

Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology

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Abstract

The Moraceae family is one of the most abundant and ecologically important families in Neotropical rainforests and is very well-represented in Amazonian fossil pollen records. However, difficulty in differentiating palynologically between the genera within this family, or between the Moraceae and Urticaceae families, has limited the amount of palaeoecological information that can be extracted from these records. The aim of this paper is to analyse the morphological properties of pollen from Amazonian species of Moraceae in order to determine whether the pollen taxonomy of this family can be improved. Descriptive and morphometric methods are used to identify and differentiate key pollen types of the Moraceae (mulberry) and Urticaceae (nettle) families which are represented in Amazonian rainforest communities of Noel Kempff Mercado National Park (NKMNP), Northeast Bolivia. We demonstrate that *Helicostylis*, *Brosimum*, *Pseudolmedia*, *Sorocea* and *Pourouma* pollen can be identified in tropical pollen assemblages and present digital images of, and a taxonomic key to, the Moraceae pollen types of NKMNP. Indicator species, *Maquira coriacea* (riparian evergreen forest) and *Brosimum gaudichaudii* (open woodland and upland savanna communities), also exhibit unique pollen morphologies. The ability to recognise these ecologically important taxa in pollen records provides the potential for much more detailed and reliable Neotropical palaeovegetation reconstructions than have hitherto been possible. In particular, this improved taxonomic resolution holds promise for resolving long-standing controversies over the interpretation of key Amazonian Quaternary pollen records.

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1. Introduction

There is considerable controversy regarding the interpretation of Amazonian fossil pollen records (Colinvaux and de Oliveira, 2000; Pennington et al., 2000; Bush, 2002; Bush et al., 2004; Mayle et al., 2004; Anhufo et al., 2006), which hampers progress in our understanding of Late Quaternary vegetation dynamics, the testing of climate and ‘earth-system’ models (Valdes, 2000; Cowling et al., 2005) and in obtaining improved estimates of past carbon storage (Behling, 2002; Mayle and Beerling, 2004; Beerling and Mayle, 2006). Much of this controversy arises from the sparse distribution of fossil pollen sites within the Amazon Basin and the extent to which they are representative of Amazonia as a whole. More problematic, however, is our inability to identify many Amazonian pollen

types to species, or even genus level, resulting in poor taxonomic resolution in many fossil pollen records. Pennington et al. (2000) point out that, when operating at such a low taxonomic resolution, up to 80% of fossil pollen types attributed to ‘tropical rain forest’ taxa, equally characterise ‘seasonally dry-forest’ taxa (e.g. Pleistocene pollen assemblages of Lake Pata in central Amazonia, Colinvaux et al., 1996). This sizeable overlap may be overcome with the increasing availability of pollen rain data that establish pollen signatures for tropical forest communities based upon differences in the abundance of their constituent taxa (e.g. Bush et al., 2004; Weng et al., 2004; Gosling et al., 2005). Similarly, improving the taxonomic resolution at which Amazonian pollen can be identified, should allow these communities to be much more readily differentiated by the presence or absence of ecosystem-specific indicator taxa.

The mulberry family (Moraceae) comprises ca. 37 genera and over 1100 species worldwide and is one of the most abundant and ecologically important families growing in tropical rainforests of

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Central and South America (Datwyler and Weiblen, 2004). This family forms part of the Rosidae and is closely allied to the Urticalean rosids that include Cannabaceae, Celtidaceae, Urticaceae, Cecropiaceae and Ulmaceae. In general, Moraceae plants are monoecious or dioecious trees and shrubs, and are adapted to a wide range of moist tropical evergreen forest habitats including well-drained *terra firme* forest, liana dominated forest, as well as seasonally-inundated and riparian forests (Killeen, 1998). They exhibit high Family Importance Values (FIV; a composite index of relative density, diversity and dominance) across the Amazon Basin and are well-represented in drought-adapted liana forests (FIV=19; *Salvias Project*, 2007) as well as *terra firme* forests (FIV=32) in northeast Bolivia. Moraceae species are at their most abundant and diverse in *várzea* (seasonally flooded) forests of tropical lowland Amazonia, exemplified by high importance values in Ecuador (FIV=44; Balslev et al., 1987), Peru (FIV=51; Nebel et al., 2001a,b) and northeast Bolivia (FIV=80; *Salvias Project*, 2007).

Constituent species are highly specialised and adapted to a diverse range of habitats. The *várzea* tree *Maquira coriacea* (Karsten) C. C. Berg, for example, is restricted to, and regularly dominates, flood-plain forests of the Amazon, Orinoco and upper Rio Paraguay Basins (Nebel et al., 2001a,b). In contrast, *Helicostylis tomentosa* (Poeppig & Endlicher) J. F. Macbride, flourishes in well-drained (*terra firme*) tall evergreen rainforests and liana forests (Killeen, 1998). The shrub *Brosimum gaudichaudii* Trecul prefers rather more arid environments and grows in *cerrado* (savanna woodland with 10–60% tree cover; Eiten 1972) and *cerradão* (almost closed-canopy dense dry woodland; Eiten 1972) communities along the southwestern margin of the Amazon Basin (De Oliveira-Filho, 1992; Marchant et al., 2002).

Such diversity and importance of species within the Moraceae family is, however, not well captured in Amazonian fossil pollen records. Moraceae pollen is generally only identified to the family taxonomic level and has hitherto been grouped together with the nettle family (Urticaceae) because of morphological similarity between grains (e.g. Colinvaux et al., 1996; Haberle and Maslin, 1999; Behling and Hooghiemstra, 2000; Mayle et al., 2000). Pollination strategies of constituent genera are mostly anemophilous and therefore regularly over-represented in pollen spectra (Gosling et al., 2005). Indeed, Moraceae/Urticaceae type pollen regularly accounts for 10–60% of total pollen counts and is considered to indicate the presence of closed-canopy lowland tropical rain forest communities when pollen abundance is >30% (Mayle et al., 2004; Gosling et al., 2005). *Ficus* and *Castilla* are exceptions, exhibiting obligate mutualism with pollinating fig-wasps and thrips, respectively (Bush and Riviera, 2001; Sakai, 2001; Datwyler and Weiblen, 2004). These two genera are cleistogamous and therefore heavily under-represented in pollen assemblages. Bush and Riviera (2001) have calculated that, in the pollen flora of Barro Colorado Island, *Ficus* has a very low R-rel value (% mean pollen influx/% basal area) of 0.03. Notwithstanding a few attempts to separate *Brosimum* (Irrion et al., 2006) and *Ficus* (Bush and Colinvaux 1988; Liu and Colinvaux, 1988) from the Moraceae/Urticaceae category in

pollen assemblages, little work has been done to identify constituent pollen types of such a potentially important diagnostic family to a higher taxonomic resolution.

Here, we present the first detailed analysis of the morphological properties of Moraceae and Urticaceae pollen grains of the Amazon Basin. Using descriptive and morphometric methods we attempt to differentiate between pollen of the constituent genera of the Moraceae and Urticaceae families represented within different kinds of rainforest community in Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. In particular, we aim to provide a pollen-taxonomic key that can be used by Neotropical palynologists to identify Moraceae and Urticaceae genera and species.

2. Study area

Taxa were selected for palynological study from detailed floristic inventories of plant communities within Noel Kempff Mercado National Park (NKMNP), a 15,230 km² biological reserve in northeast Bolivia that occupies part of the Madeira–Tapajós ecoregion (Olson et al., 2001; Fig. 1). The park is situated on an ecotone spanning 22 pristine plant communities, from moist evergreen rainforest in the north, to *cerrado* in the east, and semi-deciduous dry-forest communities in the south, and provides a physical setting that supports considerable ecosystem diversity (Killeen et al., 2003). Two black-water rivers, the Rio Iténez and Rio Paraguá define the eastern and western boundaries of NKMNP, respectively. Precambrian rocks of the Huanchaca Plateau (600–900 m a.s.l.) characterise the eastern half of the park, and Tertiary alluvial deposits of the lowland penplain (200–250 m a.s.l.), the western half.

The vegetation of the Huanchaca Plateau consists mainly of *cerrado* savanna communities, which are well-adapted to thin soils overlying the basement rocks of the Precambrian Shield. Here, moist evergreen gallery forest is confined to valleys or depressions with sufficiently thick soils (Killeen, 1998). In contrast, a variety of evergreen rainforest communities dominate the neighbouring alluvial plains, which are characterised by moist deep soils. High evergreen rainforest and liana forest grow on well-drained (*terra firme*) soils, while riparian and seasonally-flooded rainforests, as well as seasonally-flooded savannas, are associated with the seasonal flooding regime of the Rio Paraguá. Such high ecosystem diversity (*beta* diversity) within the park is responsible for a diverse range of Moraceae species (Killeen, 1998), many of which are restricted to specific kinds of rainforest. Fossil pollen analyses of sediments from the two large lakes in NKMNP, Laguna Chaplin (14° 28' S, 61° 04' W) and Laguna Bella Vista (13° 37' S, 61° 33' W), have revealed changes in vegetation, fire dynamics, and climate, over the last 50,000 years (Mayle et al., 2000; Burbidge et al., 2004; Fig. 1).

3. Materials and methods

3.1. Selection of species for palynological study

Detailed floristic inventories were obtained from 1 ha (500 × 20 m) study plots from each of the 22 plant communities

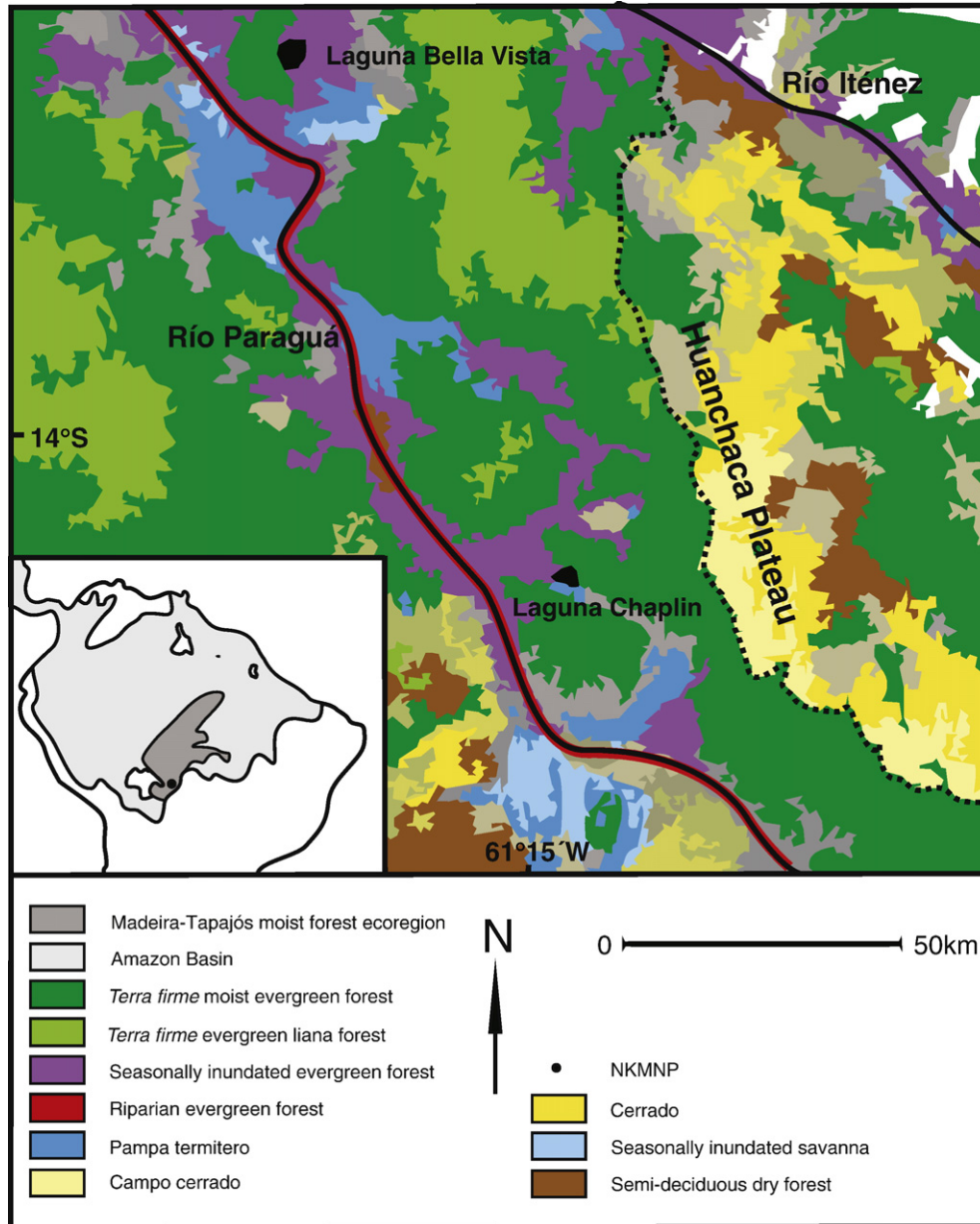


Fig. 1. Location map (inset) and distribution of plant communities within Noel Kempff Mercado National Park (NKMNP), northeast Bolivia. Modified from Killeen and Schulenberg (1998).

within NKMNP between 1993 and 2000 by Killeen (1998) and are readily available from the *Salvias Project database* (2007). Every woody plant ≥ 10 cm d.b.h. (diameter at breast height) has been measured and all tagged specimens are stored at the herbarium of the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia. Identification was made by comparison with specimens held in the collection in Santa Cruz and at the Missouri Botanical Gardens (Killeen and Schulenberg, 1998). Standardized nomenclature presented here is in accordance with publications cited in the *International Plant Names Index* (2007), a combination of Index Kewensis, the Gray Card Index and the Australian Plant Names Index. Pollen of key species of each genus of Moraceae and Urticaceae recorded in these vegetation study plots was analysed (Table 1).

Of all the ecosystems in the study area, the following four rainforest communities exhibited the greatest abundance and diversity of Moraceae species: *terra firme* tall evergreen forest, evergreen liana forest, seasonally-inundated evergreen forest and riparian evergreen forest. Species represented in other plant communities included *Brosimum alicastrum* (gallery forest lining savanna rivers on the Huanchaca plateau; Killeen, 1998), *Brosimum gaudichaudii* (cerradão, cerrado), and two *Pourouma* species, *Pourouma guianensis* and *P. minor* (gallery forest, semi-deciduous dry forest) that have recently been reclassified as Cecropiaceae (IPNI, 2007) but share similar pollen-morphological characteristics with Moraceae/Urticaceae.

The Urticaceae species were not represented in any rainforest or cerrado plots within NKMNP, with the sole exception of

Table 1
Results of descriptive and morphometric analyses of pollen grains examined including habitat details for parent taxa

Species	Specimen no.	Family	Habitat	<i>n</i>	Polarity	# Apertures	Mean <i>E</i> (μm)	Mean <i>P</i> (μm)	Mean <i>D</i> (μm)	<i>P/E</i>	Shape class (<i>P/E</i>)	<i>P/D</i>	Shape class (<i>P/D</i>)	Other distinctive features	Annulus	Pore size (μm)	Sculpturing	Operculum
<i>Brosimum alicastrum</i> Swartz	JW10038	Moraceae	TEF ^{ab}	30	Isopolar	2	18.0	18.0	16.5	1.00	Spheroidal	1.09	Prolate spheroidal	*	Yes	3	Scabrate	Yes
<i>Brosimum guianense</i> (Aublet) Huber	JR6295	Moraceae	RF ^a , IRF ^a , TEF ^b	30	Isopolar	2	15.5	15.5	12.0	1.00	Spheroidal	1.29	Subprolate	*	Yes	1.5–2	Scabrate	Yes
<i>Brosimum lactescens</i> (Moore) C.C. Berg	AJ1095	Moraceae	SIF ^b , IRF ^a , TEF ^a	30	Isopolar	2	18.5	18.0	16.5	0.98	Spheroidal	1.10	Prolate spheroidal	*	Yes	3	Scabrate	Yes
<i>Brosimum lactescens</i> (Moore) C.C. Berg	JR 6336	Moraceae	SIF ^b , IRF ^a , TEF ^a	30	Isopolar	2	18.0	18.0	16.0	0.99	Spheroidal	1.11	Prolate spheroidal	*	Yes	3	Scabrate	Yes
<i>Brosimum gaudichaudii</i> Trecul	KF4074	Moraceae	CE ^{ab} , PT ^a	30	Isopolar	2	12.5	14.5	11.0	1.19	Subprolate	1.37	Prolate	*	Yes	1.5–2	Psilate	No
<i>Brosimum gaudichaudii</i> Trecul	TK2138	Moraceae	CE ^{ab} , PT ^a	30	Isopolar	2	12.0	14.5	11.0	1.23	Subprolate	1.35	Prolate	*	Yes	1.5–2	Psilate	No
<i>Pseudolmedia laevigata</i> Trecul	G1913	Moraceae	SIF ^a , RF ^a	30	Isopolar	3–4	16.0	13.5	*	0.84	Suboblate	*	*	angulaperturate	No	2	Psilate	No
<i>Pseudolmedia laevis</i> (Ruiz & Pavon) J. F. Macbride	DN9312	Moraceae	SIF ^a , TEF ^a , LF ^a	30	Isopolar	3–4	19.0	17.5	*	0.92	Spheroidal	*	*	angulaperturate	No	2–3	Psilate	No
<i>Pseudolmedia macrophylla</i> Trecul	EM898	Moraceae	TEF ^a	30	Isopolar	3–4	20.0	18.5	*	0.92	Spheroidal	*	*	angulaperturate	No	2	Psilate	No
<i>Maquira coriacea</i> (Karsten) C.C. Berg	SB19657	Moraceae	RF ^{ac} , IRF ^{ac}	30	Isopolar	3–4–5	18.5	15.5	*	0.84	Suboblate	*	*	angulaperturate	No	2	Scabrate	No
<i>Helicostylis scabra</i> (J.F. Macbride) C.C. Berg	WP1210	Moraceae	TEF ^a , LF ^a	30	Isopolar	2–3	12.0	9.0	*	0.78	Suboblate	*	*	angulaperturate	No	1.5	Scabrate	No

<i>Helicostylis tomentosa</i> (Poeppig & Endlicher) J.F. Macbride	MT1190	Moraceae	TEF ^a , LF ^a	30	Isopolar	2–3	12.5	9.5	*	0.76	Suboblate	*	*	angulaperturate	No	1.5	Scabrate	No
<i>Helicostylis tomentosa</i> (Poeppig & Endlicher) J.F. Macbride	R7591	Moraceae	TEF ^a , LF ^a	30	Isopolar	2–3	12.0	9.5	*	0.79	Suboblate	*	*	angulaperturate	No	1.5	Scabrate	No
<i>Ficus citrifolia</i> Miller	A757	Moraceae	GF ^a , SDF ^a	30	Isopolar	2	12.0	8.0	*	0.65	Oblate	*	*	*	No	1–1.5	Psilate	No
<i>Ficus pertusa</i> Linnaeus	TK6855	Moraceae	SIF ^b , IRF ^a , TEF ^a	30	Isopolar	2	9.5	6.0	*	0.63	Oblate	*	*	*	No	1–1.5	Psilate	No
<i>Ficus paraensis</i> (Miquel) Miquel	J3109	Moraceae	TEF ^a	30	Isopolar	2	14.5	9.0	*	0.64	Oblate	*	*	*	No	1–1.5	Psilate	No
<i>Pourouma guianensis</i> Aublet subsp. Guianensis	IGV2818	Cecropiaceae	TEF ^{ab} , LF ^a	30	Isopolar	2	13.5	14.0	10.5	1.04	Spheroidal	1.34	Prolate	*	Yes	1.5	Coarsely scabrate	Yes
<i>Pourouma minor</i> Benoist	TK3899	Cecropiaceae	GF ^a , TEF ^b	30	Isopolar	2	12.5	15.0	10.5	1.19	Subprolate	1.44	Prolate	*	Yes	1.5	Coarsely scabrate	Yes
<i>Sorocea guilleminiana</i> Gaudichaud-Beaupré	RF13719	Moraceae	TEF ^a , LF ^a , SIF ^a , SDF ^a	30	Isopolar	2	14.5	14.5	12.5	1.05	Spheroidal	1.16	Subprolate	*	No	2	Coarsely scabrate	Yes
<i>Sorocea guilleminiana</i> Gaudichaud-Beaupré.	TK1120	Moraceae	TEF ^a , LF ^a , SIF ^a , SDF ^a	30	Isopolar	2	15.0	15.0	12.5	0.99	Spheroidal	1.20	Subprolate	*	No	2	Coarsely scabrate	Yes
<i>Sorocea hirtella</i> Mildbraed	G554	Moraceae	RV ^a	30	Isopolar	2	12.5	12.5	11.5	0.98	Spheroidal	1.10	Prolate spheroidal	*	No	2	Scabrate	Yes
<i>Maclura tinctoria</i> Steudel.	G75565	Moraceae	TEF ^{ab} , LF ^a	30	Isopolar	2–3	12.5	12.0	10.5	0.99	Spheroidal	1.16	Subprolate	*	No	2	Scabrate	Yes
<i>Urera caracasana</i> Grisebach	TK5928	Urticaceae	LF ^a , TFG ^d	30	Isopolar	3	12.5	10.5	12.5	0.86	Suboblate	*	*	*	Yes	1–1.5	Psilate	Yes
<i>Pouzolzia poeppigiana</i> (Wedell) Killip	MC14	Urticaceae	TFG ^a	30	Isopolar	3	13.0	11.0	13.0	0.85	Suboblate	*	*	*	Yes	1–1.5	Psilate	No

Pollen-morphological terminology follows Punt et al. (2007): *E*, equatorial diameter; *P*, polar diameter; *D*, depth (third focal plane of ellipsoid pollen grains). Habitats: TEF, *terra firme* evergreen forest; RF, riparian evergreen forest; IRF, inundated riparian evergreen forest; SIF, seasonally-inundated evergreen forest; CE, cerrado (upland savanna); PT, pampa termitera (seasonally-flooded savanna); LF, *terra firme* liana forest; GF, gallery forest; SDF, semi-deciduous dry forest; RV, riparian vegetation; TFG, tree fall gaps. ^aKilleen and Schulenberg (1998); ^bMarchant et al. (2002); ^cNebel et al. (2001a,b); ^dOrozco-Segovia et al. (1987).

Urera, which is found in liana forests with a negligible importance value (IVI) of 0.35. Given that Urticaceae is an herbaceous family, it is possible that plants below 10 cm d.b.h. may have been present in the plots and consequently not listed in the floral inventories. However, this shade-intolerant herbaceous family is unlikely to be found within the understory of closed-canopy rainforest communities where it would be out-competed by tree species better adapted to light-restricting environments. Indeed, *Urera caracasana* is a fast-growing pioneer species which flourishes only when openings occur as a result, for example, of tree fall (Orozco-Segovia et al., 1987). Furthermore, the understory of both riparian and seasonally-inundated communities is sparsely populated due to flooding throughout much of the year (Killeen, 1998) and woody species <10 cm d.b.h. are poorly represented. Of the Urticaceae, *U. caracasana* and *Pouzolzia poeppigiana* were selected for morphometric analyses.

3.2. Pollen processing and microscopic analysis

Mature male flowers were collected from the herbaria of the ‘Noel Kempff Mercado’ Natural History Museum in Santa Cruz, Bolivia and the Royal Botanic Garden Edinburgh, Scotland. Sufficient pollen for processing was collected from all taxa except *Brosimum acutifolium*. Samples were soaked in 10% NaOH for a few hours (to soften the material and extract humic acids), sieved through a 250 μm sieve, and prepared for light microscopy following the standard acetolysis method of Faegri and Iversen (1989). Residues were suspended in silicone oil for morphometric analysis. For each species, measurements were made on mature pollen grains ($n=30$) at $\times 1000$ magnification under an oil immersion Olympus BX 50 light microscope. Digital images were taken with a Canon Eos 350D digital camera. Morphological descriptions included size, aperture number, sculpturing, polarity, symmetry and the presence/absence of annulus and operculum. The shape class of individual grains was obtained by measurement of the following

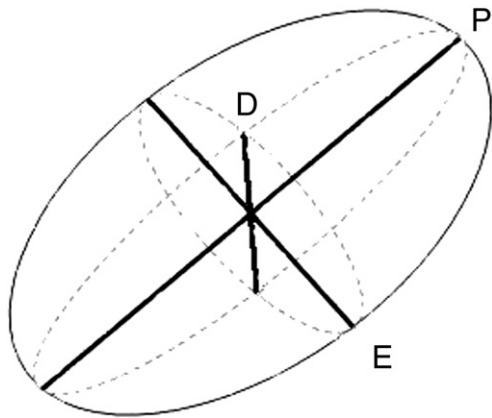


Fig. 2. Schematic diagram illustrating the three parameters measured to distinguish the shape class of ellipsoid diporate pollen grains. P =Length of polar axis, E =length of the longest equatorial diameter, D =length of the shortest equatorial diameter.

geometric parameters: the polar axis length (P) and the length of the longest equatorial diameter (E) were measured on all grains with a precision of 0.5 μm . The length of the shortest equatorial diameter, depth (D), was measured at the same precision to distinguish between ellipsoid diporate grains (Fig. 2). Shape classes were quantified using P/E and P/D ratios, respectively, and described according to Erdtman (1943). The non-parametric Mann Whitney U -test was used to test for significance between the measured parameters. Terminology follows that of Punt et al. (2007).

4. Results

Table 1 provides a summary of the quantitative parameters measured for all pollen specimens alongside habitat requirements for parent species. Digital images of studied pollen grains are presented in Fig. 3 and a taxonomic key to the genera and species of Moraceae and Urticaceae pollen types of NKMNP is given in Appendix A alongside concise pollen descriptions. All grains are isopolar monads with tectate exines; pores are always circular and some grains exhibit a slight protrusion or thickening of the exine around the pores (annulus *sensu* Punt et al., 2007). Sculpturing of the sexine is usually psilate or scabrate. The shape class (P/E) varies between oblate and subprolate, with grains of some genera, such as *Brosimum* and *Sorocea*, exhibiting spheroidal characteristics. The shape class (P/D) for diporate grains varies from prolate (e.g. *Pourouma*) to spheroidal (e.g. *Brosimum lactescens*, *B. alicastrum*). All 3–4 and 5 porate grains are angulaperturate in polar view. Specific pollen-morphological characteristics are described below.

4.1. Pollen-morphological characteristics

4.1.1. Size

In general, pollen grains are small, with the mean length of the polar axis (P) varying between 6 ± 0.5 μm for *Ficus pertusa* and 18.5 ± 2 μm for *Pseudolmedia macrophylla*, and the mean equatorial diameter (E) varying between 9.5 ± 0.5 μm and 20 ± 1.5 μm for the same species, respectively (Table 1). Most grains can clearly be allocated to two distinct size classes according to their equatorial diameter (E), with the exception of *Pseudolmedia laevigata*, *Brosimum guianense*, *Sorocea guilleminiana* and *Ficus paraensis*, which fall along a gradient between these classes (Fig. 4A). The larger size class, with a combined mean value of 18 ± 2 μm , includes *Pseudolmedia laevis*, *P. macrophylla*, *Maquira coriacea*, and *Brosimum*, except for *B. gaudichaudii*. The smaller size class consists of *B. gaudichaudii*, *Helicostylis*, *Pourouma*, *Sorocea*, *Ficus*, *Maclura tinctoria* and both Urticaceae species, *Urera caracasana* and *Pouzolzia poeppigiana*, which have a combined mean value of 12.5 ± 1.5 μm . Differences in the mean length of the polar axis (P) of grains show a similar trend, although the boundaries between size classes are less clear (Fig. 4B). Grains with the shortest mean polar axis length are *Ficus* and *Helicostylis* and both Urticaceae species. *Helicostylis* and *Ficus* have mean polar axis lengths of 9.5 ± 1 and 7.5 ± 1.5 μm , respectively, significantly smaller ($p<0.01$; Mann–

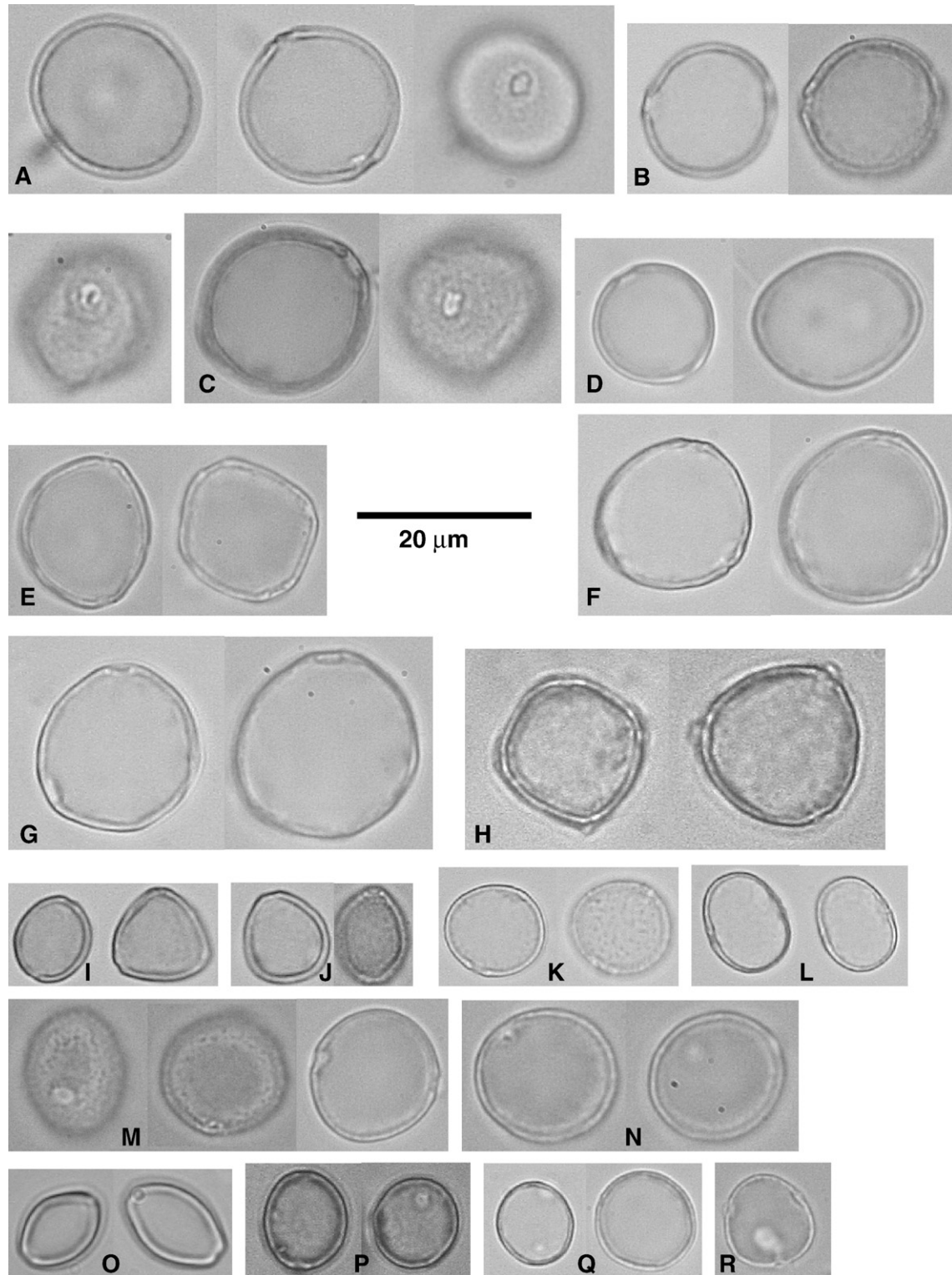


Fig. 3. Light micrographs of Moraceae/Urticaceae pollen found in NKMNP ($\times 1000$ magnification), A: *Brosimum alicastrum*, B: *B. guianense*, C: *B. lactescens*, D: *B. gaudichaudii*, E: *Pseudolmedia laevigata*, F: *P. laevis*, G: *P. macrophylla*, H: *Maquira coriacea* I: *Helicostylis scabra*, J: *H. tomentosa*, K: *Pourouma guianensis*, L: *P. minor*, M: *Sorocea guilleminiana*, N: *S. hirtella*, O: *Ficus citrifolia* P: *Maclura tinctoria*, Q: *Urera caracasana*, R: *Pouzolzia poeppigiana*.

Whitney *U*-test) than the Urticaceae species, *U. caracasana* and *P. poeppigiana*, which have a combined mean polar axis length of $10.5 \pm 1 \mu\text{m}$.

4.1.2. Apertures

The number of pores allows the subdivision of key pollen types and, when allied with other morphological features, is of

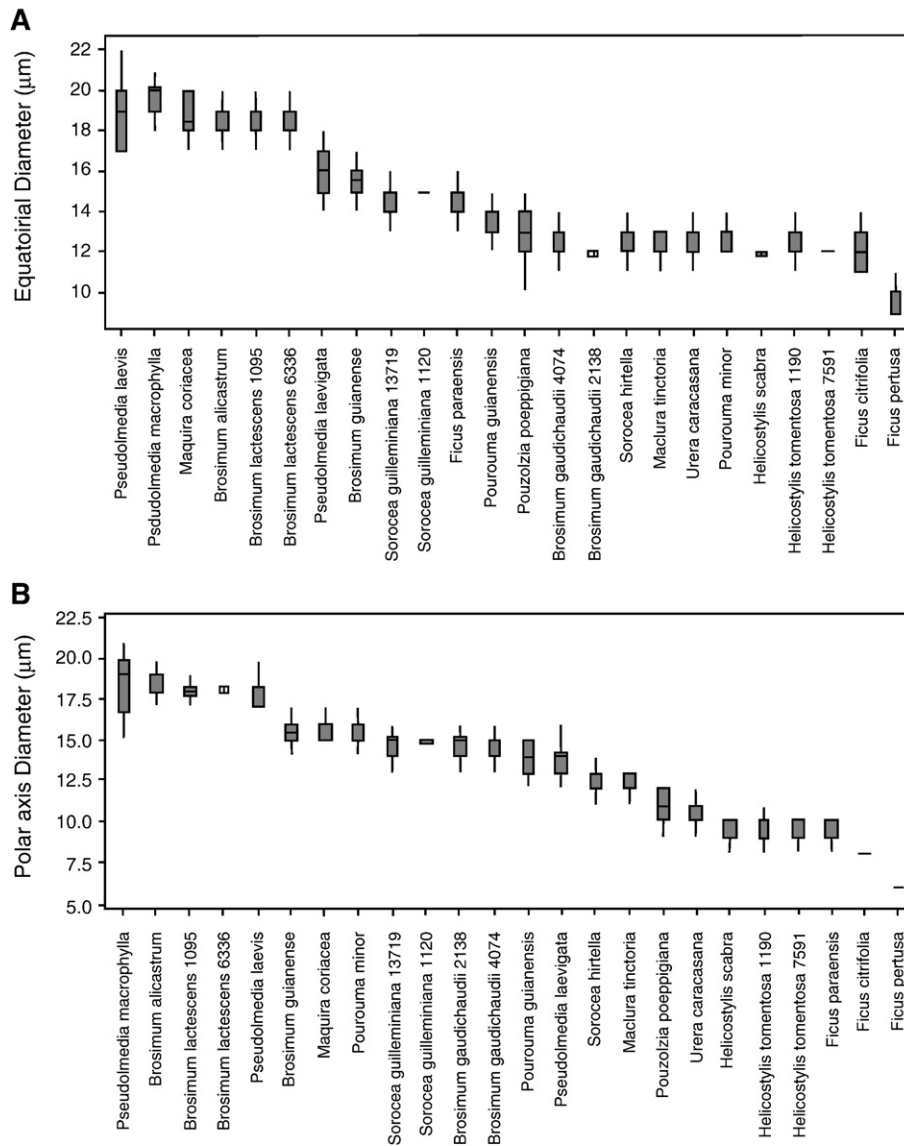


Fig. 4. Box plots of (A) longest equatorial diameter, and (B) polar axis length of the Moraceae and Urticaceae pollen within NKMNP. Stems represent the range of the data; the boxes show the interquartile range. The species collection number is shown to differentiate between two specimens of the same species.

great diagnostic value (Appendix A). *Brosimum*, *Pourouma*, *Sorocea* and *Ficus* are diporate and reveal no variability in pore numbers (Table 1). *Helicostylis* and *Maclura tinctoria* are 2–3 porate (Fig. 3I–J; P), *Pseudolmedia* 3–4 porate (Fig. 3E–G) and *Maquira coriacea* 3–4–5 porate (Fig. 3H). Both pollen types of the Urticaceae family, *Ureia caracasana* and *Pouzolzia poeppigiana*, have three pores and display no variability in their number (Fig. 3Q–R). With the exception of *Brosimum gaudichaudii*, *Brosimum* has the largest pores with a mean diameter of 3 µm (Fig. 3A–C). Most other genera have a mean pore diameter ranging from 1 to 2 µm, and *U. caracasana*, *P. poeppigiana* and *Ficus* exhibit the smallest mean pore diameter of 1–1.5 µm. *Brosimum*, *Pourouma*, and both Urticaceae specimens reveal a distinct thickening (annulus) around the pores, in particular *Brosimum lactescens*, *B. alicastrum* and *B. guianensis* (Fig. 3A–C). In contrast, the genera *Pseudolmedia*, *Helicostylis*, *Sorocea*, *Ficus* and

species *M. tinctoria* and *M. coriacea* do not. Opercula are present in *Sorocea*, *Pourouma*, *M. tinctoria*, *U. caracasana*, and *Brosimum* (except for *B. gaudichaudii*).

4.1.3. Shape

Shape classes according to both the P/E and P/D ratios vary significantly between the constituent pollen types of the Moraceae and Urticaceae families (Fig. 5A; Appendix A). Grains with a spheroidal shape class ($P/E=0.88–1.14$) include *Brosimum alicastrum*, *B. lactescens*, *B. guianense*, *Pseudolmedia laevis*, *P. macrophylla*, *Pourouma guianensis*, *Maclura tinctoria* and *Sorocea*. Only *Pourouma minor* and *Brosimum gaudichaudii* have a subprolate shape class ($P/E=1.14–1.33$) and *Pseudolmedia laevigata*, *Maquira coriacea*, *Helicostylis* and the Urticaceae are suboblate ($P/E=0.75–0.88$). *Ficus* is the only genus which has an oblate shape class ($P/E=0.5–0.75$). Tri- and stephano-porate grains, including

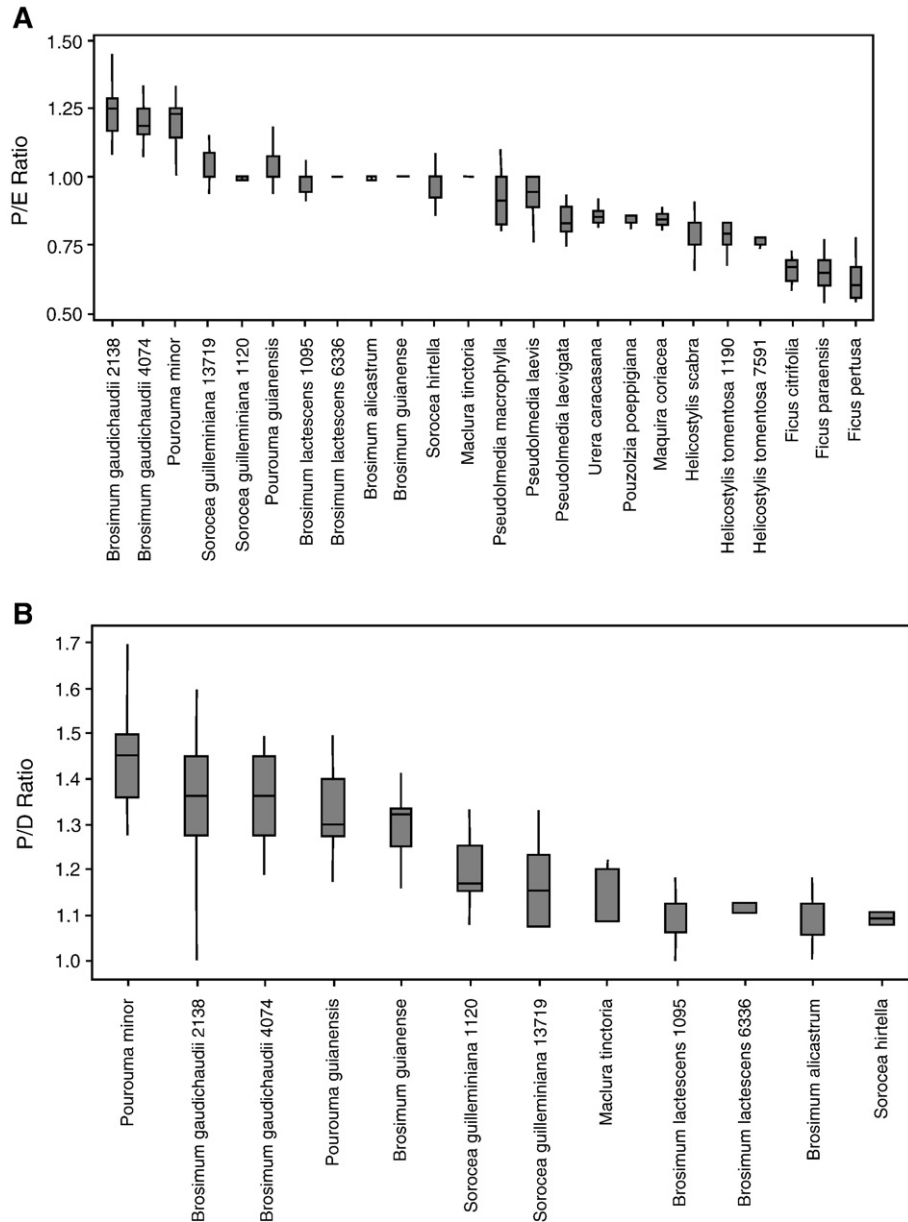


Fig. 5. Box plots of (A) P/E ratio, and (B) P/D ratio of the Moraceae and Urticaceae pollen within NKMNP. Stems represent the range of the data; the boxes show the interquartile range. The species collection number is shown to differentiate between two specimens of the same species.

Pseudolmedia, *Helicostylis*, and *M. coriacea* are angulaperturate (*sensu* Punt et al., 2007; with the apertures situated at the angles of the outline in polar view; Fig. 3E–J), with the exception of *M. tinctoria* and both Urticaceae species.

Diporate ellipsoid grains can be classified into different classes according to their P/D ratio (Fig. 5B; Appendix A). *Brosimum alicastrum*, *B. lactescens*, and *Sorocea hirtella* are spheroidal ($P/D=0.88–1.14$), *Brosimum guianense*, *Sorocea guilleminiana* and *Maclura tinctoria* are subprolate ($P/D=1.14–1.33$), and *Brosimum gaudichaudii* and *Pourouma* are prolate ($P/D=1.33–2.00$). Despite being within the same shape class as *Sorocea guilleminiana* ($P/D=1.18$) and *M. tinctoria* ($P/D=1.16$), *Brosimum guianense* has a significantly different P/D ratio (1.29; $p < 0.05$ Mann–Whitney U -test).

4.1.4. Surface sculpturing

The surface sculpturing of *Brosimum* is finely scabrate, with the exception of *Brosimum gaudichaudii* which is psilate (Table 1; Fig. 2D; Appendix A). *Maquira coriacea*, *Maclura tinctoria*, *Helicostylis*, *Pourouma* and *Sorocea* are also finely scabrate, whilst the latter two species are coarsely scabrate (Fig. 3K–M). *Pseudolmedia*, *Ficus*, and the Urticaceae species, *Urera caracasana* and *Pouzolzia poeppigiana*, are psilate.

5. Discussion

The following discussion is divided into two sections. The first focuses on the differentiation between key Moraceae

pollen types of NKMNP and their ecological significance. The second section outlines implications for the interpretation of fossil pollen records at the local (NKMNP) and basin-wide spatial scales.

5.1. Distinctive pollen types

5.1.1. *Helicostylis*

Helicostylis can be readily distinguished from other pollen types. Its key diagnostic features are its size ($P=9.5\pm 0.85\ \mu\text{m}$; $E=12\pm 0.5\ \mu\text{m}$), number of pores (2–3), shape class ($P/E=0.78$; suboblate) and finely scabrate sculpturing (Table 1). It can be differentiated from the morphologically similar *Ficus* by its sculpturing and shape class (Fig. 3I–J, O; Appendix A). *Helicostylis* is finely scabrate and has a suboblate shape class according to its P/E ratio. In contrast, *Ficus* is psilate and has a distinctly oblate shape class (mean P/E of 0.65). However, *Ficus* is rare in both modern and fossil pollen assemblages because it is cleistogamous (Bush and Riviera, 2001; see above). It is absent from pollen records of Laguna Bella Vista and Laguna Chaplin (Mayle et al., 2000; Burbridge et al., 2004), as well as from modern pollen traps in *terra firme* evergreen rainforest study plots of NKMNP (Gosling et al., 2005), even though it is abundant in the vegetation (Salvias Project database, 2007).

Within NKMNP, *Helicostylis* is well-represented in moist evergreen *terra firme* rainforest (Importance Value Index; $IVI=4.5$; Salvias Database, 2007), seasonally-inundated rainforest ($IVI=6.2$) and evergreen liana forest ($IVI=2.7$). However, it is ecologically less important in riparian forest communities ($IVI=0.6$). Its palynological importance across Amazonia is implied by its basin-wide geographic distribution (VAST, 2007; Fig. 6D).

5.1.2. *Brosimum*

Brosimum is another key pollen type that is readily identifiable within NKMNP. Its constituent species, *Brosimum alicastrum*, *B. lactescens* and *B. guianensis*, are diporate, have P/E ratios that are distinctly spheroidal ($P/E=0.98\text{--}1.00$), are finely scabrate, and have a distinct annulus surrounding the pores (Fig. 3A, B and C). Furthermore, *B. alicastrum* and *B. lactescens* produce large grains with mean equatorial diameters (E) and polar axis lengths (P) measuring $18.5\pm 1\ \mu\text{m}$ and $18\pm 1\ \mu\text{m}$, respectively. *B. guianensis* may be confused with *Sorocea* by its size and shape class (Table 1), but can be

distinguished from this taxon by the presence of its annulus (Appendix A).

Brosimum species are late-successional and strongly represented in both riparian and seasonally-flooded forest communities within NKMNP (Killeen, 1998) and across the Amazon Basin (VAST, 2007; Fig. 6B). *B. lactescens*, for example, has an IVI of 38.6 within riverine forests and *B. guianensis* is represented in both riparian and inundated forest communities with an IVI of 3.42 and 5.3, respectively. Neither is represented in well-drained (*terra firme*) forest communities, so abundance of their pollen in the fossil record would indicate that riparian and/or flooded forests were present in the catchment in the past.

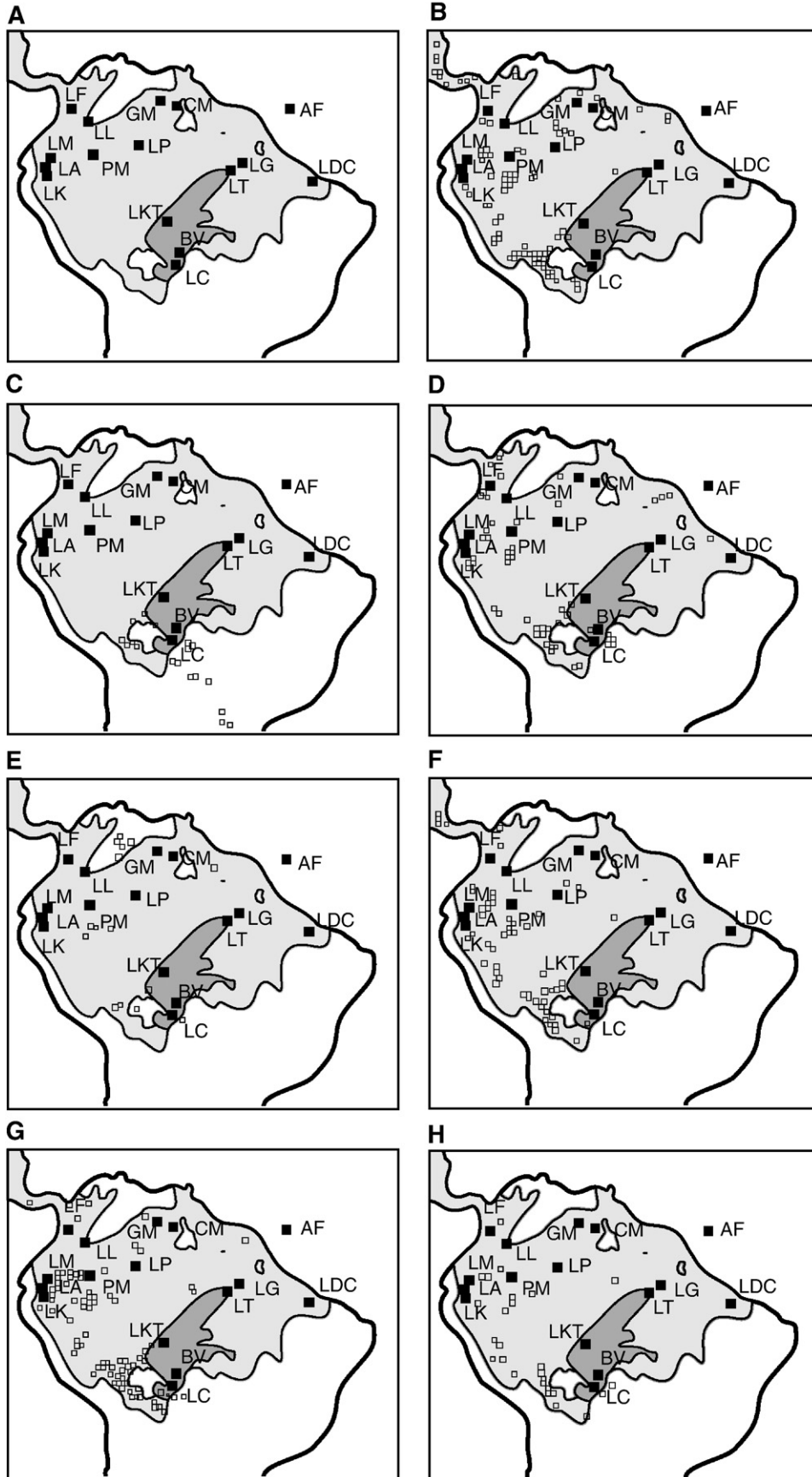
The pollen of *Brosimum gaudichaudii* (Fig. 3D) is an interesting exception which can be readily differentiated from that of other *Brosimum* species by its shape classes ($P/E=1.21$, subprolate; $P/D=1.36$, prolate), psilate sculpturing and small size (mean equatorial diameter (E) and polar axis length (P) of $12\ \mu\text{m}$ and $14.5\ \mu\text{m}$, respectively). Pollen grains of *B. gaudichaudii* and *Pourouma minor* are more difficult to distinguish from one another because they have a very similar shape classes (Table 1; Fig. 4A–B). However, unlike *B. gaudichaudii*, *Pourouma minor* exhibits a thickening of the exine around the pores (Fig. 3L) and is coarsely scabrate.

Brosimum gaudichaudii is a shrub that grows in both cerradão (almost closed-canopy dense dry woodland; Eiten 1972) and *cerrado* (savanna woodland with 10–60% tree-cover; Eiten 1972) communities of NKMNP (Killeen, 1998), as well as in seasonally-flooded savannas, both in Bolivia (*pampa termitera*) and Brazil (*murundus*) (Fig. 6C; De Oliveira-Filho, 1992). Presence of this pollen type therefore has implications for the interpretation of the Moraceae/Urticaceae signal within fossil pollen records in ecotonal regions of the Amazon Basin, such as Laguna Chaplin and Laguna Bella Vista (Fig. 1; Mayle et al., 2000; Burbridge et al., 2004).

5.1.3. *Pseudolmedia* and *Maquira coriacea*

Pseudolmedia and *Maquira* are difficult to distinguish from each other palynologically, although their pollen can be readily differentiated from that of other genera (Fig. 2E–G and Appendix A). *Pseudolmedia* pollen is 3–4 porate, psilate, angulaperturate, and relatively large, with a mean equatorial diameter (E) and polar axis length (P) of $18.5\pm 2\ \mu\text{m}$ and $16.5\pm 2.5\ \mu\text{m}$, respectively. *Maquira coriacea* is 3–4–5 porate, scabrate, angulaperturate and has a mean equatorial diameter (E) and polar axis length (P) of $18.5\pm 1\ \mu\text{m}$ and $15.5\pm 0.5\ \mu\text{m}$

Fig. 6. Geographic distribution of parent taxa of Moraceae pollen types differentiated in this paper (filled squares) plotted alongside the distribution of key Holocene and Late glacial fossil pollen sites in the Amazon lowlands (open squares). The light grey area represents the Amazon Basin and the dark grey area the Madeira–Tapajós moist forest ecoregion. Mapped species are based on output from the VAScular Tropicos (VAST) Nomenclatural Database (2007) provided by the Missouri Botanical Gardens, and are indicative of the presence/absence of plants at specific sites. A: Fossil pollen sites: LF, Laguna Funza (Van't Veer and Hooghiemstra, 2000); LL, Laguna Loma Linda (Behling and Hooghiemstra, 2000); LM, (Liu and Colinvaux, 1985); LA, Laguna Ayauch (Bush and Colinvaux, 1988); LK, Laguna Kumpak (Liu and Colinvaux, 1988); PM, Pantano de Monica (Behling et al., 1999); LP, Lagoa Pata (Colinvaux et al., 1996); GM, Guaiquinima massif (Rull, 2005a,b); CM, Chimanta Massif (Rull, 2005b); LKT, Katira (Van der Hammen and Absy, 1994); BV, Laguna Bella Vista; LC, Laguna Chaplin (Burbridge et al., 2004; Mayle et al., 2000); LT, Lago Tapajós (Irion et al., 2006); LG, Lagoa Geral and Lagoa Comprida (Bush et al., 2000); LDC, Lagoa do Caço (Ledru et al., 2001); AF, Amazon Fan (Haberle and Maslin, 1999). B: *Brosimum alicastrum*, *B. guianense* and *B. lactescens*, C: *B. gaudichaudii*, D: *Helicostylis tomentosa* and *H. scabra*, E: *Maquira coriacea*, F: *Pourouma guianensis* and *P. minor*, G: *Pseudolmedia laevigata*, *P. laevis* and *P. macrophylla*, H: *Sorocea guilleminiana* and *S. hirtella*.



(Fig. 3H). Both can be differentiated from *Helicostylis* by their size, shape class and sculpturing (Table 1). If pollen preservation is poor, it may not be possible to reliably distinguish between 3–4 porate pollen grains of *M. coriacea* and *Pseudolmedia*. However, pentaporate grains can unequivocally be identified as *Maquira*, as pollen of all other taxa in this study have 4 pores or less (Table 1).

Pseudolmedia species are late-successional canopy trees that grow in both well-drained and inundated rainforest communities across the Amazon Basin (VAST, 2007; Fig. 6G). This genus is particularly prominent in *terra firme* plots of NKMNP, where *Pseudolmedia laevis* and *P. macrophylla* have IVI values of 11.7 and 6.3, respectively. Abundant *Pseudolmedia* pollen in the fossil record would therefore be indicative of evergreen rainforest. *Maquira coriacea* is ecologically restricted to riparian evergreen forest communities within the Amazon Basin (Killeen, 1998; Nebel et al., 2001a,b; Fig. 6E). It is especially important in riparian forests lining the Rio Paraguá (IVI=29) and is not recorded in any other plant community in NKMNP. The presence of this taxon in fossil pollen assemblages would therefore provide strong evidence for riparian forest.

5.1.4. *Pourouma*, *Sorocea* and *Maclura tinctoria*

Pollen grains of *Pourouma*, *Sorocea* and *Maclura tinctoria* are rather more difficult to differentiate from each other (Fig. 3K–N, P). It is, however, possible to separate them according to their *P/D* ratio (Fig. 4b; Appendix A). *Pourouma minor* and *P. guianensis* exhibit *P/D* ratios that are strongly prolate (*P/D*=1.44 and 1.33, respectively) in contrast to those of *Sorocea* and *M. tinctoria*, which are subprolate.

Pourouma guianensis is a common tree in *terra firme* tall humid evergreen (IVI=3.1) and liana forests (IVI=3.5) in NKMNP. *P. minor* is less common, although Killeen (1998) reports its presence in gallery forests within the park and both species are present across the Amazon Basin (VAST, 2007; Fig. 6F). *Sorocea* species inhabit a wide range of plant communities within NKMNP, albeit at low abundance; e.g. *S. guillemianiana* grows in both *terra firme* (IVI=0.47) and seasonally-inundated (IVI=2.8) rainforest communities, as well as in semi-deciduous dry forests and savannas, (Killeen, 1998). It too has a range extending across Amazonia (Fig. 6H). *Maclura tinctoria* is adapted to a wide range of forest types extending from southern Mexico to northern Argentina (Marchant et al., 2002), and is present in NKMNP in evergreen liana forest (IVI=0.42) and dry forest (Killeen, 1998), although it is uncommon. In summary, *Pourouma*, *Sorocea* and *M. tinctoria*, considered as a group, are indicative of a variety of forest types, and are therefore of lower palaeoecological value than other Moraceae genera.

5.1.5. Intra-species variability in aperture number

A number of fossil (Colinvaux et al., 1997; Bush et al., 2000) and modern pollen diagrams (Weng et al., 2004; Gosling et al., 2005) have sub-divided Moraceae/Urticaceae pollen solely on the basis of the number of apertures. The evidence presented here (Table 1; Fig. 2) demonstrates that, in general, such characterisation is of limited taxonomic value because sev-

eral Moraceae genera have pollen with the same number of pores (e.g. *Brosimum*, *Ficus*, *Pourouma*, and *Sorocea* all have diporate pollen grains), whilst others have pollen with variable pore number (e.g. *Pseudolmedia* spp.: 3–4 porate, *Maquira coriacea*: 3–4–5 porate, *Helicostylis* spp.: 2–3 porate, *Maclura tinctoria*: 2–3 porate). Use of pore number as a taxonomic criterion for this family is therefore best applied in conjunction with other diagnostic characters such as surface sculpture, pore characteristics, and grain shape.

5.2. Palaeoecological implications

5.2.1. Noel Kempff Mercado National Park

The ability to palynologically differentiate the constituent genera of Moraceae and Urticaceae means that there is now the potential for making more reliable and detailed palaeovegetation reconstructions than has hitherto been possible. As well as applying this increased taxonomic resolution to future fossil pollen studies of new sites, it is also fruitful to re-examine previously studied sites to improve upon, or at least test, earlier palaeoenvironmental reconstructions. The two most obvious sites for re-analysis of their Moraceae/Urticaceae pollen records are Laguna Chaplin and Laguna Bella Vista, since they are both located within the NKMNP study area, are surrounded by a mosaic of different kinds of rainforest, and reveal a 50,000 year record of rainforest–savanna dynamics (Fig. 1; Mayle et al., 2000; Burbridge et al., 2004). Differentiating between the different Moraceae/Urticaceae pollen types should reveal whether the Late Holocene increase in abundance of this pollen type is due to development of *terra firme* rainforest or seasonally-flooded/riverine forest or a combination of the two. If the rise in Moraceae pollen at these sites is solely due to seasonally-flooded/riparian genera, then this may point to local hydrological changes in the nearby river flood-plain, whereas expansion of genera from upland *terra firme* rainforest would be more convincing evidence for a change to a wetter climate. Identification of pollen of *Brosimum gaudichaudii* in the fossil record could be of even greater significance. Abundance of this taxon in the pollen record would challenge the assumption that abundance of Moraceae pollen is indicative of rainforest (Colinvaux and de Oliveira, 2000, Mayle et al., 2004; Gosling et al., 2005) because *B. gaudichaudii* is currently restricted to, and indicative of, rather more arid environments to the south of the Amazon Basin, including well-drained savanna (*cerrado*), dense closed-canopy dry forest (*cerradão*), and seasonally-flooded savanna (Fig. 6C; De Oliveira-Filho, 1992; Killeen, 1998; Marchant et al., 2002). It is clear, therefore, that a taxonomic re-evaluation of the Moraceae/Urticaceae type pollen of the fossil pollen assemblages of Laguna Chaplin and Laguna Bella Vista could potentially lead to palaeoclimatic inferences quite different from those previously made by the authors in the initial studies (i.e. Mayle et al., 2000; Burbridge et al., 2004).

5.2.2. Amazon Basin

It would seem reasonable to assume that the pollen-morphological differences revealed here, should hold true within the floristically-distinct Madeira–Tapajós moist forest

ecoregion, which encompasses our study area (Fig. 1). For example, applying these results to the Rio Tapajós lake sediments (Fig. 6A; Irion et al., 2006), which lie within this ecoregion, could determine whether the Holocene rainforest signal at this site predominantly reflects local riparian rainforest bordering the river basin, or instead *terra firme* rainforest across a much larger area beyond the river basin.

The widespread geographic distribution of the taxa differentiated palynologically in this paper (Fig. 6), and the dominance of Moraceae pollen in all fossil pollen sites that have so far been studied in Amazonia (Mayle et al., 2004), clearly illustrates the importance of our findings for palaeoecology of the basin as a whole. It would be particularly useful to apply our findings to the previously-published Late Quaternary pollen records of the Amazon Fan (Haberle, 1997; Haberle and Maslin 1999), in order to help resolve the controversy over their significance for the Quaternary history of Amazonia's rainforests. Some have argued that the dominance of Moraceae/Urticaceae pollen throughout the glacial-Holocene sequence is evidence that Amazonia was largely covered by rainforest throughout this period (e.g. Haberle and Maslin 1999; Colinvaux et al., 2000), whereas others have suggested that it may simply reflect gallery or riparian forest lining the rivers during glacial periods, which masked pollen from savannas or dry-forests beyond, consistent with the glacial aridity hypothesis (e.g. Haffer, 1969; Van der Hammen, 1974; Prado and Gibbs, 1993; Pennington et al., 2000; Haffer and Prance, 2001). If the glacial Moraceae/Urticaceae pollen signal was found to comprise predominantly riparian or seasonally-flooded rainforest species, such as *Brosimum lactescens*, *B. guianensis*, or *Maquira coriacea*, this would be strong evidence that the Amazon Fan pollen record primarily reflects riverine rainforests rather than *terra firme* vegetation beyond. In contrast, a glacial Moraceae pollen signal that was instead dominated by *Helicostylis* and/or *Pseudolmedia* would demonstrate a regional *terra firme* rainforest signal.

The diversity and importance of Amazonian genera of the Moraceae family has, until now, not been captured in fossil pollen records of the Amazon Basin. Our results suggest that ecosystem-specific indicator taxa of this family may be differentiated from each other palynologically, and should therefore be used to improve the interpretation of fossil pollen records. These results will not only permit the palynological differentiation of different rainforest communities, but they will also improve our knowledge of the spatial extent of Amazonian rainforests during the Quaternary. Moreover, an improved understanding of the historical biogeography of the Amazon Basin would provide better estimates of past carbon storage, which may, in turn, provide invaluable data for the testing of climate and vegetation models.

6. Conclusions

An important limitation of previous Neotropical pollen studies is that pollen of the constituent genera of Moraceae and Urticaceae have not been differentiated from each other and have generally been considered as a single Moraceae/Urticaceae pollen type. In this study we examined pollen grains of each species

of these two families recorded in NKMNP, NE Bolivia, measuring the following morphological features: shape and size of the grain, pore characteristics and number, and surface sculpture. When considering these parameters in combination, we find that it is possible to differentiate between pollen of the following taxa within the Moraceae family: *Helicostylis* spp., *Brosimum* spp., *Brosimum gaudichaudii*, *Pseudolmedia* spp., *Sorocea* spp., *Pourouma* spp., and *Maquira coriacea*. Furthermore, these Moraceae pollen types can be distinguished from Urticaceae pollen (*Urera* and *Pouzolzia*). This improved taxonomic resolution provides the potential for differentiating between different kinds of rainforest, especially riparian/seasonally-flooded rainforest versus *terra firme* rainforest, as well as potentially identifying savanna/woodland communities. Consequently, much more detailed palaeovegetation reconstructions can now be achieved for Amazonia than have hitherto been possible.

Acknowledgements

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Appendix A. A taxonomic key to pollen types of Moraceae and Urticaceae genera and species of NKMNP; terminology *sensu* Punt et al. (2007) and format *sensu* Roubik and Moreno (1991). **Pourouma* has been re-classified as Cecropiaceae in IPNI (2007).

1a. Diporate	
2a. Grain psilate	
3a. $P/E=1.19-1.23$ (subprolate)	<i>Brosimum gaudichaudii</i>
3b. $P/E=0.63-0.65$ (oblate)	<i>Ficus citrifolia</i> <i>Ficus pertusa</i> <i>Ficus paraensis</i>
2b. Grain finely scabrate	
4a. $P/E=0.98-1$ (spheroidal)	
5a. Porus with a distinct annulus	<i>Brosimum alicastrum</i> <i>Brosimum guianense</i> <i>Brosimum lactescens</i>
5b. Porus without annulus	<i>Sorocea hirtella</i> <i>Maclura tinctoria</i> <i>Helicostylis scabra</i> <i>Helicostylis tomentosa</i>
4b. $P/E=0.76-0.79$ (suboblate)	
2c. Grain coarsely scabrate	
6a. $P/D=1.34-1.44$ (prolate)	<i>Pourouma minor</i> *
6b. $P/D=1.16-1.2$ (subprolate)	<i>Pourouma guianensis</i> *
	<i>Sorocea guilleminiana</i>
1b. Triporate	
7a. Grain psilate	
8a. Grain angulaperturate	<i>Pseudolmedia laevigata</i> <i>Pseudolmedia laevis</i> <i>Pseudolmedia macrophylla</i>
8b. $P/D=0.85-0.86$ (spheroidal)	<i>Urera caracasana</i> <i>Pouzolzia poeppigiana</i>

(continued on next page)

Appendix A (continued)

7b. Grain finely scabrate	
9a. Grain angulaperturate	<i>Helicostylis scabra</i> <i>Helicostylis tomentosa</i> <i>Maclura tinctoria</i>
9b. $P/D=1.16$ (subprolate)	
1c. Pantoporate (4–5 pores)	
9a. 4-porate	
10a. Grain psilate	<i>Pseudolmedia laevigata</i> <i>Pseudolmedia laevis</i> <i>Pseudolmedia macrophylla</i> <i>Maquira coriacea</i>
10b. Grain finely scabrate	
9b. 5-porate	

Pollen descriptions

Brosimum alicastrum Swartz
Diporate; sexine finely scabrate; pores 3 μm diameter; $P=17\text{--}20$ μm , $E=16\text{--}20$ μm , $D=15\text{--}18$ μm ; $P/E=1$ (spheroidal); $P/D=1.09$ (prolate–spheroidal).

Brosimum gaudichaudii Trécul
Diporate; sexine psilate; pores 1.5–2 μm diameter; $P=13\text{--}16$ μm , $E=11\text{--}14$ μm , $D=9\text{--}13$ μm ; $P/E=1.19\text{--}1.23$ (subprolate); $P/D=1.35\text{--}1.37$ (prolate).

Brosimum guianense (Aublet) Huber
Diporate; sexine finely scabrate; pores 1.5–2 μm diameter; $P=14\text{--}17$ μm , $E=14\text{--}17$ μm , $D=11\text{--}13$ μm ; $P/E=1$ (spheroidal); $P/D=1.29$ (subprolate).

Brosimum lactescens (Moore) C.C. Berg
Diporate; sexine finely scabrate; pores 3 μm diameter; $P=17\text{--}20$ μm , $E=16\text{--}20$ μm , $D=16\text{--}18$ μm ; $P/E=0.98\text{--}0.99$ (spheroidal); $P/D=1.1\text{--}1.11$ (prolate spheroidal).

Ficus citrifolia Miller
Diporate; sexine psilate; pores 1–1.5 μm diameter; $P=7\text{--}9$ μm , $E=11\text{--}14$ μm ; $P/E=0.65$ (oblate).

Ficus paraensis (Miquel) Miquel
Diporate; sexine psilate; pores 1–1.5 μm diameter; $P=8\text{--}10$ μm , $E=13\text{--}16$ μm ; $P/E=0.64$ (oblate).

Ficus pertusa Linnaeus
Diporate; sexine psilate; pores 1–1.5 μm diameter; $P=5\text{--}7$ μm , $E=9\text{--}10$ μm ; $P/E=0.63$ (oblate).

Helicostylis scabra (Macbride) C.C. Berg
Diporate and triporate; sexine finely scabrate; pores 1.5 μm diameter; amb angulaperturate; $P=7\text{--}12$ μm , $E=11\text{--}13$ μm ; $P/E=0.78$ (suboblate).

Helicostylis tomentosa (Poeppig & Endlicher) J.F. Macbride
Diporate and triporate; sexine finely scabrate; pores 1.5 μm diameter; amb angulaperturate; $P=8\text{--}10$ μm , $E=11\text{--}13$ μm ; $P/E=0.76\text{--}0.79$ (suboblate).

Maclura tinctoria Steudel
Diporate and triporate; sexine finely scabrate; pores 2 μm diameter; $P=11\text{--}13$ μm , $E=11\text{--}13$ μm , $D=9\text{--}12$ μm ; $P/E=0.99$ amb (spheroidal); $P/D=1.16$ (subprolate).

Maquira coriacea (Karsten) C.C. Berg
Diporate, triporate and pantoporate (4 and 5 pores); sexine finely scabrate; pores 2 μm diameter; amb angulaperturate; $P=15\text{--}17$ μm , $E=17\text{--}20$ μm ; $P/E=0.84$ (suboblate).

Pourouma guianensis Aublet Subsp. *guianensis*
Diporate; sexine coarsely scabrate; pores 1.5 μm diameter; $P=12\text{--}15$ μm , $E=11\text{--}15$ μm , $D=9\text{--}12$ μm ; $P/E=1.04$ (spheroidal); $P/D=1.34$ (prolate).

Pourouma minor Benoist
Diporate; sexine coarsely scabrate; pores 1.5 μm diameter; $P=13\text{--}16$ μm , $E=12\text{--}14$ μm , $D=10\text{--}11$ μm ; $P/E=1.19$ (subprolate); $P/D=1.44$ (prolate).

Pouzolzia poeppigiana (Weddell) Killip
Triporate; sexine psilate; pores 1–1.5 μm diameter; amb spheroidal; $P=9\text{--}12$ μm , $E=10\text{--}14$ μm , $P/E=0.85$ (suboblate).

Pseudolmedia laevigata Trécul
Triporate and 4-porate; sexine psilate; pores 2 μm diameter; amb angulaperturate; $P=11\text{--}15$ μm , $E=14\text{--}18$ μm ; $P/E=0.84$ (suboblate).

Pseudolmedia laevis (Ruiz & Pavon) J.F. Macbride
Triporate and 4-porate; sexine psilate; pores 2–3 μm diameter; amb angulaperturate; $P=15\text{--}21$ μm , $E=17\text{--}22$ μm ; $P/E=0.92$ (spheroidal).

Pseudolmedia macrophylla Trécul
Triporate and 4-porate; sexine psilate; pores 2 μm diameter; amb angulaperturate; $P=15\text{--}21$ μm , $E=19\text{--}25$ μm ; $P/E=0.92$ (spheroidal).

Sorocea guilleminiana Gaudichaud-Beaupré
Diporate; sexine coarsely scabrate; pores 2 μm diameter; $P=13\text{--}16$ μm , $E=14\text{--}17$ μm , $D=12\text{--}13$ μm ; $P/E=0.99\text{--}1.05$ (spheroidal); $P/D=1.16\text{--}1.2$ (subprolate).

Sorocea hirtella Mildbraed
Diporate; sexine finely scabrate; pores 2 μm diameter; $P=10\text{--}14$ μm , $E=11\text{--}14$ μm , $D=11\text{--}12$ μm ; $P/E=0.98$ (spheroidal); $P/D=1.1$ (prolate spheroidal).

Urera caracasana Grisebach
Triporate; sexine psilate; pores 1–1.5 μm diameter; amb spheroidal; $P=7\text{--}12$ μm , $E=9\text{--}14$ μm ; $P/E=0.86$ (suboblate).

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