Peñaloza-Bojacá *et al*., 2020).

**Phaeoceros tenuis** (Spruce) Hässel, *Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich* 91: 303. 1986. Fig. 5L.

Morphology: Trilete spore. Polar view subtriangular. Laesura with straight rays reaching the equator. Exospore 3.5 µm thick. Granular. Size: 48-76 µm (Prieto & Quattrocchio, 1993).

Ecological procedence: cosmopolitan genus is represented on compact, moist soil, and on rock in moist environments, exposed or partially shaded microhabitats (Peñaloza-Bojacá *et al*., 2020).

*Pteridaceae (Polypodiopsida, Polypodiales)*
**Jamesonia flexuosa** (Kunth) Christenh., *Phytotaxa* 19: 21. 2011. Fig. 5M.

Morphology: Trilete spore. Polar view subtriangular, with rounded angles. Sinuous laesura, with small coalescent ridges, reaching to the inner margin of the cingulum. Exospore including the cingulum is 5.5 µm thick. Size: 56-71 µm (Contreras-Duarte *et al*., 2006; Della & Prado, 2020).

Ecological procedence: this taxon is part of the natural vegetation of the Iberá Wetlans (Arbo & Tressens, 2002) and occurs in humid places inside of cloud forest from southern Mexico to Bolivia, and north and southeast of Brazil to Uruguay (Della & Prado, 2020; Della *et al*., 2020).

**Pellaea sp.** Fig. 5N

Morphology: Trilete spore. Polar view triangular. Rays of the laesurae straight, 2/3 of radius to almost the internal margin of cingulum. Exospore cingulum surrounds the spore, 5.4 µm thick. Central part of distal face verrucate/rugulate, low warts occasionally joined forming loins. Size: 37-48 µm.

Comparisons: few specimens recorded herein are similar to *Pellaea cordifolia* (Sessé & Moc.) A.R. Sm. (Arreguín-Sánchez *et al*., 1996; Pérez-Jiménez *et al*., 2020) and *Pellaea ovata* (Desv.) Weath. (Gómez *et al*., 2013) differing in having smooth proximal and less ornamented distal face.

Ecological procedence: this genus is including terrestrial or rupicolous species, some of humid shaded areas of hygrophilous forests and others tolerate slight exposition to light in open areas. Particularly, *Pellaea cordifolia* and *P. ovata* (Hirai & Prado, 2021) are known in South America (Anton & Zuloaga, 2021; Arbo & Tressens, 2002).

*Selaginellaceae (Lycopodiopsida, Selaginellales)*
**Selaginella** aff. **marginata** (Humb. & Bonpl. ex Willd.) Spring, *Flora* 21: 194. 1838. Fig. 5O.

Morphology: Trilete microspore. Polar view

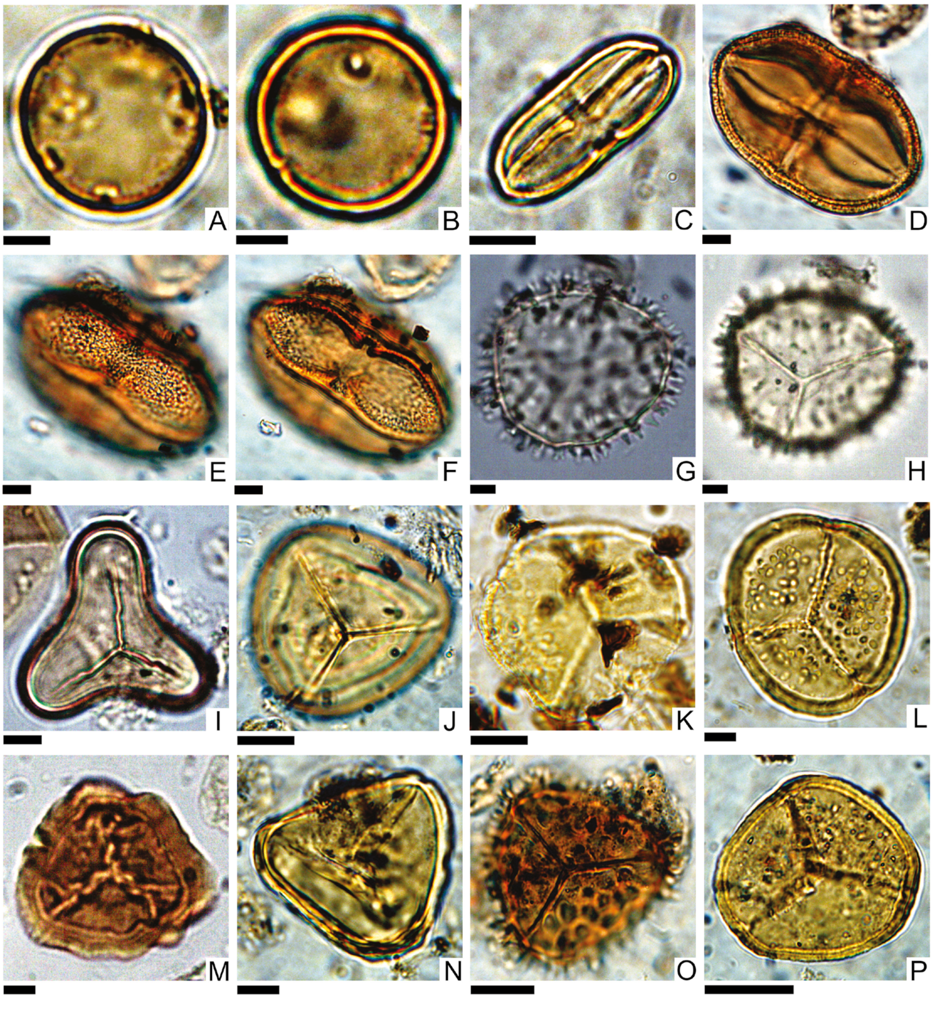


**Fig. 5.** Palynomorphs of *Phyllostylon*, *Eryngium*, *Cissus*, *Anthoceros*, *Cyathea*, *Phlegmariurus*, *Phaeoceros*, *Jamesonia*, *Pellaea*, and *Sellaginella*. **A**: *Phyllostylon rhamnoides*, general view in superior focus (100x). **B**: General view in optical section (100x). **C**: *Eryngium elegans*, equatorial view in optical section (100x). **D**: *Cissus verticillata*, equatorial view in optical section (100x). **E**: Equatorial view in superior focus (100x). **F**: Equatorial view where apertures are appreciated (100x). **G**: *Anthoceros* aff. *Lamellatus*, polar view in optical section (100x). **H**: Polar view where the trilete is appreciated (100x). **I**: *Cyathea* aff. *Multiflora*, polar view in superior focus (100x). **J**: *Phlegmariurus* aff. *Mandiocanus*, polar view in superior focus (100x). **K**: *Phaeoceros bulbiculosus*, polar view in optical section (100x). **L**: *Phaeoceros tenuis*, polar view in superior focus (100x). **M**: *Jamesonia flexuosa*, polar view in superior focus (100x). **N**: *Pellaea* sp., polar view in optical section (100x). **O**: *Selaginella* aff. *Marginata*, polar view where the trilete is appreciated (100x). **P**: *Sphagnum* sp., polar view in optical section (100x). Scales= 10 µm.

subtriangular. Laesura with straight rays reaching to the equator. Exospore thin 1-2 µm thick. Baculate with less frequent spinose and verrucate ornamentation. Size: 17-37 µm. Micro-megaspores belonging to this taxon were described from Argentina (Morbelli, 1977; Morbelli *et al*., 2001) and from Brazil (Lorscheitter *et al*., 1998).

Ecological procedence: perennial herbaceous represented in *Selaginella sellowii* Hieron. grass of the natural vegetation of Corrientes (Fontana, 2018).

*Sphagnaceae (Sphagnopsida, Sphagnales)*
**Sphagnum sp.** Fig. 5P.

Morphology: trilete spore. Polar view subtriangular, with rounded angles. Rays of the laesurae reach the equator. Exospore 2-4.5 µm thick. Finely rugged. Size: 20-26 µm (Fuertes & Rodríguez, 2009).

Ecological procedence: moss well represented in marshes of the natural vegetation of the Iberá System (Arbo & Tressens, 2002).

## Discussion

*Local and extra- local taxa and plant associations during the Holocene*

The first stage of the Mid Holocene, between 6990 and 5800 cal year BP is characterized mostly by local taxa such as *Imperata brasiliensis*, *Echinochloa crus-galli*, *Echinochloa polystachya*, *Hymenachne pernambucensis*, *Cyperus rotundus*, *Crinum americanum*, *Cypella herbertii*, *Empetrum* aff. *rubrum, Polygala leptocaulis*, *Myriophyllum aquaticum* and *Ludwigia peploides*, which integrate marsh grasslands and hygrophilous communities suggesting locally humid conditions in the studied area (Fernandez Pacella & Lara, 2019) (Fig. 6).

A later stage of the Mid Holocene, between 5800 and 5141 cal year BP is characterized by local taxa of Poaceae, Cyperaceae, *Typha dominguensis*, *Sphagnum* sp., representing a characteristic wetland association. The presence of *Typha* suggests waterlogged or flooded soils with slow-moving water and poor drainage conditions (Cabrera, 1976; Carnevalli, 1994). These plant communities, characteristic of lakes, swampy depressions and low floodplains, would indicate for this later stage of the Mid Holocene, sub-humid to humid conditions (Fernandez Pacella & Lara, 2019) (Fig. 6).

Between 5141 and 3506 cal year BP was characterized by a prevalence of local herbaceous vegetation composed of *Anthemis cotula*, *Conyza pampeana, Baccharis trimera, Gutierrezia resinosa, Bidens subalternans, Gaillardia megapotamica, Senecio bonariensis, Amaranthus muricatus, Eryngium elegans* and Poaceae, characteristic of psammophilous herbaceous steppe (Fig. 6). The

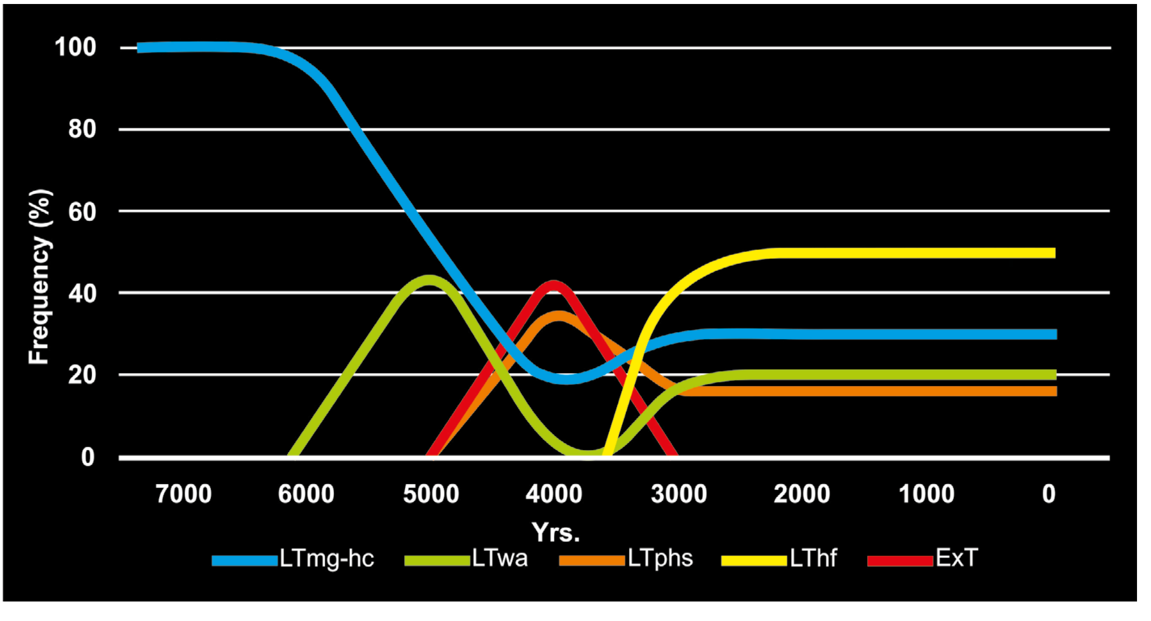


**Fig. 6.** Floristic representation of local and extra-local taxa and plant associations during the Holocene. **LTmg-hc**: local taxa-marsh grasslands and hygrophilous communities. **LTwa**: local taxa-wetland association. **LTphs**: local taxa-psammophilous herbaceous steppe. **LThf**: local taxa-hygrophilous forest. **ExT**: extra-local taxa.

presence of Chenopodiaceae suggests periodic desiccation of the water bodies (Tonello & Prieto, 2008). These results suggest dry environmental conditions (Fernandez Pacella *et al*., 2011; Fernandez Pacella & Lara, 2019). During this stage, different extra-local species are documented, which indicate the beginning of the development of various types of forests known today as Forests of *Schinopsis balansae* and *Myracrodruon balansae* ("quebrachal") of the humid Chaco phytogeographic region, better represented in Chaco, Formosa and northern Santa Fe provinces, with impoverished remains in the NW of Corrientes (Fontana, 2018). The main species documented herein are *Anadenanthera colubrina, Myracrodruon balansae, Calliandra parvifolia, Myrcianthes pungens, Phyllostylon rhamnoides, Pisonia aculeata, Prosopis alba, Schinopsis balansae, Schinus longifolia, Trichilia elegans*, *Justicia brasiliana* and *Serjania perulacea.* This type of forest develops in highest topographic areas free of floods characterized by soils with lower moisture gradients (well-drained) and a higher proportion of fine particles (Maldonado & Hohne, 2006; Morello & Rodríguez, 2009). Among these taxa, *Anadenanthera* was recorded from the Miocene to Pliocene in Patagonia and its last record is extended into the Holocene of the Iberá Wetland (Fernandez Pacella, 2015).

From 3484 cal year BP until the present (Late Holocene) the palynologic record shows a prevalence of herbaceous local vegetation composed of marshy taxa and wetland association (Fig. 6). Local taxa from the "Hygrophilous Forest", represented by *Senegalia bonariensis, Celtis iguanaea, Polygonum acuminatum***,** *Polygonum convolvulus, Cissus verticillata, Plinia rivularis, Tecoma stans, Thinouia mucronata, Chrysophyllum marginatum, Mikania cordifolia, Cyathea atrovirens, Jamesonia flexuosa, Phlegmariurus mandiocanus, Pellaea* sp., *Phaeoceros tenuis* and *Phaeoceros bulbiculosus* also documented in variable frequency (Fernandez Pacella *et al*., 2011; Fernandez Pacella & Lara, 2019). This Hygrophilous Forest developed in this interval, forms a strip that extends along small floodplain valleys close to "madrejones" or ponds with reservoirs, sometimes superimposed on the grasslands (Eskuche, 2004; Garcia *et al*., 2013). It is characterized by low to medium trees in less dense forests that allows enough light input for the establishment of herbaceous communities as part of the understory vegetation. The interpretation of "humid forests community" is clearly supported by the abundance of epiphytes and creeping taxa giving an idea of a jungle type environment (Carnevalli, 1994; Fontana, 2018).

*Comparison with modern vegetation*

All the species described herein are still part of the flora of Corrientes. For example, *Selaginella* aff. *marginata* present in the Mburucuyá National Park (Meza Torres *et al*., 2013) constitutes the herbaceous community of "*Selaginella sellowii grass*" that grows on eroded soils in the open forests of *Schinopsis balansae* and *Myracrodruon balansae* of north-western Corrientes (Bauni & Homberg, 2015; Fontana, 2018). These forests characterized by tree and shrubby forms herein documented as well (*Anadenanthera colubrina, Myracrodruon balansae, Calliandra parvifolia, Myrcianthes pungens, Phyllostylon rhamnoides, Pisonia aculeata, Prosopis alba, Schinopsis balansae, Trichilia elegans*, *Justicia brasiliana, Serjania perulacea*).

*Syagrus romanzoffiana* and *Schinus longifolia* represent the extensive palm groves particularly on the western coast of the Paraná River in the NW of Corrientes. They develop in floodplain valleys of some streams and depressed areas with soils bearing a high content of fine materials (silt and clays), mixed with sand, brought by the river, generally subjected to frequent, non-permanent floods (Fontana, 2018).

The local herbaceous taxa *Imperata brasiliensis*, *Echinochloa crus-galli*, *Echinochloa polystachya*, *Hymenachne pernambucense*, *Cyperus rotundus*, *Eryngium elegans*, *Cypella herbertii*, *Myriophyllum aquaticum, Empetrum* aff. *rubrum, Polygala leptocaulis*, *Ludwigia peploides*, *Typha dominguensis, Celtis iguanaea*, *Anthemis cotula*, *Conyza pampeana, Baccharis trimera, Mikania cordifolia, Gutierrezia resinosa, Bidens subalternans, Gaillardia megapotamica, Senecio bonariensis, Amaranthus muricatus* and *Sphagnum* sp., are currently part of the hygrophilous communities of marsh- grasslands, wetlands and psammophilous herbaceous steppe of the Iberá Wetland (Arbo & Tressens, 2002).

*Senegalia bonariensis, Polygonum acuminatum***,** *Polygonum convolvulus, Cissus verticillata, Plinia rivularis, Tecoma stans, Thinouia mucronata, Chrysophyllum marginatum, Cyathea atrovirens, Jamesonia flexuosa, Phlegmariurus saururus,* *Pellaea* sp., *Phaeoceros tenuis* and *Phaeoceros bulbiculosus*, represent varied habits from tree to epiphyte of the Hygrophilous Forests in the W, N and center of Corrientes (Carnevalli, 1994; Fontana, 2018).

## Conclusion

The 55 pollen and spore types described and illustrated in this contribution reaffirm diversified floras existed during the Mid-Late Holocene in Corrientes. Of them, 46 pollen grains correspond to 27 families of angiosperms and 9 trilete spore-types of ferns, lycophytes and bryophytes, obtained from six lakes of this wetland. Forty-two (42) taxa of these lived in the Iberá wetland (local taxa), whereas 13 extra-local ones would have arrived chiefly through air currents. This ecologic/procedence differentiation of species and their relative frequency per sample in each core (pollen diagrams) presented by Fernandez Pacella *et al*. (2011), Fernandez Pacella (2013), Fernandez Pacella & Lara (2019) was applied to interpret environmental characteristics and the evolution of the Iberá vegetation. Therefore, the identification of pollen grains up to species level enhances paleoenvironmental reconstructions based on more accurate ecological information and geographic distribution. Some local species as, considered in this studied region, were temperate-environmentally restricted and, for example, during the first stage of the Late Holocene, characteristic species of psammophilous herbaceous steppe were documented. On the other hand, in a later stage of the Late Holocene, several species appeared indicating the beginning of the development of "Hygrophilous Forest". Instead, other species such as grasses are dominant throughout the Holocene in Corrientes. This work broadens the knowledge of the palynological flora of northeastern Argentine and, will help to differentiate the local vegetation from the extra-local in future interpretations.

## Authors contribution

Both authors have jointly and equally carried out the data collection, interpretation and writing of the manuscript.

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