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FIRST QUATERNARY BRAZILIAN CAVE POLLEN RECORD: MORPHOLOGICAL DESCRIPTIONS, TAXONOMIC AND ECOLOGICAL DATA

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ABSTRACT – This paper presents descriptions, and taxonomic and ecological data by the angiosperm pollen grains recovered from Quaternary sediments of the Gruta do Urso Cave, Tocantins State, Northern Brazil. Among recovered assemblage, 44 types of angiosperm pollen were identified. Most of the pollen types described here are related to the modern aboreal-shrub and herbaceous-subshrub taxa currently present in the plant communities of the Cerrado biome: (i) forest formations (Annonaceae, *Aspidosperma*, *Ilex*, *Celtis*, *Trema*, *Tournefortia*, *Protium*, Combretaceae-Melastomataceae type, *Croton*-type, Moraceae-Urticaceae type, cf. *Bauhinia brevipes*, *Cassia*, *Pithecellobium*, *Peixotoa*, and *Cedrela*); (ii) savannah formations (*Anacardium*, *Astronium*, Asteraceae Tribu Eupatorieae, *Caryocar*, Cyperaceae, *Eriotheca*-type, *Ludwigia*, *Pseudobombax* spp., *Ouratea*, *Qualea,* and *Utricularia*), and (iii) grasslands (Poaceae). Regarding the diversity of pollen types registered, the most representative botanical families were: Fabaceae (8), Malvaceae (4), Euphorbiaceae (3), Anacardiaceae (3), Apocynaceae (2), Cannabaceae (2), Sapindaceae (2) and Poaceae (2), which also occur in the Cerrado-Caatinga transition. Pollen data show paleovegetation during the Last Glacial Maximum and Holocene times out of the cave, and provides a reliable source for paleoecological, paleoenvironmental and paleoclimatic investigations.

Keywords: palynology, Quaternary, paleovegetation, Brazilian savannah.

RESUMO – Este artigo apresenta as descrições morfológicas, dados taxonômicos e ecológicos de grãos de pólen de angiospermas recuperados de sedimentos quaternários da Gruta do Urso, Estado do Tocantins, Norte do Brasil. Foram registrados 44 tipos polínicos que se relacionam com os táxons arbustivo-arbóreos e arbustivo-herbáceos ocorrentes atualmente nas comunidades vegetacionais do bioma Cerrado: (i) formações florestais (Annonaceae, *Aspidosperma*, *Ilex*, *Celtis*, *Trema*, *Tournefortia*, *Protium*, Tipo Combretaceae-Melastomataceae, Tipo *Croton*, Tipo Moraceae-Urticaceae, cf. *Bauhinia brevipes*, *Cassia*, *Pithecellobium*, *Peixotoa* e *Cedrela*); (ii) cerrado *sensu stricto* (*Anacardium*, *Astronium*, Asteraceae Tribo Eupatorieae, *Caryocar*, Cyperaceae, Tipo *Eriotheca*, *Ludwigia*, *Pseudobombax* spp., *Ouratea*, *Qualea* e *Utricularia*) e (iii) gramíneas (Poaceae). Quanto à diversidade polínica, as famílias botânicas mais representativas foram: Fabaceae (8), Malvaceae (4), Euphorbiaceae (3), Anacardiaceae (3), Apocynaceae (2), Cannabaceae (2), Sapindaceae (2) e Poaceae (2), que também ocorrem na transição dos biomas Cerrado-Caatinga. Os dados polínicos refletem a paleovegetação do entorno da caverna durante o Último Máximo Glacial e Holoceno, e constituem uma fonte confiável para as investigações paleoecológicas, paleoambientais e paleoclimáticas.

Palavras-chave: palinologia, Quaternário, paleovegetação, Cerrado.

INTRODUCTION

Quaternary pollen analysis from conventional sites (lake sediments and paleosols) in the Cerrado areas and its transitions (*i.e.* Caatinga, Amazonian forests, and savannah) summarize the pulses of expansion and retraction among dry and humid forests due to climatic changes during the last ~ 50,000 years BP (Absy *et al.*, 1991; Ledru, 1993; Van der Hammem & Absy, 1994; Ledru *et al.*, 1996; Salgado-Labouriau *et al.*, 1997; Behling *et al.*, 1999; De Oliveira *et al.*, 1999; Barberi *et al.*, 2000; Behling & Hooghiesmtra, 2000; Ledru *et al.*, 2001). However, paleoecological information from karstic cave deposits is still scarce in Brazil and, in any case, restricted to the southeastern region, in Minas Gerais and Rio de Janeiro States (Parizzi *et al.*, 1998; Barth *et al.*, 2009).

Cave pollen deposits, such as speleothems and surface sediments, are challenged by generally poor preservation of their palynomorphs, and the post-depositional alteration of the pollen assemblages (Leroi-Gourhan & Renault-Miskovsky, 1977; Carrión *et al.*, 1999), which increase difficulties with interpretation (Bryant & Holloway, 1983). Nevertheless, in some cases, pollen may indicate the local and regional plant communities, and display value as paleoenvironmental proxy, especially in arid and semi-arid territories (Carrión *et al.*, 1995, 1999). In addition, pollen may aid in the stratigraphic and taphonomic resolution of these deposits, since palynomorphs are good indicators of transport conditions via water, wind, or animals (Carrión *et al.*, 1995; Navarro Camacho *et al.*, 2000). Another important source of pollen associated with cave deposits are human and other animal coprolites, which may contain dietary information (Chaves & Renault-Miskovsky, 1996; Carrión *et al.*, 2005).

Here we show pollen qualitative data concerning the Cerrado plant communities, with the goal of establishing a base for paleoecological and paleoclimatic regional studies on the Brazilian savannah.

STUDY SITE

Geography, geology and age

The study site, Gruta do Urso Cave (12º42'47"S; 46º24'28"W) (Figure 1), is located in Aurora do Tocantins, Tocantins State, Northern Brazil. The region is characterized by massive limestones and is geologically situated in the context of the Bambuí Group, with large concentration of caves (CPRM, 2006). The relative age of these deposits is based on Brazilian fossil mammals that are loosely dated as Late Pleistocene–Early Holocene (Cartelle, 1999; Castro *et al.*, 2013). This assignment is based both on the comparison to well-known Argentinian faunas (Marshall *et al.*, 1984; Cione & Tonni, 2005) and on several radiometric dates (Faure *et al.*, 1999; Neves & Piló, 2003; Auler *et al.*, 2006; Hubbe *et al.*, 2007). In the case of Aurora do Tocantins, the peccary *Catagonus stenocephalus* collected in Gruta dos Moura was ESR dated, yields an age of 20,000 years BP (Avilla *et al.*, 2013), which can be supported by faunistic assemblage. Although some taxa show wider biochrons, as *Pachyarmatherium* and *Catagonus* (Porpino *et al.*, 2009; Gasparini *et al.*, 2010), *Propraopus sulcatus* (Lund, 1842) is restricted to Late Pleistocene (Castro *et al.*, 2013), and the equid *Equus* (*Amerhippus*) *neogeus* (Lund, 1840) is a guide-fossil for Lujanian (Late Pleistocene–earliest Holocene) (Cione & Tonni, 1999, 2005; Maldonado *et al.*, 2016).

Regional modern climate and vegetation

The Tocantins State shows sub-humid dry, humid sub-humid and humid climates, according to Thornthwaite-Mather climate classification. The average annual rainfall is about 1,300 mm in the southeast of the Tocantins State, while the average air temperature ranges from 18 to 28° C and 5–6 months dry season occurs from April to October (Dias *et al.*, 2008). The occurrence of regional semideciduous and deciduous seasonal forests are associated with geological environments, crystalline emplacements and orogenic tracks in various soil classes, especially on rocky outcrops, cambisoils, ultisoils, and latosoils (Haidar *et al.*, 2013).

The modern Cerrado flora is the result of a combination of physical, geomorphological and anthropogenic factors as latitude, depth of the water table fires, agricultural activities, pasture management systems, and wood selective collection (Ribeiro & Walter, 2008).

The Cerrado biome has a great floristic richness, with more than 6,389 native taxa, belonging to 6,062 species of phanerogams, among arboreal-shrub and herbaceous-subshrub taxa. *Byrsonima* (Malpighiaceae), *Didymopanax* (Araliaceae), *Qualea* (Vochysiaceae) and *Caryocar* (Caryocaraceae) are the main arboreal taxa (Ribeiro & Walter, 2008). The most common family are: Fabaceae, Poaceae, Asteraceae, Rubiaceae, Melastomataceae, Euphorbiaceae, Malpighiaceae, Myrtaceae, Lythraceae and Orchidaceae (Mendonça *et al.*, 2008). Cerrado biome is composed of several plant communities: (i) Forest Formations (Riparian Forest, Gallery Forest, Dry Forest and Cerradão); (ii) Savannah Formations (Cerrado *sensu stricto* and Palm Swamps/ Swamps) and (iii) Grasslands (UNESCO, 2002; Ribeiro & Walter, 2008; Mendonça *et al.*, 2008). Cerrado is considered a biodiversity hotspot, and Tocantins State is a priority area for flora conservation covering three of the Brazilian biomes: the Cerrado, the Caatinga and the Amazon Forest (UNESCO, 2002; Ratter *et al.*, 2003).

MATERIAL AND METHODS

Sampling, processing and pollen descriptions

Twenty-one samples were collected: four by surface sample sediments and seventeen subsurface sample sediments positioned at cave sites. Each sample was collected at 10 cm intervals until subsurface until -50 cm maximum depth, according to stratigraphic deposition (Figure 1). Radiocarbon (^{14}C) ages (AMS- accelerator mass spectrometry) were obtained at the Laboratory of Ion Beam Physics, ETHZ (Zürich) (Table 1). All samples (ca. 10–30g of sediment each) were treated by chemical attack avoiding organic matter oxidation (Mendonça Filho *et al.*, 2002), using

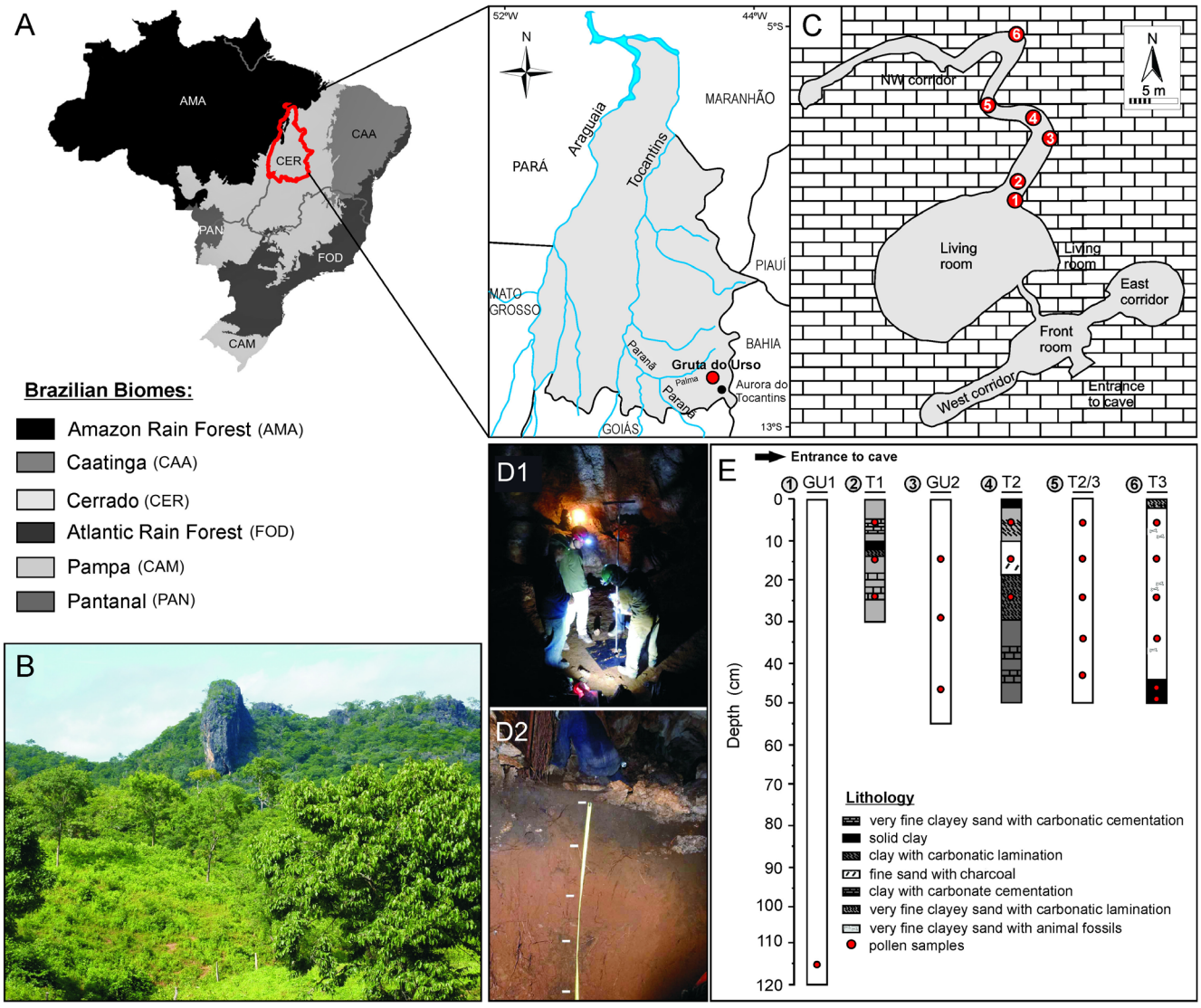

Figure 1. A, location map of the Gruta do Urso Cave, Tocantins State, Central-North Brazil and geographic position of Cerrado biome. **B**, view from the entrance to the cave showing the current cerrado arboreal vegetation. **C**, cave sites sampled for pollen: **1**, GU1; **2**, T1; **3**, GU2; **4**, T2; **5**, T2-3 and **6**, T3. **D1**, surface and **D2**, stratigraphic palynological samples. **E**, palynological samples position and lithology. The cave sites GU1, GU2 and T2-3 have no lithological description.

Table 1. Radiocarbon dates from Gruta do Urso Cave organic sediments using the Program CALIB Rev 7.0.4. (http://calib.qub.ac.uk/calib/) (Stuiver & Reimer, 1993) and the calibration curve IntCal13, with 95% probability (Reimer *et al.*, 2013).

Sample depth (cm)	Lab. code	^{14}C date BP	Cal. Yr BP 2σ range 95% probability	Cal. Yr BP average	δ^{13}C (‰)
T2-3 (10–20)	ETH–65503	6848 ± 30	7742–7613	7677	-20,4
GU2 (40–55)	ETH–65502	16773 ± 53	20436–20034	20235	-20,8
GU2 (20–40)	ETH–65501	17568 ± 57	21469–20985	21227	-21,8
T3 (20–30)	ETH–65504	20135 ± 70	24425–23972	24108	-14,9

hydrochloric and fluoric acids to dissolve carbonates and silicates respectively, and heavy liquid separation with zinc chloride (D=2.0) to concentrate the organic residue. The pollen slides were mounted in glycerin (glycerol) for light microscopy analysis.

The pollen descriptions were based on characters such as polarity, symmetry, number, position and character of apertures, exine ornamentation, shape, and size. These morphological characteristics should provide a sound basis for correlations between fossil and modern palynomorphs,

permitting their taxonomic classification (Erdtman, 1969; Salgado-Labouriau, 1973) (Table 2). Pollen were identified by comparison with the pollen reference collection of Álvaro Xavier Moreira Palynological Laboratory, Department of Botany of the Museu Nacional, Universidade Federal do Rio de Janeiro and published pollen atlases for Cerrado and Amazonian flora and other Quaternary pollen descriptions (Barth, 1966; Salgado-Labouriau, 1973; Roubik & Moreno, 1991; Colinvaux *et al.*, 1999; Bush & Weng, 2007; Gonçalves-Esteves *et al.*, 2007; Freitas & Carvalho, 2012; Cassino & Meyer, 2013; Freitas *et al.*, 2013).

Pollen taxonomy follows the classification system established in the Angiosperm Phylogeny Group III guidelines (APG IV, 2016). The descriptive terminology follows the International Code of Botanical Nomenclature (**ICBN**) and glossary of pollen and spore terminology (Punt *et al.*, 2007). All the photomicrographs (Figures 2 to 4) were taken on a transmitted light Nikon Eclipse E-100 microscope under 400x and 1000x magnification, using Moticam 3.0 MP software.

RESULTS AND DISCUSSION

Chronology

Radiocarbon (^{14}C) dates from of the pollen stratigraphy levels confirm Late Glacial Maximum (24,108 to 20,235 cal yr BP) and Early–Middle Holocene ages (7,677 cal yr BP) for the sedimentary deposits (Table 1).

Table 2. Pollen grains descriptions, taxonomic, and ecological data.

Pollen taxa / Cave Site	Descriptions	Remarks
MAGNOLIIDS		
ANNONACEAE		
Annonaceae Juss. (Figure 2.A1–2) GU2 (40–55 cm)	Tetrad, medium size, apolar, elliptic to rounded ambitus, inaperturate, exine baculate; frequently folded. Diameters: 30 x 30 μm; exine: 1 μm; bacula: 1 μm	Occurrence in modern cerrado pollen rain from Central Brazil (Salgado-Labouriau, 1973; Cassino *et al*., 2015) and Amazonian Quaternary lake sediments (Colinvaux *et al*., 1999)
MONOCOTS		
BROMELIACEAE		
Bromeliaceae Juss. (Figure 2.B) GU2 (40–55 cm)	Monad, medium size, heteropolar, elliptic ambitus, monosulcate with large sulcus and columela conspicuous, reticulate-heterobrochate exine. Polar diameter: 30 μm; equatorial diameter: 19 μm; exine: 2 μm; columela: 2 μm (Souza *et al.*, 2004)	Morphological characters resembling the genus *Dyckia*, present in gallery forest from cerrado and Amazonian savannahs (UNESCO, 2002; Mendonça *et al*., 2008; Gosling *et al*., 2009). Registered on coastal Holocene sediments in Southeastern Brazil (Freitas & Carvalho, 2012)
CYPERACEAE		
Cyperaceae Juss. (Figure 2.C) GU1 (100–120 cm)	Monad, medium size, heteropolar, circular ambitus, triporate, circular pore with conspicuous annulus, scabrate exine, irregular. Polar diameter: 50 μm; equatorial diameter: 40 μm; pore: 4 μm; annulus: 4 µm; pori: 4 μm	Morphological characters suggest affinities with the genus *Scleria* spp. (Roubik & Moreno, 1991). Compound herbaceous-subshrub layer of the moist grasslands and *Campo Sujo* communities from Central Brazil (Munhoz & Felfili, 2006, 2007) and herbaceous layer in the inselbergs from Northeastern Brazil (Araujo *et al*., 2008). Some species were registered in amphibious or emergent flora in Cerrado wetlands (Moreira *et al.*, 2011). Occurrence in modern swamps from Central Brazil (Salgado-Labouriau, 1973; Cassino *et al.*, 2015) and Amazonian savannahs (Bush & Weng, 2007; Gosling *et al*., 2009). Registered on Quaternary peat bogs and palm swamp sediments from distinct areas from Central Brazil (Ledru, 1993; Salgado-Labouriau *et al*., 1997; Cassino & Meyer, 2013)
POACEAE		
Poaceae type 1 (Figure 2.D) GU1 (100–120 cm)	Monad, medium size, heteropolar, circular ambitus, monosulcate, pore with conspicuous annulus, psilate exine, spheroidal. Polar diameter: 35 μm; equatorial diameter: 35 μm; pore: 2 μm; annulus: 2 μm	Most native grasslands have polar diameter between 30-40 μm (Salgado-Labouriau, 1973). Regional occurrence in modern cerrado, caatinga, cerrado-caatinga transition and Amazonian savannah floras (Salgado-Labouriau, 1973; Colinvaux *et al*., 1999; Gosling *et al*., 2005, 2009; Chaves, 2013; Cassino *et al*., 2015). Compound herbaceous-subshrub layer of the moist grasslands and *Campo Sujo* communities from Central Brazil (Munhoz & Felfili, 2006, 2007), cerrado and caatinga mixed forests (Passos & Dubreuil, 2004) and inselbergs from Northeastern Brazil (Araujo *et al.*, 2008). Found also in aquatic flora in palm swamps from Cerrado (Moreira *et al*., 2011). Commonly recorded on Quaternary sediments from Central Brazil (Ledru, 1993; Salgado-Labouriau *et al.*, 1997; Lorente & Meyer, 2010) and Quaternary coastal and marine sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al.*, 2013)

Table 2. Cont.

Pollen taxa / Cave Site	Descriptions	Remarks
Poaceae type 2 (Figure 2.E) GU1 (100–120 cm)	Monad, large size, heteropolar, monoporate, pore with conspicuous annulus, psilate exine, spheroidal, irregular. Polar diameter: 33µm; equatorial diameter: 25 µm; pore: 2 µm; annulus	
EUDICOTS		
MALPIGHIALES		
CARYOCARACEAE		
Caryocar F. Allam. (Figure 2.F1–4) GU2 (20–40 cm)	Monad, large size, isopolar, triangular ambitus, parasyncolporate, with very and narrow long colpes, distinctly lalongate endoaperture with sharp ends and constriction in the median region, reticulate exine (in mesocolpium) and rugulate exine (in apocolpium), with apocolpium forming a triangle conspicuous; protuberance in equatorial view; prolate (P/E: 1.62). Size in equatorial view: polar diameter: 65 μm; equatorial diameter: 40 μm; exine: 4 μm. Size in polar view: 40 x 40 μm	Arboreal component from cerrado and caatinga mixed forests (Passos & Dubreuil, 2004) and transition environments between swamps and cerrado vegetation in western Bahia State (Reis, 2008). Occurring in the modern cerrado pollen rain and Amazonian *Terra Firme* and savannah pollen rain (Barth, 1966; Salgado-Labouriau, 1973; Colinvaux *et al.*, 1999; Gosling *et al*., 2005, 2009; Cassino *et al*., 2015) and palm swamp Quaternary sediments (Lorente & Meyer, 2010)
EUPHORBIACEAE		
Actinostemon Mart. Ex Klotzsch (Figure 2.2.G1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, tricolporate, microreticulate exine, prolate (P/E: 1.37); lalongate and conspicuous endoaperture. Polar diameter: 40 μm; equatorial diameter: 29 μm; exine: 1 μm	Occurring on Holocene coastal sediments in Southeastern Brazil (Freitas & Carvalho, 2012)
Type *Croton* (Figure 2.H1–2) GU2 (40–55 cm)	Monad, medium size, apolar, circular ambitus, inaperturate, pilate exine with croton pattern, spheroidal. Diameters: 39 x 35 μm; exine: 3 μm	Components of the herbaceous-subshrub layer of the moist grassland's community from Central Brazil (Munhoz & Felfili, 2007). Occurrence in modern pollen rain cerrado, amazon and cerrado-caatinga transition (Salgado-Labouriau, 1973; Colinvaux *et al*., 1999; Chaves, 2013). Shrub taxa present in the thorny woodlands, dry forests and inselbergs from Northeastern Brazil (Alcoforado-Filho *et al*., 2003; Araujo *et al*., 2008). Registered during Quaternary times in Amazonian Quaternary lake sediments (Colinvaux *et al*., 1999), and coastal and marine sediments in Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)
Sebastiania Bertol. (Figure 2.I1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, tricolporate, reticulate to microreticulate exine, subprolate (P/E: 1.24); circular endoaperture. Polar diameter: 31 μm; equatorial diameter: 25 μm; exine: 4 μm	Shrub taxa registered in both Cerrado and Caatinga biomes (Rodal & Nascimento, 2006). Occurrence in modern cerrado (Salgado-Labouriau, 1973; Cassino et al., 2015) and Amazonian pollen rain (Colinvaux *et al*., 1999; Gosling et al., 2009). Found on Amazonian Quaternary lake sediments (Colinvaux *et al*., 1999) and Quaternary sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)
MALPIGHIACEAE		
Peixotoa A.Juss. (Figure 2.J1–2) GU2 (10–20 cm)	Monad, apolar, circular ambitus, pantoporate with presence of colpoids, rugulate exine, spheroidal. Diameters: 30 x 30 μm; pore: 3 μm; exine: 3 μm (Gonçalves-Esteves *et al.*, 2007)	Occurring in modern cerrado pollen rain (Cassino *et al*., 2015) and Quaternary marine sediments from Southeastern Brazil (Freitas *et al*., 2013)
OCHNACEAE		
Ouratea Aubl. (Figure 2.K1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, subcircular ambitus, tricolporate, scabrate exine, prolate-spheroidal (P/E: 1.09); small colpi, endoabertura lalongada. Polar diameter: 35 μm; equatorial diameter: 32 μm; exine: 2 μm	Shrub taxa that occur in pollen rain from cerrado and Amazonian savannahs (Gosling *et al*., 2009; Cassino *et al*., 2015). Occurring on Holocene palm swamp sediments (Lorente & Meyer, 2010) and coastal sediments from Southeastern Brazil (Freitas & Carvalho, 2012)
FABALES		
FABACEAE-CAESALPINIOIDEAE		
cf. *Bauhinia brevipes* Vogel (Figure 2.L1–2) GU2 (40–55 cm)	Monad, large size, isopolar, circular ambitus, tricolpate, pilate exine. Diameters: 105 x 105 μm; bacula (in most), scabrae, clavae and gemmae: 4 μm; exine: 5 μm (Moreira *et al.*, 2013)	Arboreal taxa present on thorny woodlands and uplands dry forests from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Occurrence in modern flora from cerrado and Amazonian savannahs (Salgado-Labouriau, 1973; Gosling *et al*., 2009). Found on Quaternary sediments of Amazonian lakes (Colinvaux *et al*., 1999) and coastal and marine sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)

Table 2. Cont.

Pollen taxa / Cave Site	Descriptions	Remarks
Cassia L. (Figure 2.M1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, tricolporate, scabrate exine, prolate (P/E: 1.34); lalongate endoaperture; colpi wide as long as grain. Polar diameter: 31 μm; equatorial diameter: 23 μm; exine: 2 μm	Present in modern cerrado, caatinga and caatinga-cerrado pollen flora (Salgado-Labouriau, 1973, Chaves, 2013). Also registered on Quaternary sediments from Amazonian lakes (Colinvaux *et al*., 1999)
Fabaceae (Figure 2.N1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, tricolporate, microreticulate exine, prolate (P/E: 1.73). Polar diameter: 43 μm; equatorial diameter: 25 μm; exine: 2 μm	Present in modern cerrado pollen rain from Central Brazil (Salgado-Labouriau, 1973). Occurring on Quaternary Amazonian lakes and lagoonal sediments from Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)
Senna Mill. (Figure 3.A1–2) GU2 (20–40 cm)	Monad, medium size, isopolar, tricolporate, microreticulate exine, prolate (P/E: 1.59); large colpi, lolongate endoaperture. Polar diameter: 35 μm; equatorial diameter: 22 μm; exine: 2 μm (Barth and Bousada, 1964)	Arboreal taxa registered on the thorny woodlands from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Occurrence in modern shrub cerrado pollen rain (Cassino *et al*., 2015) and Quaternary palm swamp sediments from Central Brazil (Lorente & Meyer, 2010)
FABACEAE-FABOIDEAE		
Vigna Savi (Figure 3.D1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, circular ambitus, triporate, reticulate-heterobrochate exine; spheroidal, circular pore. Polar diameter: 30 μm; equatorial diameter: 30 μm; exine: 3 μm (Bush and Weng, 2007)	Arboreal taxa that occurs in modern Amazonian flora (Carreira *et al*., 1996)
Zollernia Maximil. & Nees (Figure 3.E1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, tricolporate, microrreticulate exine, subprolate (P/E: 1.19). Polar diameter: 25 μm; equatorial diameter: 21 μm; exine: 3 μm	On Holocene lagoonal sediments from Southeastern Brazil (Freitas & Carvalho, 2012)
FABACEAE-MIMOSOIDEAE		
Acacia Mill. (Figure 3.B1–2) GU2 (20–40 cm)	Polyad, medium size, apolar, circular ambitus, periporate, psilate exine; 16 grains rounded-trapezoid shape (13 μm). Diameters: 45x45 μm; exine: 1 μm (Du Bocage *et al*., 2008)	Arboreal taxa present in Deciduous Thorny Vegetation from northeastern Brazil (Alcoforado-Filho *et al*., 2003), with occurrence in modern cerrado, caatinga and Amazonian savannah and Terra Firme pollen rain (Ledru, 1991; Gosling *et al*., 2005, 2009; Chaves, 2013). On Quaternary sediments from Central Brazil and other areas (Ledru, 1993; De Oliveira *et al*., 1999; Ledru *et al*., 2001; Behling, 2002; Lorente & Meyer, 2010)
Pithecellobium Mart. (Figure 3.C1–2) GU1 (100–120 cm)	Polyad, medium size, apolar, elliptic ambitus, 4-porate, reticulate exine; 16 grains rounded-trapezoid shape (10 µm). Diameters: 45 x 45 μm; exine: 2 μm	Arboreal taxa of the Deciduous Thorny Vegetation inland areas from Northeastern Brazil (Alcoforado-Filho *et al*., 2003) that occurs in modern pollen rain from Central Brazil and Amazonia savannahs (Salgado-Labouriau, 1973; Ledru, 1991; Gosling *et al*., 2009). On Quaternary sediments from Central Brazil and other areas (Ledru, 1993; De Oliveira *et al*., 1999; Ledru *et al*., 2001; Behling, 2002; Lorente & Meyer, 2010)
ROSALES		
CANNABACEAE		
Celtis L. (Figure 3.F1–2) GU2 (40–55 cm)	Monad, small size, isopolar, spheroidal, triporate, scabrate exine, oblate. Diameters: 18 x 18 μm; exine: 1 μm (Barth *et al*., 1975)	Arboreal layer of the thorny woodlands from Northeastern Brazil (Alcoforado-Filho *et al*., 2003) and many Neotropical forest ecosystems (Absy *et al*., 1991; Ledru 1993; De Oliveira *et al*., 1999; Ledru *et al*., 2001). Occurring in many modern pollen rain from cerrado, caatinga and Amazon biomes (Ledru, 1991, Gosling *et al*., 2005, 2009; Chaves, 2013, Cassino *et al*., 2015). Occurring also on Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999), peat bogs from Central Brazil (Lorente & Meyer, 2010) and coastal Holocene sediments from Southeastern Brazil (Freitas & Carvalho, 2012)
Trema Lour. (Figure 3.G1–2) GU2 (40–55 cm)	Monad, small size, apolar, diporate, scabrate exine. Polar diameter: 18µm; equatorial diameter: 18 µm; exine: 1 µm (Barth *et al*., 1975)	Arboreal taxa that occurs in modern cerrado pollen rain from Central Brazil (Cassino *et al*., 2015) and savannah and Terra Firme Amazonian ecosystems (Gosling *et al*., 2005, 2009). Registered on Quaternary Amazonian lake sediments (Absy *et al*., 1991; Colinvaux *et al*., 1999), palm swamps sediments from Central Brazil (Salgado-Labouriau *et al*., 1997) and coastal Holocene sediments from Southeastern Brazil (Freitas & Carvalho, 2012)

Table 2. Cont.

Pollen taxa / Cave Site	Descriptions	Remarks
MYRTALES		
Type Combretaceae-Melastomataceae (Figure 3.H1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, circular ambitus, hexalobulate, heterocolporate with three colpi alternating with three pseudocolpi, lalongate endoaperture, microreticulate exine. Polar diameter: 25 μm; equatorial diameter: 25 μm; exine: 1 μm	Present in modern cerrado, caatinga and Amazon biomes (Salgado-Labouriau, 1973; Gosling *et al*., 2005, 2009; Chaves 2013; Cassino *et al*. 2015). Compound herbaceous-subshrub layer of the moist grasslands community from Central Brazil (Munhoz & Felfili, 2008). Indicator and/ or preferential taxa in the cerrado-amazon transition (Haidar *et al*., 2013). Arboreal taxa registered in Quaternary sediments in Central Brazil (Ledru, 1993; Salgado-Labouriau *et al*., 1997; Ledru *et al*., 2001; Behling, 2002; Cassino & Meyer, 2013) and Amazonian areas (Asby *et al*., 1991; Colinvaux *et al*., 1999). Also occurring on Holocene coastal sediments from Southeastern Brazil (Freitas & Carvalho, 2012)
ONAGRACEAE		
Ludwigia L. (Figure 3.I) GU2 (40–55 cm)	Tetrad, large size, isopolar, circular ambitus, tricolporate, rugulate-verrucate exine; lalongate endoaperture. Polar axis: 95 μm; equatorial axis: 90 μm	*Ludwigia irwinii* is amphibious aquatic plant that occuring in association with *Utricularia foliosa, Paspalum morichalense, Eleocharis acutangula*, *E. plicarhachis, Rhynchospora corymbosa, Eryngium pandanifolium* and *Panicum parvifolium* and occupied shallowest zones of palm swamps from Cerrado North-Central zones (Moreira *et al*., 2011). Present in modern swamps pollen rain from Central Brazil (Cassino *et al*., 2015). On Quaternary palm swamp sediments (Lorente & Meyer, 2010), and coastal and marine sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)
VOCHYSIACEAE		
Qualea Aubl. (Figure 3.J1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, sub-triangular ambitus, tricolporate, lalongate endoaperture, microreticulate exine, prolate-spheroidal (P/E: 1.10); Polar diameter: 31 μm; equatorial diameter: 28 μm; colpi: 24 μm; exine: 2 μm	*Qualea parviflora* is a generalist specie that prefers more fertiles soils, to distrophyc and humid conditions of the gullies (Felfili & Fagg, 2007). Occurrence in transition environments between swamps and cerrado vegetation in western Bahia State (Reis, 2008). In modern cerrado and amazon pollen rain (Ledru, 1991; Gosling *et al*., 2005)
MALVALES		
MALVACEAE		
Abutilon Mill. (Figure 3.K1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, prolate-spheroidal, tricolporate, brevicolpi, echinate exine. Diameters: 44 x 42 μm; exine: 2 μm	Registered on Quaternary Amazonian lakes sediments (Colinvaux *et al*., 1999) and Quaternary coastal-marine sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)
Type *Eriotheca* Schottand Endl. (Figure 3.L1–2) T2/3 (20–30 cm)	Monad, medium size, isopolar, planoaperturate, tricolporate, reticulate-heterobrochate exine, spheroidal (P/E=1). Polar axis: 35µm; equatorial axis: 35 μm; exine: 2 μm (Abreu *et al.*, 2014)	Present in modern cerrado pollen rain from Central Plateau and wooded savannahs from Central Brazil and Amazonian areas (Salgado-Labouriau, 1973; Gosling *et al*., 2009; Cassino *et al*., 2015). On Quaternary palm swamp sediments from Southeastern Brazil (Lorente & Meyer, 2010)
Pseudobombax cf. *longiflorum* (Figure 3.M) GU1 (100–120 cm)	Monad, large size, isopolar, planoaperturate, tricolcolporate, reticulate-heterobrochate exine, prolate-spheroidal (P/E=1.02); colpi. Polar diameter: 50 μm; equatorial diameter: 49 μm; exine: 3 μm (Abreu *et al.*, 2014)	Arboreal layer of the thorny woodlands from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Occuring in Quaternary Amazonian lakes sediments (Colinvaux *et al*., 1999)
Pseudobombax cf. *marginatum* (Figure 3.N) GU2 (20–40 cm)	Monad, large size, isopolar, planoaperturate, tricolcolporate, reticulate-heterobrochate exine, spheroidal (P/E=1); densely columellate; fine (in mesocolpium) and irregular (apocolpium) brochi (Abreu *et al.*, 2014). Polar diameter: 65 μm; equatorial diameter: 65 μm; exine: 2 μm	arboreal layer of the thorny woodlands from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Occuring in modern cerrado pollen rain from Central Plateau (Salgado-Labouriau, 1973) and registered in Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999) and Quaternary coastal-marine sediments from Southeastern Brazil (Freitas & Carvalho, 2012; Freitas *et al*., 2013)
SAPINDALES		
ANACARDIACEAE		
Anacardium L. (Figure 3.O1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, tricolporate, striate-reticulate exine, subprolate (P/E: 1.20). Polar diameter: 35 μm; equatorial diameter: 29 μm; colpi: 29 μm; exine: 2 μm	Present in modern pollen rain from cerrado, caatinga and cerrado-caatinga transition (Salgado-Labouriau, 1973; Chaves, 2013; Cassino *et al*., 2015). On Quaternary Amazonian lake sediments and Quaternary lagoonal sediments from Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)

Table 2. Cont.

Pollen taxa / Cave Site	Descriptions	Remarks
Astronium Jacq. (Figure 4.A1–2) GU2 (20–40 cm)	Monad, medium size, isopolar, tricolporate, reticulate-heterobrochate exine, prolate-spheroidal (P/E: 1.07); lalongate constricted endoaperture; colpi as a long as a grain. Polar diameter: 43 μm; equatorial diameter: 40 μm; exine: 2 μm	Arboreal taxa registered in cerrado and caatinga biomes (Rodal & Nascimento, 2006). Present in modern pollen rain from cerrado, caatinga and cerrado-caatinga transition (Salgado-Labouriau, 1973; Chaves, 2013; Cassino *et al*., 2015). On Quaternary lake sediments (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)
Schinus L. (Figure 4.B1–2) GU1 (100–120 cm)	Monad, small size, isopolar, tricolporate, striate-reticulate-heterobrochate exine, prolate-spheroidal (P/E: 1.12); lalongate constricted endoaperture; colpi as a long as a grain. Polar diameter: 18 μm; equatorial diameter: 16 μm; exine: 1 μm	Occuring in modern arboreal cerrado, cerrado-caatinga and caatinga pollen rain (Salgado-Labouriau, 1973; Chaves, 2013; Cassino *et al*., 2015) and Quaternary sediments from Amazonia and Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)
BURSERACEAE		
Protium Burm.f. (Figure 4.C1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, tricolporate, scabrate exine, prolate (P/E: 1.17); lalongate endoaperture. Polar diameter: 33 μm; equatorial diameter: 28 μm; exine: 2 μm (Aguilar-Sierra and Melhem, 1998)	Arboreal taxa registered in Cerrado and Caatinga biomes (Rodal & Nascimento, 2006). Recorded in modern cerrado pollen rain (Cassino *et al*., 2015) and Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999)
MELIACEAE		
Cedrela P.Browne (Figure 4.D1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, pentagonal ambitus, 4-stephanocolporate, scabrate exine, subprolate (P/E: 1.3); lalongate endoaperture. Polar diameter: 26 μm; equatorial diameter: 20 μm; exine: 2 μm (Barth *et al.*, 1998)	arboreal taxa registered on cerrado, caatinga and Amazon biomes (Salgado-Labouriau, 1973; Rodal & Nascimento, 2006; Gosling *et al*., 2009). Arboreal taxa occurring in the thorny woodlands and uplands dry forests from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Recorded in Quaternary sediments from Amazonia and Southeastern Brazil (Colinvaux *et al*., 1999; Freitas *et al*., 2013)
SAPINDACEAE		
Paullinia L. (Figure 4.E1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, triangular ambitus, triporate, microrreticulate exine, irregular, circular pore. Polar diameter: 37 μm; equatorial diameter: 37 μm; exine: 2 μm	Arboreal-shrub taxa present in the thorny woodlands from Northeastern Brazil (Alcoforado-Filho *et al*., 2003) and on Quaternary sediments from Amazonian areas and Southeastern Brazil (Colinvaux *et al*., 1999; Freitas *et al*., 2013)
Allophylus Gled. (Figure 4.F1–2) GU2 (40–55 cm)	Monad, medium size, isopolar, quadrangular ambitus, 3-4-porate, scabrate exine, circular pore. Polar diameter:32µm; equatorial diameter: 32 μm; exine: 2 μm	Occuring in modern cerrado from Central Brazil, caatinga and cerrado-caatinga transition pollen rain (Salgado-Labouriau, 1973; Cassino *et al*., 2015; Chaves, 2013). Arboreal-shrub taxa present in the dry forests from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Also recorded on Holocene coastal sediments (Freitas & Carvalho, 2012)
CARYOPHYLLALES		
AMARANTHACEAE		
Type *Gomphrena* L. (Figure 4.G1–2) GU2 (40–55 cm)	Monad, medium size, apolar, circular ambitus, pantoporate (12 pores), lophate exine, with pentagonal lacune. Diameters: 19 x 19 μm; exine: 6 μm (Roubik and Moreno, 1991)	Registered on modern cerrado pollen rain (Salgado-Labouriau, 1973; Cassino *et al*., 2015) and Quaternary palm swamps sediments (Lorente & Meyer, 2010). On Quaternary sediments from Amazonian and Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)
LAMIIDS (EUASTERIDS I)		
BORAGINACEAE		
Tournefortia L. (Figure 4.H1–2) GU1 (100–120 cm)	Monad, medium size, apolar, circular ambitus, apparently inaperturate, exine gemmate, spheroidal. Diameters: 28 x 28 μm; gemmae: 5 x 3 μm; exine: 6 μm	Arboreal-shrub layer of the thorny woodlands and uplands dry forests from Northeastern Brazil (Alcoforado-Filho *et al*., 2003). Registered on modern cerrado pollen rain (Salgado-Labouriau, 1973; Cassino *et al*., 2015) and Quaternary palm swamps sediments (Lorente & Meyer, 2010). On Quaternary sediments from Amazonian and Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)
GENTIANALES		
APOCYNACEAE		
Forsteronia G. Mey. (Figure 4.I1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, circular ambitus, 3-porate, scabrate to rugulate exine, oblate-spheroidal (P/E: 0.92); pores with conspicuous annulus. Diameters: 28 x 26 μm; exine: 3 μm	Present in cerrado, caatinga, cerrado-caatinga transition and amazon pollen rain (Salgado-Labouriau, 1973; Chaves, 2013; Cassino *et al*., 2015; Rodrigues *et al*., 2016). On Quaternary Amazonian lakes sediments and lagoonal sediments from Southeastern Brazil (Colinvaux *et al*., 1999; Freitas & Carvalho, 2012)

Table 2. Cont.

Pollen taxa / Cave Site	Descriptions	Remarks
Aspidosperma Mart. and Zucc. (Figure 4.J1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, circular to trilobulate ambitus, tricolporate, rugulate exine in poles and psilate exine in mesocolpium, oblate (P/E: 1). Polar axis: 32 μm; equatorial axis: 32 μm; exine: 2 μm; (Moreira *et al.*, 2004)	Arboreal taxa registered in Cerrado and Caatinga biomes (Rodal & Nascimento, 2006). Occurrence in modern Brazilian savannah and Amazonian pollen rain (Salgado-Labouriau, 1973; Gosling *et al*., 2005, 2009). On Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999)
RUBIACEAE		
Type *Richardia-Borreria* (Figure 4.K1–2) GU2 (40–55 cm)	Monad, large size, isopolar, circular ambitus, 15-colporate, echinate exine, zonaperturate, shorti colpi. Diameters: 60 x 55 μm; exine: 2 μm	Ressembling the genus *Richardsonia* described by Salgado-Labouriau (1973). Compound herbaceous-subshrub layer of the moist grasslands and *Campo Sujo* communities of the Central Brazil (Munhoz & Felfili, 2006, 2007). Ocurrence in modern savannah from Central Brazil and Amazonian region (Salgado-Labouriau, 1973; Gosling *et al*., 2009; Cassino *et al*., 2015). On Quaternary palm swamp sediments (Lorente & Meyer, 2010)
LAMIALES		
BIGNONIACEAE		
Anemopaegma Mart. Ex. Meisn. (Figure 4.L) T2/3 (10–20 cm)	Monad, medium size, apolar, circular ambitus, inaperturate, reticulate-heterobrochate exine, spheroidal. Polar diameter: 35 μm; equatorial diameter: 35 μm; exine: 3 μm	Modern pollen rain of cerrado from Central Plateau (Salgado-Labouriau, 1973) and Quaternary palm swamp sediments (Lorente & Meyer, 2010)
SOLANALES		
SOLANACEAE		
Solanum L. (Figure 4.M1–2) GU2 (40–55 cm)	Monad, small size, isopolar, subcircular ambitus, tricolporate, microreticulate exine, oblate-spheroidal (P/E: 1). Polar diameter: 19 μm; equatorial diameter: 19 μm; exine: 1 μm	Modern pollen rain from Central Brazil (Salgado-Labouriau, 1973; Cassino *et al*., 2015) and Amazonian savannahs (Gosling *et al*., 2009). Shrub layer of the deciduous thorny vegetation and thorny woodlands from Northeastern Brazil inland mountains (Alcoforado-Filho *et al*., 2003). Recorded also in Holocene palm swamps and lagoonal sediments from Southeastern Brazil (Lorente & Meyer, 2010; Freitas & Carvalho, 2012)
CAMPANULIDS (EUASTERIDS II)		
AQUIFOLIALES		
AQUIFOLIACEAE		
Ilex L. (Figure 4.N1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, tricolporate, clavate exine, subprolate (P/E: 1.2). Polar diameter: 30 μm; equatorial diameter: 25 μm; clavae: 2 μm; exine: 3 μm	Arboreal taxa associated with Quaternary moist and montane forests in Central Brazil (Ledru, 1993; Salgado-Labouriau *et al*., 1997; Ledru *et al*., 2001; Lorente *et al*., 2010) and Amazonia (Absy *et al*., 1991). Present in the modern cerrado flora (Salgado-Labouriau, 1973; Ledru, 1993; Cassino *et al*., 2015). On Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999), peat bogs and palm swamps from Central Brazil and coastal sediments from Southeastern Brazil (Salgado-Labouriau *et al*., 2007; Lorente & Meyer, 2010; Freitas & Carvalho, 2012)
APIALES		
ARALIACEAE		
Hydrocotyle L. (Figure 4.O1–2) GU1 (100–120 cm)	Monad, medium size, isopolar, tricolporate, scabrate exine, prolate to perprolate (P/E: 2); lalongate constricted endoaperture. Polar diameter: 40µm; equatorial diameter: 20 μm; exine: 2 μm	Rooted floating aquatic macrophyte common in palm swamp ponds in the North-Central brazilian savannah (Moreira *et al*., 2011). Occurring in modern swamp pollen rain from Central Brazil (Salgado-Labouriau, 1973; Cassino *et al*., 2015). On Quaternary Amazonian lake sediments (Colinvaux *et al*., 1999) and peat bogs, palm swamps and coastal sediments from Southeastern Brazil (Salgado-Labouriau *et al*., 2007; Lorente & Meyer, 2010; Freitas & Carvalho, 2012)

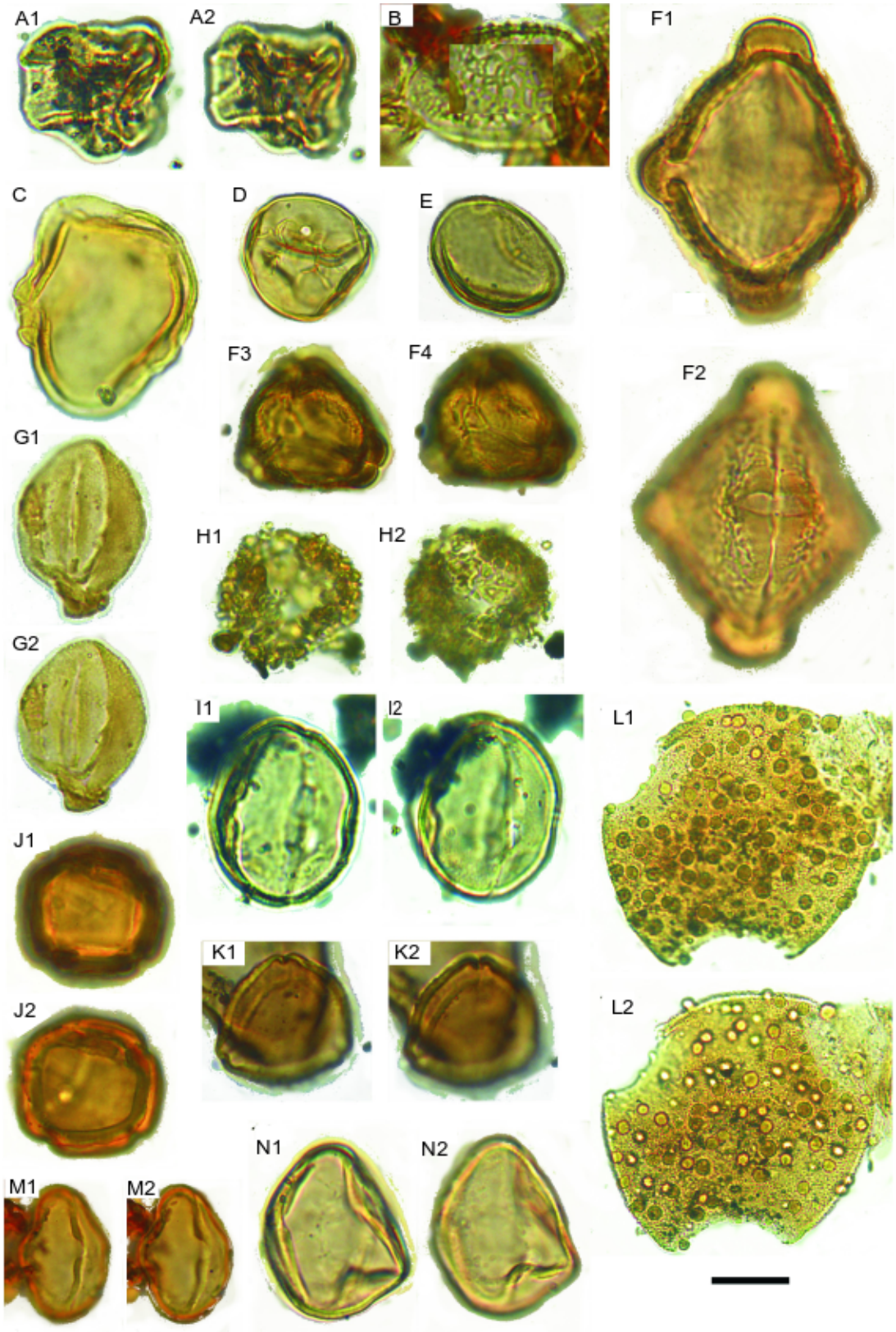

Figure 2. Photomicrographs of angiosperm pollen grains. Magnoliids: **A**, Annonaceae (tetrad tetragonal, **1**-upper and **2**-lower focus). Monocots: **B**, Bromeliaceae (polar view, with detail in the reticulated exine); **C**, Cyperaceae (pollen at different focal depths); **D**, Poaceae type 1 (polar view, upper focus); **E**, Poaceae type 2 (oblique view, lower focus). Eudicots: **F**, *Caryocar* (equatorial view, **1**-optical section and **2**-upper focus and polar view, **c**-lower and **3**-upper focus); **G**, *Actinostemon* (equatorial view, **1**-upper and **2**-lower focus); **H**, *Croton*-type (**1–2**-detail in the croton pattern); **I**, *Sebastiania* (equatorial view, **1**-optical section and **2**-lower focus); **J**, *Peixotoa* (**1**-upper focus and **2**-optical section showing quadrangular contour and colporate aperture); **K**, *Ouratea* (polar view, **1**-upper focus and **2**-optical section); **L**, cf. *Bauhinia brevipes* (polar view, **1**-lower and **2**-upper focus, with detail to the sculpture element "gemmae"); **M**, *Cassia* (equatorial view, **1**-upper and **2**-optical section); **N**, Fabaceae type 1 (equatorial view, **1**-optical section and **2**-upper focus). Scale bar = 20 µm.

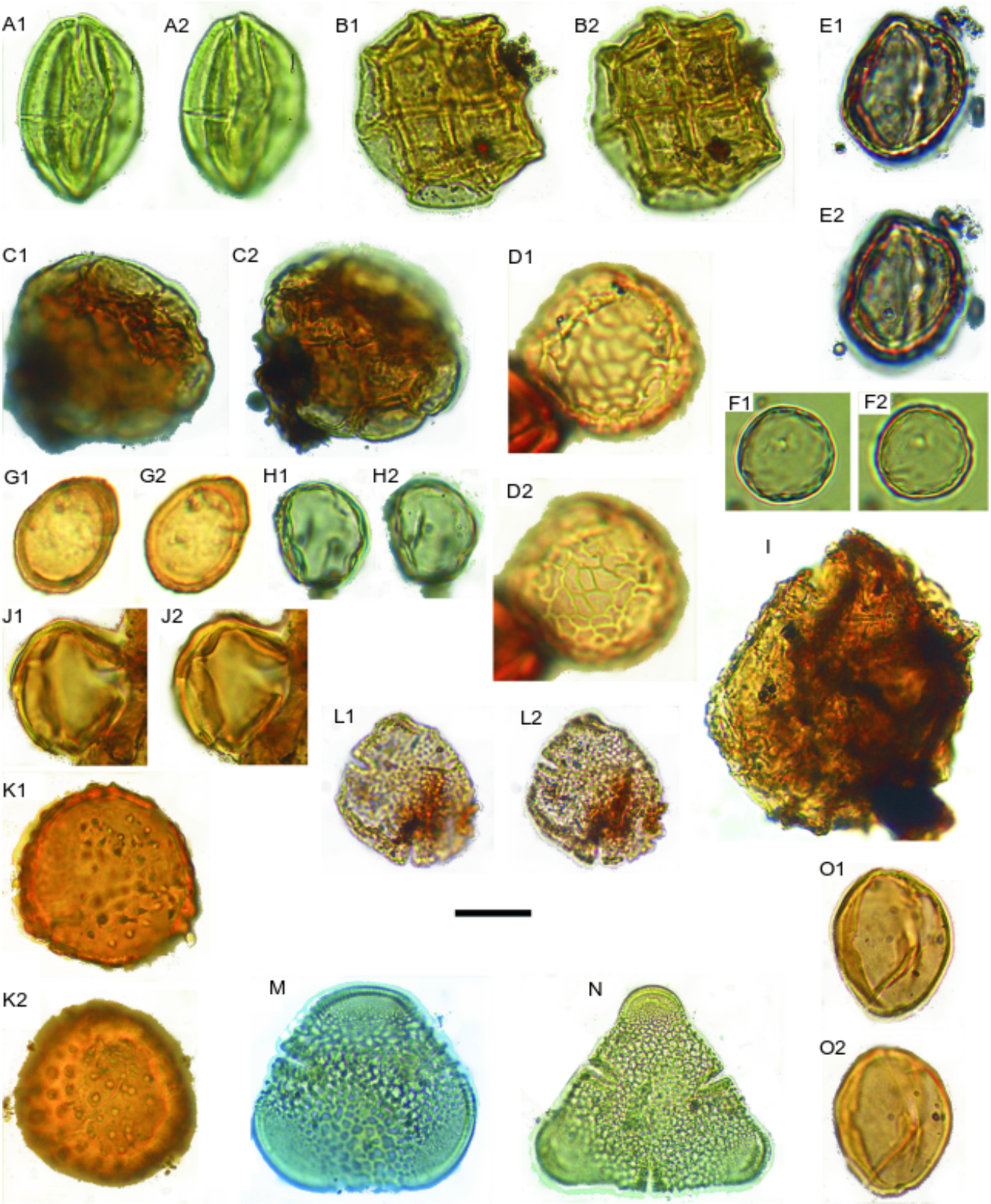

Figure 3. Photomicrographs of angiosperm pollen grains. Eudicots: **A**, *Senna* (equatorial view, **1**-optical section and **2**-upper focus); **B**, *Acacia* (**1**–**2**-polyad with 16 monads); **C**, *Pithecellobium* (**1**–**2**-polyad with 16 monads); **D**, *Vigna* (polar view, **1**-lower focus with detail in the endoaperture/pore and **2**-upper focus); **E**, *Zollernia* (equatorial view, **1**-optical section and b-lower focus); **F**, *Celtis* (equatorial view, **1**-lower focus and **2**-optical section); **G**, *Trema* (equatorial view, **1**-optical section and **2**-upper focus); **H**, Melastomataceae/ Combretaceae (equatorial view, **1**-optical section and **2**-upper focus); **I**, *Ludwigia* (polar view, upper focus); **J**, *Qualea* (equatorial view, a-optical section and b-upper focus); **K**, *Abutilon* (polar view, **1**- optical section with detail in the spines/ echinated exine and **2**-upper focus); **L**, *Eriotheca*-type (polar view, **1**-distal and **2**-upper focus); **M**, *Pseudobombax* cf. *longiflorum* (polar view, upper focus); N, *Pseudobombax* cf. *marginatum* (polar view, upper focus); **O**, *Anacardium* (equatorial view, **1**-optical section and **2**-upper focus with details in the reticulate-striate exine). Scale bar = 20 μm.

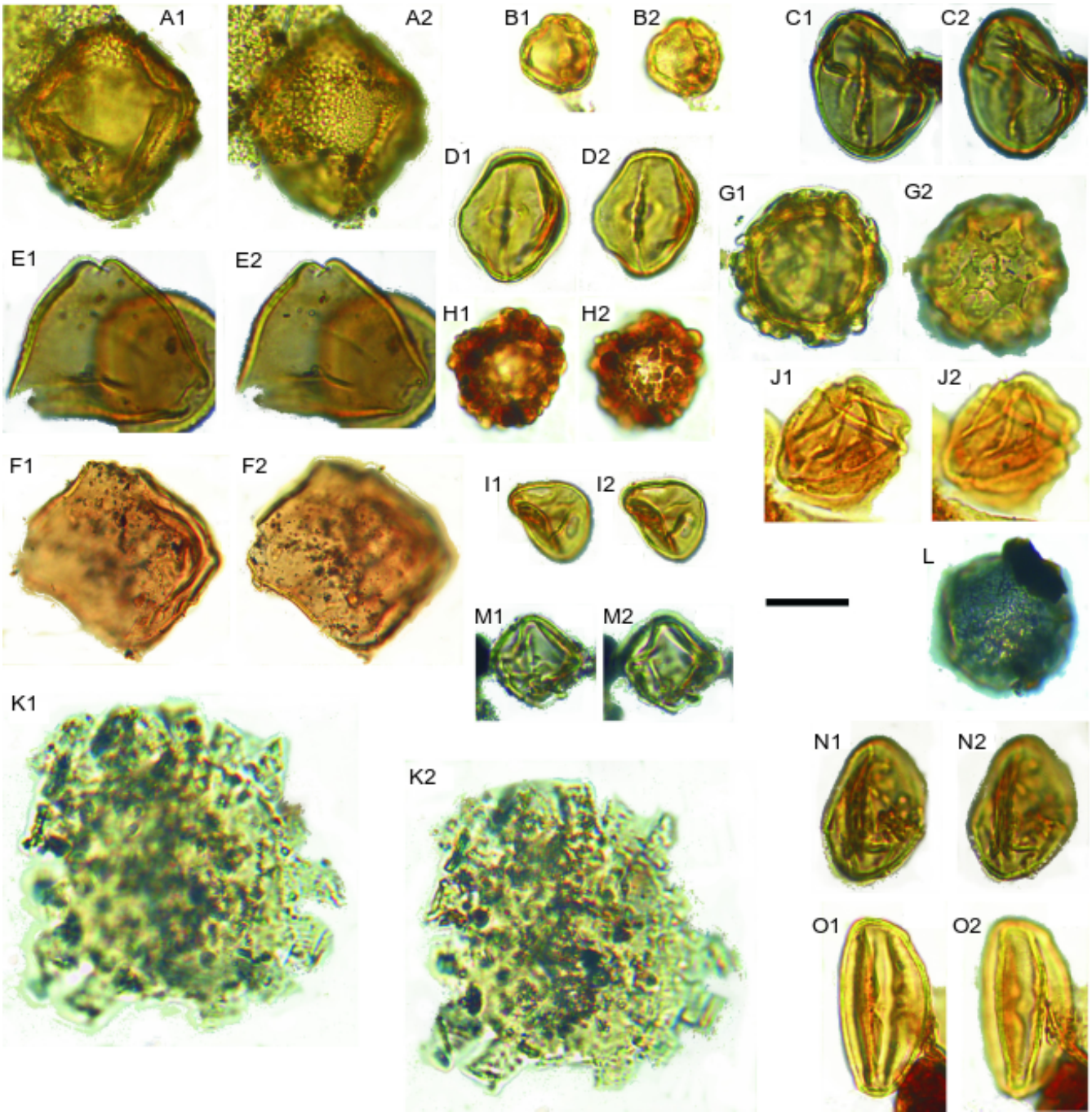

Figure 4. Photomicrographs of angiosperm pollen grains. Eudicots: **A**, *Astronium* (equatorial view, **1**-optical section and **2**-upper focus); **B**, *Schinus* (equatorial view, **1**-optical section and **2**-upper focus); **C**, *Protium* (equatorial view, **1**-optical section and **2**-upper focus); **D**, *Cedrela* (equatorial view, **1**-optical section and **2**-upper focus with detail in the scabrate exine); **E**, *Paullinia* (polar view, **1**-optical section and **2**-upper focus); **F**, *Allophylus* (polar view, **1**-upper and **2**-lower focus); **G**, *Gomphrena*-type (**1**-optical section and **2**-upper focus); 8, *Tournefortia* (**1**-optical section and **2**-upper focus); **H**, *Forsteronia* (equatorial view, **1**-upper and **2**-optical section); **I**, *Aspidosperma* (polar view, **1**-optical section and **2**-upper focus); **J**, *Richardia/ Borreria*-type (polar view, **1**-upper and **2**-lower focus); **K**, *Anemopaegma* (focus on sculpture); **L**, *Solanum* (equatorial view, **1**-optical section and **2**-upper focus); **M**, *Ilex* (equatorial view, **1**-lower focus show the typical clavate sculpture and **2**-upper focus); **N**, *Hydrocotyle* (equatorial view, **1**-optical section and **2**-upper focus). Scale bar = 20 µm.

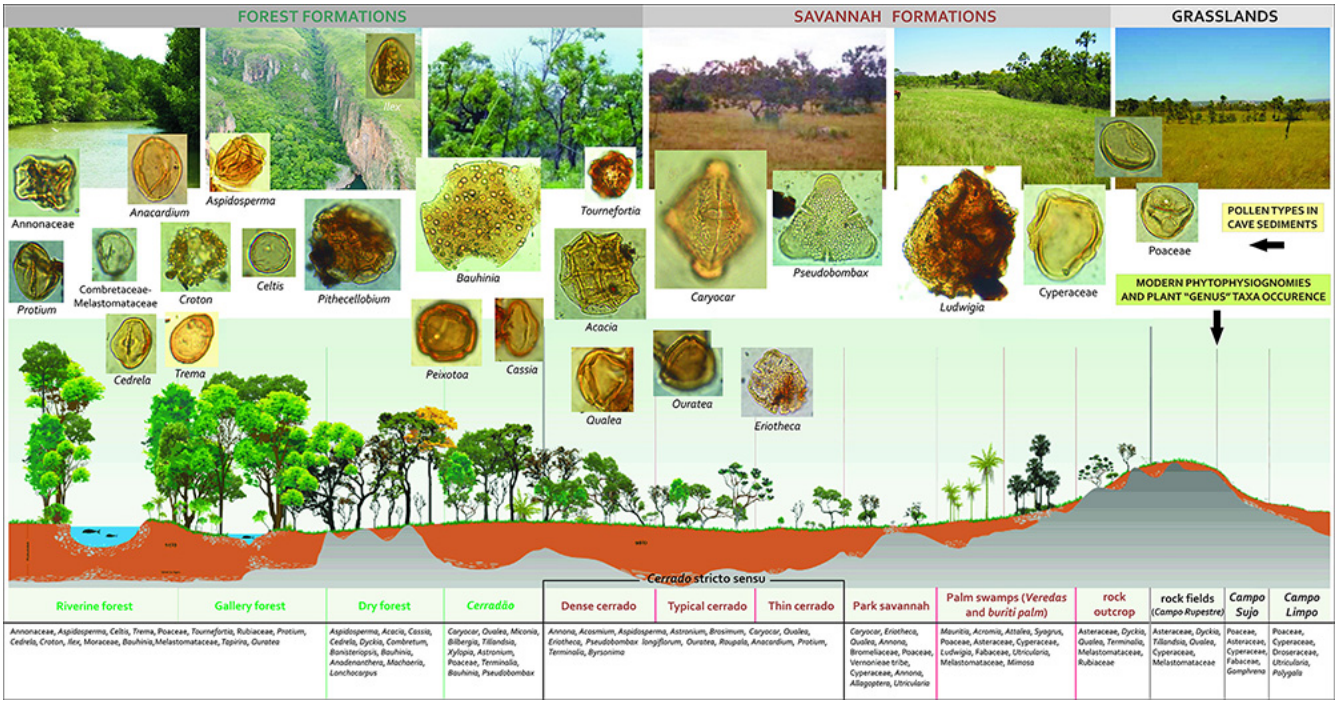

Figure 5. Main pollen taxa identified in cave sediments and its affinities with the Cerrado modern phytophysiognomies (adapted from Ribeiro & Walter, 2008 and Cassino *et al.*, 2015).

Pollen data

Cave pollen samples resulted in the taxonomic identification, morphological descriptions, photomicrography's and paleoecological data of 44 angiosperm pollen types distributed on 26 families and 36 genera detailed on Table 2. Pollen taxa showed generally good preservation. The most diverse botanical families were: Fabaceae (8), Malvaceae (4), Euphorbiaceae (3), Anacardiaceae (3), Apocynaceae (2), Cannabaceae (2), Sapindaceae (2) e Poaceae (2), which also occur in the transition of the Cerrado-Caatinga biomes.

Pollen types are related with phytosociological and floristic data for distinct topographical areas in North-Central and Northeastern Brazil (Colinvaux *et al.*, 1999; Alcoforado-Filho *et al.*, 2003; Rodal & Nascimento, 2006) and modern pollen rain to Cerrado, Caatinga and Amazon Forest biomes (Gosling *et al.*, 2005, 2009; Chaves, 2013, Cassino *et al.*, 2015; Santos *et al.*, 2015) (Figure 5; Table 2).

CONCLUSIONS

The pollen taxa described in this work reveal a wide spectrum of arboreal-shrub and herbaceous-subshrub taxa composing a mosaic of plant communities (forests formations, savannah formations and grasslands), common in the Cerrado biome, along the Quaternary. The pollen assemblages (Annonaceae, *Astronium*, *Caryocar*, *Qualea*, *Bauhinia brevipes*, *Peixotoa*, Eriotheca-type, *Cassia*, *Cedrela, Pseudobombax* spp., *Aspidosperma*, *Vigna,* and *Ouratea*) clearly show the typical Cerrado *sensu stricto* during the Last Glacial Maximum and Holocene times. Some pollen taxa were also recorded adjacent to Cerrado ecosystems (*i.e.* Caatinga and Amazon Forest). These data provide a potential framework for paleoecological, paleoenvironmental, and paleoclimatic reconstructions.

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