

Additions to the Pantepui pollen flora (Venezuelan Guayana): the Maguire Collection

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Received 3 September 2010; Accepted 15 November 2010

Abstract

This work is a pollen-morphological study of various plant species from Pantepui (Venezuelan Guayana), a region with high biodiversity and endemism, where global warming is expected to have a high impact. The study consists of a series of morphological descriptions of selected taxa from the Maguire pollen reference slide collection of The New York Botanical Garden (NYBG). The collection was initiated under the supervision of Senior Curator Bassett Maguire to advance systematic, palynological, and medical studies; today it has become also useful for other disciplines such as paleoecology, paleoclimatology or forensic studies. The aim of this pollen-morphological study is to enhance the database of pollen descriptions and illustrations for identification purposes, to be used in the ongoing paleoecological reconstructions and, eventually, in other types of studies using pollen, particularly from the Guayanan tepui summits.

Key words: Guayana; Pollen morphology; Taxonomy; *Tepuis*; Venezuela.

Resumen

Adiciones a la flora polínica de Pantepui (Guayana venezolana): la colección Maguire.- Este trabajo es un estudio sobre la morfología polínica de varias especies de plantas de Pantepui (Guayana venezolana), una región con elevada biodiversidad y un alto grado de endemismo, donde se espera un fuerte impacto del calentamiento global. El estudio consiste en una serie de descripciones morfológicas de taxones pertenecientes a la colección Maguire de láminas de referencia del Jardín Botánico de Nueva York (NYBG). La colección fue iniciada bajo la dirección del Curador Jefe Basset Maguire con el objeto de avanzar en estudios de sistemática, palinología y medicina; aunque actualmente también resulta útil en otras disciplinas, como por ejemplo la paleoecología, la paleoclimatología o los estudios forenses. El objetivo de este estudio de morfología polínica es aumentar la base de datos de descripciones e ilustraciones polínicas con propósitos de identificación taxonómica, para ser utilizada en reconstrucciones paleoecológicas y otro tipo de estudios actualmente en desarrollo, en particular en las cimas de los tepuis de Guayana.

Palabras clave: Guayana; Morfología polínica; Taxonomía; *Tepuis*; Venezuela.

INTRODUCTION

This paper is part of a series devoted to the pollen-morphological study of vascular plant species from the Venezuelan Guayana (Fig. 1), particularly from the characteristic sandstone tabular mountains (*tepuis*), initiated by Salgado-Labouriau & Villar (1992) and continued by Rull (2003). The biodiversity and endemism of this region are striking, but the origin and evolution of such exceptional biotic features has been object of intense debate, which is still ongoing (Rull, 2010). On the other hand, the tepuian flora is expected to be seriously affected by relatively rapid biodiversity loss under ongoing global warming. Hence, paleoecological and paleoclimatic studies on this region can provide useful information about biogeographical and evolutionary processes as well as the effects of climate change on the tepuian biota.

Besides the papers mentioned above, which are monographic for the pollen of the Guayana region, the available literature dealing with this subject is scarce and organized taxonomically. Rapateaceae and Asteraceae are the most thoroughly studied families in this sense, although the knowledge of Asteraceae is restricted to some genera of Mutisioideae (Carlquist, 1961; Tellería, 2008; Funk *et al.*, 2009; Ubiergo *et al.*, 2009). Accordingly, the aim of this study, as well as the previously mentioned works, is to enhance the database of pollen descriptions and illustrations for identification purposes, to be used in the ongoing pollen-based paleoecological reconstructions (Rull *et al.*, 2010) and, eventually, in other types of studies using pollen. This work is based on the Maguire pollen reference slide collection, initiated in the forties of the past century by Senior Curator B. Maguire of the New York Botanical Garden (NYBG) to make progress in biological research. Most genera and/or species studied here are endemic to the Guayana region or even to the Pantepui province or a single tepui.

Study area: Pantepui

In the local indigenous language (Pemón), “tepuí” means “stone bud”, and is the name for the characteristic sandstone/quartzite tabular mountains of Guayana (Fig. 2). They vary in altitude and extension, ranging from around 1100 to 3000 m (typically 2000–2600 m) of maximum elevation,

and with a surface of < 1 to > 1000 km² (typically 200–500 km²) (Huber, 1995a). The tepui summits are more or less flat and hold unique and specialized life forms and communities, as well as a high diversity and an amazing degree of endemism (Rull, 2009). This biotic singularity led to the creation of the Pantepui biogeographical province, which embraces all the tepui summits above 1500 m elevation (Huber, 1988, 1994). Vascular plants are the better known organisms of Pantepui, with almost 2500 species, of which > 60% are endemic to the Guayana region and > 40% are endemic to Pantepui, including 25% species endemic to a single tepui (Berry & Riina, 2005). Similarly, most tepuian vegetation types are unparalleled worldwide (Huber, 2005). Pantepui is mostly pristine due to its remoteness and inaccessibility; only a few of the tepui summits can be reached by foot after several days of walking and climbing. Indigenous people living in the surrounding lowlands and midlands do not visit the tepui summits because they consider them the home of gods and access is not allowed. On the other hand, there is no potential for commercial profit through activities such as mining, agriculture, cattle raising, etc. (Gorzula & Huber, 1992; Huber, 1995b). Tourism and biopiracy are restricted by severe regulations that, unfortunately, also hinder scientific research (Rull & Vegas-Vilarrúbia, 2008; Rull *et al.*, 2008a). The main threat for the Pantepui biota is global warming that, according to recent estimates, would determine significant biodiversity losses by upward migration and the corresponding habitat loss and fragmentation for many endemic species (Rull & Vegas-Vilarrúbia, 2006; Rull *et al.*, 2008b; Nogué *et al.*, 2009).

MATERIAL AND METHODS

Slides for this study are part of the Maguire pollen reference slide collection preserved in The New York Botanical Garden (NYBG; see <http://www.nybg.org/>). The collection comprises 3650 preparations of modern pollen representing 153 vascular plant families, of which 11 are non-seed plants. Some preparations include duplicate slides. Most vouchers are deposited in the Steere Herbarium of NYBG and can be viewed on-line (<http://www.nybg.org/>). The collection was initiated under the supervision of Senior Curator Bassett Maguire (1904–1991) to advance systematic, palynological, and medical studies. Research utilizing

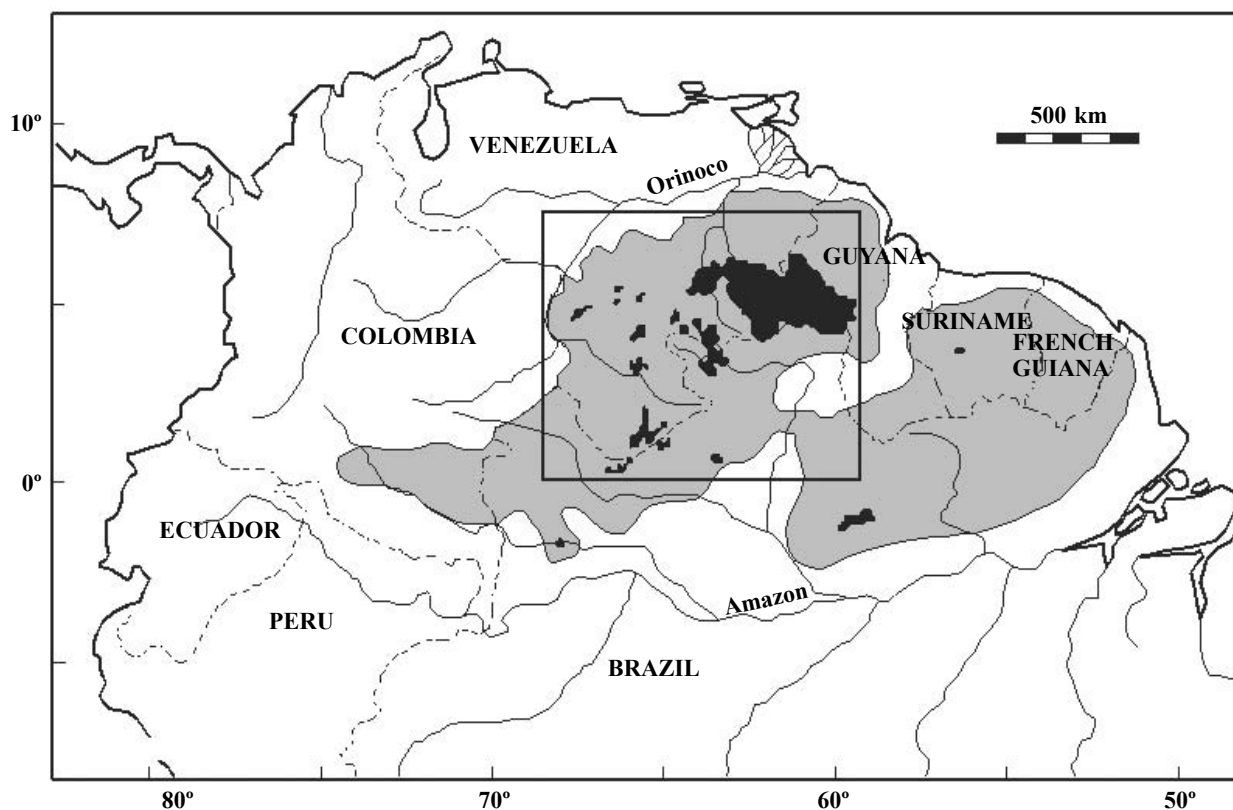


Figure 1. Map of northern South America, showing the approximate extension of the Guayana Shield (in grey) and the Precambrian sandstones and quartzites of the Roraima group (in black), on which the tepuis are modelled (Briceño & Schubert, 1990). The region under study (the Venezuelan Guayana) is indicated by a box.



Figure 2. Example of a tepui: picture of the Roraima tepui [Photograph by V. Rull].

these specimens will undoubtedly surpass the original objectives by serving fields as for example paleoecology, climate change or forensic studies, among others. The breadth of the collection is international in scope with the greatest geographic representation in tropical America, particularly the Guayana region of northern South America. Systematic strengths of the collection reflect Maguire's interest in plant groups with high species diversity or endemism in the Guayana (e.g., Clusiaceae, Gentianaceae, Rapateaceae, and Velloziaceae). Samples for the Maguire collection were mostly obtained from dried or fluid preserved collections housed at NYBG, but also include dried or fresh material as well as prepared slides from other institutions. Pollen grains were chemically treated with KOH, acetolysis, a combination of the two, or were untreated, and mounted in glycerin jelly. The slides are stored in vertical sleeves in a steel cabinet (see Howard & Boom, 1990, Fig. 11).

Measurements for this work have been taken in all the available well-preserved grains; the number of grains used in each case is indicated after the measurements ($n=x$). Measurements were taken using the photographic software DPXViewer 1.14.9 and a DeltaPix InfinityX camera. A number of species could not have been described because of the absence of suitable pollen grains due to bad preservation. These taxa are listed in the appendix for reference. Taxa are ordered alphabetically by families, following the classification of the Flora of the Venezuelan Guayana (Steyermark *et al.*, 1995-2005). For each plant species there is a morphological description accompanied by some photographs of the pollen grains found in the slide. The descriptions follow the Rull (2003) style for consistency, and use the standard nomenclature system of Punt *et al.* (2007). The title of every description summarizes the genus and species, the species authors, the pollen catalogue number, the collector, the collection location, as well as other information present on the label of the slide. Within the description, colpi and ora sizes are expressed as length x width (regarding the direction of the polar axis, in equatorial view), and grain size, as length of the polar axis x equatorial diameter. Also, the more recently accepted name of the species is noted where necessary, as well as the literature where pollen of other species of the same

genera from the Venezuelan Guayana are described, if any. The following abbreviations have been used in the text and descriptions: PV, polar view; EV, equatorial view; P/E, ratio of the length of the polar axis (P) to the equatorial diameter (E) (this ratio is the basis of a system of shape classes, Punt *et al.*, 2007). Finally, the photographs are ordered by pollen morphology (monads, tetrads and polyads, and the number and type of apertures). The scale bar in the plates is always 10 μm long, except for the images of *Moronobea jenmanii* Engl. in Mart. var. *fanshawei* Maguire and *Irlbachia cardonae* (Gleason) Maguire, where it is 20 μm long.

POLLEN DESCRIPTIONS

Asteraceae

Glossarion rhodanthum Maguire & Wurdack (Plate 1: 6-9)

(NY 2584; B. Maguire *et al.* 37126; Neblina)

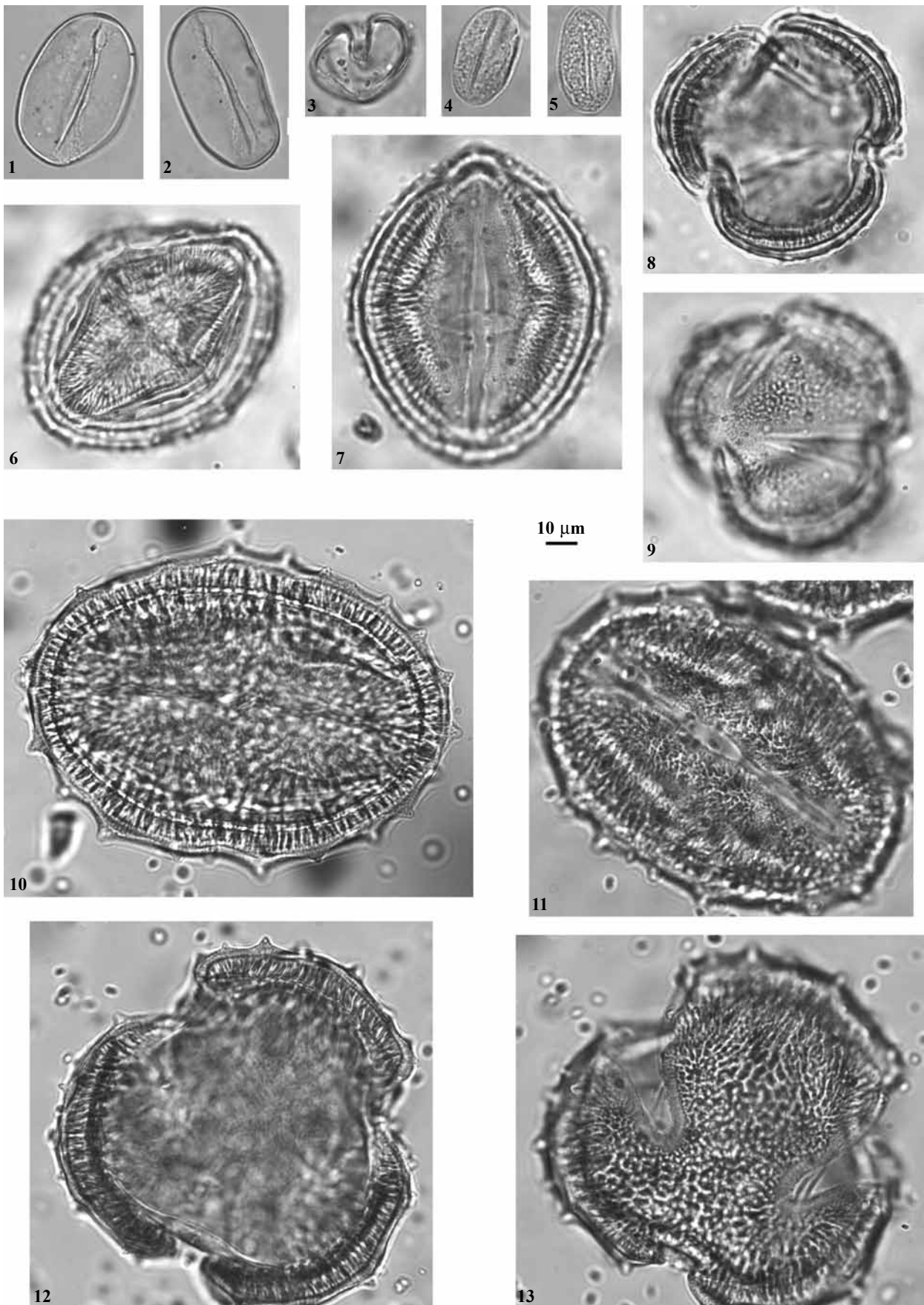
Monads. Isopolar, subprolate (P/E = 1.27), amb circular slightly lobate. Tricolporate, zonoaperturate. Ectocolpi long, sharp ends, fusiform (74.2 x 4.2 μm), marginate. Ora fusiform, lalongate (7.4 x 25.8 μm). Exine 8.8 μm thick (excluding spines), crescentic (in polar view, very thick exine in the medium of the intercolpium, gradually thinning towards the colpi), caveate, tectate, echinate, supracteal spines triangular (*ca.* 3 μm long and 3 μm wide at the base) with slightly rounded ends. Collumellae gradually more dense and/or smaller near the margo. Sexine thicker than nexine. Grain size (excluding spines): 89.8-102.8 x 71.4-80.5 μm , $n = 10$.

Gongylolepis benthamiana R. Schomb. (Plate 1: 10-13)

(NY 2586; T. Koyama & G. Agostini 7366; Venezuela)

Monads. Isopolar, subprolate to prolate (P/E = 1.33), amb circular slightly lobate. Tricolporate, zonoaperturate. Ectocolpi long, rounded ends, elliptic (83.2 x 4.2 μm), margo thick (4.0 μm), psilate. Ora elliptic, lolongate (19.9 x 12.3 μm). Exine 9.3 μm thick (excluding spines), caveate, tectate, echinate, supracteal spines triangular (*ca.* 4 μm long and *ca.* 5 μm at the base) with slightly

Plate 1. 1-3, *Kunhardtia rhodantha* (Rapateaceae); 4-5, *Barbacenia magalhaesii* (Velloziaceae); 6-9, *Glossarion rhodanthum* (Asteraceae); 10-13 *Gongylolepis benthamiana* (Asteraceae).



rounded ends. Sexine thicker than nexine. Grain size: 112.4-133.6 x 87.2-103.0 μm (excluding spines), $n = 11$.

***Stenopadus cucullatus* Maguire (Plate 2: 14-17) (NY 2592; B. Maguire & C. K. Maguire 35029; Venezuela)**

Monads. Isopolar, prolate (P/E = 1.53), amb circular slightly lobate. Tricolporate, zonoaperturate. Ectocolpi long, rounded ends, elliptic (74.8 x 3.7 μm), slightly marginate. Ora fusiform, lalongate (7.6 x 23.6 μm). Exine 3.1 μm thick, thicker at the poles (4.8 μm), tectate, psilate (columellae visible through the tectum). Sexine thicker than nexine. Grain size: 91.5-101.5 x 56.6-69.9 μm , $n = 11$.

Comments: *Stenopadus* sp. described in Rull (2003).

Bonnetiaceae

***Bonnetia celiae* Maguire (Plate 2: 18-21) (NY 957; B. Maguire 35327; Venezuela)**

Monads. Isopolar, subprolate (P/E = 1.31), amb sub-triangular, angulaperturate. Tricolporate, zonoaperturate. Ectocolpi long, sharp ends, fusiform (50.8 x 9.7 μm), marginate. Ora elliptic, lalongate (12.8 x 8.8 μm), annulus present. Exine 4.7 μm thick, semitectate, perforate. Sexine thicker than nexine. Grain size: 54.0-74.4 x 43.1-57.3 μm , $n = 9$.

Comments: *Bonnetia lanceifolia* Maguire, *B. roraimae* Oliver and *B. sessilis* Benth. are described in Salgado-Labouriau & Villar (1992) and Rull (2003).

***Bonnetia roraimae* Oliv. ex Thurn (Plate 2: 22-24) (104; Maguire 33421)**

Monads. Isopolar, oblate-spheroidal (P/E = 0.97), amb circular-triangular, angulaperturate. Tricolporate, zonoaperturate. Ectocolpi long, sharp ends, fusiform (27.4 μm x 3.8 μm). Ora circular (9.3 μm diameter), sometimes operculate. Exine 2 μm thick, semitectate, perforate. Sexine thicker than nexine. Grain size: 29.1-41.2 x 27.3-43.0 μm , $n = 6$.

Comments: *Bonnetia roraimae* is described in Salgado-Labouriau & Villar (1992) and Rull (2003).

Clethraceae

***Clethra alnifolia* L. (Plate 2: 25-28) (NY 3008; Martha's Vineyard, Mass, 18 Sept 1964; F. C. Mackoever)**

Monads. Isopolar, prolate-spheroidal (P/E = 1.13), amb circular. Tricolporate, zonoaperturate. Ectocolpi long (21.6 μm), shape difficult to distinguish. Ora lalongate, constricted, fastigium present. Exine 2.0 μm thick, tectate, psilate. Sexine and nexine approximately of the same thickness. Grain size: 25.9-32.9 x 23.4-30.1 μm , $n = 10$.

Comments: *Clethra guianensis* Klotzsch ex. Meisn. is described in Rull (2003).

Clusiaceae

***Clusia cochlitheca* Maguire (Plate 2: 29-30) (NY 3476; B. Maguire 36900)**

Monads. Amb triangular, angulaperturate. Tricolporate, operculate (operculum not always present), zonoaperturate. Ectocolpi short (12.3 μm), ora difficult to see. Exine 1.1 μm thick, semitectate, perforate. Sexine and nexine indistinguishable for measuring. Grain size: 28.3-32.7 μm , median in PV, $n = 5$.

Comments: Description based on grains in PV. *Clusia melchiorii* Gleason is described in Rull (2003).

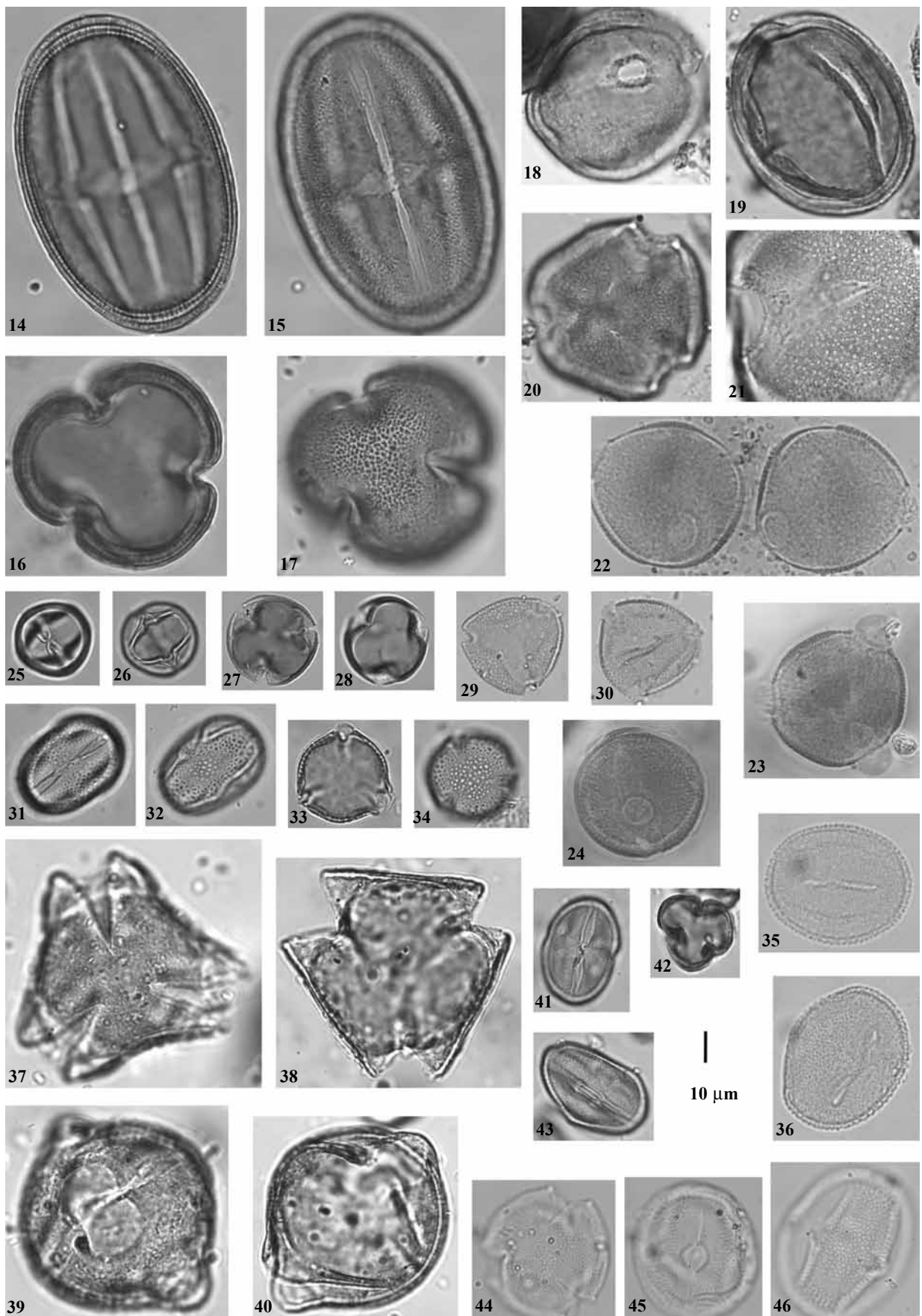
***Clusia orthoneura* Standl. (Plate 2: 31-34) (NY 3483; B. Maguire 62205)**

Monads. Isopolar, subprolate (P/E = 1.25), amb triangular-circular, angulaperturate. Tricolporate, operculate (operculum not always present), zonoaperturate. Ectocolpi long (29.5 μm), marginate, constricted in the equatorial region, sharp ends. Ora difficult to distinguish. Exine 1.8 μm thick, semitectate, reticulate, heterobrochate (lumina slightly smaller near the colpi). Sexine slightly thinner than nexine. Grain size: 31.5-37.6 x 25.3-32.4 μm , $n = 20$.

***Hypericum uliginosum* H. B. K. (Plate 2: 35-36) (NY 753; E. P. Killip & A. C. Smith 20487; Colombia)**

Monads. Isopolar, subprolate (P/E = 1.22).

Plate 2. 14-17, *Stenopadus cucullatus* (Asteraceae); 18-21, *Bonnetia celiae* (Bonnetiaceae); 22-24, *Bonnetia roraimae* (Bonnetiaceae); 25-28, *Clethra alnifolia* (Clethraceae); 29-30, *Clusia cochlitheca* (Clusiaceae); 31-34 *Clusia orthoneura* (Clusiaceae); 35-36, *Hypericum uliginosum* (Clusiaceae); 37-40, *Neotatea neblinae* (Clusiaceae); 41-43, *Tovomita weddelliana* (Clusiaceae); 44-46, *Tapeinostemon longiflorum* (Gentianaceae).



Tricolporate, zonoaperturate. Ectocolpi long (27.5 μm), rounded ends, marginate, ora difficult to see. Exine 2.3 μm thick, semitectate, perforate. Sexine thicker than nexine. Grain size: 46.5-51.4 x 38.5-41.6 μm , n = 4.

***Moronobea jenmanii* Engl. in Mart. var. *fanshawei* Maguire (Plate 3: 82-84)
(NY 2315; S. S. Tillett & C. L. Tillett 44904; B. Guiana)**

Monads. Isopolar, subprolate (P/E = 1.18), amb circular-quadrangular angulaperturate. Tetracolporate (sometimes pentacolporate), zonoaperturate. Ectocolpi 94.3 μm long and narrow. Ora difficult to see. Exine 4.7 μm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Grain size: 169.2-184.0 x 140.0-166.3 μm , n = 10.

***Neotatea neblinae* Maguire (Plate 2: 37-40)
(NY 2415; B. Maguire 42178; Neblina)**

Monads. Isopolar, prolate-spheroidal (P/E = 1.04), amb triangular, angulaperturate. Tricolporate, zonoaperturate. Ectocolpi long, fusiform, sharp ends (47.8 x 4.3 μm). Ora lalongate (15.1 x 28.3 μm), slightly constricted in the middle, fastigium present. Exine 3.3 μm thick, semitectate, perforate. Sexine slightly thicker than nexine. Grain size: 54.2-67.2 x 53.3-65.3 μm , n = 10.

***Tovomita weddelliana* Planch. & Triana (Plate 2: 41-43)
(NY 3528; L. Aristeguieta & G. Agostini 6344; Venezuela)**

Monads. Isopolar, prolate (P/E = 1.47), amb circular lobate, fossaperturate. Tricolporate, zonoaperturate. Ectocolpi long (28.0 μm), marginate, constricted in the equatorial region, sharp ends. Ora only visible in optical section. Exine 1.7 μm thick, semitectate, perforate. Sexine and nexine approximately of the same thickness. Grain size: 29.9-37.1 x 20.5-25.6 μm , n = 10.

Droseraceae

***Drosera roraimae* (Klotzsch ex Diels) Maguire (Plate 4: 89-91)
(NY 2781; B. Maguire 42338)**

Tetrads, uniplanar (rhomboidal and tetragonal) or multiplanar (decussate and tetrahedral). Individual grains inaperturate, heteropolar (distal pole clavate-microechinate and proximal pole conspicuously folded), oblate-suboblate (P/E = 0.75), amb subcircular. Exine 3.5 μm thick, intectate, microechinate and clavate. Sexine thicker than nexine. Individual grain size: 33.0-44.3 x 46.6-54.2 μm , n = 16. Tetrad diameter: 60.3-74.4 μm , n = 8.

Comments: *Drosera* sp. described in Salgado-Labouriau & Villar (1992) and Rull (2003).

Ericaceae

***Bejaria glauca* Humb. & Bonpl. var. *coarctata* Mansf. & Sleumer (Plate 4: 92-94)
(NY 1391; B. Maguire & C. K. Maguire # 44345; Ecuador)**

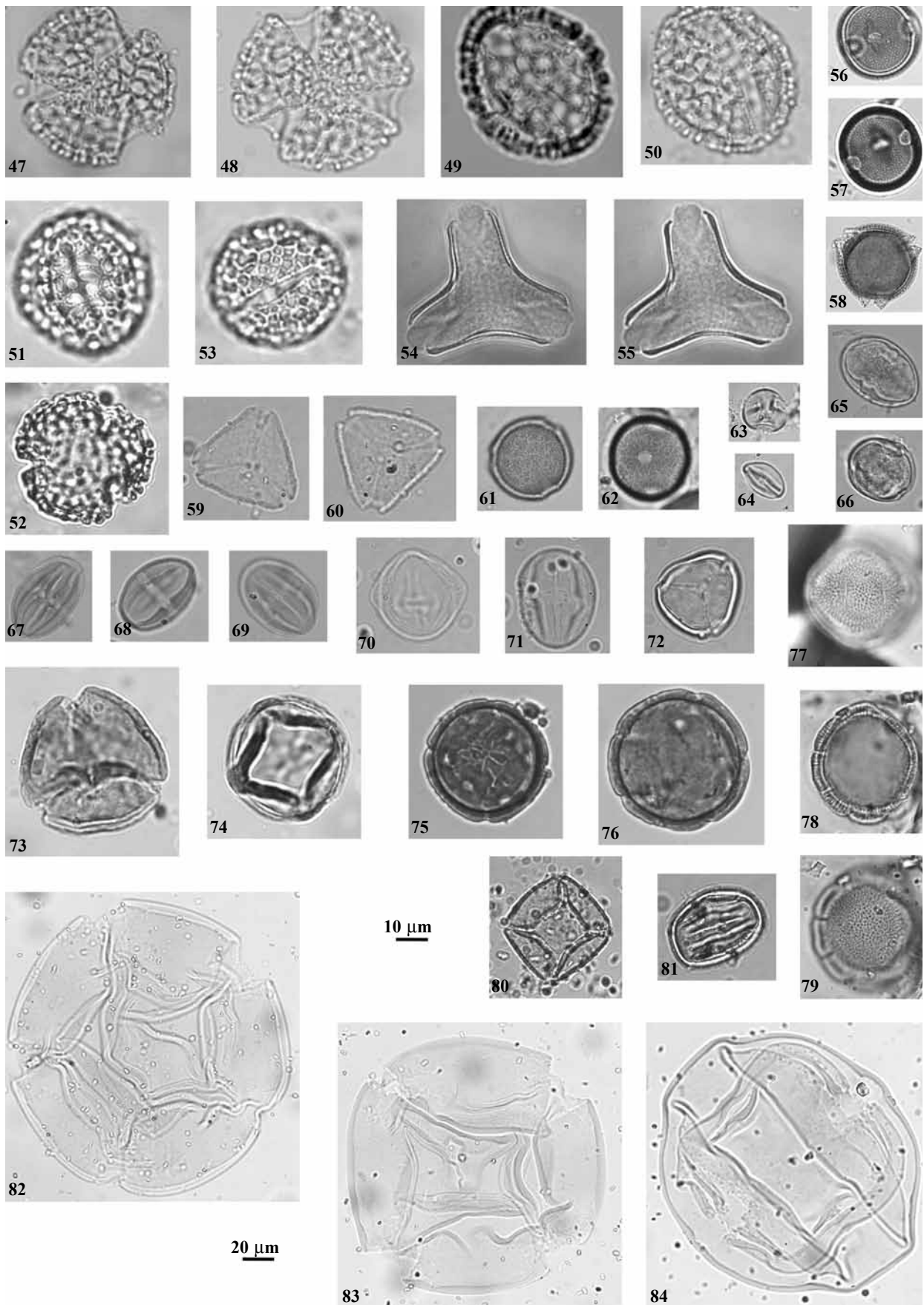
Tetrads, multiplanar, tetrahedral or decussate, outline circular slightly lobate. Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.74), amb circular, tricolporate. Half ectocolpi 8.1 μm long, narrow, slightly marginate. Ora difficult to distinguish. Exine 2.3 μm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 30.5-37.3 x 41.1-48.8 μm , n = 10. Tetrad diameter: 56.0-67.3 μm , n = 10.

Comments: *Bejaria aestuans* Mutis ex L., in Steyermark *et al.* (1995-2005).

***Cavendishia duidae* A. C. Sm. in Gleason (Plate 5: 104-105)
(NY 1399; Maguire *et al.* 29707; Venezuela)**

Tetrads, multiplanar tetrahedral or decussate, outline circular-triangular slightly lobate. Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.72), amb circular, tricolporate. Half ectocolpi

Plate 3. 47-50, *Chorisepalum ovatum* var. *ovatum* (Gentianaceae); 51-53, *Macrocarpaea neblinae* (Gentianaceae); 54-55, *Psittacanthus obovatus* (Loranthaceae); 56-58, *Diacidia galphimoides* (Malpighiaceae); 59-60, *Myrcia bolivarenses* (Myrtaceae); 61-62, *Ouratea gillyana* (Ochnaceae); 63-64, *Freziera sericea* (Ternstroemiaceae); 65-66, *Philacra duidae* (Ochnaceae); 67-69, *Philacra steyermarkii* (Ochnaceae); 70, *Poecilandra pumila* (Ochnaceae); 71, *Tyleria spathulata* (Ochnaceae); 72, *Schoepfia flexuosa* (Olacaceae); 73-74, *Duranta mutisii* (Verbenaceae); 75-76, *Banisteriopsis inebrians* (Malpighiaceae); 77-79, *Borreria laevis* (Rubiaceae); 80-81, *Heliamphora neblinae* var. *neblinae* (Sarraceniaceae); 82-84, *Moronobea jenmanii* var. *fanshawei* (Clusiaceae).



9.5 µm long, narrow, slightly marginate. Ora difficult to distinguish. Exine 1.6 µm thick, psilate, tectate. Sexine and nexine indistinguishable for measuring. Individual grain size: 32.2-38.2 x 40.8-55.4 µm, n=10. Tetrad diameter: 57.8-71.8 µm, n = 10.

***Disterigma humboldtii* Nied. (Plate 5: 108-110) (NY 1406; J. A. Steyermark, J. J. Wurdack 1156; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular-triangular. Viscin threads absent. Individual grains heteropolar, suboblate (P/E = 0.80), amb circular, tricolporate. Half ectocolpi 17.4 µm long, narrow, marginate. Ora difficult to distinguish. Exine 2.7 µm thick, psilate, tectate. Sexine and nexine indistinguishable for measuring. Individual grain size: 31.1-35.6 x 37.4-47.5 µm, n = 19. Tetrad diameter: 51.5-61.4 µm, n = 19.

***Ledothamnus atroadenus* Maguire, Steyererm. & Luteyn var. *atroadenus* (Plate 5: 111-112) (NY 1413; J. J. Wurdack # 34190; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular slightly lobate (sometimes triangular-circular). Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.73), amb circular, tricolporate. Half ectocolpi 10.8 µm long, narrow, marginate. Ora difficult to distinguish. Exine 2.8 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 28.8-34.6 x 40.2-45.8 µm, n=11. Tetrad diameter: 51.3-60.7 µm, n = 11.

Comments: *Ledothamnus luteus* Maguire, Steyererm. & Luteyn described in Salgado-Labouriau & Villar (1992) and Rull (2003).

***Mycerinus chimantensis* Maguire, Steyererm. & Luteyn (Plate 5: 106-107) (NY 1422; J. A. Steyermark & J. J. Wurdack 825; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular slightly lobate. Viscin threads absent. Individual grains heteropolar, suboblate (P/E = 0.84), amb circular, tricolporate. Half ectocolpi 16.8 µm long but often difficult to distinguish. Ora difficult to distinguish. Exine 2.2 µm thick, psilate, tectate. Sex-

ine and nexine approximately of the same thickness. Individual grain size: 39.3-48.4 x 43.6-53.6 µm, n = 10. Tetrad diameter: 71.6-80.5 µm, n = 7.

***Notopora schomburgkii* Hook.f. (Plate 6: 115-116) (NY 1668; B. Maguire *et al.* 46150A; British Guiana)**

Tetrads, multiplanar, tetrahedral or decussate, outline triangular or quadrangular. Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.74), amb circular, tricolporate. Half ectocolpi 20.3 µm long, narrow, marginate. Ora difficult to distinguish. Exine 3.1 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 40.5-49.9 x 56.5-63.7 µm, n = 10. Tetrad diameter: 75.7-90.4 µm, n = 10.

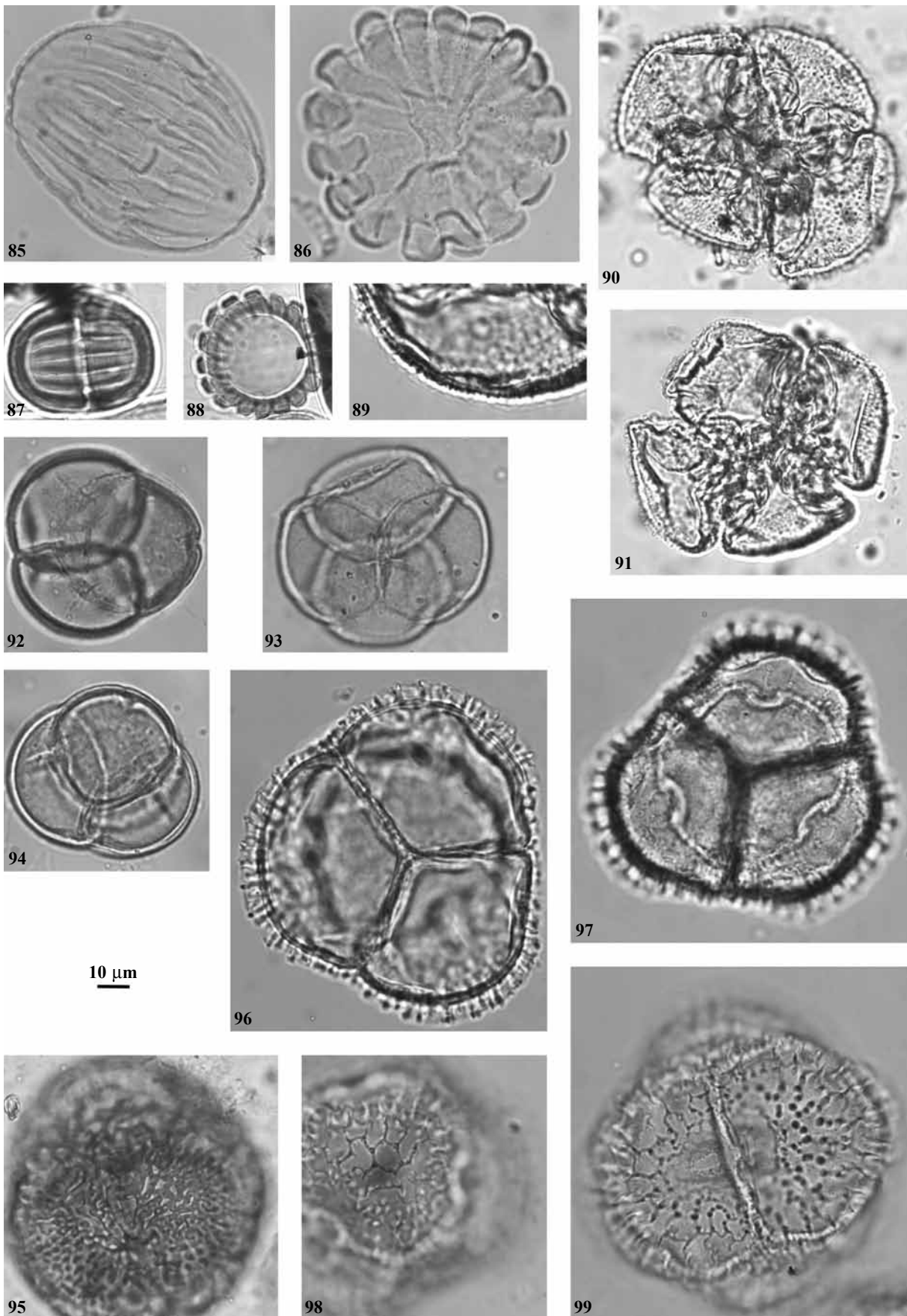
***Notopora smithiana* Steyererm. & Maguire (Plate 6: 117-120) (NY 3494; J. A. Steyermark & J. J. Wurdack 823; Chimantá, Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular-triangular. Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.72), amb circular, tricolporate. Half ectocolpi 19.1 µm long, 3.8 µm wide, sharp ends, sometimes appear narrow. Ora difficult to distinguish, probably lalongate (10.4 µm wide). Exine 2.9 µm thick, microrugulate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 37.3-42.1 x 52.5-59.0 µm, n = 11. Tetrad diameter: 70.1-77.3 µm, n = 11.

***Orthaea paruensis* Spruce (Plate 6: 121-124) (NY 1424; K. D. Phelps & C. B. Hitchcock 477; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular-triangular. Viscin threads absent. Individual grains heteropolar, suboblate (P/E = 0.77), amb circular, tricolporate. Half ectocolpi 13.6 µm long, narrow, marginate (half margo: 16.2 x 3.3 µm). Ora difficult to distinguish but they seem lalongate (10.7 µm wide). Exine 2.7 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 30.1-34.7 x 39.1-45.7 µm, n = 12. Tetrad diameter: 55.9-62.1 µm, n = 12.

Plate 4. 85-86, *Utricularia foliosa* (Lentibulariaceae); 87-88, *Monnina chanduyensis* (Polygalaceae); 89-91, *Drosera roraimae* (Droseraceae); 92-94, *Befaria glauca* var. *coarctata* (Ericaceae); 95, *Symbolanthus elisabethae* (Gentianaceae); 96-99, *Schultesia heterophylla* (Gentianaceae).



***Tepuia cardonae* A. C. Sm. (Plate 5: 113-114)
(NY 1671; J. A. Steyermark & J. J. Wurdack
1039; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular or subtriangular. Viscin threads absent. Individual grains heteropolar, oblate (P/E = 0.69), amb circular, tricolporate. Half ectocolpi 10.8 µm long, narrow. Ora difficult to distinguish. Exine 3.2 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 24.1-39.1 x 38.5-54.9 µm, n = 9. Tetrad diameter: 47.6-62.6 µm, n = 9.

Comments: *Tepuia venusta* Camp. described in Salgado-Labouriau & Villar (1992) and Rull (2003).

***Thibaudia cupatensis* Huber (Plate 6: 125-126)
(NY 1436; B. Maguire *et al.* # 42263; Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular, slightly lobate. Viscin threads absent. Individual grains heteropolar, suboblate (P/E = 0.76), amb circular, tricolporate. Half ectocolpi 16.8 µm long, narrow, marginate. Ora difficult to distinguish. Exine 2.4 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Individual grain size: 39.4-46.9 x 52.3-58.6 µm, n = 10. Tetrad diameter: 68.2-78.8 µm, n = 10.

Comments: *Thibaudia nutans* Klotzsch ex Mansf. described in Salgado-Labouriau & Villar (1992) and Rull (2003).

Gentianaceae

***Chorisepalum ovatum* Gleason var. *ovatum*
(Plate 3: 47-50)
(NY 2500; B. Maguire *et al.* 27921; Venezuela)**

Monads. Isopolar, subprolate (P/E = 1.21), amb circular. Tricolporate, zonoaperturate. Ectocolpi long and wide (36.1 x 3.9 µm), sharp ends, constricted at the equatorial region. Ora apparently lolongate, but difficult to distinguish. Exine 4.5 µm thick, semitectate, reticulate, irregularly heterobrochate (lumina smaller in polar regions), simplicolumellate. Sexine thicker than nexine. Grain size: 48.0-54.2 x 35.0-44.9 µm, n = 6.

***Irlbachia cardonae* (Gleason) Maguire (Plate 6:
127-129)
(NY 2531; B. Maguire *et al.* 33917; Venezuela)**

Polyad, constituted by 16 grains, outline circular. Individual grains heteropolar (only distal pole echinate), suboblate (P/E = 0.78), amb circular. Apertures difficult to distinguish due to the sculpture (Gentianaceae are normally tricolporate). Exine 4.7 µm thick (excluding spines), reticulate, semitectate, echinate (4-5 big curved spines per grain with rounded ends: 22.5 µm long, 13.4 µm base diameter), supracteal granula and verrucae irregularly distributed. Sexine thicker than nexine. Individual grain size: 43.0-57.8 x 56.9-69.7 µm, n = 7. Polyad diameter 190.9-210.2 µm (excluding spines), n = 5.

***Macrocarpaea neblinae* Maguire & Steyermark
(Plate 3: 51-53)
NY 2723; B. Maguire *et al.* 37103; Venezuela)**

Monads. Isopolar, prolate-spheroidal (P/E = 1.06), amb circular. Tricolporate, zonoaperturate. Ectocolpi long, sharp ends, sometimes slightly rounded, fusiform (28.5 x 2.3 µm), marginate. Ora elliptic (6.5 x 4.3 µm), lolongate. Exine 3.8 µm thick, semitectate, reticulate irregularly heterobrochate, simplicolumellate. Sexine thicker than nexine. Grain size: 41.7-45.1 x 38.8-43.0 µm, n = 10.

Comments: *Macrocarpaea tepuiensis* (Gleason) Steyermark described in Rull (2003).

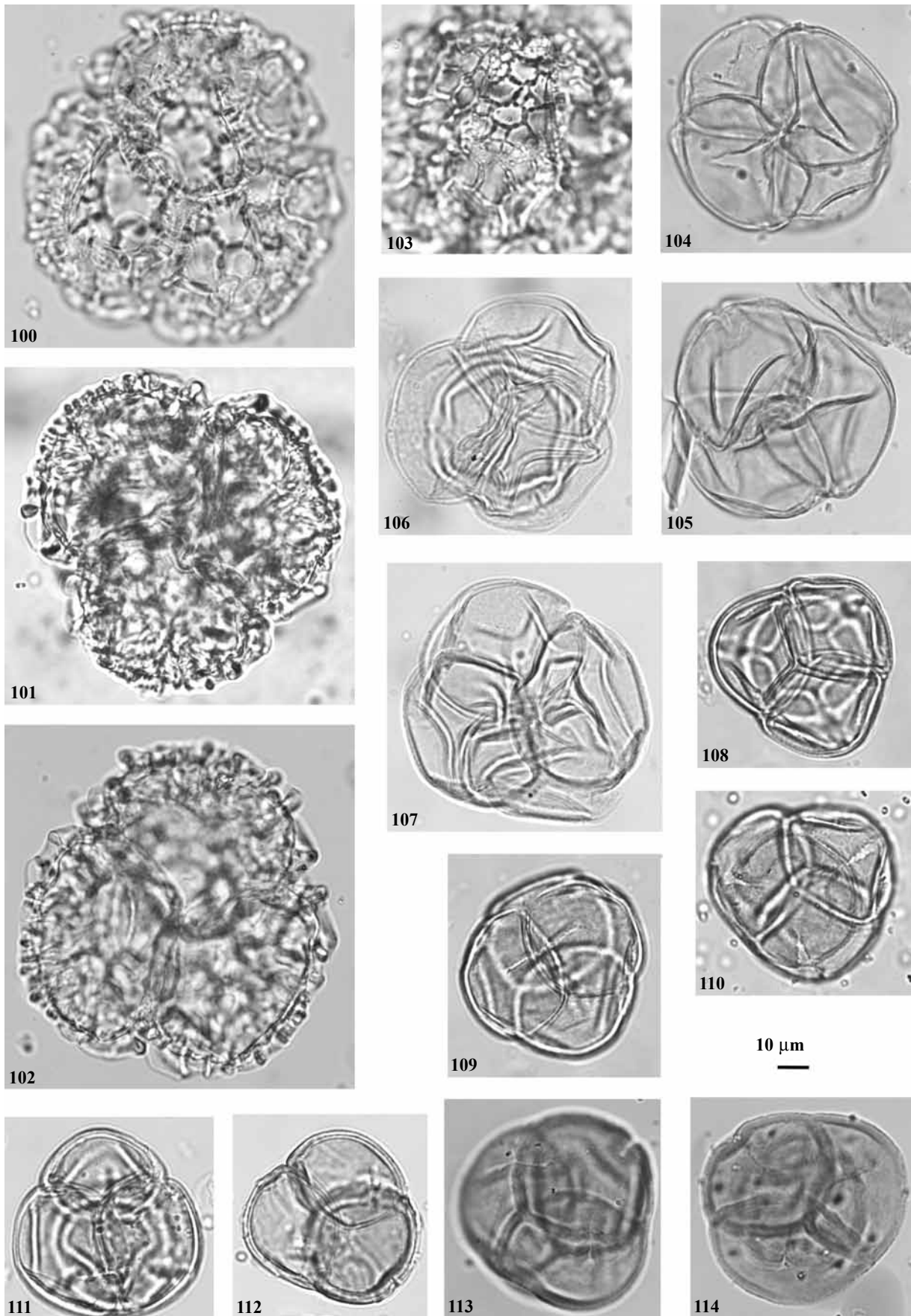
***Neblinantha neblinae* Maguire (Plate 5: 100-103)
(NY 2541; B. Maguire *et al.* 60527; Neblina)**

Tetrads, multiplanar, tetrahedral or decussate. Individual grains heteropolar, oblate (P/E = 0.72), amb circular-slightly lobate. Tricolporate, colpi and ora difficult to observe due to the sculpture pattern. Exine 7.7 mm thick, semitectate, reticulate, heterobrochate, simplicolumellate. Sexine thicker than nexine. Individual grain size: 47.5-54.0 x 63.2-77.9 µm, n = 10. Tetrad diameter: 90.3-103.8 µm, n = 10.

***Schultesia heterophylla* Miq. (Plate 4: 96-99)
(NY 2565; J. J. Wurdack & N. G. L. Guppy 15;
Venezuela)**

Tetrads, multiplanar, tetrahedral or decussate, outline circular-triangular. Individual grains hetero-

Plate 5. 100-103, *Neblinantha neblinae* (Gentianaceae); 104-105, *Cavendishia duidae* (Ericaceae); 106-107, *Mycerinus chimantensis* (Ericaceae); 108-110, *Disterigma humboldtii* (Ericaceae); 111-112, *Ledothamnus atroadenus* var. *atroadenus* (Ericaceae); 113-114, *Tepuia cardonae* (Ericaceae).



polar, oblate to suboblate ($P/E = 0.75$), amb circular. Triporate, pori elliptic ($7.2 \mu\text{m}$ long, $8.9 \mu\text{m}$ wide), annulate. Exine $8.0 \mu\text{m}$ thick, semitectate, reticulate heterobrochate. Sexine thicker than nexine. Individual grain size: $46.7\text{-}54.0 \times 63.4\text{-}73.3 \mu\text{m}$, $n = 11$. Tetrad diameter: $88.3\text{-}97.9 \mu\text{m}$, $n = 11$.

***Symbolanthus elisabethae* Gilg (Plate 4: 95)
(NY 1266; J. A. Steyermark 75662; Venezuela,
Bolivar, June 1953)**

Tetrads, multiplanar, tetrahedral or decussate. Apertures difficult to observe due to the sculptural pattern. Exine $5\text{-}6 \mu\text{m}$ thick, semitectate, reticulate heterobrochate, simplicolumellate. Sexine thicker than nexine. Tetrad diameter: $85.8\text{-}90.0 \mu\text{m}$, $n = 4$.

***Tapeinostemon longiflorum* Maguire & Steyermark
(Plate 2: 44-46)**

(NY 2579; J. A. Steyermark 103937; Venezuela)

Monads. Isopolar, subprolate ($P/E = 1.30$), amb circular. Tricolporate, zonoaperturate. Ectocolpi long ($30.3 \mu\text{m}$) and narrow, sharp ends. Ora circular ($6.4 \mu\text{m}$ diameter). Exine $3.0 \mu\text{m}$ thick, semitectate, perforate. Sexine thicker than nexine. Grain size: $43.3\text{-}53.9 \times 35.6\text{-}42.0 \mu\text{m}$, $n = 6$.

Lentibulariaceae

***Utricularia foliosa* L. (Plate 4: 85-86)**

(NY 1646; E. Asplund 5793; Ecuador)

Monads. Isopolar, subprolate ($P/E = 1.29$), amb circular slightly multilobate. Polyzonocolporate (17 apertures). Ectocolpi long ($68.7 \mu\text{m}$) and narrow, endocingulum present (zonorate). Exine $2.0 \mu\text{m}$ thick, psilate. Sexine and nexine indistinguishable. Grain size: $81.63\text{-}88.1 \times 63.9\text{-}66.5 \mu\text{m}$, $n = 3$.

Comments: *Utricularia quelchii* N. E. Brown described in Rull (2003) and Salgado-Labouriau & Villar (1992).

Loranthaceae

***Psittacanthus obovatus* Eichl. (Plate 3: 54-55)**

(NY 1612; P. C. Hutchinson 1363 H. G. H.; Peru)

Monads. Amb subtriangular concave, angulaper-

turate. Tricolp(or)ate, zonoaperturate, syncolp(or)ate. Exine psilate, tectate.

Comments: One single pollen grain found (PV).

Malpighiaceae

***Banisteriopsis inebrians* C. V. Morton (Plate 3: 75-76)**

(NY 2703; B. A. Krukoff-8550; Brazil)

Monads. Spheroidal. Pantoporate, with irregular colpoids in several directions. Pori elliptic ($3.4 \times 2.1 \mu\text{m}$), with diffuse outline. Exine $3.8 \mu\text{m}$ thick, tectate, psilate. Sexine thicker than nexine. Grain diameter: $37.5\text{-}46.2 \mu\text{m}$, $n = 10$.

***Diacidia galphimoides* Griseb (Plate 3: 56-58)
(NY 670; B. Maguire 44091)**

Monads. Isopolar, prolate-spheroidal ($P/E = 1.04$), amb circular-triangular, angulaperturate. Tricolporate, zonoaperturate. Ectocolpi short, sharp ends, fusiform ($13.2 \times 3.2 \mu\text{m}$). Ora elliptic, lalongate ($4.4 \times 6.2 \mu\text{m}$), fastigium present. Exine $1.7 \mu\text{m}$ thick, semitectate, reticulate heterobrochate, lumina size decreasing towards the apertures and the polar region. Nexine slightly thicker than sexine. Grain size: $24.7\text{-}28.9 \times 22.9\text{-}27.4 \mu\text{m}$, $n = 11$.

Comments: The slide has the epithet *duckei*, however this name was never published.

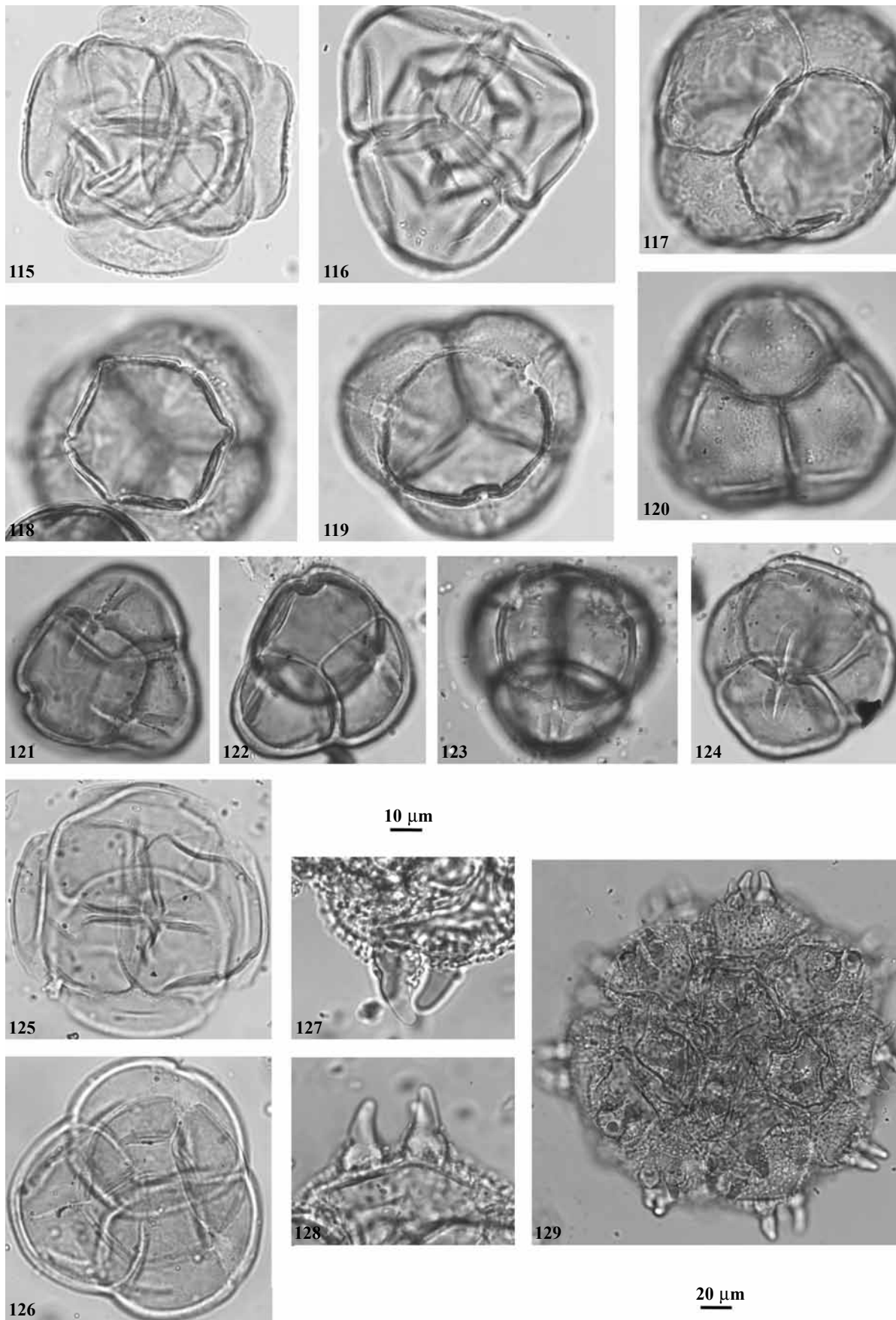
Myrtaceae

***Myrcia bolivarensis* (Steyermark.) McVaugh (Plate 3: 59-60)**

(NY 2193; S. S. Tillett & C. L. Tillett 45012; B. Guiana)

Monads. Isopolar, amb triangular, angulaperturate. Tricolporate, syncolporate. Exine $1.7 \mu\text{m}$ thick, reticulate or areolate with undulating surface (difficult to observe due to bad preservation). Sexine and nexine difficult to distinguish for measuring. Grain size: $29.2\text{-}33.8 \mu\text{m}$, median in PV, $n = 10$.

Comments: Description based on grains in PV. *Myrcia bonnetia-sylvestris* (Steyermark.) Steyermark described in Salgado-Labouriau & Villar (1992) and Rull (2003).



Ochnaceae

Ouratea gillyana (Dwyer) Sandwith & Maguire (Plate 3: 61-62)

(B. Maguire & D. B. Fanshawe 32629; 311)

Monads. Isopolar, spheroidal (P/E = 1.00), amb circular. Tricolporate, zonoaperturate. Ectocolpi apparently fusiform but difficult to observe (9.9 µm long, n=2), ora slightly elliptic lalongate (4.7 x 3.9 µm). Exine 1.4 µm thick, psilate and tectate (columellae visible through the tectum). Sexine and nexine approximately of the same thickness. Grain size: 23.2-26.7 x 23.1-27.1 µm, n = 10.

Philacra duidae (Gleason) Dwyer (Plate 3: 65-66) (NY 279; G. H. H. Tate 529)

Monads. Isopolar, prolate (P/E = 1.36), amb circular. Tricolporate, zonoaperturate. Ectocolpi long (19.5 µm) and narrow. Ora elliptic, lalongate: 3.5 µm long (n = 7) x 7.9 µm wide (n = 4). Exine 1.0 µm thick, psilate and tectate (columellae visible through the tectum). Sexine and nexine indistinguishable for measuring. Grain size: 24.2-26.9 x 17.9-19.3 µm, n = 10.

Philacra steyermarkii Maguire (Plate 3: 67-69) (NY 277; J. A. Steyermark 93615)

Monads. Isopolar, prolate (P/E = 1.40), amb apparently circular-triangular, angulaperturate. Tricolporate, zonoaperturate. Ectocolpi long (21.9 µm) and narrow, constricted in the equatorial region. Ora elliptic, lalongate (3.4 x 7.9 µm), sometimes constricted. Exine 1.6 µm thick, psilate and tectate (columellae visible through the tectum). Sexine and nexine approximately of the same thickness. Grain size: 26.2-31.1 x 18.6-22.1 µm, n = 12.

Poecilandra pumila Steyermark (Plate 3: 70) (NY 297; B. Maguire & S. S. Tillett 43800)

Monads. Isopolar, oblate-spheroidal (P/E = 0.99), amb circular. Tricolporate, zonoaperturate. Ectocolpi long (21.2 µm) and narrow, ora apparently elliptic lalongate, fastigium present. Exine 1.3 µm thick, psilate and tectate. Sexine and nexine indistinguishable for measuring. Grain size: 27.3-32.2 x 26.6-31.7 µm, n = 10.

Tyleria spathulata Gleason (Plate 3: 71) (NY 295; B. Maguire *et al.* 30092)

Monads. Isopolar, prolate-spheroidal (P/E = 1.13), amb circular slightly lobate. Tricolporate, zonoaperturate. Ectocolpi long (23.4 µm, n = 3) and narrow (2.0

µm, n = 1), sharp ends, slightly marginate. Ora elliptic, lalongate (3.2 x 6.4, n = 1). Exine 1.3 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Grain size: 24.0-32.5 x 20.2-26.4 µm, n = 11.

Olacaceae

Schoepfia flexuosa Roem. & Schult. (Plate 3: 72) (NY 3037; J. A. Steyermark & J. J. Wurdack 326, Feb. 2, 1955; Chimantá, Venezuela)

Monads. Isopolar, amb triangular-rounded, angulaperturate. Tricolporate, syncolporate. Exine 1.52 µm thick (measured in PV), psilate. Sexine and nexine approximately of the same thickness. Grain size: 25.7-32.1 µm, median in PV, n = 6.

Comments: Described in Maguire *et al.* (1974), on the same slide.

Polygalaceae

Monnina chanduyensis Chod. (Plate 4: 87-88) (NY 809; F. W. Pennell 14467; Peru)

Monads. Isopolar, prolate (P/E = 1.34), amb circular slightly multilobate. Polyzonocolporate (17 colpori). Ectocolpi long (34.4 µm) and narrow, endocingulum present (zonorate). Exine 4.0 µm thick, psilate to slightly scabrate, tectate (columellae visible through the tectum). Nexine thicker than sexine. Grain size: 45.7-52.7 x 30.8-39.5 µm, n = 6.

Rapateaceae

Kunhardtia rhodantha Maguire (Plate 1: 1-3) (NY 3056; B. Maguire & L. Politi 27954; Cerro Sipapo, Venezuela, Jan. 1, 1949)

Monads. Heteropolar, oblate (P/E = 0.65). Monosulcate, sulcus long (39.8 µm). Exine 1.5 µm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Grain size: 27.4-36.9 x 33.0-56.6 µm, n = 10.

Comments: Described in Carlquist (1961).

Rubiaceae

Borreria laevis (Lam.) Griseb. (Plate 3: 77-79) (NY 815; H. H. Smith 87; Colombia)

Monads. Isopolar, oblate-spheroidal (P/E = 0.94), amb circular. Polyzonocolporate (9 colpi), short and narrow (5.4 µm long, 0.8 µm wide), ends sharp.

Exine 2.7 μm thick, tectate, psilate (columellae visible through the tectum). Sexine thicker than nexine. Grain size: 29.8-36.6 x 30.8-38.5 μm , $n = 8$.

Comments: *Borreria remota* (Lam.) Bacigalupo & E. L. Cabral, in Steyermark *et al.* (1995-2005).

Sarraceniaceae

Heliamphora neblinae Maguire var. *neblinae* (Plate 3: 80-81)

(NY 2736; B. Maguire *et al.* 37019; Venezuela)

Monads. Isopolar, prolate (P/E = 1.41), amb usually quadrangular, angulaperturate. Tretracolporate, zonoaperturate. Ectocolpi long (20.3 μm) and narrow. Os indistinct, sometimes visible in optical section. Exine 1.3 μm thick, psilate, tectate. Sexine and nexine approximately of the same thickness. Grain size: 30.0-31.2 x 21.4-22.8 μm , $n = 3$.

Comments: *Heliamphora minor* Gleason described in Salgado-Labouriau & Villar (1992) and Rull (2003).

Ternstroemiaceae

Freziera sericea Humb. & Bonpl. (Plate 3: 63-64) (NY 209; 892)

Monads. Isopolar, prolate (P/E = 1.46), amb circular. Tricolporate, zonoaperturate. Ectocolpi long (11.7 μm) and narrow, os indistinct. Exine 0.7 μm thick, psilate. Sexine and nexine indistinguishable for measuring. Grain size: 14.0-15.5 x 9.3-11.2 μm , $n = 10$.

Comments: *Eurya sericea* (Kunth) Szyszyl., in Hokche *et al.* (2008).

Velloziaceae

Barbacenia magalhaesii L. B. Sm. (Plate 1:4-5) (NY 438; B. Maguire *et al.* 49062; Brazil)

Monads. Heteropolar, oblate (P/E = 0.61). Mono-sulcate, sulcus long. Exine < 1 μm thick, perforate. Sexine and nexine indistinguishable for measuring. Grain size: 16.9-24.6 x 30.6-36.4 μm , $n = 5$.

Verbenaceae

Duranta mutisii L. f. (Plate 3: 73-74) (NY 1526; W. H. Camp E-5203, Ecuador)

Monads. Isopolar, spheroidal (P/E = 1.00), amb triangular, angulaperturate. Tricolporate, zonoaper-

turate. Ectocolpi long, sharp ends. Exine 3.8 μm thick, psilate, tectate. Sexine thicker than nexine. Grain size: 39.7-42.6 x 40.7-40.9 μm , $n = 3$.

Comments: *Duranta obtusifolia*, in Steyermark *et al.* (1995-2005).

ACKNOWLEDGEMENTS

The authors are grateful to O. Huber, who noticed the existence of the Maguire pollen collection and encouraged its study. The comments of one anonymous reviewer contributed to the improvement of the manuscript. Funding was provided by the Higher Council for Scientific Research (CSIC) of Spain and the Biological Sciences Commission of the Institute for Catalan Studies (IEC).

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Appendix. List of species/slides of the Maguire collection analyzed, which pollen grains are unsuitable for a morphological study.

<p>Acanthaceae <i>Justicia carthaginensis</i> Jacq. (NY 846; O. L. Haught 4753; Colombia)</p>
<p>Annonaceae <i>Duguetia riberensis</i> Aristeg. ex Mass & Boon (NY 658; L. Aristeguieta 5308; S. America)</p>
<p>Boraginaceae <i>Cordia leucophylctis</i> Hook. f. (NY 862; Chapin 1125; Indefatigable Is., Galapagos)</p>
<p>Cyatheaceae <i>Cyathea arborea</i> (L.) Sm. (NY 2995; E. L. Little, Jr., 22 June 1950; El Verde, Puerto Rico)</p>
<p>Dennstaedtiaceae <i>Hypolepis repens</i> (L.) Presl. (NY 1546; Cuatrecasas 16092; Colombia)</p>
<p>Dryopteridaceae <i>Diplazium lindbergii</i> (Mett.) Christ (NY 1524; Holdridge 1608; Ecuador)</p>
<p>Fabaceae <i>Inga</i> aff. <i>punctata</i> Willd. (NY 769; G. Tessmann 3443; Peru)</p>
<p>Lamiaceae <i>Hyptis capitata</i> Jacq. (NY 754; Toro 44; Colombia)</p>
<p>Myrsinaceae <i>Cybianthus brownii</i> Gleason (NYBG 2363; Maguire 32104; Brit Guiana)</p>
<p>Myrtaceae <i>Eugenia florida</i> D. C. (NY 2170; H. S. Irwin et al. 55206; Suriname)</p>
<p>Ochnaceae <i>Elvasia quinqueloba</i> Spruce (# 34812; B. Maguire & J. J. Wurdack, 287)</p>