A Pollen Atlas of Premontane Woody and Herbaceous Communities from the Upland Savannas of Guayana, Venezuela

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A pollen atlas of premontane woody and herbaceous communities from the upland savannas of Guayana, Venezuela

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Descriptions and photomicrographs of pollen grains from 245 angiosperm species commonly found in contemporary plant communities of the upland savannas of Guayana, Venezuela are presented. Most of the species are frequent in woody communities as shrublands, evergreen montane and gallery forest of the premontane altitudinal belt (400–1800 m above sea level). In contrast with previous contributions which emphasised species from highland and/or flooded environments, most species considered here grow on lowland to upland well-drained soils. The high numbers of taxa considered herein means that the utility of this contribution transcends palaeoecology and impinges on, for example, reproductive biology, forensic palynology, aerobiology and melissopalynology in Guayana and the wider Neotropical realm.

Keywords: neotropical pollen; premontane forest; upland savanna; Gran Sabana; Guayana; Venezuela

1. Introduction

In the Neotropics, the diversity of pollen types in sedimentary records and pollen rain samples from woody communities can reach several hundred types (Behling et al. 1999; Colinvaux et al. 1999; Berrío et al. 2000; Van der Hammen and Hooghiemtra, 2000; Bush and Rivera 2001; Weng et al. 2004; Gosling et al. 2005; Burn et al. 2010). A high proportion of these are of unknown origin. In the last few decades several studies have advanced the understanding of Neotropical pollen, and numerous illustrated catalogues and atlases have been published (Hooghiemstra 1984; Roubik and Moreno 1991; Herrera and Urrego 1996; Colinvaux et al. 1999; Rull 2003; Bush and Weng 2007). Nevertheless, the great variability in pollen morphology between species of the same genera and within families necessitates the creation of more reference collections for pollen identification in high-diversity tropical environments. In the upland savannas of Guayana (Gran Sabana, Canaima National Park), the construction of additional pollen atlases is also necessary due to the particular composition and structure of the plant communities. This reflects the unique character of the geology of this region and its location on an upland plateau. Most current pollen atlases available for tropical South America are based on species from the Amazon lowlands or the Andean highlands.

An illustrated pollen key by Rull (2003) for Gran Sabana and *Pantepui* (the latter including both higher slopes and summits of the *tepui* table mountains) provided pollen descriptions for 85 taxa in 36 families. Most pollen types in this work are from flooded upland environments or peat bogs above 1800 m above sea level (asl). Hence, species of premontane (400–1500/1800 m asl) evergreen forest growing on well-drained soils were weakly represented, although these communities are dominant in both the uplands (>70% of plant cover according to Delgado et al. 2009) and the lowlands of Canaima National Park (>80% of plant cover). The contribution of Rull (2003) is therefore useful for the identification of the commonest pollen types found in flooded gallery forest from the uplands and/or highland-tepui environments. However, detailed palaeoecological research on woody communities growing on well-drained soils of the Gran Sabana plateau and adjacent areas requires additional tools for pollen identification.

We present pollen descriptions and photomicrographs of 245 species belonging to 194 genera and 68 families, collected from specimens stored in the National Herbarium of Venezuela. The most abundant upland genera included by Rull (2003) are also treated here. Pollen photomicrographs are accompanied by brief descriptions. This work allows the identification

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of high-, intermediate- and low-abundance pollen types found in new sediment cores from the forest-savanna transitions of the upland savannas of Gran Sabana (Leal 2010). Furthermore, given the relatively high numbers of taxa that are considered, the utility of this contribution transcends palaeoecology and provides an important contribution to reproductive biology, forensic palynology, aerobiology, melissopalynology and other related fields.

2. Methods

2.1. Study site and species selection

The upland savannas of Guayana are located in the southeast of Canaima National Park in the Venezuelan portion of the Precambrian Guayana Shield (Figure 1). Gran Sabana covers 18,000 km^2 with a plateau at 400–1500 m asl. In contrast to the rest of the park where evergreen forests represent >80% of plant cover, the Gran Sabana is characterised by the coexistence of evergreen premontane forest and huge treeless savannas, the latter occupying 30% of total plant cover (Delgado et al. 2009). Both the forest and savanna communities, plus sparser floras such as palm swamps, broadleaved grasslands, fernlands and shrublands, are distributed in a mosaic-like pattern mainly controlled by soil types and climate.

The climate is humid submesothermic, with mean annual temperatures between 21 and 24°C. Mean annual rainfall is between 1600 and 4000 mm (Hernández 1994a). Air temperature and rainfall vary markedly along complex spatial gradients determined by altitudinal changes and topography (Huber and Febres 2000). A 2–3 month dry season ocurs from January to March, coinciding with the southwards migration of the intertropical convergence zone (ITCZ). The regolith is generally derived from sandstones of the Roraima Group, and this unit

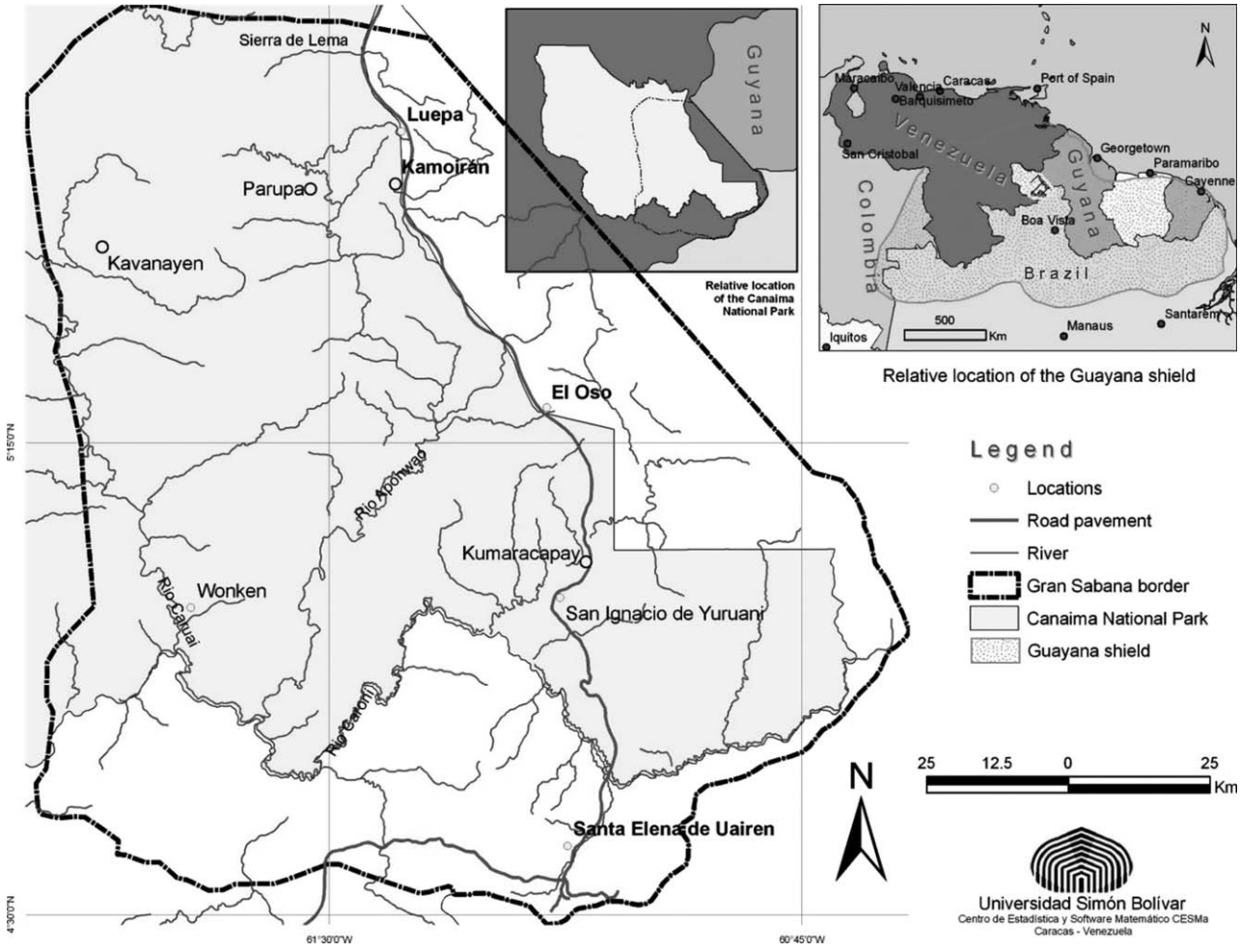


Figure 1. The location of the Gran Sabana in the Canaima National Park, southeast Venezuela, provided by Raul Ramirez-Arbeláez (CesMa, USB).

produces acidic nutrient-poor soils (Dezzeo and Fölster 1994).

The commonest vegetation type in Gran Sabana is evergreen premontane forest, which is found on well-drained soils, and the evergreen gallery forest. These include Lauraceae (e.g. *Ocotea guianensis*), *Alchornea triplinervia* (Euphorbiaceae), *Alexa* sp. (Leguminosae), *Anaxagorea* sp. (Annonaceae), *Byrsonima stipulacea* (Malpighiaceae), *Clusia* spp. (Clusiaceae), *Dimorphandra macrostachya* (Fabaceae), *Euterpe tenuiramosa* (Arecaceae), *Henriettea ramiflora* (Melastomataceae), *Licania micrantha* (Chrysobalanaceae), *Matayba venezuelana* (Sapindaceae), *Pourouma guianensis* (Cecropiaceae), *Pouteria bangii* (Sapotaceae), *Protium heptaphyllum* (Burseraceae), *Ruizterania ferruginea* (Vochysiaceae), *Tachigali guianensis* (Fabaceae), *Simarouba amara* (Simaroubaceae) and *Sloanea picapica* (Elaeocarpaceae) (see Huber 1986; Hernández 1994b).

Treeless savanna is the second-most important vegetation type, and is dominated by *Trachypogon spicatus*, *Axonopus anceps* (Poaceae) and Cyperaceae spp. (Bilbao et al. in press). Many other herbaceous and scrubby communities are also present, including broadleaved grasslands (''herbazales'') unique to the Guayana Shield, which are composed of *Stegolepis ptaritepuiensis* (Rapateaceae), *Bocchinia micrantha* (Bromeliaceae), Poaceae, Cyperaceae, Eriocaulaceae and Xyridaceae (see Huber 1994a, 1994c, 1994d; 1995). Palm swamps (''morichales'') are also present; these are dominated by *Mauritia flexuosa* (Arecaceae), Poaceae and Cyperaceae (see Huber 1994c, 1994d). Shrublands (the ''sclerophyllus shrublands'' of Huber 1989) are also important in the uplands and comprise species of *Clusia* (Clusiaceae), *Humiria* (Humiriaceae), *Bonnetia* (Theaceae), *Gongylolepis* (Asteraceae), *Thibaudia, Notopora* (Ericaceae), *Cyrilla* (Cyrillaceae) and Melastomataceae (Huber 1989; 1995).

The angiosperm genera considered here were chosen on the basis of their importance in living communities and the availability of fertile herbarium specimens. They include all the vegetation types described above, and were selected on the basis of the botanical and ecological literature of the area (Steyermark 1966; Huber 1986, 1989, 1990, 1994a, 1994b, 1994c, 1994d; Schubert and Huber 1989; Hernández 1999; Fölster and Dezzeo 1994; Hernández and Fölster 1994; Hernández 1994b; Steyermark et al. 1995; Ramirez et al. 2007; Bilbao et al. 2009; Bilbao et al., in press). Only the most important genera living between 400 and 1800 m asl were chosen, and genera only observed above 1800 m were excluded. These highland taxa belong to a different phytogeographical unit termed *Pantepui* (Huber 1994b) and were described by Rull (2003).

2.2. *Sampling, processing and presentation of results*

This atlas is based entirely on specimens curated in the National Herbarium of Venezuela, which were identified by expert taxonomists. The procedures of Jarzen and Jarzen (2006) for sample collection from herbarium specimens were followed, dissecting anthers from mature flowers, immediately prior to anthesis. In the laboratory, the anthers were gently macerated and acetolysed following standard procedures (Erdtman 1986).

The pollen grains were described using the terminology of Punt et al. (2007). Aspects considered were: (a) aggregation of grains; (b) symmetry; (c) shape and size in equatorial view (EV) and polar view (PV); (d) presence, number and type of apertures; and (e) exine thickness, stratification and sculpture. The synoptic pollen descriptions are based on the above characteristics, they are ordered alphabetically in families and dicots and monocots are considered separately. The maximum, mean (in parentheses) and minimum sizes for each pollen type are given. The overall exine thickness and the relative thickness of the sexine with respect to nexine are also included. The ratio of the polar axis length and the equatorial axis width (P/E) was used to classify grains by their EV shape (Erdtman 1986). A single description is given for two or more pollen grains that have identical characteristics (e.g. genera of Poaceae and Cyperaceae) to save space. Notes on the ecology, altitudinal distribution of species and the abundance of each pollen type in surface soils or in Holocene sedimentary records are also given briefly. In this case, pollen abundance is expressed as percentage of the pollen sum (ΣP) found by Leal (2010). Photomicrographs for each type in EV and PV showing the main taxonomic characters are given in Plates 1–14.

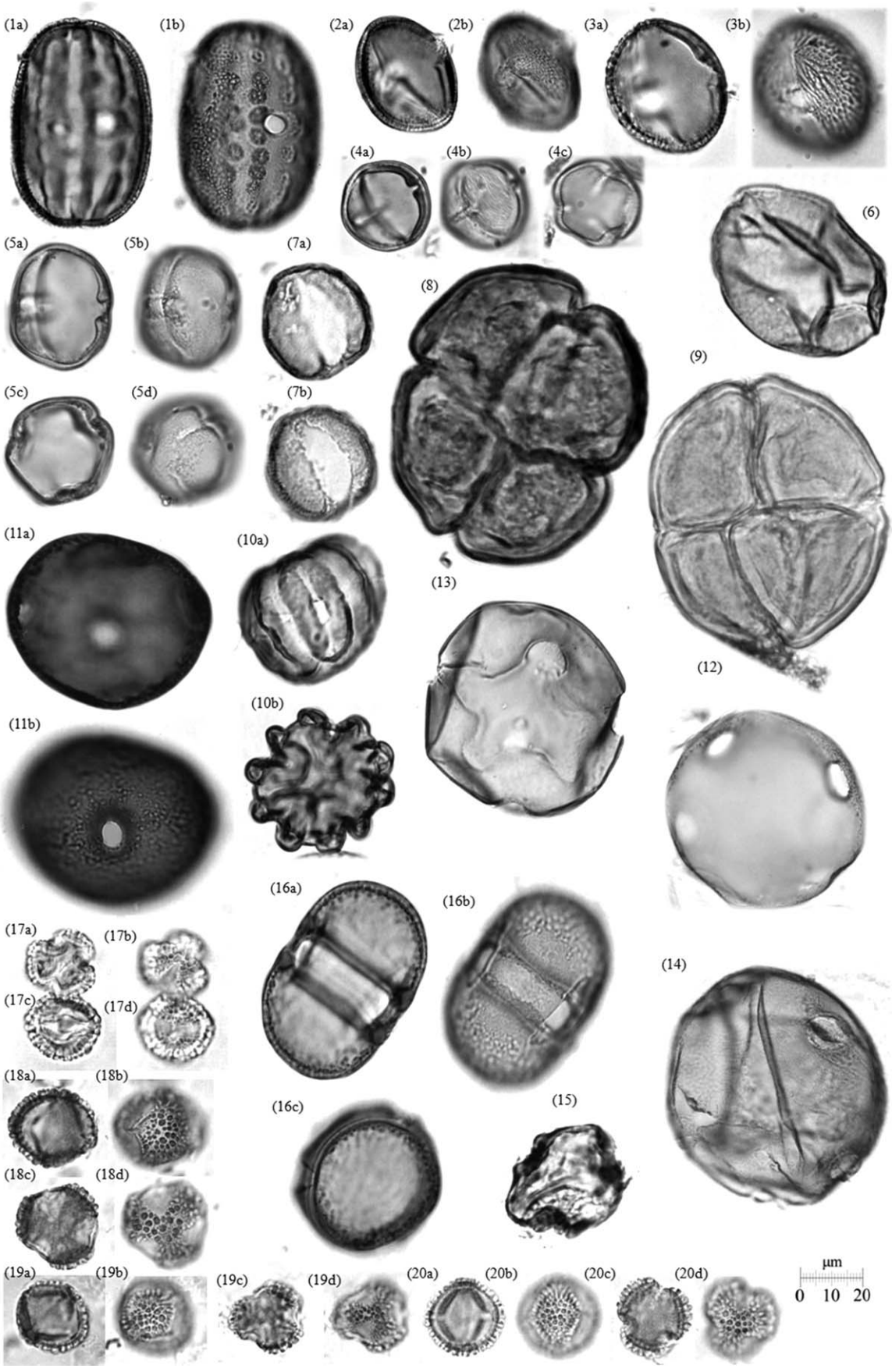
3. Systematic section

3.1. *DICOTS*

ACANTHACEAE

Justicia kunhardtii Leonard (Plate 1, fig. 1)

Monads. EV prolate, 55.5(57)58.5 × 30(36)40.5 μm. P/E = 1.90. PV oval 33–34.5 × 43.5–45 μm. Di-zonoporate. Pori wide, circular-ovoid, 7–8 μm diameter. Exine 4–5 μm, columellae conspicuous, sexine = nexine. A pattern of rounded elements formed by microreticula and exhibiting a longitudinal arrangement is observed; this is a common character in this family. General exine sculpture is microreticulate-microscabrate. Herb 60 cm tall, growing in open savannas on sandstone or sandy soils (400–1700 m asl). Observed only in sediments from broadleaf grasslands (ΣP < 0.5%).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ANACARDIACEAE

Anacardium giganteum W. Hancock ex Engl. (Plate 1, fig. 2)

Monads. EV prolate-spheroidal, 28.5(29)30 × 27(28)28.5 μm. P/E = 1.06. PV circular, 27(28)30 μm. Tricolporate, colpi as long as grain, pori lalongate-rectangular, 4.5(5)6 × 10.5(13)15 μm. Exine 3 μm, columellae conspicuous, sexine = nexine, microreticulate, making a pattern of slight longitudinal striae. Tree in macrothermic forest (0–600 m asl). A similar pollen type was observed in surface soils of forest (ΣP < 0.5%).

Astronium obliquum Griseb. (Plate 1, fig. 3)

Monads. EV subprolate 30(34)40.5 × 25.5(28)30 μm. P/E = 1.20. PV circular-trilobate, 24(27)28.5 μm. Tricolporate, colpi as long as grain, pori lalongate-rectangular (3 × 6 μm). Exine 1.5 μm, columellae visible, sexine = nexine. Microreticulate-heterobrochate, with reticula making a pattern of longitudinal striae. Tree 30 m tall, deciduous macrothermic forest (100–800 m asl). Observed in most forest soils (ΣP > 5%).

Tapirira guianensis Aubl. (Plate 1, fig. 4)

Monads. EV prolate-spheroidal, 22.5(24)27 × 22.5(26.4)25.5 μm. P/E = 1.03. PV circular-trilobate, 19.5(22)22.5 μm. Tricolporate, colpi narrow (1.5–2 μm wide), as long as grain, pori lalongate (1.5–4.5 × 15–18 μm). Exine 1.5 μm, sexine = nexine, with a very fine and diffuse striate pattern. Tree 30 m tall, deciduous or evergreen premontane or gallery forest (0–1200 m asl). Observed in soils from gallery forest, savanna/forest boundaries and morichales (ΣP > 5%).

Thyrsodium spruceanum Benth. (Plate 1, fig. 5)

Monads. EV subprolate, 31.5(35)37.5 × 28.5(30)31.5 μm. P/E = 1.20. PV circular-trilobate, 27(20)30 μm. Tricolporate, colpi as long as grain, narrow (1.5–3 μm), pori lalongate (4.5–7.5 × 9–22.5 μm). Exine 1.5 μm, sexine = nexine, microreticulate-striate. Tree 20 m tall, in deciduous, semideciduous and evergreen forest (0–1200 m asl). Observed rarely in forest soils (ΣP < 0.5%).

ANNONACEAE

Anaxagorea petiolata R.E. Fr. (Plate 1, fig. 6)

Monads. Spherical-ovoid, 45(49)52.5 μm. Inaperturate. Exine thin (1 μm) generally easily folded, translucent, psilate. Tree 6–15 m tall, premontane forest (300–1300 m asl). Observed rarely in forest soils (ΣP < 0.5%).

Bocageopsis multiflora (Mart.) R.E. Fr. (Plate 1, fig. 7)

Monads. Spherical-ovoid, 25.5(32)36 μm. Monocolpate, colpi as long as grain, covering 1/3 of total grain width. Exine 1.5 μm, columellae visible, sexine = nexine, microreticulate. Tree 20 m tall in evergreen premontane forest (200–600 m asl). Observed rarely in forest soils (ΣP < 0.5%).

Xylopia calophylla R.E. Fr. (Plate 1, fig. 8)
Xylopia frutescens Aubl. (Plate 1, fig. 9)

Uniplanar tetrads, tetragonal, 84 × 59 μm. Grains ovoid-rectangular, 34.5(39)45 × 25.5(30)34.5 μm. Inaperturate. Exine thin (1.5 μm), sexine > nexine, very translucent, psilate. Tree 15 m tall. Semideciduous and evergreen forest (100–600 m asl). Observed rarely in forest soils (ΣP < 0.5%).

APOCYNACEAE

Aspidosperma decussatum Woodson (Plate 1, fig. 10)

Monads. EV suboblate, 30(35)37.5 × 36(40.5)43.5 μm. P/E = 0.87. PV polygonal-circular, 37.5(39)42 μm. Penta-zono-colporate, colpi as long as grain, 3 μm wide, pori small rectangular (7.5 × 3 μm). Conspicuous thickened margo present, extended toward apocolpium. Pseudocolpi present alternated with apertures. Exine thin (1.5 μm), sexine = nexine, psilate. Tree 20 m tall in gallery forest (80–600 m asl). Observed rarely in forest soils (ΣP < 0.5%).

Galactophora schomburgkiana Woodson (Plate 1, fig. 11)

Monads. EV suboblate, 53 × 63 μm. P/E = 0.85. PV circular, 55.5(66)72 μm. Tri-zono-porate, pori circular (6 μm diameter), with thickened annulus (4–5 μm thick). Exine thin (1–3 μm), sexine = nexine, scarbrate. Erect shrub 1–5 m tall. Sandy savannas, flooded and open areas or tepui summits (200–2000 m asl). Observed in sediments from herbazales and morichales (ΣP < 1%).

Mandevilla benthamii (A. DC.) K. Schum. (Plate 1, fig. 12)

Monads spheroidal, 95(109)117.5 μm. Zono-porate, with 3–6 circular to oval annulate pori

Plate 1. ACANTHACEAE: *Justicia kunhardtii* (1). ANACARDIACEAE: *Anacardium giganteum* (2), *Astronium obliquum* (3), *Tapirira guianensis* (4), *Thyrsodium spruceanum* (5). ANNONACEAE: *Anaxagorea petiolata* (6), *Bocageopsis multiflora* (7), *Xylopia calophylla* (8), *Xylopia frutescens* (9). APOCYNACEAE: *Aspidosperma decussatum* (10), *Galactophora schomburgkiana* (11), *Mandevilla benthamii* (12), *M. scabra* (13), *M. subcarnosa* (14), *Rhigospira quadrangularis* (15), *Tabernaemontana cerea* (16). AQUIFOLIACEAE: *Ilex divaricata* (17), *I. jenmanii* (18), *I. parvifructa* (19), *I. retusa* (20). For figs. 12, 13 and 14, the scale bar represents 40 μm.

(15–25 × 12.5–20 μm). Exine thin (2.5 μm), sexine = nexine, microscabrate. Shrub 80 cm tall, in open savannas and shrublands on sandy soils, sandstone or igneous rocks, and also in tepui summits (400–2100 m asl). Not observed in soils from Gran Sabana.

Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K. Schum. (Plate 1, fig. 13)
Mandevilla subcarnosa (Benth.) Woodson (Plate 1, fig. 14)

Monads. Spherical, 120–140 μm diameter. Pantoporate, with 4–6 circular to oval annulate pori (19–24 × 28–35 μm). Exine thin (1.5–3 μm), sexine = nexine, fragile, microscabrate. Liana in humid premontane forest (0–600 m asl). *Mandevilla subcarnosa* is also present in the tepuian forest (until 2000 m asl). Observed rarely in forest soils ($\Sigma P < 0.5\%$).

Rhigospira quadrangularis (Müll. Arg.) Miers (Plate 1, fig. 15)

Monads, oblate, 30(33)37.5 μm. Tri-zono-porate, pori circular (6 μm diameter), with a thickened darkened annulus. Exine 1.5 μm in mesocolpi and 4 μm in oral section, microrugulate. Tree 30 m tall, evergreen forest (100–1000 m asl). Observed rarely in forest soils ($\Sigma P < 0.5\%$).

Tabernaemontana cerea (Woodson) Leeuwenb. (Plate 1, fig. 16)

Monads. EV prolate, 52.5(59)63 × 37.5(43)49.5 μm. P/E = 1.40. PV circular, 43.5(46)49.5 μm. Tetra-zono-colporate, colpi short, occupying 1/2 of grain length (33.6–48 × 7.2–12 μm), pori lalongate (c. 22 × 6 μm). Additionally an equatorial pseudocolpus is observed, giving a zonorate appearance. The colpus equatorialis has a thickened and darkened margo. Exine 3–4 μm, sexine > nexine. Verrucate. Tree 1–6 m tall, growing in the understory of evergreen forests. Observed rarely in forest soils ($\Sigma P < 0.5\%$).

AQUIFOLIACEAE

Ilex divaricata Martius ex Reisseck in C. Martius (Plate 1, fig. 17)
Ilex jenmanii Loes. (Plate 1, fig. 18)
Ilex parvifructa Edwin (Plate 1, fig. 19)
Ilex retusa Klotzsch in R.M. Schomb. (Plate 1, fig. 20)
Ilex chimantaensis T.R. Dudley (Plate 2, fig. 21)

Monads. EV oblate-spheroidal, 19(22)23 × 22.5(24)28 μm. P/E = 0.90. PV circular-trilobate, 20(22)22.5 μm. Tricolporate, colpi as long as grain, pori small and circular, inconspicuous. Exine 6 μm, sexine > nexine, clavate. Large sculptural elements (2–4 μm long × 1–2 μm wide). Shrub 2 m tall, in shrublands on sandstone outcrops or sandy soils. Some species growing in gallery forest (100–600–1200 m asl, and some species above 2000 m asl). Very common in soils from gallery forest and morichales ($\Sigma P = 5–10\%$).

ARALIACEAE

Schefflera coriacea (Marchal ex Thurn) Harms (Plate 2, fig. 22)

Monads. EV oblate-spheroidal, 30(34)37.5 × 34.5(36)37.5 μm. P/E = 0.94. PV subangular, 28.5(34)37.5 μm. Tricolporate, colpi narrow (1.5 μm), as long as grain, pori lalongate-rectangular. Exine 1–2 μm, columellae densely distributed, sexine = nexine, microreticulate-microscabrate. Tree 5–20 m tall. Gallery forest on sandstone and tepuian forests (800–1800 m asl). This genus is very common in gallery forests and premontane forest soils reaching $\Sigma P = 10–30\%$.

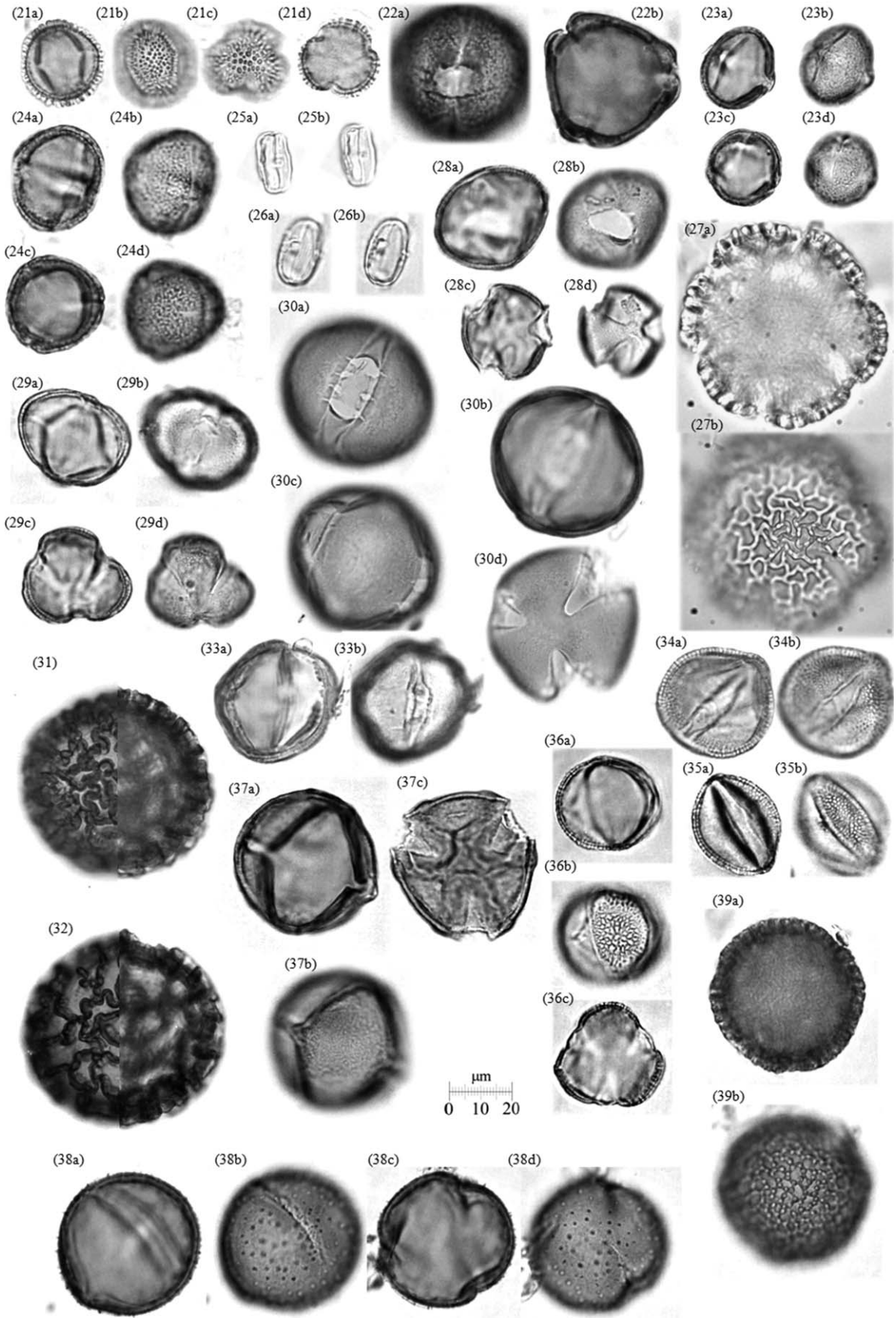
Schefflera duidae Steyerm. (Plate 2, fig. 23)

Monads. EV prolate-spheroidal, 21(23)25.5 × 19.5(21)22.5 μm. P/E = 1.12. PV subangular, 19.5(20)21 μm. Tricolporate, colpi as long as grain, narrow (1.5 μm), pori lalongate (c. 3 × 7 μm). Exine thin (1–2 μm), sexine = nexine, microreticulate. Shrub or climbing tree 5–6 m tall. In gallery forests on sandstone (800–1800 m asl). This genus is very common in gallery forests and premontane forest soils reaching $\Sigma P = 10–30\%$.

Schefflera sessiliflora Splithof-Heerschop ex. Frodin (Plate 2, fig. 24)

Monads. EV prolate-spheroidal 25.5(28)30 × 24(25)27 μm. P/E = 1.11. PV subangular, 22.5(24)25.5 μm. Tricolporate, colpi as long as grain, 1 μm width, pori lalongate-concave (6 × 8 μm). Exine 1.5–2 μm, sexine = nexine, microreticulate. Tree 5 m tall, in gallery forest (1400–1800 m asl). This genus is very common in gallery forests and premontane forest soils reaching $\Sigma P = 10–30\%$.

Plate 2. *Ilex chimantaensis* (21). ARALIACEAE: *Schefflera coriacea* (22), *S. duidae* (23), *S. sessiliflora* (24). BEGONIACEAE: *Begonia fischeri* (25), *B. pieurii* (26), BIGNONIACEAE: *Anemopaegma parkeri* (27), *Arrabidaea candicans* (28). *A. grosourdyana* (29), *Digomphia laurifolia* (30), *Distictella obovata* (31), *Amphilophium granulosum* (32), *Parabignonia steyermarkii* (33), *Stizophyllum riparium* (34), *Tabebuia capitata* (35), *T. ochracea* (36). BORAGINACEAE: *Bourreria cumanensis* (37), *Cordia exaltata* (38), *C. spinescens* (39), For figs. 31 and 32, the scale bar represents 40 μm.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BEGONIACEAE

Begonia fischeri Schrank (Plate 2, fig. 25)
Begonia prieurii A. DC. (Plate 2, fig. 26)

Monads. EV prolate, 17(18)19 × 8(9.5)13 μm. P/E = 1.86. PV circular-trilobate, 10(11)13.5 μm. Tricolporate, colpi narrow, as long as grain, with costae. Pori lalongate, covering 1/2 of total grain width. Exine thin (<1 μm), translucent psilate to slightly striate. Erect herb, 0.8–1.5 m tall, in open swamps (50–800 m asl). Occasionally observed in morichales (ΣP > 1%).

BIGNONIACEAE

Anemopaegma parkeri Sprague (Plate 2, fig. 27)

Monads. EV suboblate, 48(52)57 × 63(67)70 μm. P/E = 0.8. PV circular, 57(61)66 μm. Penta-zonocolpate, colpi as long as grain (6–7 μm wide), with rounded endings and a psilate membrane that shows a pattern of latitudinal breakages (a common diagnostic character in the family). Exine 4.5–6 μm, sexine > nexine, reticulate-cristate, lumina 6–7.5 μm wide, with an irregular shape, muri 1.5–3 μm thick. Liana. Evergreen forests (100–900 m asl). Observed rarely in forest soils (ΣP > 0.5%).

Arrabidaea candicans DC. (Plate 2, fig. 28)
Arrabidaea grosourdyana (Baill.) Sandwith (Plate 2, fig. 29)

Monads. EV suboblate, 21(25)28.5 × 27(31)36 μm. P/E = 0.81. PV circular-trilobate, 22.5(28)31.5 μm. Tricolporate, colpi as long as grain, with rounded endings, covering 1/4 of grain width. Pori circular to elliptical, 7–8 μm diameter, formed by breakages in the colpus membrane. Exine 1.5 μm, densely columellate, sexine = nexine, microreticulate-microscarbrate. Liana of evergreen forests (100–1200 m asl). Very common in forest soils (ΣP = 5%).

Digomphia laurifolia Benth. (Plate 2, fig. 30)

Monads. EV suboblate, 46(49)55 × 55(57)60 μm. P/E = 0.86. PV circular-trilobate, 48(53)60 μm. Tricolpate, colpi as large as grain, wide (covering 1/4 of total grain width), with rounded endings and a psilate membrane that exhibits the typical latitudinal breakages of this family. Exine 1 μm, densely columellate, sexine nexine, microscabrate. Shrub or small tree in shrublands and in tepui slopes and summits (700–2500 m asl). Not observed in sediments from Gran Sabana.

Distictella obovata Sandwith (Plate 2, fig. 31)
Amphilophium granulosum (Klotzsch) L. Lohmann (Plate 2, fig. 32)

Monads. Spherical-ellipsoidal, 84(91)96 × 72(84)86 μm. Inaperturate. Exine 7.5–9 μm, sexine > nexine, reticulate-cristate, lumina 22.5 μm width, with scattered verrucae into the lacunae. Muri thick (4 μm), probably multibaculate, with variable height, giving a cristate appearance. Liana in montane forests. Observed occasionally in forest soils (ΣP < 0.5%).

Parabignonia steyermarkii Sandwith (Plate 2, fig. 33)

Monads. EV prolate, 34.5(38)40.5 × 24(27)28.5 μm. P/E = 1.44. PV circular, 33(35.5)37.5 μm. Tricolporate, wide colpi (3–5 μm), as long as grain, with rounded endings and a psilate membrane. Pori lolongate, 7–8 × 5–6 μm. Exine 1.5–3 μm, granulate-microscabrate. Liana in humid cloud forest (400–1200 m asl). Observed very frequently in forest soils (ΣP = 5%).

Stizophyllum riparium (Kunth) Sandwith (Plate 2, fig. 34)

Monads. EV suboblate, 30(33)37.5 × 36(39)45 μm. P/E = 0.85. PV circular-trilobate, 30(33)34.5 μm. Tricolpate, colpi as long as grain, covering 1/4 of total grain width, with rounded endings and a psilate membrane, which exhibits the breakage pattern common in the family. A thin psilate margo is also present (1 μm thick). Exine (2–3 μm), sexine = nexine, microreticulate. Liana in evergreen forest (200–900 m asl). Observed rarely in forest soils (ΣP < 0.5%).

Tabebuia capitata (Bureau & K. Schum.) Sandwith (Plate 2, fig. 35)

Monads. EV prolate, 30(31)31.5 × 19.5(22)24 μm. P/E = 1.40. PV circular-trilobate, 22.5(26)31.5 μm. Tricolpate, colpi as long as grain, with rounded endings, narrow, 1.5–3 μm wide. Exine 1 μm, densely columellate, sexine = nexine, microreticulate. Tree in evergreen forest (200–500–1000 m asl). Observed frequently in forest soils (ΣP < 3%).

Tabebuia ochracea (Cham.) Standl. (Plate 2, fig. 36)

Monads. EV suboblate, 24(26)28.5 × 30(31)33 μm. P/E = 0.83. PV subangular, 25.5(29)31.5 μm. Tricolpate, colpi wide, reaching 1/4 of grain width, as large as grain, with rounded endings and a psilate membrane. Exine 1 μm, densely columellate, sexine = nexine, reticulate-heterobrochate. Tree in evergreen forests (0–900 m asl). Observed frequently in forest soils (ΣP < 3%).

BORAGINACEAE

Bourreria cumanensis (Loefl.) O.E. Schulz (Plate 2, fig. 37)

Monads. EV suboblate, 36(38)40.5 × 43.5(46)49.5 μm. P/E = 0.83. PV subangular, 40.5(43)46.5 μm. Tricolporate, colpi as long as grain, 7–8 μm width. In

PV colpi are joined by arcii. Pori elliptical, lalongate, 4–8 × 9–15 μm. Exine 1–3 μm, sexine = nexine, microrugulate. Tree or shrub (5–10 m tall) in deciduous or semideciduous forests (0–600 m asl). Rarely observed in forest soils (ΣP < 0.5%).

Cordia exaltata Lam. (Plate 2, fig. 38)

Monads. EV oblate-spheroidal, 36(38)40.5 × 39(41)43.5 μm. P/E = 0.93. PV circular-trilobate, 39(40.5)42 μm. Tricolporate, colpi as long as grain, 3 μm wide, with a microscabrate membrane. Pori sometimes inconspicuous, lalongate (3 × 15 μm). Exine 3 μm, sexine = nexine, with scattered very thin and short spines. Tree 25 m tall, in evergreen forests (200–800 m asl). Very abundant in soils of a recently burned forest (reaching ΣP > 20%), but usually rare in most forest soils (ΣP < 1%).

Cordia spinescens L. (Plate 2, fig. 39)

Monads spheroidal, 40.5(42)43.5 μm. Tri-zono-porate, pori 3–8 μm diameter. Exine 4–5 μm, sexine > nexine. Semi-reticulate, lumina 4–8 μm wide and muri 1.5–2 μm thick. Shrub 3 m tall. Shrublands (200–1000 m asl). Only observed in soils of broadleaved grasslands (ΣP > 0.5%).

Tournefortia candidula (Miers) I.M. Johnst. (Plate 3, fig. 40)

Monads. EV subprolate-rectangular, 22.5(25)27 × 18(19.5)21 μm. P/E = 1.30. PV circular, 18(19.5)21 μm. Tricolporate, colpi narrow (1.5–3 μm), as long as grain. Pori lalongate-concave (3–4 × 4–11 μm), pseudocolpus present. Exine 1.5–3 μm, psilate. Shrub 1–2 m tall. Savannas and savanna-forest boundaries and gaps in deciduous forests (200–1300 m asl). Rarely observed in forest soils (ΣP > 0.1%).

BURSERACEAE

Bursera simaruba (L.) Sarg. (Plate 3, fig. 41)

Monads. EV prolate-spheroidal, 42(43.5)45 × 39(42)45 μm. P/E = 1.08. PV circular, 37.5(41.5) 43.5 μm. Tri-zono-porate. Pori circular (6–9 μm diameter) with a thicker annulus-vestibulum (2–3 μm wide × 3–4 μm thick). Exine 3 μm, columellae conspicuous, reticulate-striate, with striae distributed in a centripetal fashion from the poles to the equator. Tree 25 m tall, in deciduous and semideciduous forests (50–700 m asl). Rarely observed in forest soils (ΣP > 0.1%).

Dacryodes glabra Cuatrec. (Plate 3, fig. 42)

Monads. EV prolate-spheroidal, 37.5(38)40.5 × 33(35)37.5 μm. P/E = 1.08. PV subangular, 30(33)34.5 μm. Tricolporate, colpi narrow (<1 μm), covering 1/2 of grain length, pori lalongate, 4 × 7 μm, with rounded edges. Exine 1.5–3 μm, psilate, thickened in the oral zone. Shrub 1–7 m tall, in gallery forests, shrublands and tepui mires (0–1000 m asl). Not observed in soils or sediments from Gran Sabana.

Protium guianense (Aubl.) Marchand (Plate 3, fig. 43)
Tetragastris panamensis (Engl.) Kuntze (Plate 3, fig. 44)

Monads. EV subprolate, 31.5(33)34.5 × 25.5(27)28.5 μm. P/E = 1.23. PV subangular, 22.5(27)30 μm. Tricolporate, colpi narrow (<1 μm), covering 1/2 of grain length, pori lalongate (4 × 7 μm), with rounded edges. Exine 1.5–3 μm, psilate, thickened in the oral zone. *Protium guianense* is a 3–20 m tall tree that occurs in evergreen forests. *Tetragastris panamensis* is a tree 40 m tall occurring in semideciduous or evergreen forests (50–1000 m asl). This pollen type is very abundant in most forest soils (ΣP = 10–30%).

CAMPANULACEAE

Centropogon cornutus (L.) Druce (Plate 3, fig. 45)

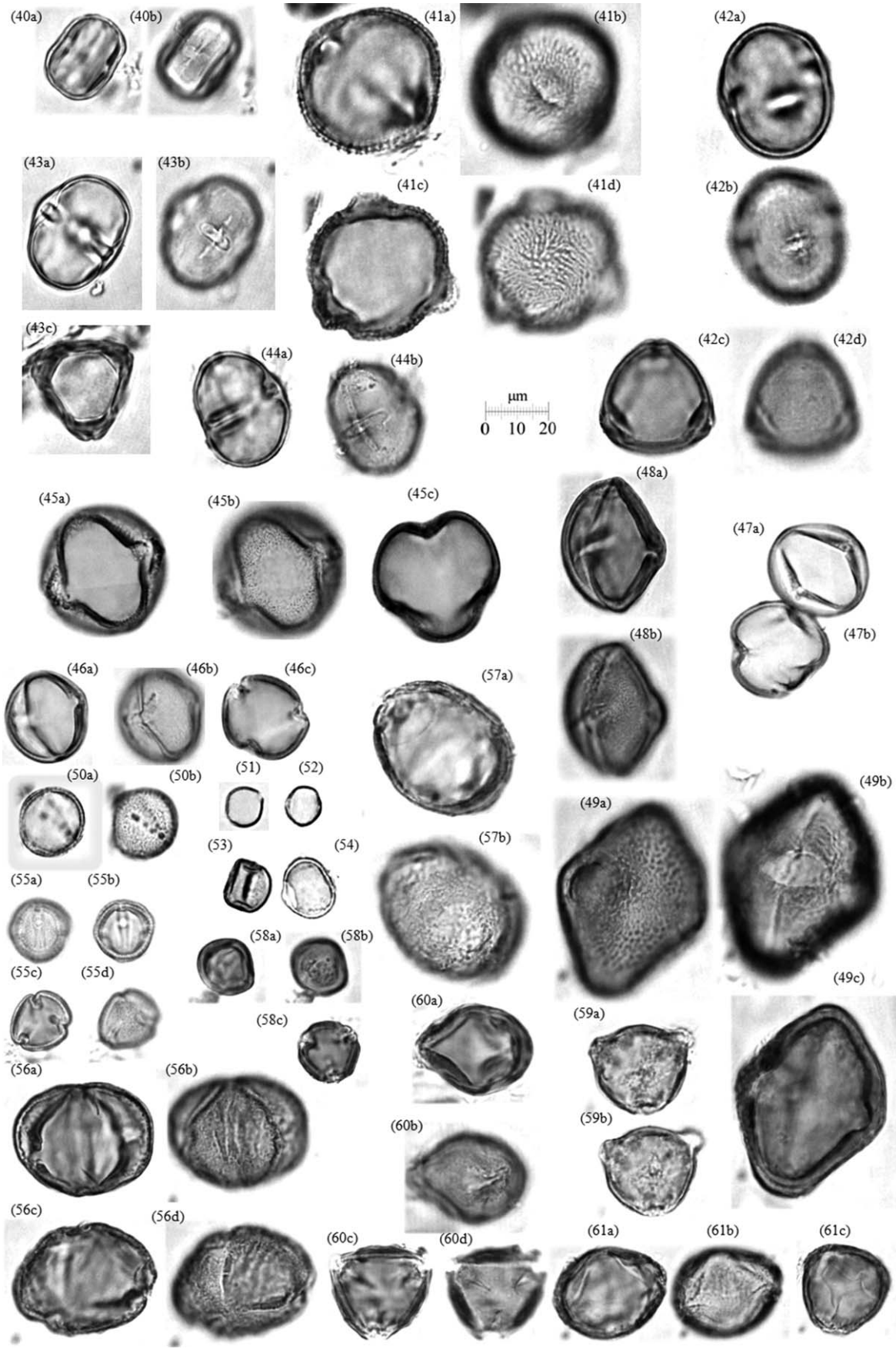
Monads. EV oblate-spheroidal, 33(35)37.5 × 34.5(37)40.5 μm. P/E = 0.96. PV circular-trilobate, 33(34.5)36 μm. Tricolporate, colpi as long as grain, 7–8 μm wide, with rounded endings, and a rugulate-striate membrane. Pori circular (3–7 μm diameter). Exine 1.5–2 μm, columellae densely distributed, sexine > nexine, rugulate. Herb or small shrub, in humid areas along riversides, and open disturbed areas (0–1800 m asl). Never observed in sediments from Gran Sabana.

Lobelia galpinii Schltr. (Plate 3, fig. 46)

Monads. EV oblate-spheroidal, 24(25)25.5 × 27(28.5)30 μm. P/E = 0.96. PV circular trilobate, 24(27.5)30 μm. Tricolporate, colpi as long as grain, 3–5 μm wide, with a rugulate-striate membrane. Colpi with round endings and constrained in equator, pori lalongate (3 × 8 μm). Exine 1.5 μm, sexine > nexine, microrugulate, showing a slightly striate pattern. Small prostrate herb, in lagoons, riversides and morichales (50–1200 m asl). Never observed in sediments from Gran Sabana.

Siphocampylus reticulatus (Willd. ex Roem. & Schult.) Klotzch & H. Karst. ex Vatke. (Plate 3, fig. 47)

Monads. EV oblate-spheroidal, 25.5(28)31.5 × 27(28.5)30 μm. P/E = 0.98. PV circular-trilobate, 25.5(28)30 μm. Tricolporate, colpi as long as grain, 4–5 μm wide, with rounded endings, constrained at equator. Pori small, inconspicuous, circular (2–3 μm diameter). Exine 1.5 μm, almost psilate, with a very slight microrugulate sculpture. Shrub 2 m tall in forested slopes and occasionally in savannas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(600–1200–1400 m asl). Never observed in sediments from Gran Sabana.

CARYOCARACEAE

Anthodiscus mazarunensis Gilly (Plate 3, fig. 48)

Monads. EV subprolate-rhomboidal, 31.5(34.5) 37.5 × 25.5(28.5)33 μm. P/E = 1.21. PV subangular, 25.5(28)31.5 μm. Tricolporate, colpi as long as grain, narrow, pori lalongate (1.5–3 × 4–6 μm). Exine 3 μm, reticulate-rugulate. Tree 25 m tall. Evergreen forests, on sandy soils along rivers (100–2000 m asl). Never observed in sediments from Gran Sabana.

Caryocar montanum Prance (Plate 3, fig. 49)

Monads. EV subprolate-rhomboidal, 52.5(54)55.5 × 45(48)51 μm. P/E = 1.13. PV subangular, 37.5(41)45 μm. Tricolporate, colpi as long as grain, narrow, pori lalongate, 9–10 × 20–23 μm. Exine 3–5 μm, reticulate-rugulate, rugulae 1 μm thick. Tree 30 m tall in submontane-montane evergreen forest (1200–2000 m asl). Frequently observed in forest soils (ΣP < 0.5%).

CARYOPHYLLACEAE

Polycarpaea corymbosa (L.) Lam. (Plate 3, fig. 50)

Monads. EV oblate-spheroidal, 16.5(18)19.5 × 16(18)19 μm. P/E = 0.97. PV circular, 1.5(18.5)20 μm. Tricolpate, colpi as long as grain, 2 μm wide. Exine 1–1.5 μm, columellae conspicuous, microreticulate-microrugulate. Erect herb 5–40 cm tall. Common in sandy soils of *Trachypogon* savannas (100–1000 m asl). Never observed in soils from Gran Sabana.

CECROPIACEAE

Coussapoa asperifolia Trécul (Plate 3, fig. 51)
Coussapoa crassivenosa Mildbr. (Plate 3, fig. 52)

Monads. Spheroidal-ellipsoidal, 7.5(9)10.5 × 9(10.5)12 μm. Diporate, pori small, equidistant, circular. Exine <1 μm, psilate. Hemi-epiphytic tree 20 m tall. Forests (*C. asperifolia*, 0–600 m asl, *C. crassivenosa*, 700–1700 m asl). Present rarely in forest soils (ΣP < 0.5%).

Pourouma bicolor Mart. (Plate 3, fig. 53)
Pourouma guianensis Aubl. (Plate 3, fig. 54)

Monads asymmetric, spheroidal-ellipsoidal, 15(15)15 × 13.5(16.5)19.5 μm. Diporate, pori small equidistant. Exine <1 μm, psilate. Tree 20 m tall. Evergreen forest (100–1500 m asl). Frequently found in forest soils and in sediments from morichales (ΣP < 5%).

CELASTRACEAE

Zinowiewia aymardii Steyerm. (Plate 3, fig. 55)

Monads. EV spheroidal, 15(16)16.5 × 13.5(16)18 μm. P/E = 1. PV subangular, 15(16.5)18 μm. Tricolporate, colpi as long as grain, narrow, pori circular small, 1.5–2 μm diameter with a thin psilate annulus. Exine <1 μm, columellae densely distributed, microreticulate. Tree 10–45 m tall. Evergreen forests (300–1000 m asl). Only observed rarely at a forest site.

CHRYSOBALANACEAE

Hirtella paniculata Sw. (Plate 3, fig. 56)
Hirtella scabra Benth. (Plate 3, fig. 57)

Monads. EV suboblate, 31.5(33)34.5 × 37.5(40)45 μm. P/E = 0.82. PV ovoid-subangular, 42(44)48 × 33(33.5)34.5 μm. Tricolporate, colpi as long as grain, 4–8 μm wide, pori lalongate 3–5 × 7–10 μm. Exine 1.5–2 μm, sexine > nexine. Nexine with variable thickness, granulate-microescabrate. Shrub or small tree. In open areas on sandy soils, savannas and riversides (50–1300 m asl). With very low frequency in morichales (ΣP < 0.1).

Licania discolor Pilg. (Plate 3, fig. 58)

Monads. EV suboblate, 15(17.5)21 × 19.5(21)22.5 μm. P/E = 0.83. PV triangular, 18(20)22.5 μm. Tricolporate, colpi as long as grain, narrow and pori circular, 3 × 5 μm. Exine thickened in oral zone by a translucent protruding annulus, atrium visible in PV. Exine thin (1–1.5 μm), sexine > nexine, psilate. Tree 35 m tall. Evergreen forest (50–800 m asl). This pollen type was abundant only in soils from peatly shrublands (ΣP < 5%).

Licania intrapetiolaris Spruce ex. Hook. f. (Plate 3, fig. 59)

Monads. EV suboblate, 22.5(24)25.5 × 27(28.5)30 μm. P/E = 0.84. PV subangular, 24(24.5)25.5 μm.

Plate 3. *Tournefortia candidula* (40). BURSERACEAE: *Bursera simaruba* (41). BURSERACEAE: *Dacryodes glabra* (42), *Protium guianense* (43), *Tetragastris panamensis* (44). CAMPANULACEAE: *Centropogon cornutus* (45), *Lobelia galpinii* (46), *Siphocampylus reticulatus* (47). CARYOCARACEAE: *Anthodiscus mazarunensis* (48), *Caryocar montanum* (49). CARYOPHYLLACEAE: *Polycarpaea corymbosa* (50). CECROPIACEAE: *Coussapoa asperifolia* (51), *C. crassivenosa* (52), *Pourouma bicolor* (53), *P. guianensis* (54). CELASTRACEAE: *Zinowiewia aymardii* (55), CHRYSOBALANACEAE: *Hirtella paniculata* (56), *H. scabra* (57), *Licania discolor* (58), *L. intrapetiolaris* (59), *Parinari campestris* (60), *P. maguirei* (61).

Triporate, pori lalongate (6 × 9 μm), protruding outward. Exine 1–1.5 μm, sexine > nexine, psilate. Shrub or small tree. Evergreen forest, open areas and riversides (100–1000 m asl). Not observed in Gran Sabana soils.

Parinari campestris Aubl. (Plate 3, fig. 60)
Parinari maguirei Prance (Plate 3, fig. 61)

Monads. EV suboblate-rhomboidal, 24(25)25.5 × 30(32)37.5 μm. P/E = 0.78. PV triangular, 22.5(25.5)30 μm. Tricolporate, colpi as long as grain, narrow, pori circular to oblique, small (2 μm diameter) with atrium. Exine 2–3 μm, sexine = nexine, microscabrate. Tree 25 m tall. Savanna borders and seasonally flooded riverbanks (0–900 m asl). Not observed in sediments from Gran Sabana.

Parinari excelsa Sabine (Plate 4, fig. 62)

Monads. EV suboblate-rhomboidal, 31.5(34)36 × 39(42)45 μm. P/E = 0.81. PV subangular, 33(37)40.5 μm. Tricolporate, colpi as long as grain, narrow, pori circular oblique, 6–8 μm diameter, with atrium. Exine 1.5–2 μm, sexine = nexine, microscabrate. Tree 45 m tall. Evergreen forests (100–1000 m asl). Not observed in sediments from Gran Sabana.

CLETHRACEAE

Clethra guyanensis Klotzsch ex Meisn. (Plate 4, fig. 63)

Monads. EV oblate-spheroidal, 16.5(18)19.5 × 16.5(18)21 μm. P/E = 0.98. PV circular, 16.5(17)18 μm diameter. Tricolporate, colpi as long as grain, narrow. Pori circular, 1.5–4 μm diameter. Exine 1–1.5 μm, sexine = nexine, psilate. Tree or shrub 2.5–10 m tall. Montane humid forests or tepui slopes (800–2500 m asl). This pollen type was only abundant in soils from morichales (ΣP < 5%).

CLUSIACEAE

Calophyllum brasiliense Cambess. (Plate 4, fig. 64)

Monads. EV oblate-spheroidal, 30(34)36 × 30(34)37.5 μm. P/E = 0.99. PV circular-subangular, 30(33)37.5 μm. Tricolporate, colpi as long as grain, with a thin psilate margo and a granulate membrane. Pori circular-rectangular (7–9 × 15–18 μm). Exine 1.5 μm, columellae conspicuous, sexine > nexine, granulate-perforate. Tree 30 m tall. Evergreen forests, gallery forests, morichales and seasonally flooded riverbanks (0–1400 m asl). Frequent in gallery forest soils and morichales (ΣP > 3%).

Caraipa longipedicellata Steyerm. (Plate 4, fig. 65)

Monads. EV subprolate, 48(53)55.5 × 34.5(43)46.5 μm. P/E = 1.23. PV circular, 43.5(46)48 μm. Tricolporate, colpi as long as grain, narrow, constrained at the equator making a bridge that divides the colpus in two parts, membrane psilate. Pori lalongate, with atrium, 7–8 × 12–15 μm. Exine 3 μm, columellae conspicuous, sexine = nexine, microreticulate-perforate. Tree 25 m tall. Evergreen forest, savanna borders and morichales (100–1300 m asl). Frequent in forest soils (ΣP > 3%).

Caraipa tereticaulis Tul. (Plate 4, fig. 66)

Monads. EV prolate-spheroidal, 31.5(36)37.5 × 31.5(34)36 μm. P/E = 1.05. PV circular-subangular, 30(32)34.5 μm. Tricolporate, colpi as long as grain, 4–5 μm wide, constrained at the equator, pori with annulus 3 μm thick, dividing colpus into two parts. Colpi with a psilate membrane. Pori lalongate, with atrium, 6–10 × 9–20 μm. Exine 4–5 μ thick, columellae conspicuous, sexine = nexine, microreticulate-perforate. Tree 4–30 m tall. Evergreen premontane and gallery, forests and savanna borders (800–1800 m asl). Frequent in forest soils (ΣP > 3%).

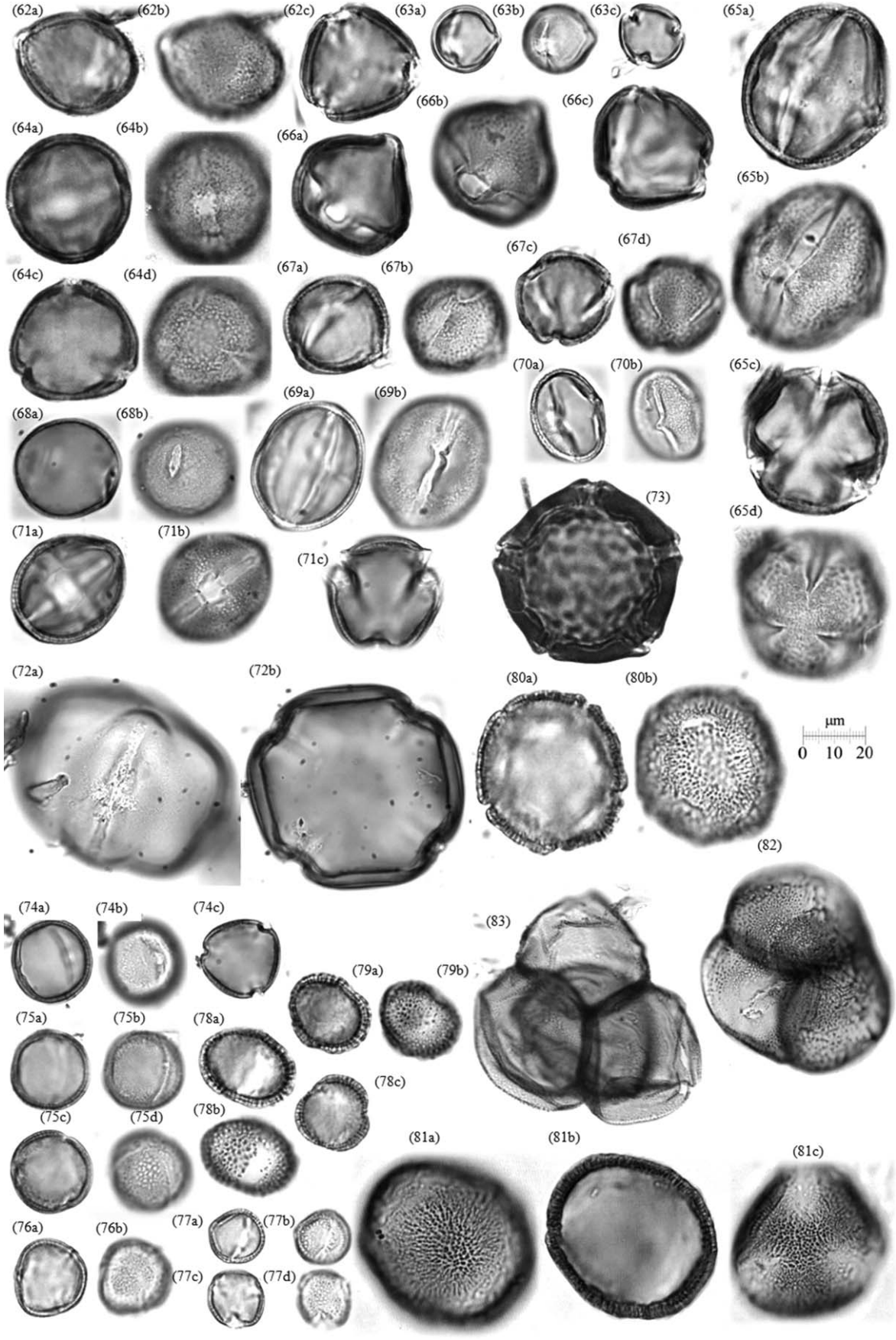
Clusia crassifolia Planch. & Triana (Plate 4, fig. 67)

Monads. EV oblate-spheroidal, 24(28)30 × 27(30)34.5 μm. P/E = 0.93. PV circular, 25.5(27)28.5 μm. Tricolporate, colpi as long as grain, with a very thin psilate margo. Pori circular 3 μm diameter. Exine 1.5–2 μm, columellae conspicuous, sexine > nexine, microreticulate. Tree 2–18 m tall. Gallery forest, tepuian shrublands, and muddy areas (1300–2300 m asl). Frequent in forest soils (ΣP > 3%).

Clusia grandiflora Splitg. (Plate 3, fig. 68)

Monads. EV suboblate, 25.5(29)31.5 × 34.5(37)39 μm. P/E = 0.80. PV circular, 31.5(34.5)37.5 μm. Tricolporate, colpi short but wide (7–11 × 4–5 μm), with a thin psilate margo. Pori lalongate fisiform (4–7 × 6–10 μm). Exine 1.5–2 μm, columellae conspicuous, sexine > nexine, microreticulate. Shrub or tree 3–30 m tall. Gallery and montane forests (0–1300 m asl). Frequent in forest soils (ΣP > 3%).

Plate 4. *Parinari excelsa* (62). CLETHRACEAE: *Clethra guyanensis* (63). CLUSIACEAE: *Calophyllum brasiliense* (64), *Caraipa longipedicellata* (65), *C. tereticaulis* (66), *Clusia crassifolia* (67), *C. grandiflora* (68), *C. pusilla* (69). *Hypericum moranense* (70), *Mahurea exstipulata* (71), *Moronobea ptaritepuiana* (72), *Symphonia globulifera* (73), *Vismia baccifera* (74), *V. macrophylla* (75), *V. guianensis* (76). CONNARACEAE: *Pseudoconnarus macrophyllus* (77). CONVOLVULACEAE: *Dicranostyles longifolia* (78), *Evolvulus glomeratus* (79), *Lysiostyles scandens* (80), *Maripa scandens* (81). CUCURBITACEAE: *Gurania acuminata* (82), *G. huberi* (83). For figs. 72 and 81–83, the scale bar represents 40 μm.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Clusia pusilla Steyerm. (Plate 3, fig. 69)

Monads. EV prolate, 33(37.5)40.5 × 24(26)28.5 μm. P/E = 1.43. PV circular-trilobate, 25.5(28)30 μm. Tricolporate, colpi as long as grain, 3–5 μm wide, with a thin psilate margo and slightly constrained at the equator. Pori inconspicuous, small, circular to lalongate (4–6 μm diameter). Exine 3 μm, columellae conspicuous, sexine > nexine, microreticulate. Shrub 2–4 m tall. Evergreen montane and tepuian forests (700–2000 m asl). Frequent in forest soils (ΣP > 3%).

Hypericum moranense Kunth (Plate 3, fig. 70)

Monads. PV subprolate, 25.5(26)28.5 × 21(22)24 μm. P/E = 1.18. PV circular-trilobate, 19.5(23)27 μm. Tricolporate, colpi as long as grain, narrow (1.5–4 μm), pori circular, small, inconspicuous (3 μm diameter). Exine 2 μm, columellae densely distributed, sexine = nexine, microreticulate. Perennial or annual herb 7–65 cm tall. Humid and open places (1200–1300 m asl). Not observed in soils from Gran Sabana.

Mahurea exstipulata Benth. (Plate 4, fig. 71)

Monads. EV prolate-spheroidal, 30(34)37.5 × 28.5(31)31.5 μm. P/E = 1.11. PV circular-trilobate, 30(31)31.5 μm. Tricolporate, colpi as long as grain, wide, with a psilate membrane, pori open 7–9 × 7–14 μm, rectangular, with atrium. Exine 3 μm, columellae densely distributed, sexine = nexine, microreticulate. Tree or shrub 2–20 m tall. Evergreen forests, frequently burned forest areas, tepui slopes and summits (100–1600–2200 m asl). Only observed rarely in gallery forest soils in northern Gran Sabana (ΣP < 0.1%).

Moronobea ptaritepuiana Steyerm. (Plate 4, fig. 72)

Monads. EV suboblate-rectangular, 55(58)60 × 72(74)77 μm. PV rhombic, angulaperturate, 65(70)72 × 72(75)82 μm. P/E = 0.78. Tetracolporate, colpi as long as grain, narrow, with a scabrate membrane. Pori lalongate, narrow. Exine 4 μm, sexine > nexine, psilate. Shrub or tree 2–30 m tall. Forests, slopes and tepuian summits (800–1900 m asl). Not observed in soils from Gran Sabana.

Symphonia globulifera L.f. (Plate 4, fig. 73)

Monads. EV oblate, 36(40)43 × 48(57)62 μm. P/E = 0.69. PV circular-polygonal. Zonoporate, with 4–6 elliptical pori, operculate. Exine 10 μm, rugulate. Tree 35 m tall. Evergreen forests, seasonally flooded gallery forest and morichales (0–1700 m asl). This pollen type has only been observed in morichales soils (ΣP < 1%).

Vismia baccifera (L.) Triana & Planch. (Plate 4, fig. 74)
Vismia macrophylla Kunth (Plate 4, fig. 75)

Monads. EV prolate-spheroidal, 22.5(24)25.5 × 22.5(23)24 μm. P/E = 1.03. PV circular-trilobate, 22.5(24)25.5 μm. Tricolporate, colpi as long as grain, pori circular, small, 3 μm diameter. Exine 1.5 μm, columellae densely distributed, sexine > nexine, microreticulate-heterobrochate. Tree 3–22 m tall, in evergreen forests (*V. baccifera*: 100–1300 m asl, *V. macrophylla*: 0–600 m asl). Present in forest soils (ΣP < 1%).

Vismia guianensis (Aubl.) Pers. (Plate 4, fig. 76)

Monads. EV prolate-spheroidal 16.5(19)21 × 18(19)21 μm. P/E = 1.01. PV circular, 18(19)21 μm. Tricolporate, colpi as long as grain, pori circular, small (1.5–3 μm diameter). Exine 1.5 μm, columellae densely distributed, sexine = nexine, microreticulate-heterobrochate. Tree 2–25 m tall. Evergreen forests and shrublands (50–1400 m asl). Present in forest soils (ΣP < 1%).

CONNARACEAE

Pseudoconnarus macrophyllus (Poepp.) Radlk. (Plate 4, fig. 77)

Monads. EV oblate-spheroidal, 13.5(15.5)16.5 × 16.5(17.5)18 μm. P/E = 0.89. PV circular, 16.5(17.5)18 μm. Tricolporate, colpi narrow as long as grain, pori circular (1 μm diameter). Exine 1 μm, sexine = nexine, columellae densely distributed, microreticulate. Liana. Evergreen forests and disturbed areas (100–900 m asl). Not observed in sediments from Gran Sabana.

CONVOLVULACEAE

Dicranostyles longifolia Ducke (Plate 4, fig. 78)
Evolvulus glomeratus Nees & Mart. (Plate 4, fig. 79)

Monads. EV oblate-spheroidal, 22.5(24)25.5 × 25.5(26)28.5 μm. P/E = 0.90. PV circular-trilobate, 21(22.5)24 μm. Tricolpate, colpi wide (covering 1/4 of grain width), as long as grain, with diffuse edges. Exine 2–3 μm, sexine > nexine, verrucate, verrucae < 1 μm wide and 1 μm long. *Dicranostyles longifolia* is a liana of montane forests (1200–1400 m asl), while *E. glomeratus* is a savanna herb. Frequent in forests soils, but at low abundances (ΣP < 1%).

Lysiostyles scandens Benth. (Plate 4, fig. 80)

Monads. Spheroidal, 42(46)52.5 μm diameter. Pantocolpate, with at least 8 to 10 narrow colpi, 6–10 μm long. Exine 2–3 μm, sexine > nexine, columellae < 1 μm tall, microverrucate. Climbing herb in evergreen forests (100–900 m asl). Not observed in sediments from Gran Sabana.

Maripa scandens Aubl. (Plate 4, fig. 81)

Monads. EV prolate-spheroidal, 52.5(55)57 μm diameter. PV subangular-square, 51(53)60 μm long.

P/E = 1.04. Tricolpate to tetracolpate, colpi wide (covering 1/4 of grain width), as long as grain, with diffuse edges. Exine 3 μm, sexine > nexine, columellae < 1 μm tall, microverrucate. Liana. Evergreen forests (100–1200 m asl). Never seen in sediments from Gran Sabana.

CUCURBITACEAE

Gurania acuminata Cogn. (Plate 4, fig. 82)
Gurania huberi Cogn. (Plate 4, fig. 83)

Tetrads, tetrahedral, 90(101)109 × 90(93)102 μm (*G. acuminata*), 150(155)158 × 123(143)155 μm (*G. huberi*). Grains spheroidal, 60(73)82.5 × 60(63)75 μm and 90(102)108 × 79.5(84)93 μm, respectively. Monoporate, apparently coaperturate. Exine 3 μm, microreticulate. Climbing herb in evergreen gallery forests (100–1200 m asl, reaching 1400 m asl for *G. huberi*). Rarely observed in forest soils (ΣP < 0.1%).

CUNONIACEAE

Weinmannia velutina O.C. Schmidt (Plate 5, fig. 84)

Monads. EV prolate, 10.5(11)12 × 4.5(6)7.5 μm. P/E = 1.85. PV circular-trilobate, 7.5(8.5)9 μm. Tricolporate, colpi as long as grain, pori small, inconspicuous. Exine thin (< 1 μm), psilate. Shrub or tree 1–15 m tall. Shrublands or tepui slope forests (900–1100–2700 m asl). Scarce in forest soils (ΣP < 0.1%).

CYRILLACEAE

Cyrilla racemiflora L. (Plate 5, fig. 85)

Monads. EV oblate-spheroidal, 8.5(9)9.5 × 10.5(11)12 μm. P/E = 0.82. EV circular, 10(11.5)12 μm. Tricolporate, colpi as long as grain, narrow, pori small, circular with atrium protruding outward. Exine 1 μm, sexine = nexine, psilate-microscabrate. Shrub 1–2 m tall. Shrublands, forests and tepuian slopes and summits (900–2000 m asl). Rare in forest soils, but abundant in peaty shrublands (ΣP = 5–10%).

DICHAPETALACEAE

Tapura guianensis Aubl. (Plate 5, fig. 86)

Monads. EV suboblate, 18 × 22 μm. P/E = 0.81. PV subangular, 18(18)19.5 μm. Tricolporate, colpi as long as grain, 1.5 μm wide, pori circular-quadrangular or lalongate-concave, 3–5 μm diameter. Exine 1.5 μm, perforate. Small tree in evergreen forests (50–800 m asl). Very infrequent in most forest soils, but abundant in few localities in southenn Gran Sabana (ΣP 5%).

DILLENIACEAE

Doliocarpus dentatus (Aubl.) Standl. (Plate 5, fig. 87)

Monads. EV prolate-spheroidal, 22(25)27.5 × 18(23)26 μm. P/E = 1.08. PV circular trilobate, 19.5(22)23 μm diameter. Tricolporate, colpi narrow, as long as grain, pori circular (3–7 μm diameter). Exine 1.5–2.5 μm, columellae conspicuous, sexine = nexine, microreticulate-heterobrochate. Liana in evergreen forests, scrubby savannas and tepui slopes (100–1000 m asl). Present in forest soils (ΣP < 3%).

DROSERACEAE

Drosera sessilifolia A. St.-Hil. (Plate 5, fig. 88)

Decussate tetrads, 54(63)78 × 57(64)75 μm. Irregular-shaped grains, spheroidal, 31.5(39)48 μm, coaperturate, apparently with 4 colpi in the distal face. Exine thin (1–2 μm), echinate, with sculptural elements < 1 μm. Herb common in sandy very damp soils (50–1000 m asl). This pollen type is only present in herbazales and morichales (ΣP < 0.5%).

ELAEOCARPACEAE

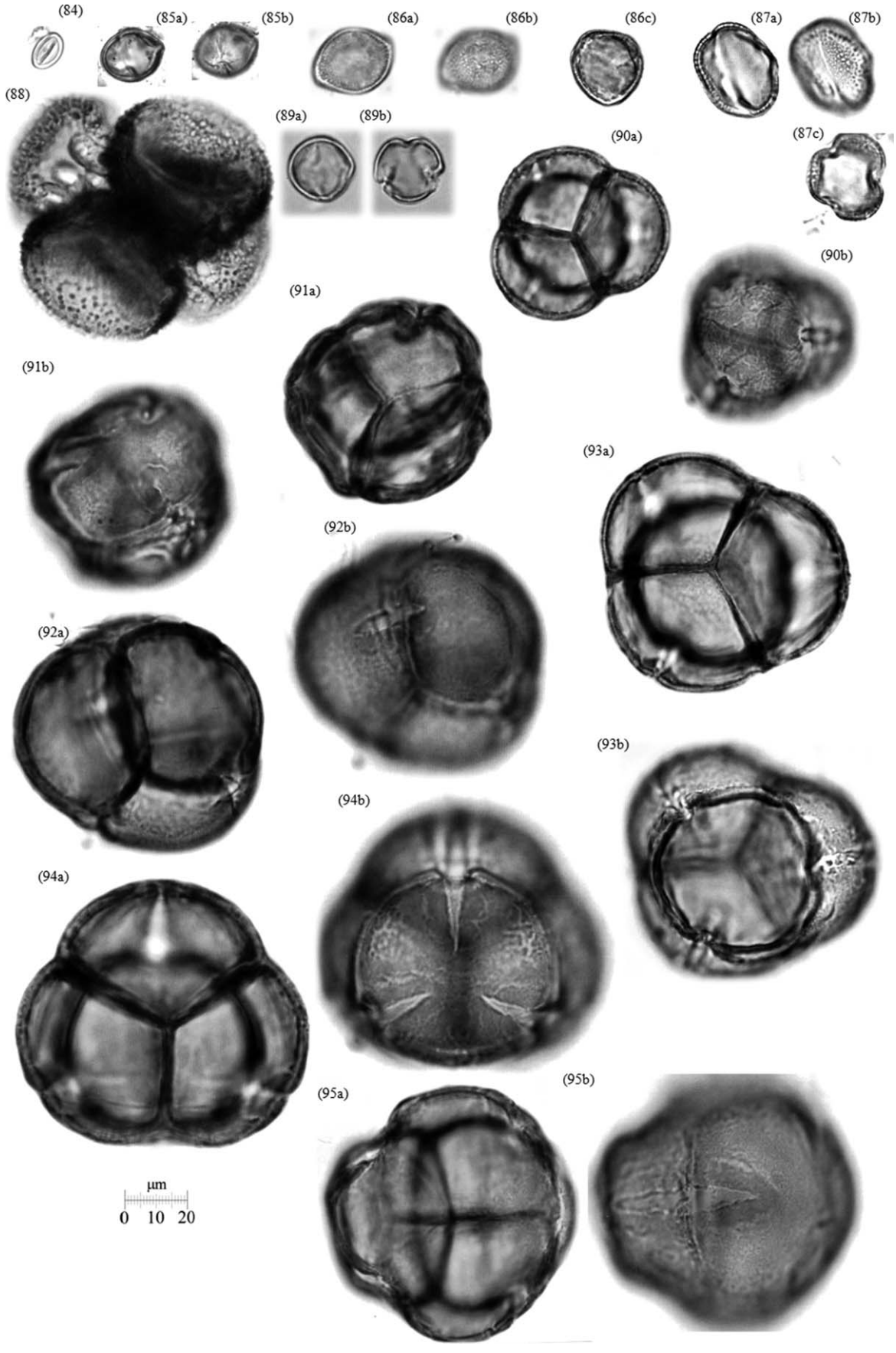
Sloanea grandiflora Sm. (Plate 5, fig. 89)

Monads. EV prolate-spheroidal, 15(15)16.5 × 15(15)16.5 μm. P/E = 1. PV circular-trilobate, 13.5(14)15 μm. Tricolporate, colpi narrow, as long as grain. Pori circular (2 μm diameter). Exine 1–1.5 μm, nexine > sexine, psilate. Tree 5–20 m tall in semideciduous or evergreen forests and gallery forests (0–600 m asl). Rare in forest soils (ΣP < 0.5%).

ERICACEAE

Agarista duckei (Huber) Judd (Plate 5, fig. 90)
Bejaria sprucei Meisn. (Plate 5, fig. 91)
Orthaea venamensis Maguire, Steyerm. & Luteyn (Plate 5, fig. 92)
Psammisia guianensis Klotzsch (Plate 5, fig. 93)
Notopora schomburgkii Hook. f. (Plate 5, fig. 94)

Tetrads tetrahedral, major axis 37.5(38.5)40.5 μm long (*A. duckei*), 45(49)52.5 μm long (*B. sprucei*), 60(61)63 μm long (*O. venamensis* and *N. schomburgkii*) and 63(66)67.5 μm long (*P. guianensis*). Grains spheroidal, diameters: 27(29)30 μm, 30(35)37.5 μm, 39(40)40.5 μm and 42(44)45 μm, respectively. Coaperturate, following Fisher's rule. Exine 1–1.5 μm, sexine > nexine, scabrate. *A duckei*, *B. sprucei* and *O venamensis* are shrubs or small trees 2–6 m tall, found in riverbanks and also on sandstone (100–1400 m asl). *P. guianensis* and *N schomburgkii* are epiphytic shrubs in montane forests (400–2300 m asl). This pollen type was observed rarely in forest soils (ΣP < 0.5%),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although Rull (2007) observed high abundances at the base of a sediment section from Santa Cruz de Mapaurí in southern Gran Sabana.

Thibaudia nutans Klotzsch ex Mansf. (Plate 5, fig. 95)

Decussate tetrads, 60(61)63 × 60(64.5)67.5 μm. Grains spheroidal, 37.5(40)45 μm. Coaperturate, tricolporate, following Fisher's rule. Exine 2.5–3 μm, sexine > nexine, scabrate. Epiphytic shrub 0.3–4.5 m tall. In savannas and forests (400–2800 m asl). Not observed in soils from Gran Sabana.

EUPHORBIACEAE

Adenophaedra grandifolia (Klotzsch) Müll Arg. (Plate 6, fig. 96)

Monads. EV prolate-spheroidal, 21(23)25.5 × 21(23)24 μm. P/E = 1.01. PV circular-trilobate, 30(33)34.5 μm diameter. Tricolporate, colpi as long as grain, narrow (1–3 μm), pori lalongate, 1.5–2 × 10–11 μm. Exine 1.5 μm, columellae conspicuous, sexine nexine, microreticulate. Tree or shrub 2–8 m tall. Montane forests along rivers (900–1300 m asl). Not observed in soils from Gran Sabana.

Alchornea triplinervia (Spreng.) Müll. Arg. (Plate 6, fig. 97)

Monads. EV oblate-spheroidal, 15(17)18 × 18(19)19.5 μm. P/E = 0.92. PV circular, 16.5(18)21 μm. Tricolporate, colpi as long as grain, narrow (1.5 μm wide), pori inconspicuous, operculate. Exine 1–2 μm, scabrate-granulate. Tree 5–20 m tall. Evergreen forests, disturbed areas (50–900 m asl). This pollen type is scarce even in forest soils, however it was found abundantly at a single locality in southernmost Gran Sabana (ΣP 10%).

Chaetocarpus schomburgkianus (Kuntze) Pax & K. Hoffm. (Plate 6, fig. 98)

Monads. EV prolate, 33(35)37.5 × 24(26)28.5 μm. P/E = 1.36. PV circular, 30(33)34.5 μm. Tricolporate, colpi as long as grain, narrow, pori lalongate, 4 × 7 μm wide. Exine 3 μm, sexine = nexine, columellae conspicuous, regulate-scabrate. Tree 6–30 m tall. Semideciduous or evergreen forests and gallery forests (0–900 m asl). Observed rarely in forest soils (ΣP < 0.5%).

Croton matourensis Aubl. (Plate 6, fig. 99)

Monads, spheroidal, 82.5(103)124.5 μm. Inaperturate. Exine 3 μm (excluding sculptural elements). Reticulate, with thickened papillae (pila) forming the nodes of the polygonal reticulum. Muri <1 μm, lumina 12–22 μm wide, pila 3–5 μm high × 6–8 μm wide. Tree 5–30 m tall. Evergreen forests (100–1200 m asl). This pollen type is very rare in forest soils, and was only observed at a single locality in southernmost Gran Sabana.

Croton subincanus Müll. Arg. (Plate 6, fig. 100)

Monads, spheroidal, 75(81)84 μm. Inaperturate. Exine 3 μm (excluding sculptural elements), with triangular pila forming the characteristic *Croton*-pattern. Pila 2–5 μm high × 1–4 μm wide. Shrub or small tree 0.3–1.5 m tall. Sandstone outcrops, gallery forests and open disturbed riverbanks and forest gaps (700–1200 m asl). This pollen type is very rare in forest soils, and only was observed in a single locality in southernmost Gran Sabana.

Hyeronima oblonga (Tul.) Müll. Arg. (Plate 6, fig. 101)

Monads. EV prolate, 24(28)31.5 × 15(16)16.5 μm. P/E = 1.36. PV circular-trilobate, 13.5(14)15 μm. Tricolporate, colpi as long as grain, very narrow, with a thin psilate margo. Pori lalongate, very open, 3–5 × 10–12 μm. Exine 1.5 μm, sexine = nexine, microscabrate. Tree 5–18 m tall. Evergreen forests (300–2300 m asl). Frequent in forest soils (ΣP < 1%).

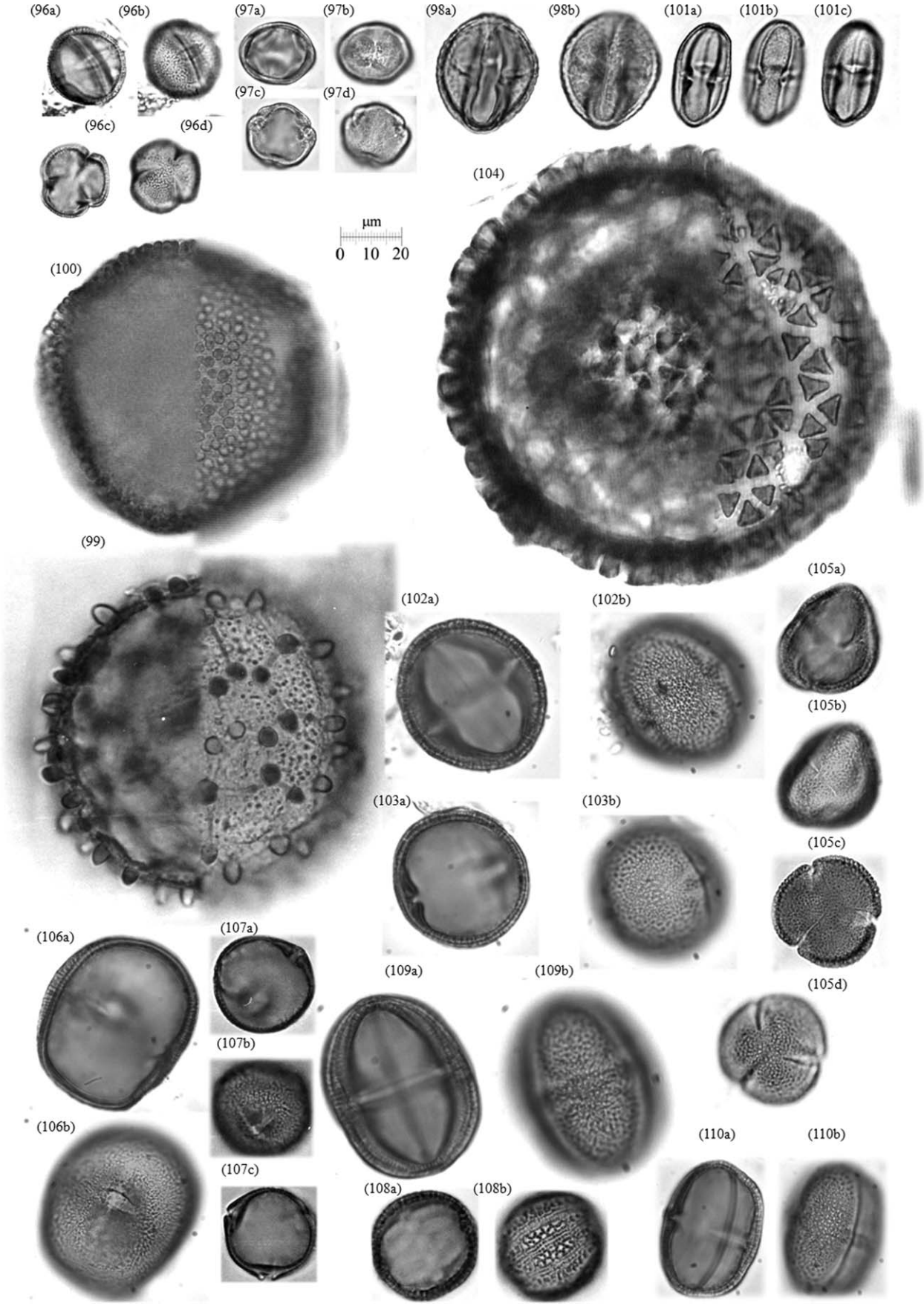
Mabea piriri Aubl. (Plate 6, fig. 102)

Monads. EV prolate-spheroidal, 46.5(49.5)52.5 × 45(45)46.5 μm. P/E = 1.09. PV circular, 42(44.5)46.5 μm. Tricolporate, colpi as long as grain, narrow (1 μm), with a thick costae. Pori inconspicuous, lalongate and narrow (3 × 8 μm). Exine 2–3 μm, columellae conspicuous, sexine = nexine, microreticulate. Tree 15–25 m tall. Evergreen forests (0–900 m asl). Frequent in forest soils (ΣP < 5%).

Mabea subsessilis Pax & K. Hoffm. (Plate 6, fig. 103)

Monads. EV prolate-spheroidal, 39(42)45 × 33(37)40.5 μm. P/E = 1.13. PV circular, 36(38)42 μm. Tricolporate, colpi very narrow, covering 2/3 of grain length, with a thin psilate margo, pori inconspicuous, pori lalongate (4–6 × 9–15 μm). Exine 3 μm (in the mesocolpori) and 6 μm (in the oral zone). Columellae conspicuous, microreticulate. Shrub or small tree 15 m tall in evergreen secondary forests (100–1500 m asl). Frequent in forest soils (ΣP < 5%).

Plate 5. CUNONIACEAE: *Weinmannia velutina* (84), CYRILLACEAE: *Cyrilla racemiflora* (85). DICHAPETALACEAE: *Tapura guianensis* (86). DILLENIACEAE: *Doliocarpus dentatus* (87). DROSERACEAE: *Drosera sessilifolia* (88). ELAEOCARPACEAE: *Sloanea grandiflora* (89). ERICACEAE: *Agarista duckeii* (90), *Bejaria sprucei* (91), *Orthaea venamensis* (92), *Psammisia guianensis* (93), *Notopora schomburgkii* (94), *Thibaudia nutans* (95).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Manihot esculenta Crantz (Plate 6, fig. 104)

Monads spheroidal, 144(146)151 μm. Inaperturate. Exine 5 μm (excluding sculptural elements). Clavate, with triangular clavae making the characteristic *Croton*-pattern. Clavae are 7–8 μm high × 9–10 μm wide. Herb or small shrub 1–4 m tall known as ''cassava'', ''yuca dulce'' or ''yuca amarga'', cultivated by local Pemón Amerindians. Never seen in sediments.

Micrandra rossiana R.E. Schult. (Plate 6, fig. 105)

Monads. EV suboblate, 25.5(27)30 × 30(31)33 μm. P/E = 0.88. PV circular-trilobate, 27(32)37.5 μm. Tricolporate, colpi very narrow, as long as grain. Pori lalongate, 1.5–2 μm × 5–7 μm. Exine 1.5 μm, columellae conspicuous, sexine > nexine, microreticulate. Tree 10–35 m tall. Evergreen forests (100–1000 m asl). Not observed in sediments.

Pera bicolor (Klotzsch) Müll. Arg. (Plate 6, fig. 106)

Monads. EV subprolate, 49.5(52.5)57 × 40.5(45)48 μm. P/E = 1.17. PV circular, 45(46.5)51 μm. Tricolporate, colpi 4 μm wide, covering 1/2 of grain length, with a thin psilate margo. Pori lalongate (4–7 × 10–15 μm), with a psilate annulus. Exine 1–3 μm in the mesocolpori and 4–5 μm in oral zone, sexine > nexine, microreticulate-perforate. Tree or shrub 30 m tall in savannas and forests on sandy (100–600 m asl). Very frequent in soils from morichales (ΣP > 3%), and in forest soils.

Pera glabrata (Schott) Poepp. ex Baill. (Plate 6, fig. 107)

Monads. EV oblate-spheroidal, 22.5(25)28.5 × 24(25.5)27 μm. P/E = 0.98. PV circular, 24(26)27 μm. Tricolporate, colpi narrow (1 μm), covering 2/3 grain length, with a thin psilate margo. Pori lalongate, pori with atrium, lalongate, 3 × 6–10 μm. Exine 1–2 μm in the mesocolpori and 3 μm in oral zone, columellae conspicuous, sexine = nexine, microreticulate-perforate. Tree or shrub 35 m tall. Evergreen forest and gallery forests, savanna-forest boundaries and shrublands (100–1300 m asl). Very frequent in soils from morichales (ΣP > 3%) and in forest soils.

Phyllanthus majus Steyerm. (Plate 6, fig. 108)

Monads. EV oblate-spheroidal, 27(28.5)30 × 27(29)30 μm. P/E = 0.97. PV circular, 25.5(28)30 μm. 8–10 zonoporate/zonocolporate, with circular pori, 3 μm diameter. Exine 3 μm, columellae conspicuous, sexine > nexine, reticulate, with bands of reticula arranged longitudinally. Shrub 1–2 m tall. Savannas and shrublands (1000–2300 m asl). Not observed in sediments.

Sapium glandulosum (L.) Morong (Plate 6, fig. 109)

Monads. EV subprolate, 46.5(50)52.5 × 36(38)42 μm. P/E = 1.31. PV circular, 34.5(39)40.5 μm. Tricolporate, colpi as long as grain, 3–5 μm wide. Pori lalongate, as wide as grain, giving a zonorate appearance. Exine 1–2 μm, sexine = nexine, psilate. Shrub or tree 20 m tall. Seasonally flooded gallery forests and secondary forests (0–600 m asl). Frequent in soils from morichales but at low percentages.

Sapium jenmanii Hemsl. (Plate 6, fig. 110)

Monads. EV subprolate, 37.5 × 28.5(30)31.5 μm. P/E = 1.25. PV circular, 30(31)34.5 μm. Tricolporate, colpi narrow, as long as grain. Pori lalongate wide, giving a zonorate appearance. Exine 3 μm, columellae densely distributed, sexine > nexine, microreticulate. Tree 40 m tall. Montane forests (300–700 m asl). Frequent in soils from morichales but at low percentages.

FABACEAE

Abarema barbouriana (Standl.) Barneby & J.W. Grimes. (Plate 7, fig. 111)

Calliandra rigida Benth. (Plate 7, fig. 112)

Polyads uniplanar, ovoid, with 16 grains, general size: 100(106)112.5 × 87.5(95)105 μm. Grains rectangular, 22.5(27.5)32.5 × 27.5(32)35 μm, inaperturate. Exine thin, 1.5 μm, psilate. Shrubs or small trees 2–9 m tall. Present in scrubby islands in the savanna, in riverbanks and tepuian mires (100–1200–2000 m asl). Very rare in forest soils.

Alexa canaracunensis Pittier (Plate 7, fig. 113)

Monads. EV oblate-spheroidal, 45(47)48 × 46.5(47)48 μm. P/E = 0.96. PV circular, 48(51)54 μm. Tetracolporate, colpi with diffuse edges, covering 1/2 of grain length, 4–6 μm wide, pori circular, 3 × 4 μm. Exine 3–5 μm, sexine > nexine, columellae densely distributed, scabrate-perforate. Tree 3–12 m tall. Evergreen forests (100–1500 m asl). Infrequent in forest soils.

Alexa confusa Pittier (Plate 7, fig. 114)

Monads. EV prolate-spheroidal, 48(52.5)55.5 × 48(50)51 μm. P/E = 1.05. PV circular, 49.5(51)52.5 μm.

Plate 6. EUPHORBIACEAE: *Adenophaedra grandifolia* (96), *Alchornea triplinervia* (97), *Chaetocarpus schomburgkianus* (98), *Croton matourensis* (99), *C. subincanus* (100), *Hyeronima oblonga* (101), *Mabea piriri* (102), *M. subsessilis* (103), *Manihot esculenta* (104), *Micrandra rossiana* (105), *Pera bicolor* (106), *P. glabrata* (107), *Phyllanthus majus* (108), *Sapium glandulosum* (109), *S. jenmanii* (110).


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Tricolporate, colpi with diffuse edges, as long as grain, 4–6 μm wide. Exine 3–5 μm, sexine = nexine, columellae densely distributed, scabrate-perforate. Tree 10–30 m tall. Evergreen forests and occasionally in savanna-forest boundaries (50–1300 m asl). Infrequent in forest soils.

Alexa cowanii Yakovlev (Plate 7, fig. 115)

Monads. EV prolate-spheroidal, 46.5(48)48 × 40.5(42)45 μm. P/E = 1.13. PV circular, 40.5(43)48 μm. Tricolporate, colpi with diffuse edges, as long as grain, 3 μm wide, pori lalongate 4–5 × 7–8 μm. Exine 3–5 μm, sexine = nexine, columellae densely distributed, scabrate. Tree 20 m tall. Evergreen forests (100–500 m asl). Infrequent in forest soils.

Bauhinia guianensis Aubl. (Plate 7, fig. 116)
Bauhinia rutilans Spruce ex. Benth. (Plate 7, fig. 117)

Monads. EV prolate, 48(51)52.5 × 33(35)37.5 μm. P/E = 1.46. PV circular-trilobate, 34.5(36.5)37.5 μm. Tricolporate, colpi with a thin margo, covering 2/3 of grain length, 4–6 μm wide, and constrained at the equator, with a psilate membrane. Pori circular, 4–8 μm diameter. Exine 1.5 μm, sexine = nexine, psilate. Liana in evergreen montane and gallery forests (100–900 m asl, as far as 1300 m asl for *B. rutilans*). Very frequent in forest soils and also in morichales (ΣP < 1%).

Cajanus bicolor DC. (Plate 7, fig. 118)

Monads. EV prolate-spheroidal, 40.5(43.5)45 × 37.5(41)42 μm. P/E = 1.10. PV triangular, 36(40)43.5 μm. Tricolporate, colpi covering 2/3 of grain length, with rounded endings, 3–5 μm wide. Pori circular, 7–9 μm diameter, with membrane protruding outward. Exine 3 μm, sexine > nexine, reticulate-heterobrochate, with lumina shrinking towards the pole, muri 1.5 μm wide, lumina 2–4 μm long × 2–6 μm wide. Shrub 1–3 m tall. Known as "quinchoncho", is widely cultivated sometimes escaping to disturbed areas (50–1000 m asl). Not observed in sediments.

Chamaecrista ramosa (Vogel) H.S. Irwin & Barneby (Plate 7, fig. 119)
Chamaecrista roraimae (Benth.) Gleason (Plate 7, fig. 120)

Monads. EV prolate, 34.5(37)37.5 × 25.5(26)27 μm. P/E = 1.40. PV circular-trilobate, 21(24)25.5 μm. Tricolporate, colpi as long as grain, narrow (3 μm wide), constrained at the equator, pori circular, 4 μm diameter, apparently with geniculum. Exine 1.5 μm, thickened in the oral zone, sexine = nexine, psilate. Shrub 1 m tall in savannas and savanna-forest boundaries (50–1200 m asl). Very frequent in forest soils, but only abundant in sediments from morichales (ΣP 5%).

Clitoria falcata Lam. (Plate 7, fig. 121)

Monads. EV subprolate, 24(25)25.5 × 19.5(21)22.5 μm. P/E = 1.19. PV circular-trilobate, 24(24.5)25.5 μm. Tricolporate, colpi narrow, as long as grain, pori circular-ovoid, 4–5 × 6 μm. Exine 1.5 μm, sexine = nexine, columellae conspicuous, microreticulate. Climbing plant in savannas and forest borders (50–1000 m asl). Not observed in sediments.

Dalbergia monetaria L.f. (Plate 7, fig. 122)

Monads. EV subprolate, 25.5(26)27 × 19.5(21)22.5 μm. P/E = 1.23. PV circular-trilobate, 22.5(23)24 μm. Tricolporate, colpi narrow (< 1 μm wide) with a thin psilate margo, as long as grain, pori circular-oblique, 4–6 μm diameter, with geniculum. Exine 1–2 μm, columellae conspicuous, sexine = nexine, psilate. Climbing shrub, small tree or liana. Semideciduous to evergreen forests, gallery forests and flooded forests along back-water rivers (50–1000 m asl). Not observed in sediments.

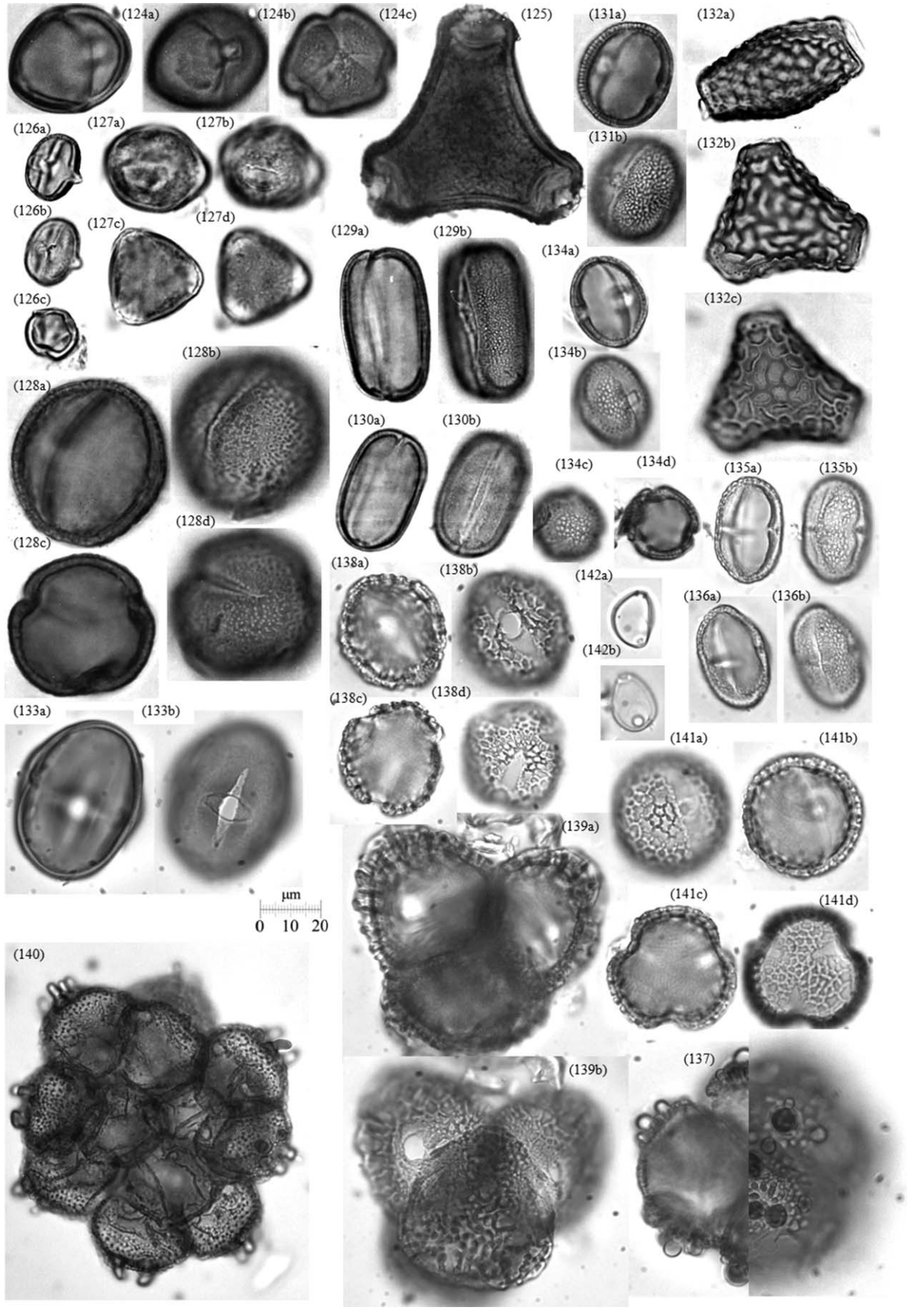
Dimorphandra davisii Sprague & Sandwith (Plate 7, fig. 123)

Monads. EV suboblate 31.5(32)33 × 36(38)40.5 μm. P/E = 0.84. PV subangular, 31.5(34)36 μm. Tricolporate, colpi as long as grain, open (3 μm wide), with a psilate membrane, pori circular annulate, 2–6 μm diameter. Exine 3 μm, columellae densely distributed, sexine = nexine, microreticulate. Tree 4–40 m tall in evergreen forests (300–1500 m asl). Not observed in sediments.

Dimorphandra macrostachya Benth. (Plate 8, fig. 124)

Monads. EV suboblate, 24(24.5)25.5 × 30(31)31.5 μm. P/E = 0.80. PV subangular, 24(26.5)28.5 μm. Tricolporate, colpi as long as grain, 2–3 μm wide, with a psilate membrane, pori circular annulate, 3–7 μm diameter. Exine 2–3 μm, sexine = nexine, microscabrate. Tree 30–40 m tall. Evergreen montane and gallery forest (100–1200 m asl). This pollen type is a dominant element in gallery forest soils at the northern and central areas of Gran Sabana (ΣP = 5–40%).

Plate 7. FABACEAE: *Abarema barbouriana* (111), *Calliandra rigida* (112), *Alexa canaracunensis* (113), *A. confusa* (114), *A. cowanii* (115), *Bauhinia guianensis* (116), *B. rutilans* (117), *Cajanus bicolor* (118), *Chamaecrista ramosa* (119), *C. roraimae* (120), *Clitoria falcata* (121), *Dalbergia monetaria* (122), *Dimorphandra davisii* (123).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Eperua falcata Aubl. (Plate 8, fig. 125)

Monads. EV oblate, 50(49)53 × 67(77)79 μm. P/E = 0.64. PV triangular-concave, 67(70)72 μm. Trizonoporate, pori open (7–8 μm diameter), with a conspicuous psilate annulus (6–8 μm thick). Exine 3 μm, sexine > nexine, rugulate. Tree 8–40 m tall in gallery forests and flooded forests (100–1200 m asl). Rarely observed in soils from morichales.

Machaerium myrianthum Spruce ex. Benth. (Plate 8, fig. 126)

Monads. EV prolate-spheroidal, 15(18)21 × 15(16)18 μm. P/E = 1.13. PV circular-trilobate, 15(17.5)19.5 μm. Tricolporate, colpi narrow, as long as grain, constrained at equator. Pori circular-ovoid-concave, protruding outward, constrained at the centre, 4–5 × 6 μm. Exine 1 μm, sexine < nexine, psilate. Liana or tree 10 m tall. Forests (200–800 m asl). Not observed in sediments.

Ormosia paraensis Ducke (Plate 8, fig. 127)

Monads. EV suboblate, 22.5(24)25.5 × 25.5(27)30 μm. P/E = 0.88. PV subangular, 25.5(26)27 μm. Tricolporate, colpi with diffuse edges, occupying 1/2 of grain length. Pori circular-oval, very wide, 4–5 × 7–8 μm, with diffuse edges. Exine thin (1.5 μm), thinned in the oral section, sexine = nexine, microscabrate-granulate. Tree 20 m tall. Forests (50–1500 m asl). Rarely observed in forest soils.

Senna bacillaris (L.f.) H.S. Irwin & Barneby (Plate 8, fig. 128)

Monads. EV prolate-spheroidal, 48(51)53 × 43(46)50 μm. P/E = 1.10. PV circular, 41(44)48 μm. Tricolporate, colpi narrow (1 μm wide), as long as grain, pori small, inconspicuous. Exine 4–5 μm, columellae densely distributed, sexine > nexine, perforate. Tree 8 m tall. Forests or bordering areas in gallery forests (50–1300 m asl). Rarely observed in gallery forest soils.

Stylosanthes guianensis (Aubl.) Sw. (Plate 8, fig. 129)

Monads. EV prolate, 37.5(39)40.5 × 21(23)25.5 μm. P/E = 1.70. PV circular. Dicolpate, colpi as long as grain, 4–6 μm wide, with a thin psilate margo and a scabrate membrane. Exine 1–2 μm, sexine = nexine, densely columellate, microreticulate. Erect herb in savannas and open places (200–1100 m asl). Seen very rarely in soils from morichales.

Stylosanthes viscosa (L.) Sw. (Plate 8, fig. 130)

Monads. EV prolate, 27(29.5)33 × 16.5(17.5)19.5 μm. P/E = 1.69. PV circular. Dicolpate, colpi as long as grain, 2 μm wide, with a microscabrate membrane and a thin psilate margo. Exine 1–1.5 μm, sexine = nexine, densely columellate, microscabrate. Erect herb in open savannas (100–900 m asl). Seen only once in soils from morichales.

Tachigali guianensis (Benth.) Zarucchi & Herend. (Plate 8, fig. 131)

Monads. EV prolate-spheroidal, 28.5(30)30 × 22.5(25)27 μm. P/E = 1.18. PV circular-trilobate, 21(23)24 μm. Tricolporate, colpi as long as grain, 4–5 μm wide, pori circular, relatively small, 3 μm diameter. Exine 1.5 μm, columellae densely distributed, sexine > nexine, microreticulate. Tree 30 m tall. Evergreen premontane and gallery forests (20–500–1200 m asl). Very frequent in soils from forests, being abundant in some localities (ΣP > 20%), but usually with a moderate to low abundance (ΣP < 5%).

Vigna linearis (Kunth) Maréchal, Mascherpa & Stainier (Plate 8, fig. 132)

Monads. EV oblate-rectangular, 35(37)41 × 69(73)77 μm. P/E = 0.51. PV triangular, 60–80 μm. Triporate, pori large and open, covering 2/3 of grain length. Exine 2–3 μm, sexine = nexine, reticulate. Lumina 4–5 μm wide, polygonal-rectangular, muri 2–3 μm thick. Herb or climbing plant in savannas, morichales and open areas (50–900 m asl). Never seen in sediments.

FLACOURTIACEAE

Casearia corymbosa Kunth (Plate 8, fig. 133)

Monads. EV subprolate, 45(46)48 × 33(37)39 μm. P/E = 1.24. PV subangular, 34.5(37)39 μm. Tricolporate, colpi covering 1/2 of grain length, 3–5 μm wide, with a psilate membrane. Pori lalongate, 4 × 12–15 μm. Exine 2–3 μm, sexine > nexine, psilate. Tree 2–12 m tall in disturbed forests (100–900 m asl). Very frequent in forest soils but at low abundances (ΣP < 1%).

Euceraea nitida Mart. (Plate 8, fig. 134)

Monads. EV subprolate, 21(22.5)24 × 18(18)19.5 μm. P/E = 1.23. PV circular-trilobate, 16.5(18)18 μm. Tricolporate, colpi as long as grain, 1–2 μm wide. Pori

Plate 8. *Dimorphandra macrostachya* (124), *Eperua falcata* (125), *Machaerium myrianthum* (126), *Ormosia paraensis* (127), *Senna bacillaris* (128), *Stylosanthes guianensis* (129), *S. viscosa* (130), *Tachigali guianensis* (131), *Vigna linearis* (132). FLACOURTIACEAE: *Casearia corymbosa* (133), *Euceraea nitida* (134), *Laetia procera* (135), *Ryania speciosa* (136). GENTIANACEAE: *Chelonanthus purpurascens* (137), *Chorisepalum carnosum* (138), *Coutoubea reflexa* (139), *Irlbachia cardonae* (140), *Tachia schomburgkiana* (141), *Voyria aphylla* (142). For fig. 140, the scale bar represents 40 μm.

lalongate, 3 × 4–7 μm. Exine 1.5 μm, columellae conspicuous, sexine = nexine, microreticulate. Shrub or small tree 10 m tall. In gallery forests, savanna-forest boundaries, and evergreen montane forests (100–1700 m asl). Frequent in forest soils at moderate abundances (ΣP 5–8%).

Laetia procera (Poepp.) Eichler (Plate 8, fig. 135)
Ryania speciosa Vahl (Plate 8, fig. 136)

Monads. EV prolate-spheroidal, 25(27)28 × 23(23.5)24 μm. P/E = 1.14. PV circular, 24–25 μm. Tricolporate, colpi as long as grain, pori circular or oblate. Exine 1 μm, sexine = nexine, microreticulate. Tree 8–40 m tall. Evergreen premontane and gallery forests (50–600 m asl). Never seen in sediments from Gran Sabana.

GENTIANACEAE

Chelonanthus purpurascens (Aubl.) Struwe & V.A. Albert (Plate 8, fig. 137)

Tetrads tetrahedral, 47(65)81 × 38.5(62)71.5 μm. Grains ovoid, 46(49)49.5 × 42(54)67.5 μm, apparently tricolporate. Exine 3 μm, with a gemmate sculpturing. Gemmae are 5–7 μm long × 3–4 μm wide. Herb or small shrub (2 m tall), in savannas and roadsides, but more common in highlands (50–2000 m asl). Only observed a single herbazal locality (ΣP < 1%).

Chorisepalum carnosum Ewan (Plate 8, fig. 138)

Monads. EV oblate-spheroidal-rhombic, 30(32) 34.5 × 33(36)39 μm. P/E = 0.88. PV circular, 30(32)34.5 μm. Tricolporate, colpi as long as grain, with rounded endings, with a thin psilate margo and a psilate membrane. Pori circular, 6–9 μm diameter, with a thin psilate annulus. Exine 3 μm, sexine = nexine, columellae conspicuous, reticulate-heterobrochate, with reticula shrinking toward poles. Climbing shrub sometimes epiphytic, 3 m tall. Montane forests and tepui summits (700–1600 m asl). Observed in herbazales and peats (ΣP < 1%).

Coutoubea reflexa Benth. (Plate 8, fig. 139)

Tetrads tetrahedral, larger axis 67(75)79 μm long. Grains spheroidal, 43(45)46 μm diameter, probably tricolporate, coaperturate, short colpi with membrane. Pori relatively small (c. 3–5 μm diameter), slightly lalongate. Exine 3 μm, sexine > nexine, reticulate-cristate, with crests 3 μm tall forming a wide reticulum. Small shrub 10–100 cm tall. Humid savannas on sandy soils (50–1000 m asl). Observed in herbazales and peats (ΣP < 1%).

Irlbachia cardonae (Gleason) Maguire (Plate 8, fig. 140)

Polyads spheroidal with 16 grains, uniplanar, 139(155)168 × 120(127)137 μm. Grains spheroidal, 41(45)53 μm diameter, apparently triporate, coaperturate, pori circular 3–5 μm diameter. Exine 3–4 μm. Columellae conspicuous, giving a baculate sculpturing. Additionally papillae were observed in the distal face. Herb 1.5 m tall in savannas and forest on tepui summits (500–2300 m asl). Observed in herbazales and peats (ΣP < 1%).

Tachia schomburgkiana Benth. (Plate 8, fig. 141)

Monads. EV spheroidal, 30(32)34.5 × 30(32)34.5 μm. P/E = 1.00. PV circular, 28.5(30)31.5 μm diameter. Tricolporate, colpi as long as grain, with rounded endings, with a thin psilate margo and a psilate membrane. Pori circular, 2–6 μm diameter, with a psilate thin annulus. Exine 2–3 μm, sexine > nexine, reticulate. Shrub 3 m tall. Montane forests on white-sandy soils or sandstone (400–1200 m asl). Observed in herbazales and peats (ΣP < 1%).

Voyria aphylla (Jacq.) Pers. (Plate 8, fig. 142)

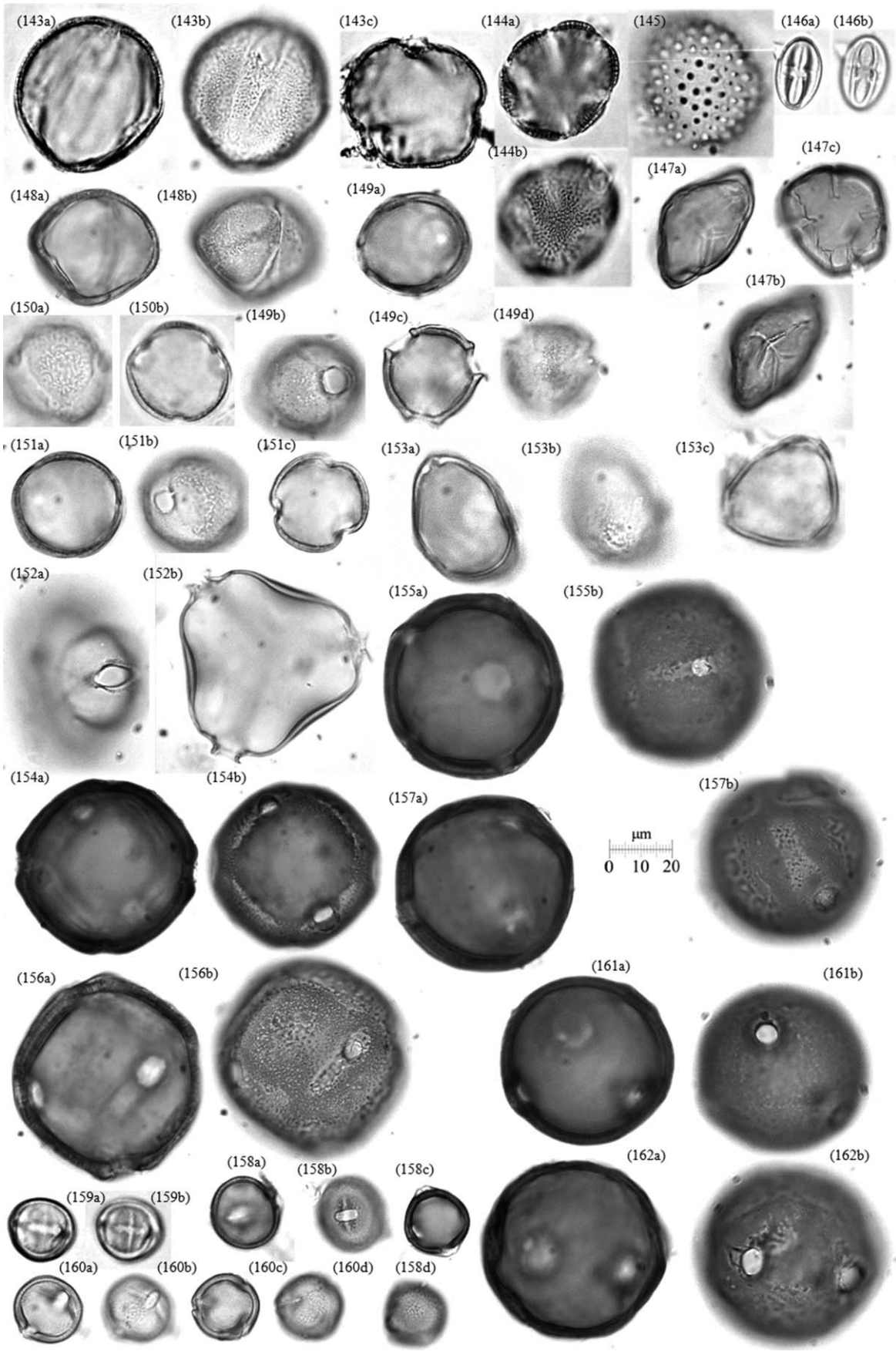
Monads, ovoid to semicircular, 7.5(9)10.5 × 12(13)13.5 μm. Diporate. Exine <1 μm, psilate, translucent. Small saprophyte 15–30 m tall. Semideciduous forests, evergreen forests, granite outcrops, on white-sand or savannas (50–1800 m asl). Never found in sediments.

GESNERIACEAE

Nautilocalyx porphyrotrichus (Leeuwenb.) Wiehler (Plate 9, fig. 143)

Monads. EV prolate-spheroidal, 42(45)49.5 × 41(43)45 μm. P/E = 1.05. PV circular-trilobate, 43(44)45 μm. Tricolporate, colpi as long as grain, pori inconspicuous, lolongate, narrow. Exine 1 μm thick, columellae densely distributed, sexine = nexine, psilate. Terrestrial herb sometimes growing on rock

Plate 9. GESNERIACEAE: *Nautilocalyx porphyrotrichus* (143). LAMIACEAE: *Hyptis atrorubens* (144). LAURACEAE: *Ocotea guianensis* (145). LACISTEMATACEAE: *Lacistema aggregatum* (146). LENTIBULARIACEAE: *Genlisea guianensis* (147), *G. roraimensis* (148). LOGANIACEAE: *Antonia ovata* (149), *Bonyunia minor* (150), *B. superba* (151). LYTHRACEAE: *Cuphea anisoclada* (152), *C. dactylophora* (153). MALPIGHIACEAE: *Banisteria lucida* (154), *Banisteriopsis pulcherrima* (155), *Heteropterys cristata* (156), *Tetrapterys pusilla* (157), *Blepharandra hypoleuca* (158), *Byrsonima crassifolia* (159), *B. verbascifolia* (160), *Hiraea tepuiensis* (161), *Tetrapterys oleifolia* (162).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outcrops. Humid forests (400–1300 m asl). Never seen in sediments.

LAMIACEAE

Hyptis atrorubens Poit. (Plate 9, fig. 144)

Monads. EV suboblate, 28.6(31.5)33 × 31(36)40 μm. P/E = 0.87. PV oval-hexalobate, 26(28)29 × 33(36)42 μm. Hexazonocolpate, colpi as long as grain, wide. Exine 1 μm, sexine = nexine. Reticulate, lumina 2–3 μm wide and muri 1 μm thick. Semi-prostrate herb, 15–50 cm tall. Humid savannas and borders of flooded forests (50–1300 m asl). Infrequent in soils from savanna-forest borders, gallery forests or morichales. Only abundant at a single locality on a riverbank in southern Gran Sabana.

LAURACEAE

Ocotea guianensis Aubl. (Plate 9, fig. 145)

Monads, ovoid-spheroidal, 25.5(30)31.5 μm. Inaperturate. Exine 1 μm, fragile, easily damaged during acetolysis (like most pollen grains of this family). Short spines (1.5 μm long × 1 μm width). Tree 20 m tall. From premontane forests to tepui summits (100–1200 m asl). Never found in sediments due to its susceptibility to oxidation.

LACISTEMATACEAE

Lacistema aggregatum (P.J. Bergius) Rusby (Plate 9, fig. 146)

Monads. EV prolate, 18(19)19.5 × 12(13)15 μm. P/E = 1.46. PV circular-trilobate, 13.5(15)16.5 μm. Tricolporate, colpi as long as grain, with costae, pori small-circular, 1–3 μm diameter, vestibulate. Exine < 1 μm, sexine = nexine, columellae inconspicuous or absent, psilate. Shrub or small tree 2–10 m tall. Forests, savanna-forest transitions, riverbanks and disturbed open areas (0–1200 m asl). It has only been observed in some soils from morichales, but at very low abundances.

LENTIBULARIACEAE

Genlisea guianensis N.E. Br. (Plate 9, fig. 147)
Genlisea roraimensis N.E. Br. (Plate 9, fig. 148)

Monads. EV suboblate, 27.5 × 32.5(34)35 μm. P/E = 0.80. PV rectangular or subangular, 32.5(34)35 μm. Tri or sometimes tetracolpate, colpi narrow, syncolpate. Exine 1 μm, sexine > nexine, psilate. Herb 10–45 cm tall. *Genlisea guianensis* grows in open flooded areas, as riverbanks or lagoons (100–400–1100 m asl) and *G. roraimensis* in humid savannas (1300–2800 m asl). It has only been observed in some soils from morichales, but at very low abundances.

LOGANIACEAE

Antonia ovata Pohl (Plate 9, fig. 149)
Bonyunia minor N.E. Br. (Plate 9, fig. 150)
Bonyunia superba M.R. Schomb. ex Progel (Plate 9, fig. 151)

Monads. EV suboblate, 19(20)24 × 22(23)25 μm. P/E = 0.86. PV subangular, 22(23)23 μm. Tricolporate, colpi as long as grain. Pori circular, open, 4–7 μm diameter. Exine 1.5 μm, sexine = nexine, microscabrate-perforate. Shrub or tree 4–10 m tall, in savannas, shrublands and gallery forest borders (500–800–1400 m asl). Recorded rarely at a single locality.

LYTHRACEAE

Cuphea anisoclada Lourteig (Plate 9, fig. 152)

Monads. EV oblate, 29(29.5)33 × 42(46)49.5 μm. P/E = 0.64. PV subangular, 36(43)49.5 μm. Triporate, pori wide, lolongate, 7–8 per 3–7 μm, with a thin annulus 1 μm wide × 2 μm tall and a vestibulum. The annulus is fused by a longitudinal arcus that is joined at the equator. Exine 1.5 μm, sexine = nexine. Psilate. Herb 50–60 cm tall. In riverbanks and waterfalls (400–1700 m asl). Frequently observed in soils from herbazales and morichales, occasionally reaching high abundances (ΣP = 5–10%).

Cuphea dactylophora Koehne (Plate 9, fig. 153)

Monads. EV suboblate, 18.7 × 22 μm. P/E = 0.85. PV subangular, 22 μm diameter. Triporate, pori wide, circular, 5–6 μm diameter. Exine 1.5 μm, sexine = nexine. Psilate. Small shrub. Frequent in mires from uplands to tepuian summits, also in riverbanks and rocky localities (200–1500 m asl). Never seen in sediments.

MALPIGHIACEAE

Banisteria lucida Rich. (Plate 9, fig. 154)

Monads spheroidal, 47(51)54 μm. 4–6 zonocolporate. Colpi with diffuse edges and rounded endings, pori circular, 4–7 μm diameter. Exine rigid, 4–5 μm thick, sexine > nexine, nexine very thin (< 1 μm). Microscabrate. Liana or climbing shrub in riverbanks and humid, disturbed sites (100–400, 1750 m asl). Infrequent in forest soils.

Banisteriopsis pulcherrima (Sandwith) B. Gates (Plate 9, fig. 155)
Heteropterys cristata Benth. (Plate 9, fig. 156)
Tetrapterys pusilla Steyerm. (Plate 9, fig. 157)

Monads spheroidal, 49.5(51)53 μm. 4–6-pantocolporate, colpi with diffuse edges and rounded endings, and pori circular, 6–9 μm diameter. Exine rigid, 4–5 μm thick, sexine > nexine, nexine thin (< 1 μm). Microscabrate. Liana or climbing ligneous plant in gallery forest trees (450–1500 m asl). Infrequent in forest soils.

Blepharandra hypoleuca (Benth.) Griseb. (Plate 9, fig. 158)

Monads. EV prolate-spheroidal, 15(16.5)18 × 13(15)16.5 μm. P/E = 1.10. PV subangular, 13(14) 15 μm. Tricolporate, colpi narrow (1 μm wide), covering 2/3 of grain length, pori lalongate with rounded ends, 2–3 × 3–6 μm, with fastigium. Exine 1.5 μm, sexine = nexine, microreticulate. Climbing shrub 3 m tall growing in sandstone outcrops, along rivers in shrublands, and in gallery forests (600–2100 m asl). This pollen type is very frequent in forest soils, reaching ΣP > 10% in some sites.

Byrsonima crassifolia (L.) Kunth (Plate 9, fig. 159)
Byrsonima verbascifolia (L.) DC. (Plate 9, fig. 160)

Monads. EV oblate-spheroidal, 15(16)18 × 12(16)19.5 μm. P/E = 0.96. PV circular, 16.5(17)18 μm. Tricolporate, colpi narrow (1 μm wide), as long as grain. Pori lalongate with rounded endings, 3 × 7–8 μm. Exine 1 μm, sexine = nexine, microreticulate. *Byrsonima crassifolia* is a shrub or small tree 2–3 m tall and *B. verbascifolia* is a sufruticose dwarf shrub 10–15 cm tall, both growing in savannas (50–1000 m asl). Observed in very low percentages in savanna-forest boundaries and in soils from morichales.

Hiraea tepuiensis Steyerm. (Plate 9, fig. 161)

Monads spheroidal, 38.5(40)42 μm. Hexapantoporate, pori circular 4–6 μm diameter, annulated. Exine rigid, 2–3 μm thick, sexine > nexine, nexine very thin (< 1 μm). Microscabrate. Ligneous liana in small trees of gallery forests (400–1500 m asl). Infrequent in forest soils.

Tetrapterys oleifolia (Benth.) Nied. (Plate 9, fig. 162)

Monads spheroidal, 44(47)52 μm. Hexazonoporate, pori circular 5–8 μm diameter, annulate. Exine rigid, 2–3 μm thick, sexine > nexine, nexine very thin (< 1 μm). Microscabrate. Shrub 50 cm tall growing in shrublands (1250 m asl). This pollen type was observed in low abundances in forest soils.

MALVACEAE

Catostemma commune Sandwith (Plate 10, fig. 163)

Monads. EV oblate, 22.5(27)33 × 45(47.5)52.5 μm. P/E = 0.57. PV circular-pentalobate, 42(48)52.5 μm. Zonocolpate, 4–5 colpi as long as grain, with a microrugulate-microscabrate membrane. Exine 3–4.5 μm, sexine = nexine, microrugulate. Tree 45 m tall in evergreen forests (50–900 m asl). Observed frequently in forest soils but in very low abundances (ΣP < 0.5%). This pollen type was found abundantly by Rull (2007) in the lowermost part of a core from Santa Cruz de Mapaurí.

Eriotheca globosa (Aubl.) A. Robyns (Plate 10, fig. 164)

Monads. EV oblate-apiculate, 24(26)30 × 36(38) 39 μm. P/E = 0.69. PV triangular, 30(33.5)36 μm. Tricolpate, fossaperturate, colpi size: 7–13 × 3–5 μm. Exine 1.5–3 μm, sexine = nexine, reticulate-heterobrochate, with lumina shrinking toward equator (1–3 μm width), and muri 1 μm thick. Deciduous tree 3–40 m tall in premontane forest (100–1300 m asl). Observed occasionally in forest soils (ΣP < 0.1%).

Peltaea trinervis (C. Presl) Krapov. & Cristóbal (Plate 10, fig. 165)

Monads, spheroidal, 120(121)132.5 μm. Pantoporate. Exine 5–7 μm, with large spines (15–25 μm long × 4–5 μm wide) densely distributed. Spines are conical with rounded endings. Shrub 0.5–2 m tall in savannas, rocky outcrops, riverbanks (50–800 m asl). Observed once from a soil from morichales.

Pochota minor (Sims) Steyerm. & W.D. Stevens (Plate 10, fig. 166)

Monads. EV oblate-apiculate, 34.5(41)45 × 60(67)67.5 μm. P/E = 0.62. PV triangular, 60(63)69 μm. Tricolpate, fossaperturate, colpi size: 9–15 μm long × 3–5 μm wide, with a 3–4 μm thick margo. Exine 1.5–3 μm, sexine = nexine, microscabrate, with scattered sharp short spines (3–5 μm long × < 1 μm wide). Tree 20 m tall, in gallery forest, montane humid forest and flooded savannas on sandstone (0–1100 m asl). Rarely observed in forest soils (ΣP < 0.5%).

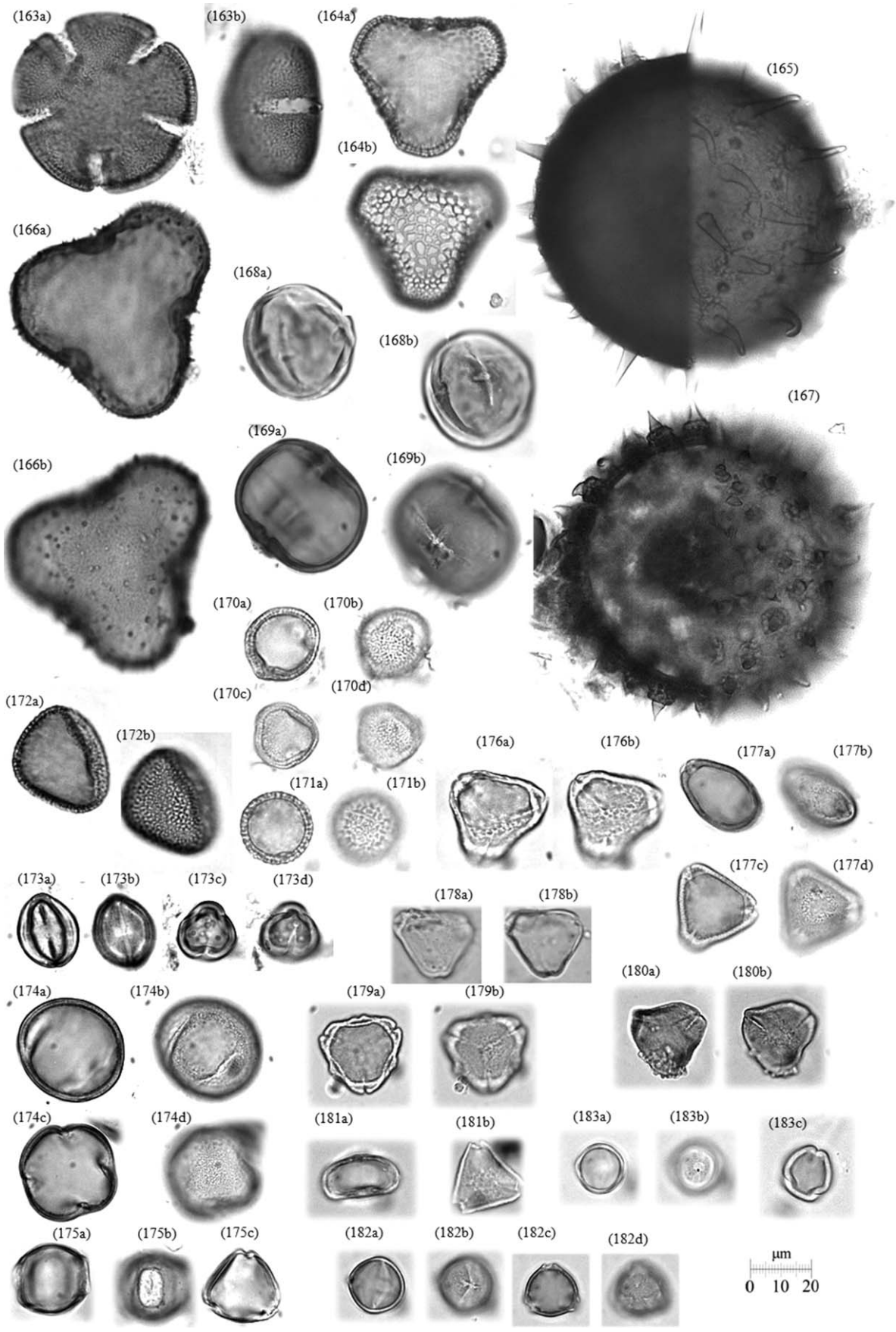
Sida linifolia Cav. (Plate 10, fig. 167)

Monads, spheroidal, 99(110)115 μm. Pantoporate. Exine 8–9 μm, with large spines (12.5–17.5 μm long × 4–5 μm wide) densely distributed. Spines with a base covered by multiple columellae with acute endings. Shrub 1 m tall in savannas, and open disturbed areas (50–1000 m asl). Not observed in sediments from Gran Sabana.

MELIACEAE

Cedrela odorata L. (Plate 10, fig. 168)

Monads. EV subprolate, 38.5(41)44 × 33(35.2) 38.5 μm. P/E = 1.17. PV circular, 32–35.5 μm.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Tetracolporate, colpi narrow with diffuse edges, covering 2/3 of grain length and with straight endings, pori lalongate with rounded endings, 3–5 × 8–12 μm. Exine 1.5 μm, sexine > nexine, psilate. Tree 30–60 m tall. Deciduous to evergreen forests (50–1200 m asl). Observed rarely in a gallery forest site.

Trichilia septentrionalis C. DC. (Plate 10, fig. 169)

Monads. EV subprolate, 35.2(40)45 × 32(34)36 μm. P/E = 1.18. PV circular, 33(34)35 μm. Tri- to tetracolporate, colpi narrow with diffuse edges, covering 2/3 of grain length, pori lalongate with rounded endings, 3–5 μm × 8–12 μm. Exine 2 μm thick, sexine > nexine, psilate. Tree 20 m tall, in evergreen forests (100–1200 m asl). Very frequent in forest soils, mainly in southern Gran Sabana. Abundances are moderate or low (ΣP 5–10%, or <1%).

MENISPERMACEAE

Abuta imene (Mart.) Eichler (Plate 10, fig. 170)

Monads. EV prolate-spheroidal, 15(16)16.5 × 13(15)16.5 μm. P/E = 1.04. PV circular-trilobate, 12(15)15 μm. Triporate, pori with diffuse borders, circular, 2–4 μm diameter. Exine 1.5 μm, sexine = nexine, columellae conspicuous, microreticulate. Liana in tall trees (20–35 m) growing in evergreen montane and gallery (100–1000 m asl). Observed rarely in forest soils.

Cissampelos andromorpha DC. (Plate 10, fig. 171)

Monads. EV spheroidal, 13(14.5)15 × 13(14.5) 15 μm. P/E = 1.00. PV subangular, 14(15)15 μm. Tricolporate, colpi with diffuse edges, covering 2/3 of grain length, very narrow. Pori diffuse, circular, 2 μm diameter. Exine 1.5 μm, sexine = nexine, columellae conspicuous, microreticulate. Liana in primary and secondary forests (100–1300 m asl). Observed rarely in forest soils.

MYRISTICACEAE

Virola surinamensis (Rol ex. Rottb.) Warb. (Plate 10, fig. 172)

Monads, semicircular to ovoid, 27.5(30)31 × 23(24)25 μm. Monocolpate, aperture covering 2/3 of grain length, narrow and with diffuse edges. Exine 2 μm, sexine = nexine, columellae conspicuous, microreticulate or semi-microreticulate. Tree 40 m tall. Evergreen forests, mainly in seasonally flooded forests (0–600 m asl). Very infrequent in forest soils, but usually observed in morichales although with very low percentages (ΣP < 1%).

MYRSINACEAE

Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult. (Plate 10, fig. 173)

Monads. EV subprolate, 15(17)18 × 13(14)15 μm. P/E = 1.17. PV circular-trilobate or tetralobate, 13(14)15 μm. Tri- to tetracolporate, colpi as long as grain, narrow, pori small, lalongate, diffuse, may be operculate. Exine 1–1.5 μm thick, psilate. Shrub 1–30 m tall. In forests (1000–2300 m asl). This pollen type is very common in forest soils with intermediate to low abundances (ΣP < 5%).

Myrsine resinosa (A.C. Sm.) Pipoly (Plate 10, fig. 174)

Monads. EV oblate-spheroidal, 23(27)29 × 27.5(28)30 μm. P/E = 0.94. PV circular-trilobate, 22(25)29 μm. Tetracolporate, colpi as long as grain, narrow. Pori small, diffuse, circular, 2–3 μm diameter. Exine 1.5–2 μm, sexine = nexine, columellae conspicuous, microreticulate or microscabrate. Shrub 2 m tall, growing in gallery forests (1200–1300 m asl). This pollen type is very common in forest soils with intermediate to low abundances (ΣP < 5%).

Myrsine nitida (Mez) Pipoly (Plate 10, fig. 175)

Monads. EV suboblate, 19 × 22.5 μm. P/E = 0.83. PV circular-trilobate, 18(20)21 μm. Tri- to tetracolporate, colpi covering 2/3 of grain length, pori open, oval, with rounded endings, and a thin psilate annulus. Exine 1.5 μm, sexine = nexine, psilate. Tree 2 m tall. In *Clusia* and *Magnolia* forests (1400–2500 m asl). This pollen type is very common in forest soils with intermediate to lower abundances (ΣP < 5%).

MYRTACEAE

Calyptranthes pulchella DC. (Plate 10, fig. 176)
Psidium acutangulum DC. (Plate 10, fig. 177)

Monads. EV oblate, 12(14)18 × 22(22.5)23 μm. P/E = 0.62. PV subangular, 18(20)22 μm. Tricolporate,

Plate 10. MALVACEAE: *Catostemma commune* (163), *Eriotheca globosa* (164), *Peltaea trinervis* (165), *Pochota minor* (166), *Sida linifolia* (167). MELIACEAE: *Cedrela odorata* (168), *Trichilia septentrionalis* (169). MENISPERMACEAE: *Abuta imene* (170), *Cissampelos andromorpha* (171). MYRISTICACEAE: *Virola surinamensis* (172). MYRSINACEAE: *Myrsine coriacea* (173), *M. resinosa* (174), *M. nitida* (175). MYRTACEAE: *Calyptranthes pulchella* (176), *Psidium acutangulum* (177), *Eugenia punicifolia* (178), *Marlierea ferruginea* (179), *Myrcia albidotomentosa* (180), *Siphoneugena dussii* (181). OCHNACEAE: *Cespedesia spathulata* (182). OLACACEAE: *Minquartia guianensis* (183). For figs. 165 and 167, the scale bar represents 40 μm.

syncolpate, pori lalongate-concave, pori 3–4 × 4–5 μm, vestibulate. Exine 1.5 μm, nexine = sexine, microreticulate. *Calyptranthes pulchella* is a shrub growing along streams in *Bonnetia* forests on tepui summits (1100–1900 m asl). *Psidium acutangulum* is a small tree (3–4 m tall), growing in gallery forests. This pollen type is frequent but at low abundance in forest soils.

Eugenia punicifolia (Kunth) DC. (Plate 10, fig. 178)

Monads. EV oblate-rectangular, 15(17)20 × 23(26)29 μm. P/E = 0.63. PV subangular, 18(23)26 μm. Tri- to tetracolporate, colpi occupying 1/2 of grain length. Exine 1.5 μm, sexine = nexine, microscabrate. Shrub 4 m tall. In forests and on rocky outcrops (50–1100 m asl). Frequent but at low abundances in forest soils.

Marlierea ferruginea (Poiret) McVaugh (Plate 10, fig. 179)

Monads. EV oblate, 13(14)14 × 22(23)24 μm. P/E = 0.59. PV subangular, 18(20)23 μm. Tricolporate, syncolpate, with pseudocolpi alternating with apertures. Exine 1.5 μm thick, sexine = nexine, columellae conspicuous, microreticulate. Shrub or small tree 4–20 m tall growing in montane and gallery forests (500–1200 m asl). Never seen in sediments from Gran Sabana.

Myrcia albidotomentosa (Amshoff) McVaugh (Plate 10, fig. 180)

Monads. EV suboblate, 11.5 × 13.2 μm. P/E = 0.88. PV subangular, 20(21)22 μm. Tricolpate, colpi covering 1/2 of grain length. Exine 1.5 μm, sexine = nexine, microrugulate or microreticulate. Shrub or small tree 1–4 m tall. In gallery forests on sandy soils, shrublands on rocky outcrops, slopes or open outcrops (650–2600 m asl). Frequent although at low abundances in forest soils.

Siphoneugena dussii (Krug & Urban) Proença. (Plate 10, fig. 181)

Monads. EV peroblate-rectangular, 9(9.5)10 × 19(21)23 μm. P/E = 0.45. PV subangular, 16.5(19)20 μm. Tricolpate, syncolpate. Exine 1.5 μm, sexine = nexine, psilate. Shrub or small tree 1.5–12 m tall. On rocky or forested shores, sloped and tepui summits (600–2200 m asl). Never seen in sediments.

OCHNACEAE

Cespedesia spathulata (Ruiz & Pavón) Planch. (Plate 10, fig. 182)

Monads. EV prolate-spheroidal, 16.5(18)19 × 16.5(17)18 μm. P/E = 1.06. PV subangular, 15(16)16.5 μm. Tricolporate, colpi as long as grain, narrow, pori lalongate. Exine 1 μm, sexine = nexine, psilate. Tree 20–30 m tall, growing in forests and disturbed areas. Never seen in sediments from Gran Sabana.

OLACACEAE

Minquartia guianensis Aubl. (Plate 10, fig. 183)

Monads. EV spheroidal, 11(12)13 × 11(12)13 μm. P/E = 1. PV circular-trilobate, 14–15 μm. Tricolporate, colpi as long as grain, pori lalongate with rounded endings, 3–4 × 2–3 μm. Exine 1 μm, sexine = nexine, psilate. Tree 4–30 m tall. Premontane and montane forests (100–1200 m asl). Never seen in sediments from Gran Sabana.

ONAGRACEAE

Ludwigia affinis (DC.) H. Hara. (Plate 11, fig. 184)

Tetrads, tetrahedral, 130–135 × 118–120 μm. Grains triangular, 90–94 μm long. Triporate, pori open and circular, 10–15 μm diameter, with a thickened annulus and atrium protruding outwards (covering 12–15 μm long in PV). Exine 4–5 μm, with variable thickness, scabrate. Herb 2.5 m tall, growing in flooded open areas (0–800 m asl). This pollen type can be found in soils from morichales, but in low abundances.

PROTEACEAE

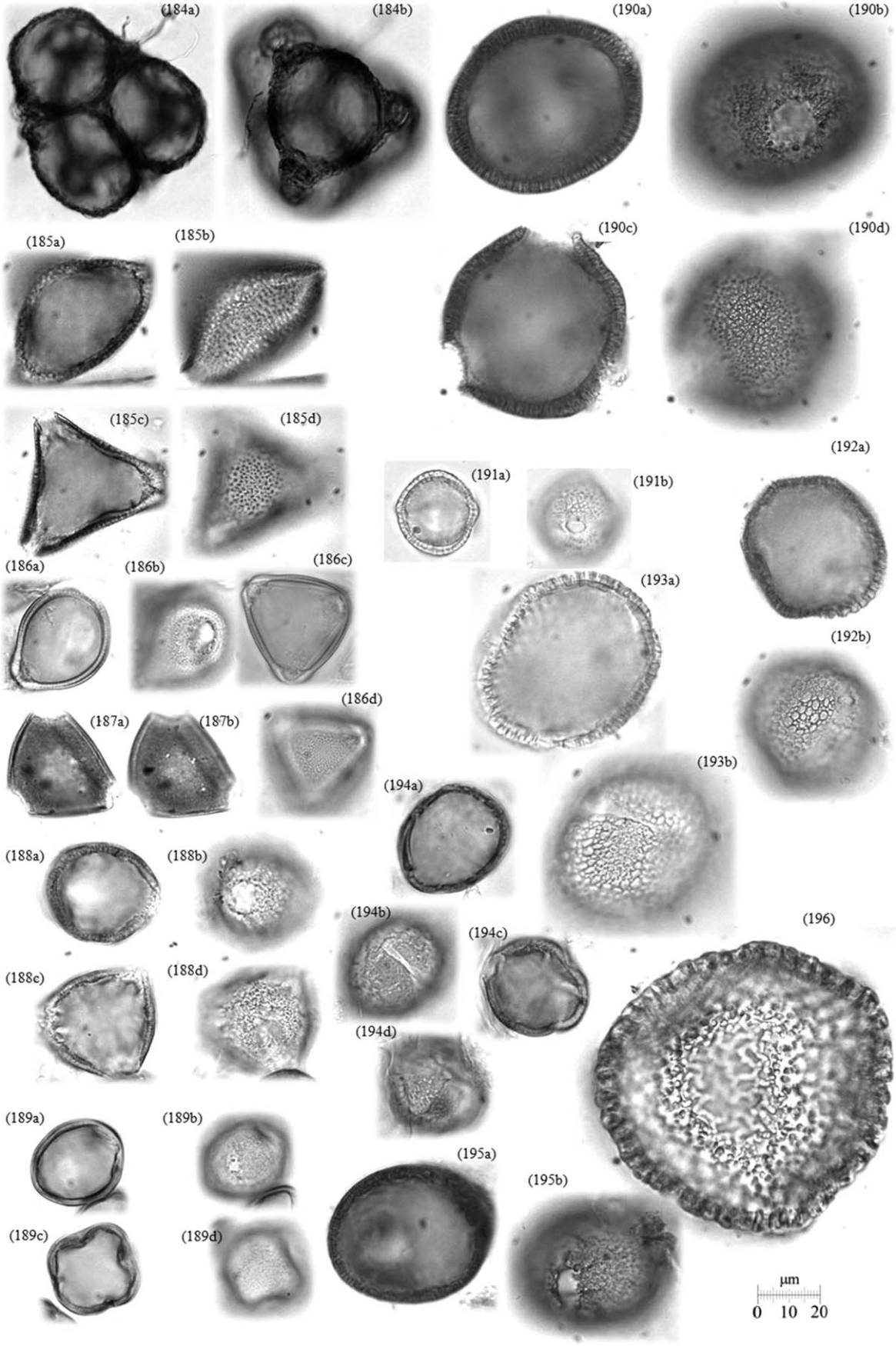
Euplassa glaziovii (Mez) Steyerm. (Plate 11, fig. 185)

Monads. EV oblate, 26(31)41 × 43(49)60.5 μm. P/E = 0.63. PV triangular, 25(26)27.5 μm. Triporate, colpori 4–6 μm, with a scabrate annulus 3–4 μm thick. Exine 2 μm, columellae conspicuous, nexine = sexine, microreticulate. Shrub 2–12 m tall. Gallery forests and savanna-forest boundaries (400–1300 m asl). Very frequent in forest soils in low abundances ($\Sigma P < 1\%$).

Panopsis rubescens (Pohl) Rusby (Plate 11, fig. 186)

Monads. EV oblate, 24(26)27.5 × 35(36)38.5 μm. P/E = 0.72. PV subangular, 25(26)27.5 μm. Triporate,

Plate 11. ONAGRACEAE: *Ludwigia affinis* (184). PROTEACEAE: *Euplassa glaziovii* (185), *Panopsis rubescens* (186), *Roupala montana* (187). RUBIACEAE: *Chiococca nitida* (188), *Coccocypselum guianense* (189), *Declieuxia fruticosa* (190), *Elaeagia maguirei* (191), *Ferdinandusa goudotiana* (192), *Geophila cordifolia* (193), *Ladenbergia lambertiana* (194), *Pagamea capitata* (195), *Palicourea corymbifera* (196). For fig. 184, the scale bar represents 40 μm.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pori 5–6 μm diameter, with a scabrate annulus 3 μm thick and atrium. Exine 2 μm, columellae conspicuous, nexine = sexine, granulate-perforate. Tree 3–15 m tall, in flooded gallery forests and morichales (50–600 m asl). Not observed in sediments.

Roupala montana Aubl. (Plate 11, fig. 187)

Monads. EV oblate, 22(25)26.5 × 32(34)38 μm. P/E = 0.74. PV subangular, 27(29)30.5 μm. Triporate, pori 6 μm diameter, with a scabrate annulus 3 μm thick. Exine 2 μm, columellae conspicuous, nexine = sexine, granulate. Tree in flooded gallery forests and morichales (50–1500 m asl). Very common in forest soils and in sediments from morichales (ΣP < 3%).

RUBIACEAE

Chiococca nitida Benth. (Plate 11, fig. 188)

Monads. EV suboblate, 24(25.5)27.5 × 29(31) 33 μm. P/E = 0.83. PV subangular, 29(31)34 μm. Tricolporate, colpi as long as grain, pori with diffuse edges, open and rounded. Exine 1.5 μm, columellae conspicuous, sexine > nexine. Microreticulate. Shrub 6 m tall, in evergreen montane and gallery forests. Some varieties are present in rocky tepuian slopes (400–1400 m asl). Infrequent in forest soils.

Coccocypselum guianense (Aubl.) K. Schum. (Plate 11, fig. 189)

Monads. EV spheroidal, 21(22)24 × 21(22)23 μm. P/E = 1.00. PV rectangular-tetralobate, 22(22)23 μm. Tetracolporate, colpi covering 2/3 of grain length, with a microscabrate membrane. Pori circular, small, diffuse. Exine 1 μm, sexine > nexine, microscabrate. Prostrate herb. In forested slopes, sandstone and granite outcrops, savanna borders along streams (50–1300 m asl). This pollen type is frequent, but scarce in forest soils.

Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze (Plate 11, fig. 190)

Monads. EV suboblate, 44(46)48 × 51(54)57 μm. P/E = 0.86. PV triangular, 52–54 μm. Tricolporate, colpi covering 2/3 of grain length, with a microscabrate membrane. Pori open, circular 8–10 μm diameter, with diffuse borders and apparently vestibulate. Exine very thick (5–6 μm), densely columellate, sexine > nexine, finely microreticulate. Small shrub 0.7–1.5 m tall, growing in savannas, rocky outcrops, on sandstone or igneous rocks (50–1300 m asl). Observed from a single locality in a forest soil.

Elaeagia maguirei Standl. (Plate 11, fig. 191)

Monads. EV prolate-spheroidal, 22(22.5)23 × 19(21.5)24 μm. P/E = 1.05. PV circular, 19(21.5)24 μm. Triporate, with circular pori 4–6 μm diameter. It is possible to observe a colpus associated with each pore, but the tricolporate character is not usually visible, due to the very diffuse borders of the colpi. Exine 2 μm, sexine > nexine; densely columellate, microreticulate-heterobrochate, with lumina shrinking toward oral area. Trees 20 m tall, in rocky tepuian slopes (1100–1800 m asl). Not observed in sediments.

Ferdinandusa goudotiana K. Schum. (Plate 11, fig. 192)

Monads. EV oblate-spheroidal, 33(35)37 × 30(36)39.5 μm. P/E = 0.95. PV circular, 36(40)43 μm. Tricolporate, colpi as long as grain, pori circular-small. Exine 3–5 μm, sexine > nexine, reticulate-heterobrochate, muri < 1 μm thick, lumina circular-polygonal < 1–2 μm wide. Tree 3–18 m tall in evergreen and seasonal forests (100–1300 m asl). Infrequent in forest soils.

Geophila cordifolia Miq. (Plate 11, fig. 193)

Monads. EV suboblate, 51(52)54 × 60.5(62)64 μm. P/E = 0.85. PV circular, 52(53)54 μm. Tri- or tetracolporate, colpi as long as grain, pori 11–15 μm diameter. Exine 3–5 μm, densely columellate, sexine > nexine, reticulate-heterobrochate, muri < 1 μm thick and lumina circular-polygonal 1–2 μm wide. Tree in evergreen forests (50–1200 m asl). Infrequent in forest soils.

Ladenbergia lambertiana (A. Braun ex Mart.) Klotzsch (Plate 11, fig. 194)

Monads. EV suboblate, 24(25)25 × 29(30)31 μm. P/E = 0.84. PV circular-trilobate, 25(27)29 μm. Tricolporate, colpi narrow, as long as grain, pori lalongate, 3 × 8–9 μm. Exine 1.5–2 μm, sexine = nexine, microscabrate. Shrub or tree 20 m tall, in borders of savannas, gallery forests, secondary forests, rocky sandstone slopes (50–2000 m asl). Infrequent in forest soils.

Pagamea capitata Benth. (Plate 11, fig. 195)

Monads. EV oblate-spheroidal, 37(37)38 × 37(38)39 μm. P/E = 0.97. PV subangular, 41(43)46 μm. Tricolporate, colpi covering 2/3 of grain length, pori lalongate with diffuse borders, 3–4 × 13–15 μm. Exine 2 μm, sexine = nexine, microreticulate. Shrub or tree 1–4 m tall, in shrublands, savannas, sandstone outcrops, or white sand lenses (0–1400 m asl). Infrequent in soils from herbazales.

Palicourea corymbifera (Müll. Arg.) Standl. (Plate 11, fig. 196)

Monads spheroidal, 62.5(64)67.5 μm. Inaperturate. Exine densely columellate, 4–5 μm, sexine > nexine, reticulate, muri 1 μm thick, lumina 3–5 μm wide. Shrub

or small tree 8 m tall, growing in evergreen montane and gallery forests (50–1200 m asl). This genus is frequent in forest soils.

Palicourea croceoides Desv. ex Ham. (Plate 12, fig. 197)

Monads spheroidal, 80 μm. Inaperturate. Exine 4–5 μm, densely columellate, sexine > nexine, microreticulate. Shrub or small tree 5 m tall. Evergreen forests (0–900 m asl). This genus is frequent in forest soils.

Palicourea rigida Kunth (Plate 12, fig. 198)

Monads spheroidal, 67.5(74)82.5 μm. Inaperturate. Exine 2 μm, densely columellate, sexine > nexine, microrugulate. Shrub 0.2–3 m tall, in savannas, rocky outcrops and open sites, shrublands, montane and gallery forests (100–1600 m asl). This genus is frequent in forest soils.

Retiniphyllum laxiflorum (Benth.) N.E. Br. (Plate 12, fig. 199)

Monads. EV subprolate, 33(34)34 × 20(23)24 μm. P/E = 1.48. PV circular, 26(27.5)29 μm. Tricolporate, colpi covering 3/4 of grain length, with psilate membrane. Pori lalongate, 2–3 × 11 μm. Exine 3 μm, sexine = nexine, densely columellate, microreticulate. Shrub or small tree 4 m tall, in savannas, rocky outcrops, montane and gallery forests (100–1600 m asl). Infrequent in forest soils.

Sabicea velutina Benth. (Plate 12, fig. 200)

Monads. EV subprolate, 35.2(36)37 × 24(29)34 μm. P/E = 1.23. PV subangular, 34–35 μm. Tricolporate, colpi with diffuse borders, sometimes difficult to observe, covering 2/3 of grain length. Pori circular, small. Exine 2 μm, sexine = nexine, densely columellate, rugulate-cristate. Climbing plant in savannas and rocky slopes (400–1800 m asl). Not observed in sediments.

Sipanea galioides Wernham (Plate 12, fig. 201)

Monads. EV prolate-spheroidal 21(23)24 × 19(21)24 μm. P/E = 1.11. PV circular-trilobate, 20(21)23 μm. Tricolporate, colpi narrow, as long as grain, pori circular-inconspicuous. Exine 1–1.5 μm, sexine = nexine, microreticulate. Herb, in dry savannas, forest borders, gallery forests, exposed slopes with montane forest cover (750–1800 m asl). Infrequent in forest soils.

SAPINDACEAE

Matayba arborescens (Aubl.) Radlk. (Plate 12, fig. 202)

Monads. EV oblate, 16.5(19)22 × 25(27)29 μm. P/E = 0.72. PV subangular, 27.5(28)30 μm. Tricolporate, syncolpate, with a thin psilate margo, and circular pori 3–7 μm diameter, vestibulate. Exine 1 μm, microreticulate. Small tree, in scrubby islands in savannas, savanna-forest edges, gallery forests, flooded forests (100–800 m asl). Frequent in forest soils (ΣP < 1%).

SAPOTACEAE

Chrysophyllum sanguinolentum (Pierre) Baehni (Plate 12, fig. 203)

Monads. EV prolate, 33(35)37 × 20(22)23 μm. P/E = 1.56. PV circular, 20–24 μm. Tricolporate, colpi covering 1/2 of grain length, pori circular, 2–6 μm diameter. Exine 2 μm, psilate. Tree 15–30 m tall, in montane and gallery forests, also in flooded forests. Very common between 500–2000 m asl. Found in forest soils (ΣP 5%), mainly in southern Gran Sabana.

Pouteria bangii (Rusby) T.D. Penn. (Plate 12, fig. 204)

Monads. EV prolate, 24(25)30 × 15(16)18 μm. P/E = 1.60. PV circular, 20–24 μm. Tricolporate, colpi covering 1/2 of grain length, pori circular, 2–6 μm diameter. Exine 2 μm, psilate. Tree 15–30 m tall. In gallery forests, evergreen montane forests and seasonally flooded forests. Found between 600–1500 m asl. Common in forest soils (ΣP 5%), mainly in southern Gran Sabana.

Pradosia beardii (Monach.) T.D. Penn. (Plate 12, fig. 205)

Monads. EV prolate, 20(25)29 × 16.5(17)19 μm. P/E = 1.50. PV circular, 27.5(28)30 μm. Tricolporate, colpi as long as grain, pori circular, 3–5 μm diameter. Exine 1 μm, sexine = nexine, psilate. Tree 3–25 m tall. Shrublands on sandy soils, in gallery forest and seasonally flooded forests (700–1800 m asl). Only observed from a single site in soil from morichales.

SIMAROUBACEAE

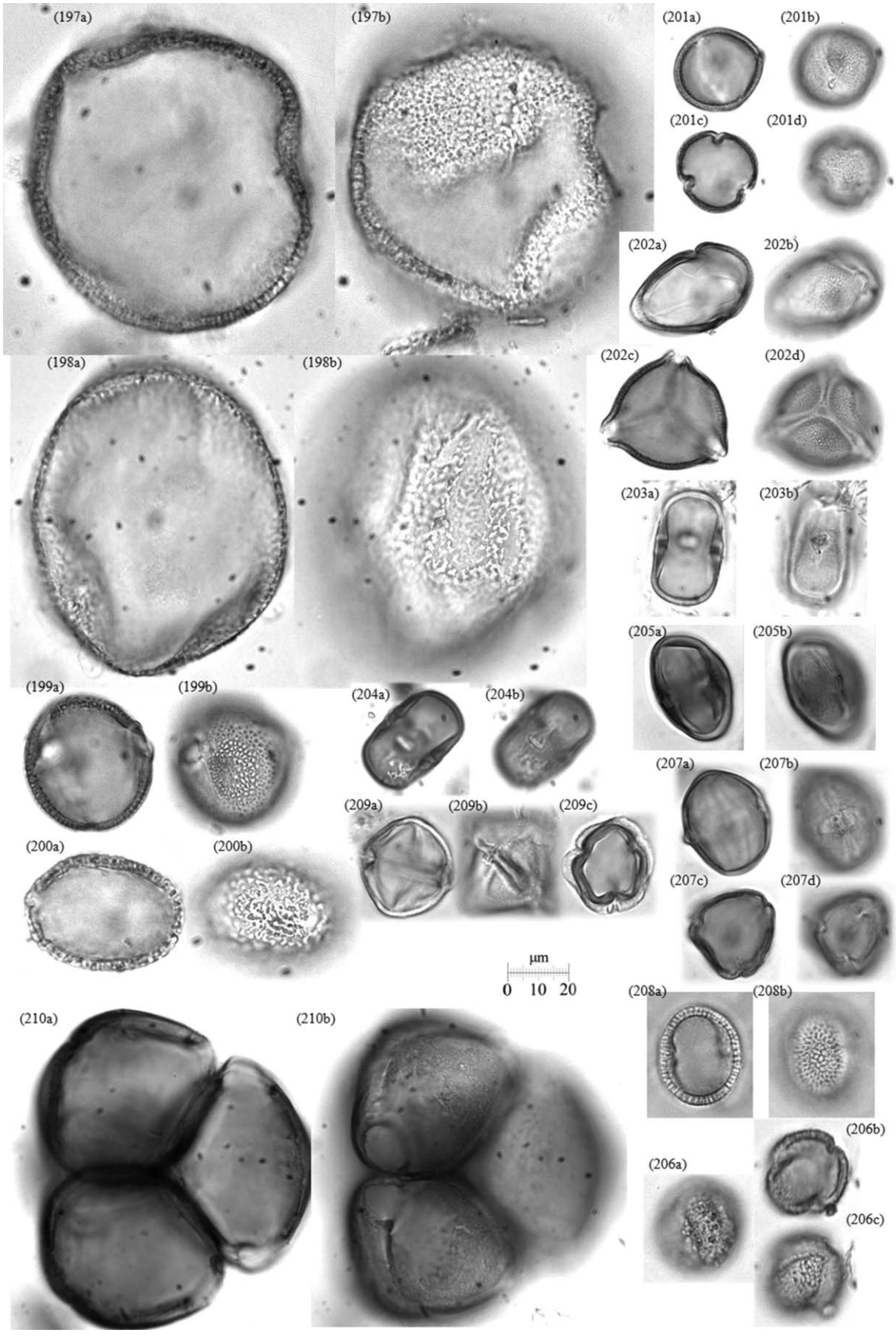
Simarouba amara Aubl. (Plate 12, fig. 206)

Monads. EV subprolate, 22(23)23 × 18–19 μm. P/E = 1.22. PV circular-trilobate, 19(19)20 μm. Tricolporate, colpi as long as grain, pori lalongate, 2–3 × 5–7 μm. Exine 1.5 μm, sexine = nexine, verrucate. Tree 20 m tall. Gallery forests (240–1300 m asl). Frequent in forest soils but in low proportions.

SOLANACEAE

Cyphomandra hartwegii (Miers) Walp. (Plate 12, fig. 207)

Monads. EV prolate-spheroidal, 25(26)27.5 × 23(25)26 μm. P/E = 1.06. PV circular-trilobate, 21(22)24 μm. Tricolporate, colpi narrow, as long as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grain. Pori lalongate, with margo forming an equatorial colpus (zonorate), protruding outwards, 2 μm thick. Exine 1.5–2 μm, sexine = nexine, psilate. Shrub or small tree, in humid forests and riverbanks (50–1300 m asl). Found in soils from morichales (ΣP < 1%).

Melananthus ulei Carvalho (Plate 12, fig. 208)

Monads. EV prolate-spheroidal, 16.5(19)22 × 18(19)19 μm. P/E = 1.03. PV circular, 20–21 μm. Tricolporate, colpi as long as grain, pori small, inconspicuous. Exine densely columellate, 2 μm, sexine > nexine, microreticulate. Shrub 0.5–1 m tall. Found in gallery forests on rocky or sandy soils (400–1300 m asl). Rare in forest soils (ΣP < 0.5%).

Solanum acerifolium Dunal (Plate 12, fig. 209)

Monads. EV subprolate, 27.5(29)32 × 23(24)26 μm. P/E = 1.18. PV circular-trilobate, 23(24)26 μm. Tricolporate, colpi wide as long as grain, constrained at the equator, pori very wide, lalongate-rectangular, 5–8 × 12–16 μm. Exine 1 μm, sexine > nexine, psilate. Shrub 0.5–3 m tall, in forest gaps (50–1800 m asl). Rare in soils from morichales (ΣP < 0.5%).

THEACEAE

Bonnetia sessilis Benth. (Plate 12, fig. 210)

Tetrads, tetrahedral, 90(97.5)106 × 88(96)104.5 μm. Grains ovoid, 64(68)71.5 × 67.5(71)78 μm, tricolporate, colpi narrow, syncolpate, pori circular, open, with a psilate margo, 11–18 μm diameter. Exine 4 μm, microscabrate. Shrub found in shrublands (100–2100 m asl). Not observed from soils in Gran Sabana.

Bonnetia tepuiensis Kobuski & Steyerm. (Plate 13, fig. 211)

Monads. EV suboblate, 35–36 × 42–43 μm. P/E = 0.82. PV subangular, 41–43 μm. Tricolporate, syncolpate, colpi with a thin psilate margo, pori circular and open, 8–10 μm diameter. Exine 2–3 μm, sexine > nexine, microreticulate. Shrub found in shrublands and tepuian forests (1000–2500 m asl). This pollen type was observed once in a herbazales soil.

Ternstroemia crassifolia Benth. (Plate 13, fig. 212)

Monads. EV prolate-spheroidal, 22(24)25 × 21(23)24 μm. P/E = 1.03. PV circular, 22(23.5)25 μm. Tricolporate, colpi narrow, as long as grain, pori lalongate-concave. Exine 1 μm, sexine = nexine, psilate. Shrub 3 m tall, growing in shrublands (1000–1400 m asl). Not observed in sediments.

VOCHYSIACEAE

Qualea paraensis Ducke (Plate 13, fig. 213)

Monads. EV prolate-spheroidal, 27.5(33)38.5 × 26(32)35 μm. P/E = 1.04. PV subangular, 30(33)36 μm. Tricolporate, colpi as long as grain, pori lalongate. Exine densely columellate, 2 μm, sexine = nexine with a pattern of very thin striae. Trees 30 m tall, in evergreen forests (100–1000 m asl). Observed rarely in forest soils.

Ruizterania ferruginea (Steyerm.) Marcano-Berti (Plate 13, fig. 214)

Ruizterania rigida (Stafleu) Marcano-Berti (Plate 13, fig. 215)

Monads. EV suboblate-rhombic, 33(37)41 × 38.5(42)46 μm. P/E = 0.87. PV triangular, 33(39)44 μm. Tricolporate, colpi as long as grain, narrow, pori with diffuse borders, circular, 11–15 μm diameter. Exine 3–6 μm, sexine = nexine, microreticulate. Shrubs or trees 2–8 m tall, in montane and gallery forests (400–1700 m asl). This pollen type is very rare in forest soils.

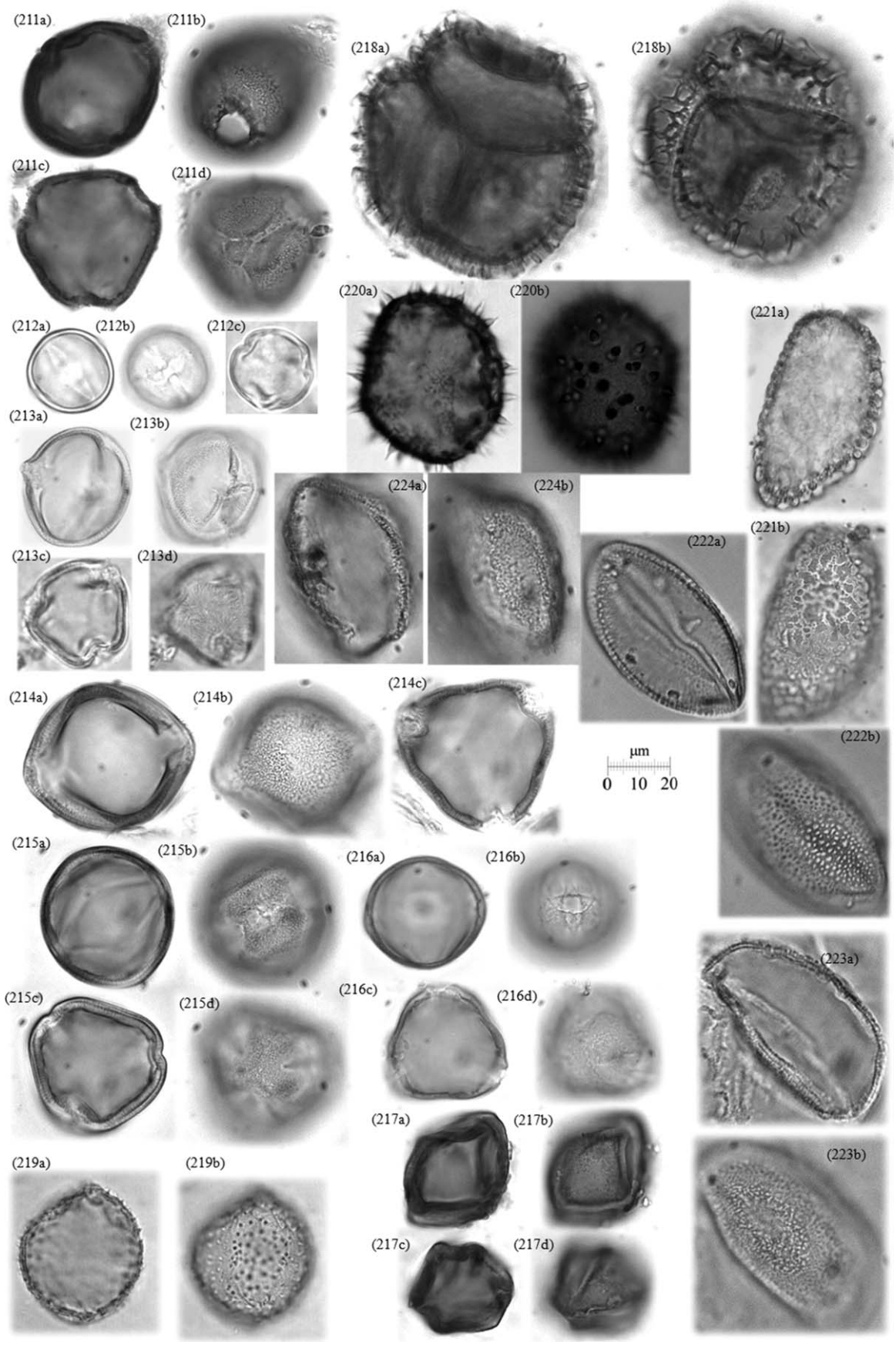
Vochysia costata Warm. (Plate 13, fig. 216)

Monads. EV oblate-spheroidal, 27.5(29)31 × 31(33)35 μm. P/E = 0.88. PV subangular, 24(27.5)32 μm. Tricolporate, colpi as long as grain, narrow, pori with diffuse borders, apparently operculate. Exine 2 μm, sexine = nexine, psilate. Tree 30 m tall. Montane forests (1000–1700 m asl). Usually this is a rare pollen type in forest soils, but in some localities was very frequent (ΣP 5–15%).

Vochysia crassifolia Warm (Plate 13, fig. 217)

Monads. EV oblate-spheroidal, 31(33)34 × 35(37)41 μm. P/E = 0.88. PV triangular, 31(35)38.5 μm. Tricolporate, colpi occupying 1/2 of grain length, pori lalongate 7–10 × 11–15 μm. Exine 2 μm, sexine = nexine, microrugulate-granulate. Tree 4–20 m tall. Gallery forests (50–1500 m asl). This pollen type was found only in one site from a forest soil in southern Gran Sabana.

Plate 12. *Palicourea croceoides* (197), *P. rigida* (198), *Retiniphyllum laxiflorum* (199), *Sabicea velutina* (200), *Sipanea galioides* (201). SAPINDACEAE: *Matayba arborescens* (202). SAPOTACEAE: *Chrysophyllum sanguinolentum* (203), *Pouteria bangii* (204), *Pradosia beardii* (205). SIMAROUBACEAE: *Simarouba amara* (206). SOLANACEAE: *Cyphomandra hartwegii* (207), *Melananthus ulei* (208), *Solanum acerifolium* (209). THEACEAE: *Bonnetia sessilis* (210). For fig. 210, the scale bar represents 40 μm.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WINTERACEAE

Drymis roraimensis (A.C. Sm.) Ehrend. & Gottsb. (Plate 13, fig. 218)

Tetrads, tetrahedral, 52(53)55 × 52(54)57 μm. Grains ovoid, 37(39)40 μm long, with at least one circular annulate pore, 10 μm diameter. Exine 5–6 μm, with a 'foot layer' 1 μm thick, columellae 4 μm long, making a cristate-reticulate pattern. Reticula with muri 1 μm thick and lumina 5–7 μm wide. Shrub or small tree 4–8 m tall, in montane and cloud forests, tepuian summits and along streams (1400–2500 m asl). Not observed in sediments.

3.2. MONOCOTS

ALISMATACEAE

Sagittaria rhombifolia Cham. (Plate 13, fig. 219)

Monads, spheroidal, 34.5(38.6)46.5 μm. Apparently dicolpate, with apertures of variable sizes, sometimes inconspicuous. Exine 1 μm, echinate, spinules <1 μm thick, 1 μm long. Aquatic herb, 1 m tall. Found along lake shores, in temporal lagoons and close to streams (50–1100 m asl). Infrequent in soils from morichales.

ARECACEAE

Mauritia flexuosa L.f. (Plate 13, fig. 220)

Monads, asymmetric, spheroidal-ovoid, 38–45 μm long. Monoporate, with an ellipsoid pore (termed an ulcus), covering 1/3 of grain length and sometimes inconspicuous. Exine 1 μm, sexine > nexine, echinate, with spines bottle-shaped, embedded in the exine, 1.5 μm thick × 5–7 μm long. Palm 8–15 m tall. Forming monospecific stands termed morichales, forming palm swamps. Palm is also present in seasonally flooded gallery forests (0–1000 m asl). This pollen type is only present in low abundances from flooded gallery forests and at medium-to-high abundances in morichales reaching a $\Sigma P > 40\%$.

BROMELIACEAE

Bilbergia macrolepis L.B. Sm (Plate 13, fig. 221)

Monads, ovoid, monocolpate, 38–40 × 63–66 μm. Colpi as long as grain. Exine 3 μm, gemmate-rugulate. Epiphytic plant in trees from evergreen and gallery forests (100–800 m asl). Not observed in sediments.

Brocchinia acuminata L.B. Sm. (Plate 13, fig. 222)

Monads, ovoid, monocolpate, 50–55 × 20–26 μm. Colpi as long as grain. Exine 1 μm, microreticulate-granulate. Terrestrial herb growing in humid sites, rocky slopes and cliffs, along streams, *Bonnetia roraimae* forests and shrublands (400–2100 m asl). Only seen in soils from herbazales, but very rare.

Brocchinia micrantha (Baker) Mez (Plate 13, fig. 223)

Monads, ovoid, monocolpate, 38–41 × 28–30 μm. Colpi as long as grain. Exine 1 μm, reticulate-heterobrochate. Terrestrial or litophytic herb, forming colonies in sandstone outcrops (400–1200 m asl). Only seen in soils from herbazales, but very rare.

Catopsis berteroniana (Schult. & Schult. f.) Mez (Plate 13, fig. 224)

Monads, ovoid, monocolpate, 65–69 × 39–41 μm. Colpi as long as grain. Exine 1 μm, microreticulate. Epiphyte, present in different vegetation types, forming shrublands to tall evergreen forests (100–1300 m asl). Not observed in sediments.

Lindmania guianensis (Beer) Mez (Plate 14, fig. 225)

Monads, ovoid, monocolpate, 46(48)49.5 × 32(36)38.5 μm. Colpi as long as grain. Exine 1 μm, reticulate-heterobochate, with lumina shrinking toward colpi. Muri <1 μm thick and lumina 1–2 μm wide. Terrestrial herb, growing close to sandstone outcrops, savannas and sandy mires. Not observed in sediments.

Puya floccosa (Linden) E. Morren ex Mez (Plate 14, fig. 226)

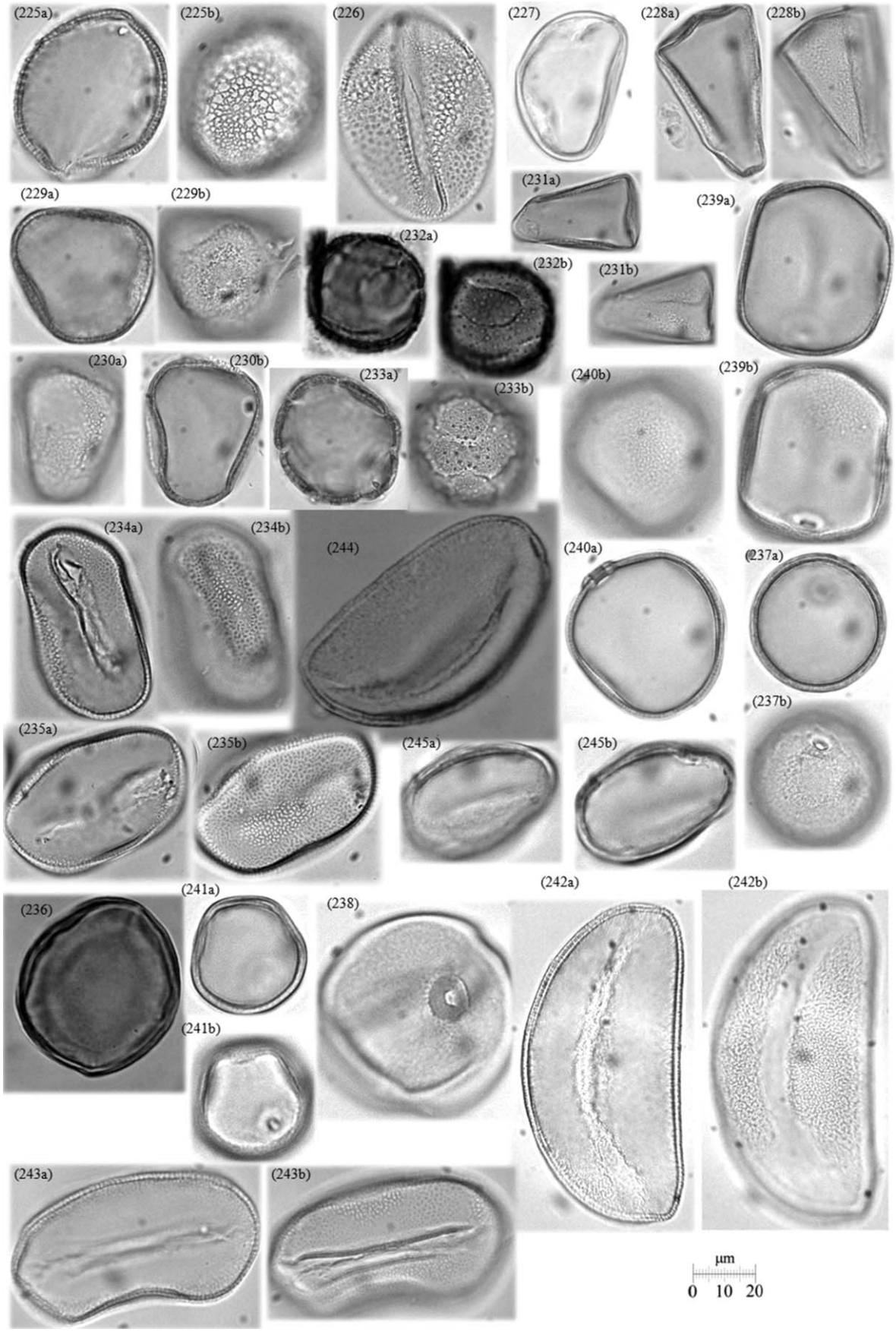
Monads, ovoid, monocolpate, 60.5(63)66 × 41(41.5)44 μm. Colpi as long as grain. Exine 1 μm, reticulate-heterobrochate, with lumina circular-polygonal. Terrestrial or litophytic herb. Single or in colonies in rocky savannas and outcrops (1000–1700 m asl). Observed occasionally from herbazales soils.

BURMANNIACEAE

Burmannia capitata (Walter ex J.F. Gmel.) Mart. (Plate 14, fig. 227)

Monads, ovoid, monocolpate, 30(31)33 × 25(26)27.5 μm, colpi wide, covering 4/5 of grain length. Exine 1 μm, psilate. Small herb growing in humid open places (50–900 m asl). Not observed in sediments.

Plate 13. *Bonnetia tepuiensis* (211), *Ternstroemia crassifolia* (212). VOCHYSIACEAE: *Qualea paraensis* (213), *Ruizterania ferruginea* (214), *R. rigida* (215), *Vochysia costata* (216), *V. crassifolia* (217). WINTERACEAE: *Drymis roraimensis* (218). ALISMATACEAE: *Sagittaria rhombifolia* (219). ARECACEAE: *Mauritia flexuosa* (220). BROMELIACEAE: *Bilbergia macrolepis* (221), *Brocchinia acuminata* (222), *B. micrantha* (223), *Catopsis berteroniana* (224).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CYPERACEAE

Bulbostylis junciformis (Kunth) C.B. Clarke (Plate 14, fig. 228)
Hypolytrum pulchrum (Rudge) H. Pfeiff. (Plate 14, fig. 229)
Lagenocarpus rigidus (Kunth) Nees (Plate 14, fig. 230)
Scleria cyperina Wild ex. Kunth (Plate 14, fig. 231)

Monads trapezoid, 33(40)44 × 29(34)43 μm. Monoporate. Exine 1 μm, sexine = nexine, columellae conspicuous, granulate. Perennial herb, in savannas on rocky or sandy soils and in shrublands (50–1300 m asl). This is one of the most common pollen types in the forest-savanna borders, morichales, herbazales or flooded depressions (ΣP > 15 < 30%).

ERIOCAULACEAE

Eriocaulon humboldtii Kunth (Plate 14, fig. 232)
Eriocaulon steyermarkii Moldenke (Plate 14, fig. 233)

Monads, spheroidal, 27.5(29.5)33 μm. Spiroaperturate. Exine spinulate, with scattered short spines <1 μm long. Terrestrial herb, partially submerged in flooded open sites: *Eriocaulon humboldtii* (50–1400 m asl), *Eriocaulon steyermarkii* (500–2700 m asl). Very abundant in flooded depressions in soils from morichales.

Paepalanthus dichotomus Klotzsch ex Körn (Plate 14, fig. 234)
Syngonanthus jenmanii (Gleason) Giul. & Hensold (Plate 14, fig. 235)

Monads ovoid, 47(51)53 × 31(31.5)33 μm. Monocolpate, covering 3/4 of grain length. Exine thin, 1 μm, microreticulate. Terrestrial plant 3–6 cm tall, growing in sandy savannas and tepui summits (*Paepalanthus dichotomus*: 1200–2100 m asl, *Syngonanthus jenmanii*, 400–2600 m asl). Not observed in sediments.

NYMPHAEACEAE

Nymphaea rudgeana G. Mey. (Plate 14, fig. 236)

Monads spheroidal, 42(44)46 μm. Inaperturate. Exine 1.5 μm, psilate. Aquatic floating or submerged herb. Lagoons and morichales (0–900 m asl). Not observed in sediments.

POACEAE

Aristida torta (Nees) Kunth (Plate 14, fig. 237)
Axonopus anceps (Mez.) Hitchc. (Plate 14, fig. 238)
Axonopus aureus P. Beauv. (Plate 14, fig. 239)
Echinolaena inflexa (Poir.) Chase (Plate 14, fig. 240)
Panicum trichoides Sw. (Plate 14, fig. 241)

Monads spheroidal, 32(33)34 μm. Monoporate, pori with a granulate annulus. Exine 1 μm, psilate. Savanna herbs (50–1500 m asl). This is by far the most abundant pollen type found in sediments from Gran Sabana. In forest soils, ΣP can reach 5–15%, while in savanna-forest boundaries, herbazales, morichales and flooded depressions, ΣP may be between 50 and 90%.

RAPATEACEAE

Stegolepis angustata Gleason (Plate 14, fig. 242)

Monads, semicircular, 77(81)86 × 37(40)44 μm. Monocolpate, colpi as long as grain. Exine 2 μm, sexine = nexine, densely columellate, microreticulate. Robust herb 1–2.5 m tall, in humid areas on sandy soils and in forest borders (800–1800 m asl). Only present in soils from herbazales (ΣP = 1–20%).

Stegolepis ptaritepuiensis Steyerm. (Plate 14, fig. 243)

Monads, ovoid, 46(49)52 × 27.5(30)33 μm. Monocolpate, colpi as long as grain. Exine 1.5 μm, sexine nexine, densely columellate, microreticulate. Herb 0.5–2 m tall. In flooded savannas on sandstone outcrops and also in tepui summits (900–2400 m asl). Only present in soils from herbazales (ΣP = 1–20%).

XYRIDACEAE

Xyris chimantae Kral & L.B. Sm. (Plate 14, fig. 244)

Monads semicircular, 46.5(62)67.5 × 30(34)37.5 μm. Monocolpate, colpi as long as grain. Exine 3 μm, densely columellate, sexine = nexine, microgranulate. Herb 0.1–0.6 m tall. Grows in savannas (800–2400 m asl). Very abundant in soils from herbazales, morichales or shallow lagoons.

Xyris setigera Oliv. (Plate 14, fig. 245)

Monads semicircular, 31(31)32 × 20(22.5)25 μm. Monocolpate, colpi as long as grain, with a thin margo and a microscabrate membrane. Exine 2 μm, psilate. Herb 0.1–0.6 m tall. Found in savannas (800–2400 m

Plate 14. *Lindmania guianensis* (225), *Puya floccosa* (226). BURMANNIACEAE: *Burmannia capitata* (227). CYPERACEAE: *Bulbostylis junciformis* (228), *Hypolytrum pulchrum* (229), *Lagenocarpus rigidus* (230), *Scleria cyperina* (231). ERIOCAULACEAE: *Eriocaulon humboldtii* (232), *E. steyermarkii* (233), *Paepalanthus dichotomus* (234), *Syngonanthus jenmanii* (235). NYMPHAEACEAE: *Nymphaea rudgeana* (236). POACEAE: *Aristida torta* (237), *Axonopus anceps* (238), *A. aureus* (239), *Echinolaena inflexa* (240), *Panicum trichoides* (241). RAPATEACEAE: *Stegolepis angustata* (242), *S. ptaritepuiensis* (243). XYRIDACEAE: *Xyris chimantae* (244), *X. setigera* (245).

asl). Very abundant in soils from herbazales, morichales or shallow lagoons.

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