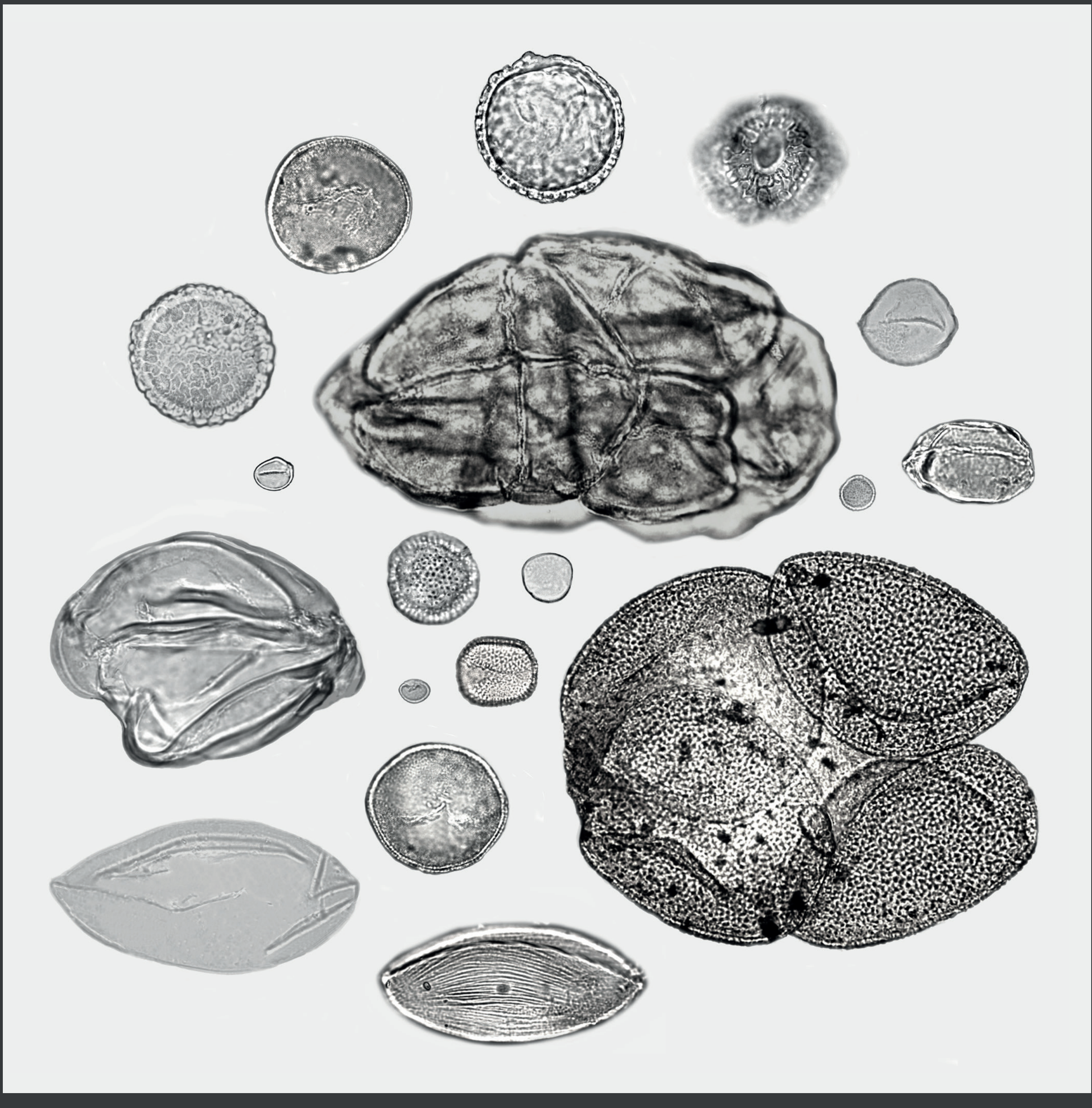
CATALOG OF ANGIOSPERM POLLEN GRAINS FROM THE RIO GRANDE DO SUL FLORA, SOUTHERN BRAZIL

VOL. 1
ANA GRADE AND MAGNOLIIDS

Maria Luisa Lorscheitter and Rinaldo Pires dos Santos



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Introduction

Only some of the pollen grains released by anthers and dispersed in the atmosphere pollinate angiosperm flowers. At the end of this journey, pollen grains deposited on the stigma of viable flowers of the same species germinate, initiating the development of an adult androphyte, which is responsible for the formation of the male gamete. The other grains are lost in the atmosphere and are deposited randomly in different environments.

Pollination is generally a long and dangerous journey, which could dry out fragile pollen grains. However, the outer resistant and protective pollen wall, the exine, is formed by sporopollenin, which is a highly resistant biological material.

Angiosperm pollen grains are spheroidal or elongated, with or without apertures, where differentiated exine facilitates germination. The apertures also allow volume-change accommodations with varying humidity, the harmomegathy (Walker 1976).

The exine structure of most angiosperm pollen grains is composed of sexine (tectum and columellae) and nexine, with distinct morphologies, depending on the taxon (Walker & Doyle 1975). The exine surface can be smooth (psilate) to densely ornamented, depending on the vector that transports the pollen grain, such as wind (smooth surface: anemophily), animal (ornate surface: zoophily), or water (smooth surface: hydrophily).

All morphological features of the pollen grain wall are genetically determined. Thus, the combination of the shape of the grain, number, position, and characteristics of the apertures, the type of structure, and the ornamentation of the exine define the species or their group (Erdtman 1952).

The resistance of the exine allows many pollen types to be preserved in appropriate sediments for quantitative palynological analyses (Birks & Birks 1980; Birks & Gordon 1985; Berglund 1986). Therefore, pollen grains are excellent working tools for reconstructing the paleoenvironment and can indicate the sequence of past environments over geological time.

The palynology of Quaternary sediments, which is aimed at reconstituting the paleoenvironment of the last millennia in the Coastal Plain and the East Plateau of Rio Grande do Sul, was conducted at the Laboratory of Palynology, Department of Botany, Institute of Biosciences, Federal University of Rio Grande do Sul (Lorscheitter 1983; Lorscheitter & Romero 1985; Lorscheitter 1992, Roth & Lorscheitter 1993; Cordeiro & Lorscheitter 1994; Neves & Lorscheitter 1995; Lorscheitter 1997; Lorscheitter & Dillemburg 1998; Lorscheitter 2003; Leal & Lorscheitter 2007; Leonhardt & Lorscheitter 2010; Scherer & Lorscheitter 2014; Spalding & Lorscheitter 2015; Masetto & Lorscheitter 2019; Roth *et al.* 2021). A reference palynological collection of the current flora of Rio Grande do Sul was essential to identify the spores and pollen preserved in these sediments. The objective of the present study was to report a catalog of angiosperm photomicrographs of this reference pollen collection, to subsidize palynological studies, particularly those in southern Brazil.

Methods

The current reference pollen presented here for paleoenvironmental analyses was extracted from exsiccate at the ICN (Instituto de Ciências Naturais) Herbarium, Department of Botany, which contains species from the flora of Rio Grande do Sul.

All reference pollen material was collected directly from the herbarium exsiccate using a magnifying glass, and the sample (anthers) was placed in a 10 ml glass centrifuge tube. Information about the exsiccate was recorded in a book, including the respective species number of the reference pollen collected and of the ICN herbarium. The samples were chemically processed by acetolysis (Faegri & Iversen 1975), with subsequent filtering of the material through 250 µm mesh. Five permanent slides were mounted for each species in glycerol-jelly (Salgado-Labouriau 1973; Faegri & Iversen 1975).

Light microscopy (DIAPAN; Leica Microsystems, Wetzlar, Germany) was used for microscopic analyses and photomicrographs. The photomicrographs were taken with a digital camera (DFC295; Leica Microsystems) connected to the microscope.

The polar axis and equatorial diameter of 10 grains were measured for each pollen species, and the average was used to obtain an approximate size. In grains with two equatorial diameters, only the largest equatorial diameter was measured. Only the diameter of the spheroidal grains was measured. Measurements were always taken within 1 week after acetolysis due to the subsequent tendency for an increase in the exine over time until the volume stabilized (Salgado-Labouriau 1973). This trend may explain why certain photomicrographs had larger pollen grain sizes than indicated in the averages, as they were taken after the respective measurements, but preserved the original morphology.

The species were named following the Missouri Botanical Garden (MOBOT) nomenclature (2023), and pollen terminology was based on Punt *et al.* (2007).

The general taxonomic ordering of the pollen material was that of APG IV (Angiosperm Phylogeny Group version IV) Byng *et al.* (2016), in the form of a catalog of photomicrographs. The taxa sequence was the same as in the APP (Angiosperm Phylogeny Poster) Cole *et al.* (2017), according to APG IV. A band with the same color as the respective APP clade was placed along the margin of each page of the catalog.

The legend of each pollen grain photomicrograph contained the name of the species, the registration number of the reference collection (left) and of the ICN Herbarium, an equatorial or polar view of the grain and respective plane of focus, and the shape of the grain, to enable a comparison. The number, position, and characteristics of apertures in the aperturate grains are indicated. The legend also includes the type of ornamentation and the average pollen grain measurements in micrometers (P = polar axis, EQ = greatest equatorial diameter). Only the grain diameter is indicated for spheroidal grains.

Characteristics of the pollen grains

The 19 species analyzed had pollen grains with a polar axis equal to or smaller than the equatorial diameter and were, therefore, spheroidal, sub-spheroidal, oblate, or peroblate. These morphological types of pollen are characteristic of primitive groups of angiosperms, although they can also occur in derived taxa.

Grains without an aperture (primitive inaperturate) were found among the pollen analyzed (6 species), but most of the others had bilateral symmetry and an elongated latitudinal aperture, the sulcus, which was parallel to the equatorial diameter and located at the distal pole, the anasulcate aperture (9 species). Other grains were sulcoidate (3 species), with an undefined sulcus. Anasulcate pollen is the most primitive and common type of pollen among primitive angiosperms, being rivaled in frequency only by primitive inaperturate pollen (Walker 1974). This anasulcate aperture characterizes *Clavatipollenites*, which represents one of the oldest fossil records of angiosperm pollen from the Lower Cretaceous in Barremian rocks, indicating its primitive condition (Hughes 1976; Walker 1976; Cronquist 1981).

Only *Drimys brasiliensis* Miers presented a circular derived aperture, the ulcus, which is primitive in terms of the location at the distal pole, the ana-ulcerate grain (characteristic of the genus). Another derived feature in *Drimys* is the arrangement of the grains in tight tetrads. Loose tetrads were observed in *Annona cacans* Warm. and *Xylopia grandiflora* A. St.-Hil. The grains were grouped in dense and elongated polyads in *Xylopia brasiliensis* Spreng.

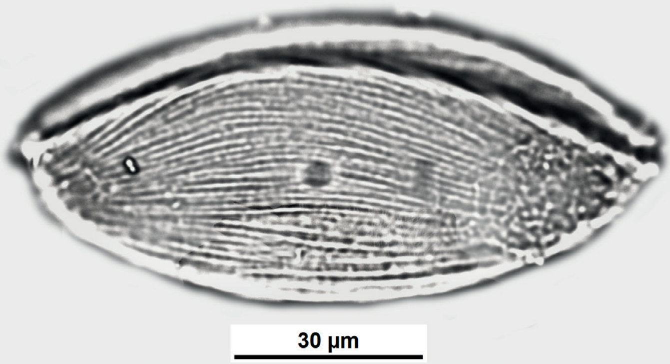
The sculpturing (ornamentation) of the pollen grains was generally very small and delicate, including those that were scabrate, striate, spinulose, microverrucate, reticulate (suprareticulate?), rugulate, or psilate. The psilate condition appears to represent the basic type of exine surface in primitive angiosperms (Walker 1976). Coarsely eureticulate grains were observed only in *D. brasiliensis*.

The primitive characteristics found in the material followed the taxonomic groups of APG IV (Byng *et al.* 2016) and APP (Cole *et al.* 2017), with ANA GRADE “EARLY ANGIOSPERMS” and MAGNOLIIDS, where the orders are included. In the APP (Cole *et al*. 2017) one of the characteristics indicated for these most primitive groups of angiosperms is the monosulcate pollen (an elongated latitudinal aperture, but without information about its position in the grain). The monosulcate grains analyzed here were all anasulcate.

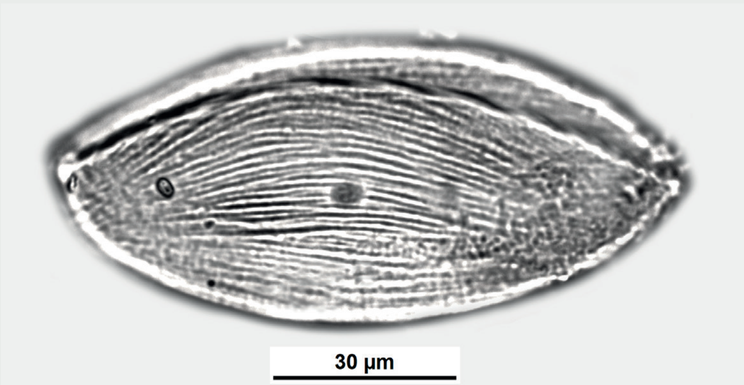
These results confirm the contribution of pollen morphology to the evolutionary understanding of primitive angiosperms.

On the next pages is the catalog containing photomicrographs of the 19 species studied, according to the ANA GRADE and MAGNOLIIDS in the APP (Cole *et al.* 2017).

Cabombaceae



Cabomba australis Speg.
793 – ICN 49881
Equatorial view: first plane
Oblate - Anasulcate - Striate
P $\bar{x}$= 54 µm EQ $\bar{x}$= 104 µm



Cabomba australis Speg.
793 – ICN 49881
Equatorial view: second plane
Oblate - Anasulcate - Striate
P $\bar{x}$= 54 µm EQ $\bar{x}$= 104 µm

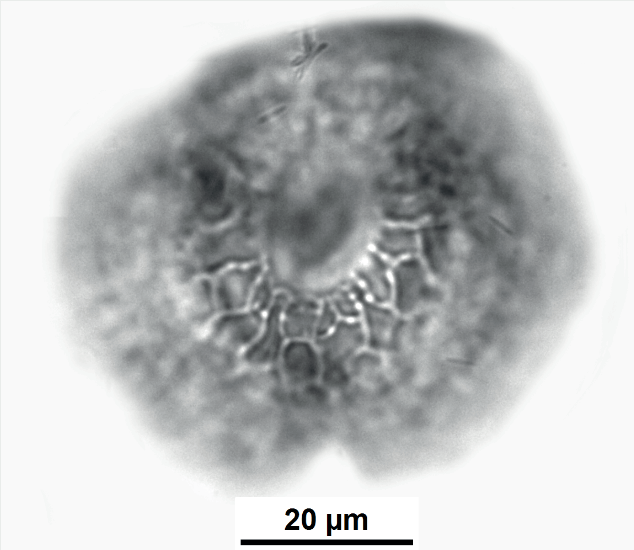
Cabomba australis Speg.
793 – ICN 49881
Polar view Distal face
Oblate - Anasulcate - Striate
P $\bar{x}$= 54 µm EQ $\bar{x}$= 104 µm

Canellaceae

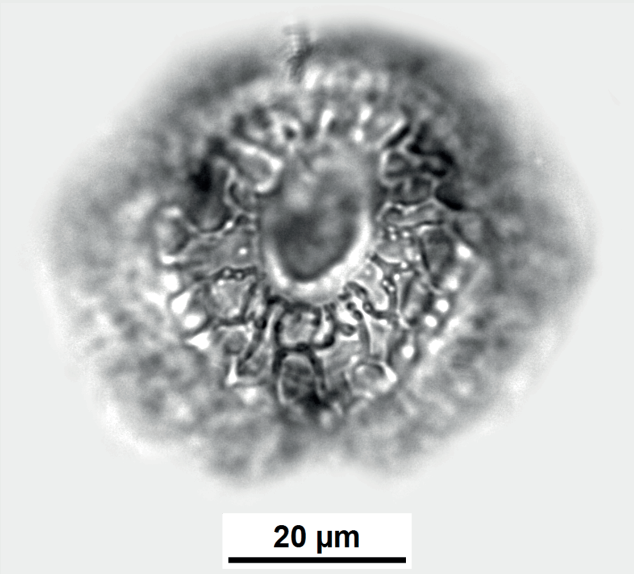
Capsicodendron dinisii (Schwacke) Occhioni
766 – ICN 48427
Polar view Distal face: first plane
Subspheroidal - Anasulcate - Rugulate
P $\bar{x}$= 20 µm EQ $\bar{x}$= 24 µm

Capsicodendron dinisii (Schwacke) Occhioni
766 – ICN 48427
Polar view Distal face: second plane
Subspheroidal - Anasulcate - Rugulate
P $\bar{x}$= 20 µm EQ $\bar{x}$= 24 µm

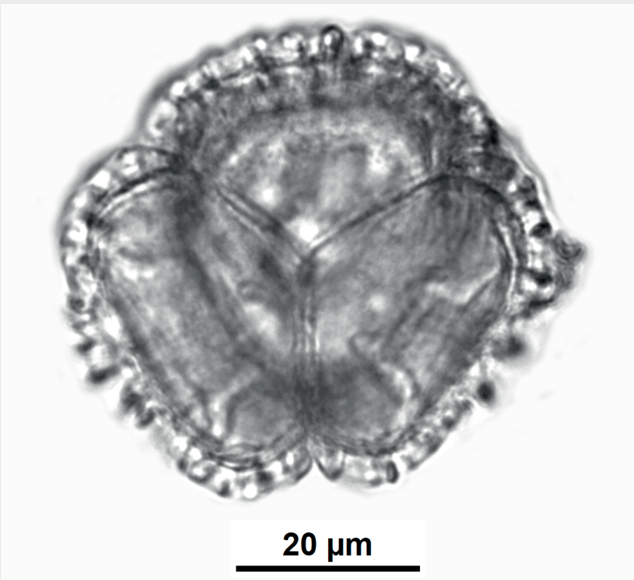
Winteraceae



Drimys brasiliensis Miers
839 – ICN 68259
Polar view Distal face: first plane
Oblate - Ana-ulcerate - Eureticulate
xP $\overline{x}$= 27 µm   EQ $\overline{x}$= 39 µm
Tetrad diameter $\overline{x}$ = 50 µm

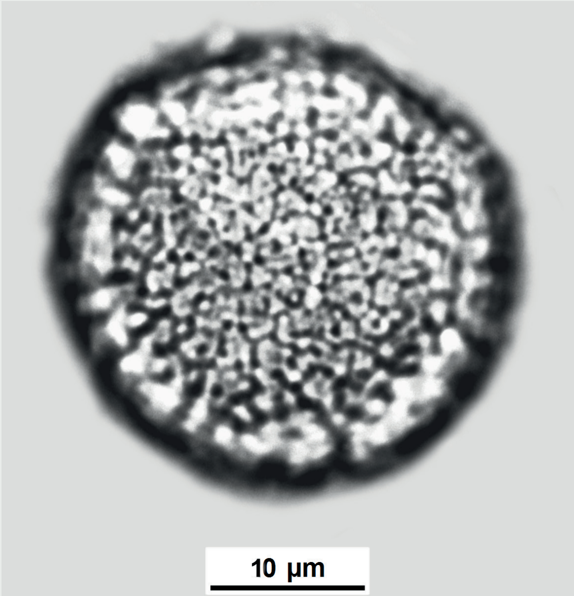


Drimys brasiliensis Miers
839 – ICN 68259
Polar view Distal face: second plane
Oblate - Ana-ulcerate - Eureticulate
P $\overline{x}$= 27 µm   EQ $\overline{x}$= 39 µm
Tetrad diameter $\overline{x}$ = 50 µm

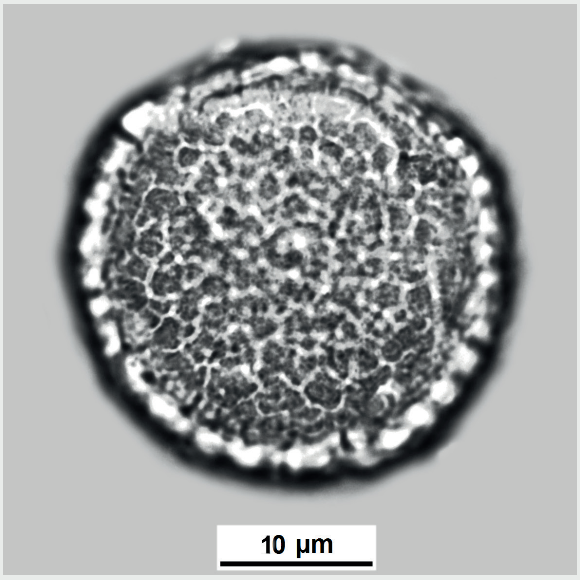


Drimys brasiliensis Miers
839 – ICN 68259
Polar view Distal face: third plane
Oblate - Ana-ulcerate - Eureticulate
P $\overline{x}$= 27 µm   EQ $\overline{x}$= 39 µm
Tetrad diameter $\overline{x}$ = 50 µm

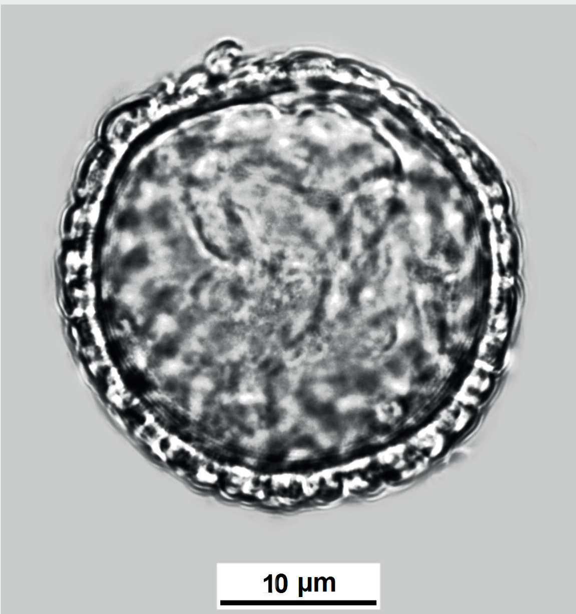
Aristolochiaceae



Aristolochia curviflora Malme
603 – ICN 40003
Equatorial view: first plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

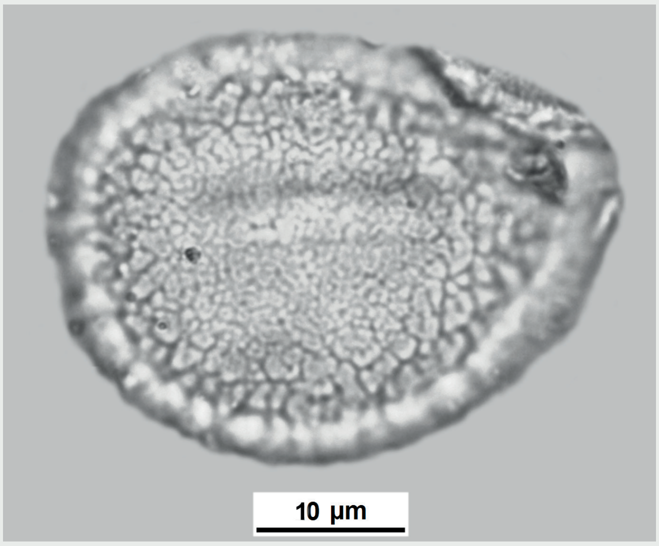


Aristolochia curviflora Malme
603 – ICN 40003
Equatorial view: second plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

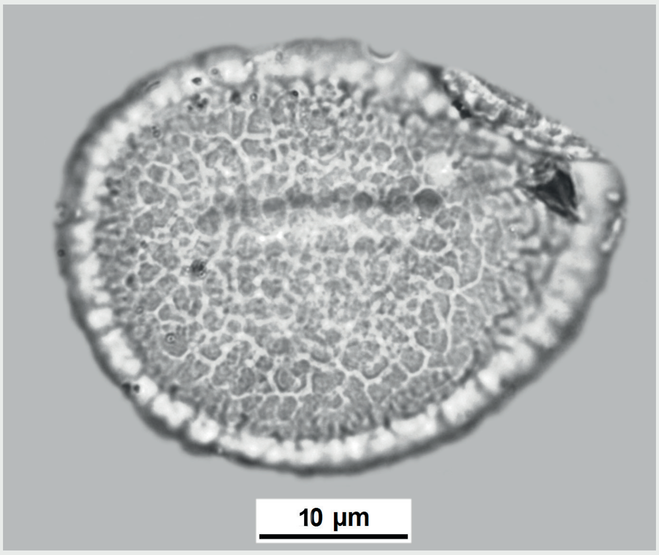


Aristolochia curviflora Malme
603 – ICN 40003
Equatorial view: third plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

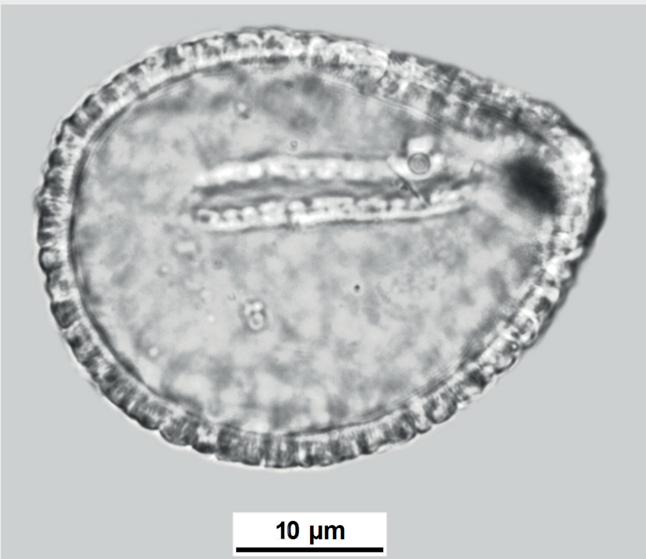
Aristolochiaceae



Aristolochia curviflora Malme
603 – ICN 40003
Polar view Proximal face: first plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

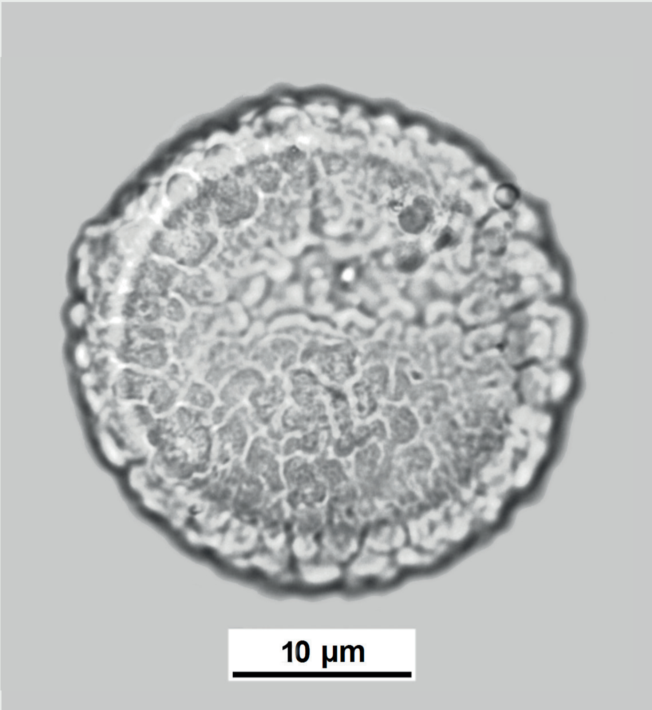


Aristolochia curviflora Malme
603 – ICN 40003
Polar view Proximal face: second plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

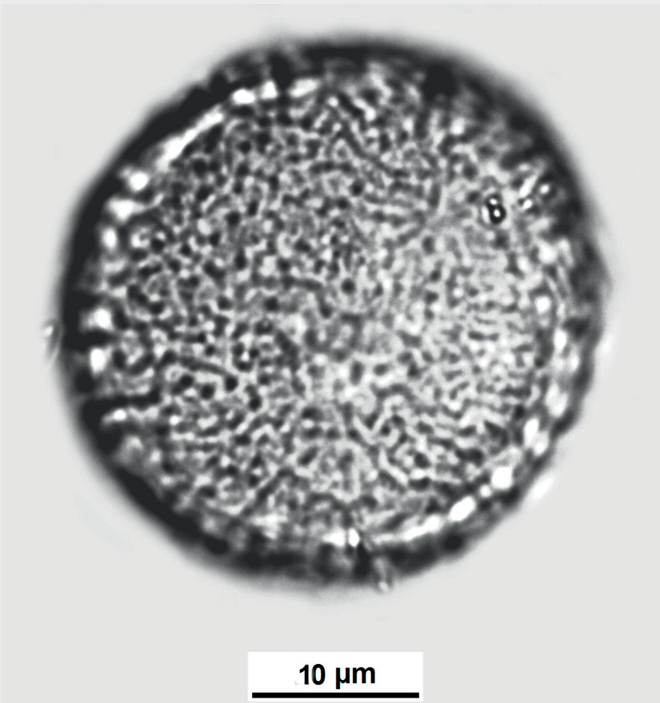


Aristolochia curviflora Malme
603 – ICN 40003
Polar view Proximal face: third plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 48 µm

Aristolochiaceae

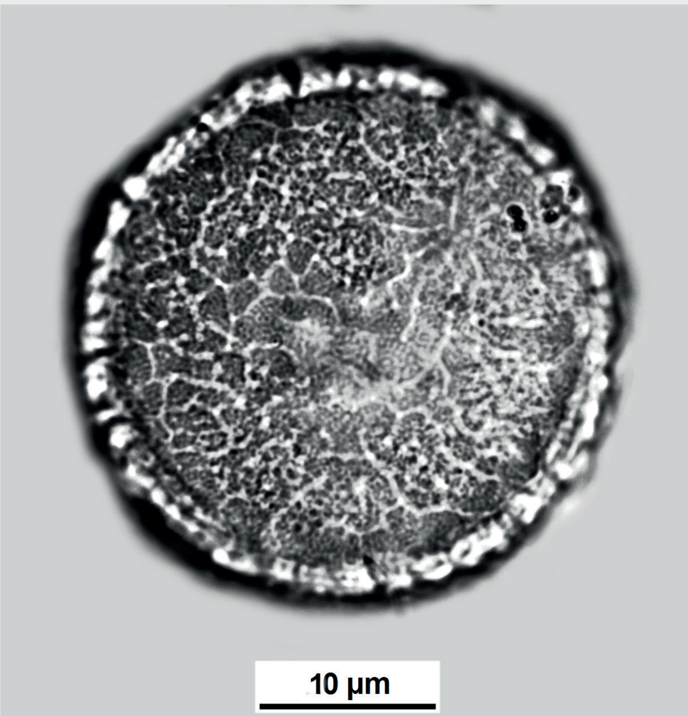


Aristolochia sessiflora DC. ex Duch.
817 – ICN 21097
Polar view Distal face: second plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 27 µm

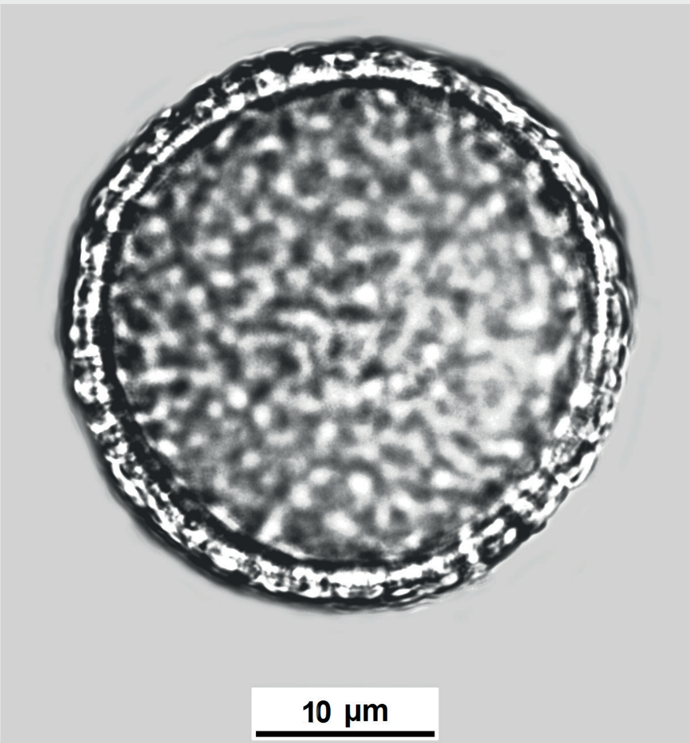


Aristolochia sessiflora DC. ex Duch.
817 – ICN 21097
Polar view Distal face: first plane
Spheroidal - Anasulcate - Rugulate
diameter $\bar{x}$= 27 µm

Aristolochiaceae

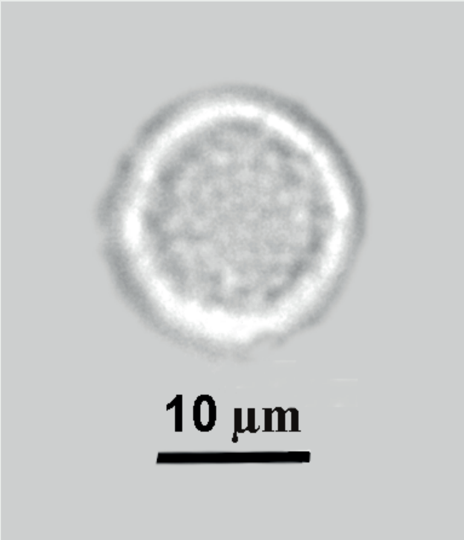


Aristolochia sessiflora DC. ex Duch.
817 – ICN 21097
Polar view Distal face: second plane
Spheroidal - Anasulcate - Rugulate
diameter $\overline{x}$= 27 µm

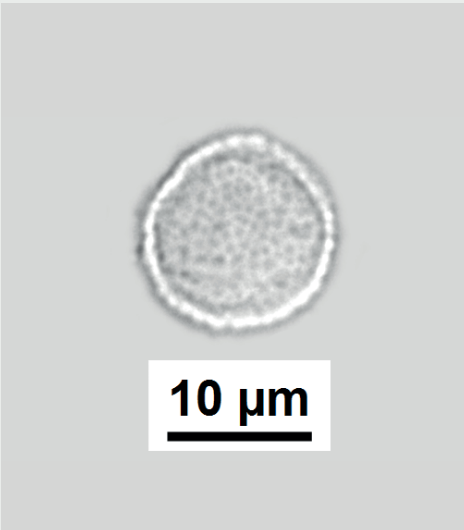


Aristolochia sessiflora DC. ex Duch.
817 – ICN 21097
Polar view Distal face: third plane
Spheroidal - Anasulcate - Rugulate
diameter $\overline{x}$= 27 µm

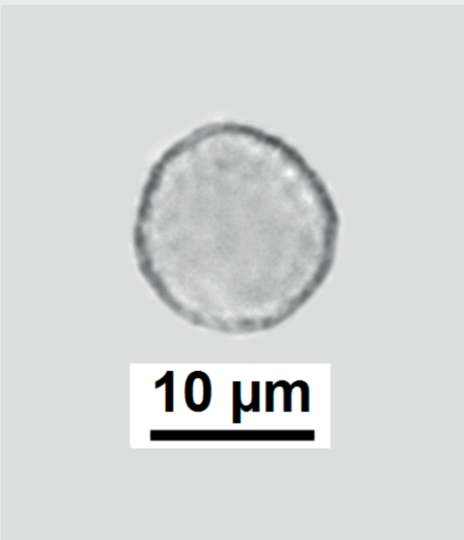
Piperaceae



Peperomia balansana C. DC.
602 – ICN 46490
Spheroidal - Inaperturate - Microverrucate: first plane
diameter $\bar{x}$= 6 μm



Peperomia balansana C. DC.
602 – ICN 46490
Spheroidal - Inaperturate - Microverrucate: second plane
diameter $\bar{x}$= 6 μm



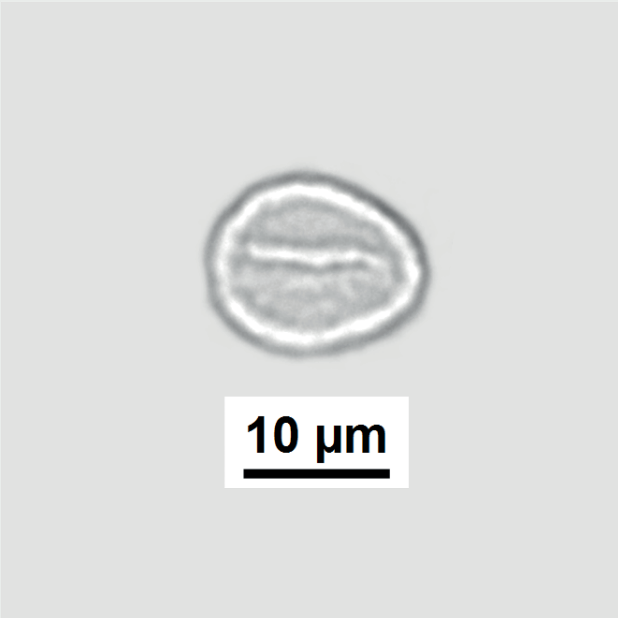
Peperomia balansana C. DC.
602 – ICN 46490
Spheroidal - Inaperturate - Microverrucate: third plane
diameter $\bar{x}$= 6 μm

Piperaceae

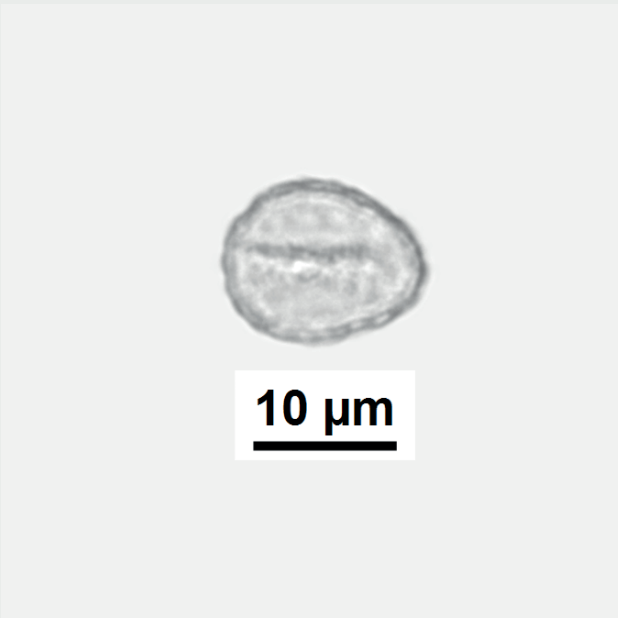
Piper gaudichaudianum Kunth
753 – ICN 4825
Equatorial view: first plane
Oblate - Anasulcate - Scabrate
P $\bar{x}$= 5 µm EQ $\bar{x}$= 8 µm

Piper gaudichaudianum Kunth
753 – ICN 4825
Equatorial view: second plane
Oblate - Anasulcate - Scabrate
P $\bar{x}$= 5 µm EQ $\bar{x}$= 8 µm

Piperaceae

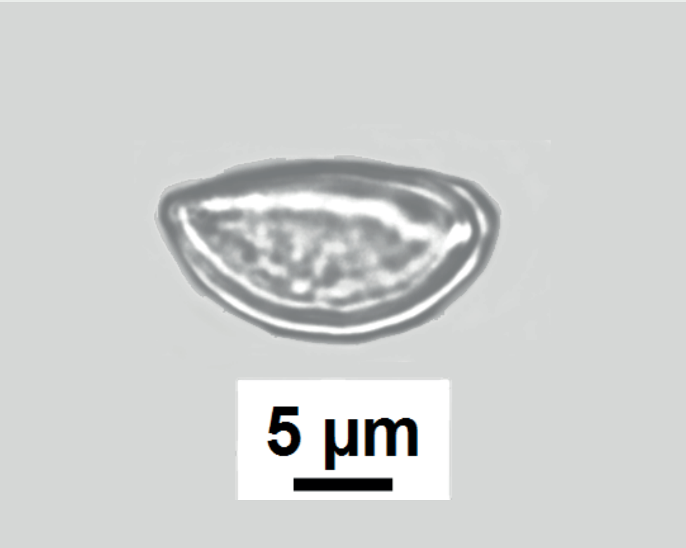


Piper gaudichaudianum Kunth
753 – ICN 4825
Polar view Distal face: first plane
Oblate - Anasulcate - Scabrate
P $\bar{x}$= 5 µm   EQ $\bar{x}$= 8 µm

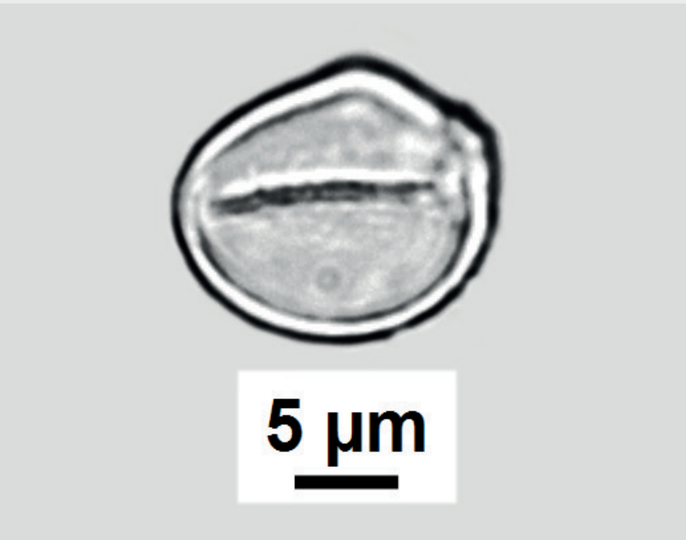


Piper gaudichaudianum Kunth
753 – ICN 4825
Polar view Distal face: second plane
Oblate - Anasulcate - Scabrate
P $\bar{x}$= 5 µm   EQ $\bar{x}$= 8 µm

Piperaceae

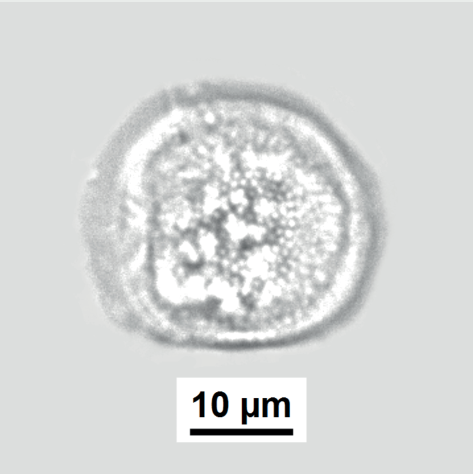


Piper martianum Kunth
600 – ICN 35107
Equatorial view
Oblate - Anasulcate - Psilate
P $\bar{x}$= 7 µm EQ $\bar{x}$= 10 µm

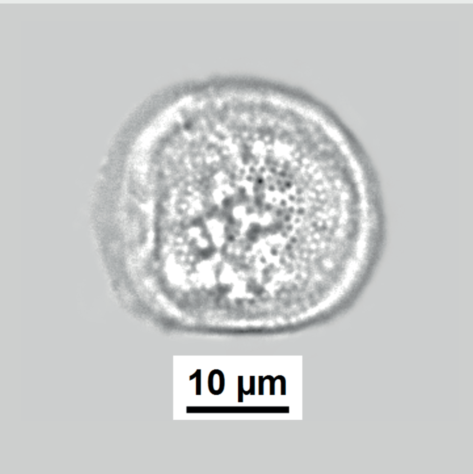


Piper martianum Kunth
600 – ICN 35107
Polar view Distal face
Oblate - Anasulcate - Psilate
P $\bar{x}$= 7 µm EQ $\bar{x}$= 10 µm

Lauraceae

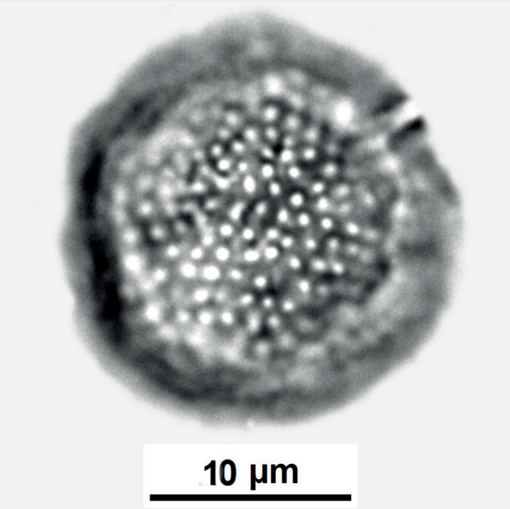


Endlicheria paniculata (Spreng.) J.F. Macbr.
287 – ICN 16246
Subspheroidal - Inaperturate - Spinulose: first plane
P $\bar{x}$= 28 µm   EQ $\bar{x}$= 37 µm
Note: Persistent remnants of cellular contents after acetolysis.

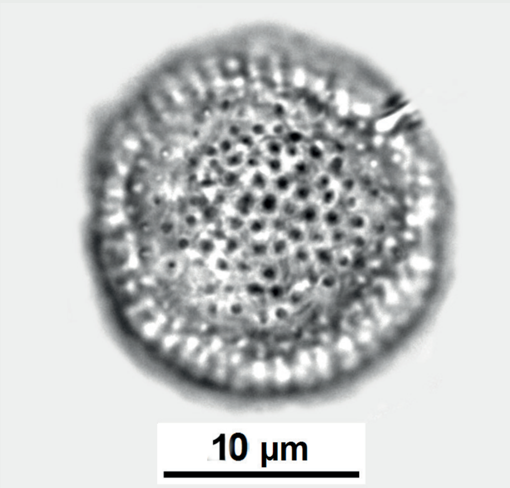


Endlicheria paniculata (Spreng.) J.F. Macbr.
287 – ICN 16246
Subspheroidal - Inaperturate - Spinulose: second plane
P $\bar{x}$= 28 µm   EQ $\bar{x}$= 37 µm
Note: Persistent remnants of cellular contents after acetolysis.

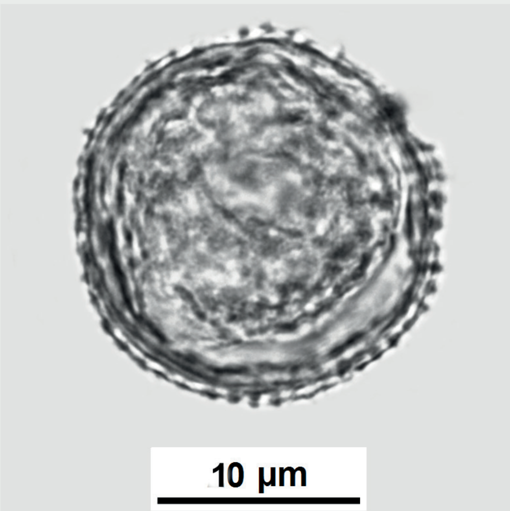
Lauraceae



Nectandra rigida (Kunth) Nees
757 – ICN 1843
Spheroidal - Inaperturate - Spinulose: first plane
diameter $\bar{x}$= 21 µm

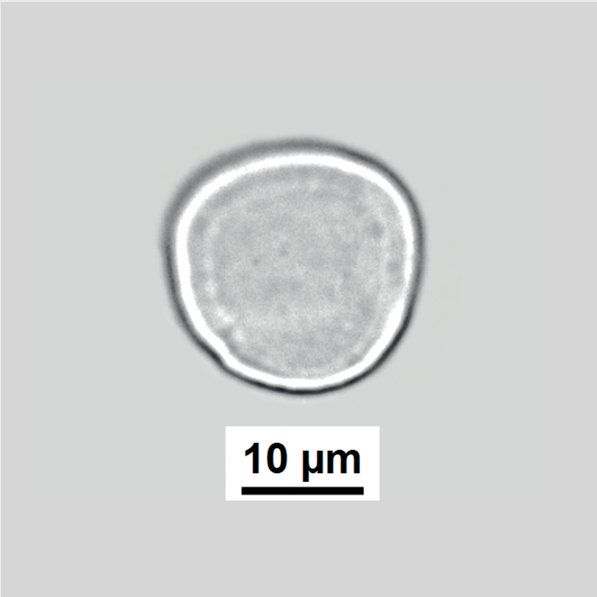


Nectandra rigida (Kunth) Nees
757 – ICN 1843
Spheroidal - Inaperturate - Spinulose: second plane
diameter $\bar{x}$= 21 µm

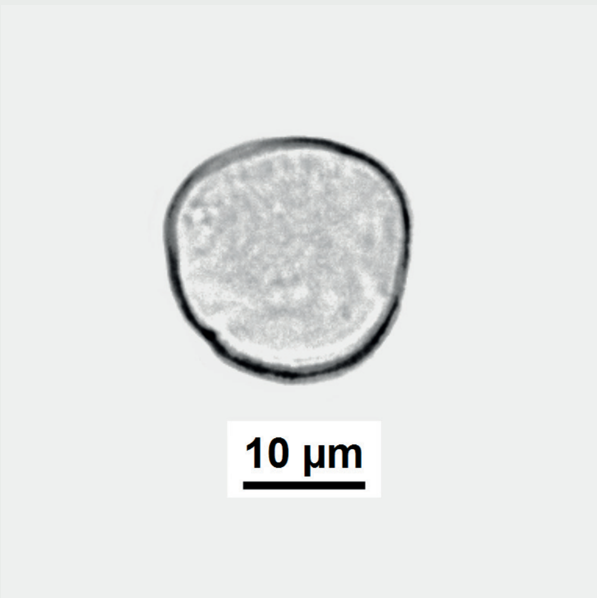


Nectandra rigida (Kunth) Nees
757 – ICN 1843
Spheroidal - Inaperturate - Spinulose: third plane
diameter $\bar{x}$= 21 µm

Monimiaceae

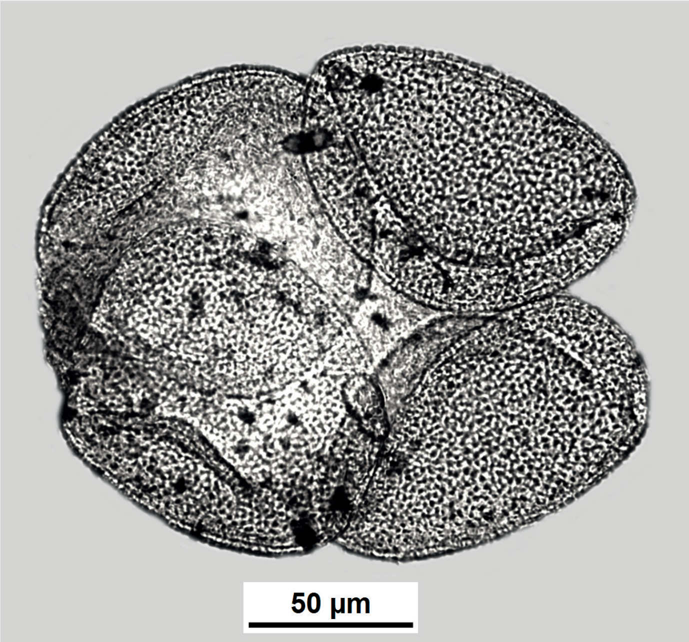


Mollinedia floribunda Tul.
282 – ICN 26352
Polar view: first plane
Subspheroidal – Inaperturate – Scabrate
P $\bar{x}$= 18 µm EQ $\bar{x}$= 22 µm

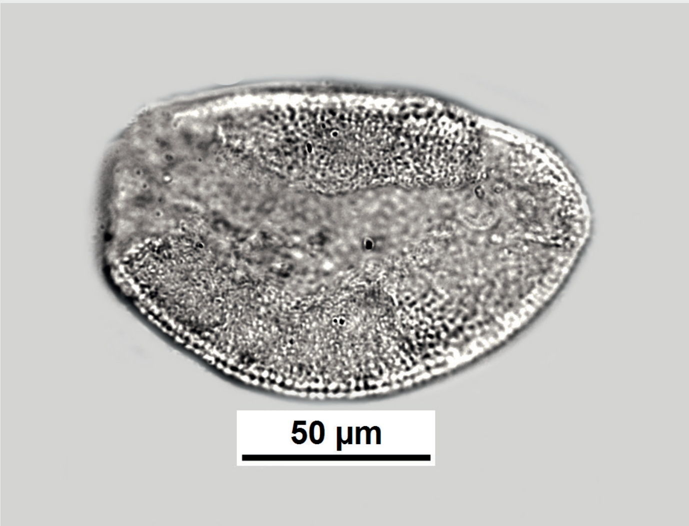


Mollinedia floribunda Tul.
282 – ICN 26352
Polar view: second plane
Subspheroidal – Inaperturate – Scabrate
P $\bar{x}$= 18 µm EQ $\bar{x}$= 22 µm

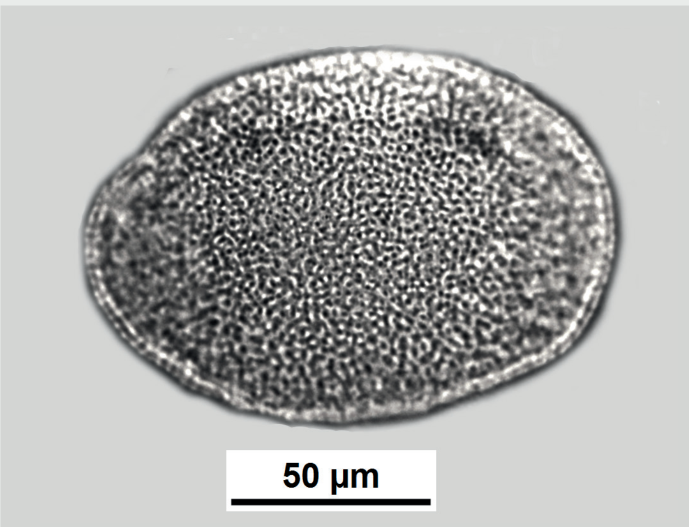
Annonaceae



Annona cacans Warm.
687 – ICN 47651
Oblate - Sulcoidate - Rugulate
P $\bar{x}$= 70 µm EQ $\bar{x}$= 106 µm
Tetrad diameter $\bar{x}$= 139 µm
Note: caracteristic loose tetrads.

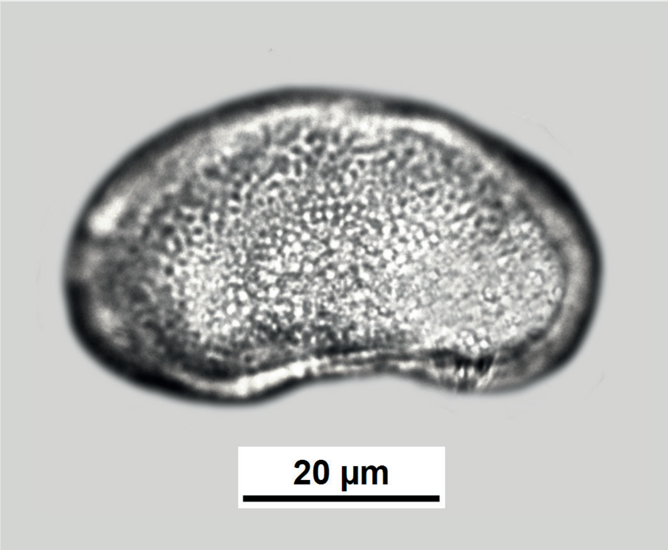


Annona cacans Warm.
687 – ICN 47651
Equatorial view - Pollen grain
Oblate - Sulcoidate - Rugulate
P $\bar{x}$= 70 µm EQ $\bar{x}$= 106 µm

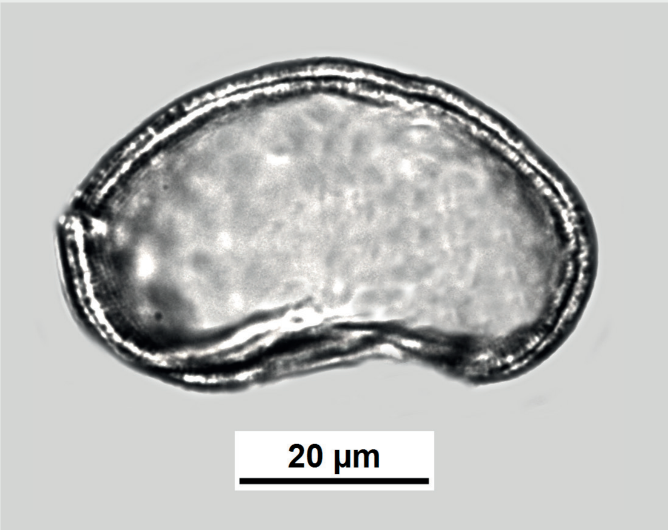


Annona cacans Warm.
687 – ICN 47651
Equatorial view - Pollen grain
Oblate - Sulcoidate - Rugulate
P $\bar{x}$= 70 µm EQ $\bar{x}$= 106 µm

Annonaceae



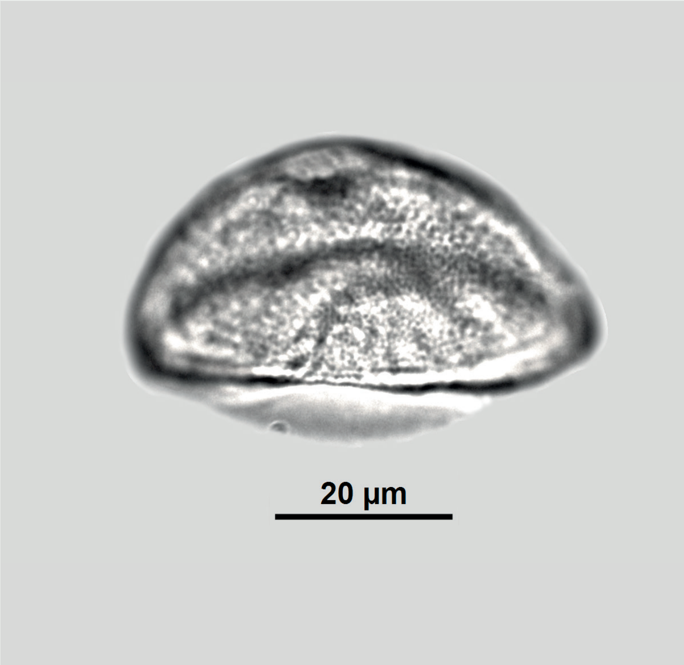
Annona emarginata (Schltdl.) H. Rainer
69 – ICN 2978
Equatorial view: first plane
Subspheroidal - Sulcoidate - Rugulate
P $\bar{x}$= 37 µm EQ $\bar{x}$= 40 µm



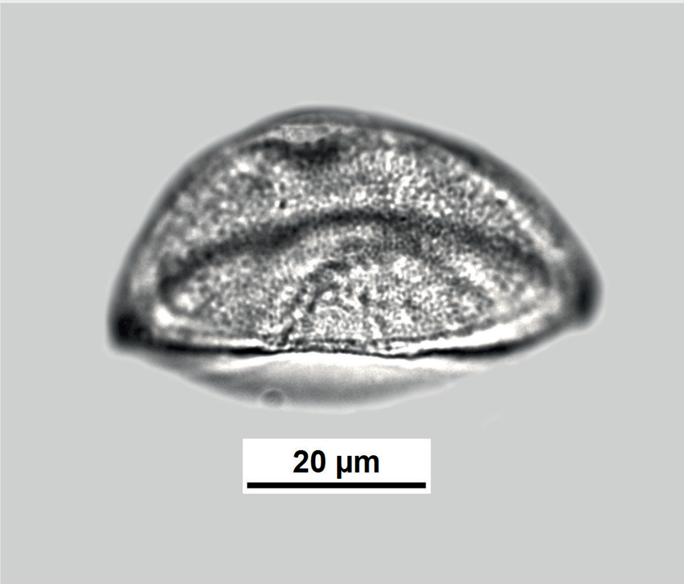
Annona emarginata (Schltdl.) H. Rainer
69 – ICN 2978
Equatorial view: second plane
Subspheroidal - Sulcoidate - Rugulate
P $\bar{x}$= 37 µm EQ $\bar{x}$= 40 µm

Annona emarginata (Schltdl.) H. Rainer
69 – ICN 2978
Polar view Distal face
Subspheroidal - Sulcoidate - Rugulate
P $\bar{x}$= 37 µm EQ $\bar{x}$= 40 µm

Annonaceae

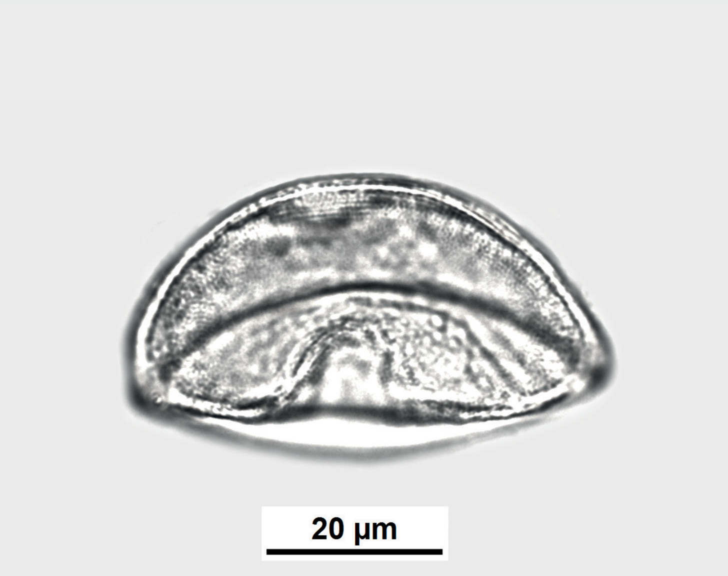


Rollinia sylvatica (A. St.-Hil.) Martius
1133 – ICN 103254
Equatorial view: first plane
Subspheroidal – Sulcoidate - Reticulate
P $\bar{x}$= 34 µm   EQ $\bar{x}$= 44 µm



Rollinia sylvatica (A. St.-Hil.) Martius
1133 – ICN 103254
Equatorial view: second plane
Subspheroidal – Sulcoidate - Reticulate
P $\bar{x}$= 34 µm   EQ $\bar{x}$= 44 µm

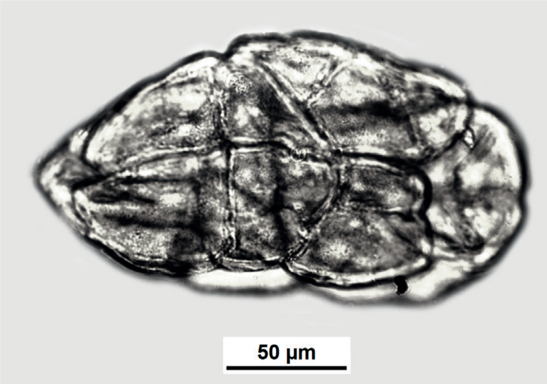
Annonaceae



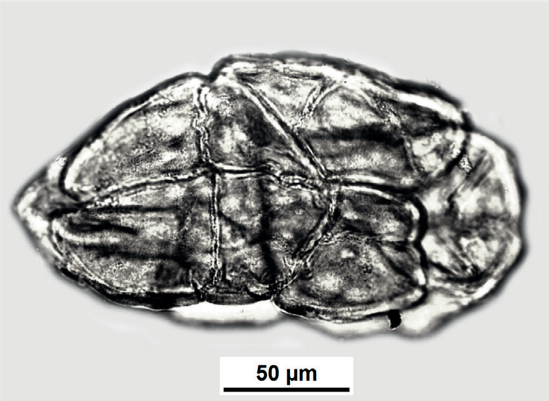
Rollinia sylvatica (A. St.-Hil.) Martius
1133 – ICN 103254
Equatorial view: third plane
Subspheroidal – Sulcoidate - Reticulate
P $\bar{x}$= 34 µm EQ $\bar{x}$= 44 µm

Rollinia sylvatica (A. St.-Hil.) Martius
1133 – ICN 103254
Polar view Distal face
Subspheroidal – Sulcoidate - Reticulate
P $\bar{x}$= 34 µm EQ $\bar{x}$= 44 µm

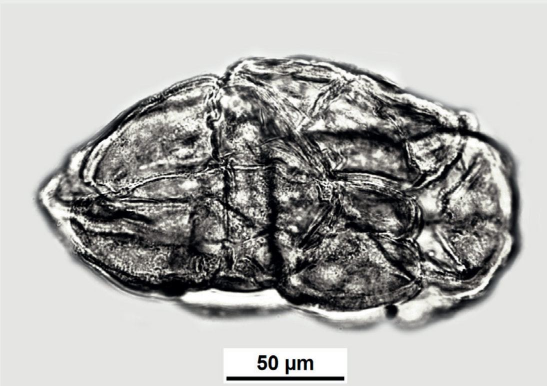
Annonaceae



Xylopia brasiliensis Spreng.
331 – ICN 2745
Subspheroidal - Inaperturate - Scabrate
P $\bar{x}$= 49 µm   EQ $\bar{x}$= 59 µm
Polyad diameters $\bar{x}$= 100 µm x 200 µm: first plane

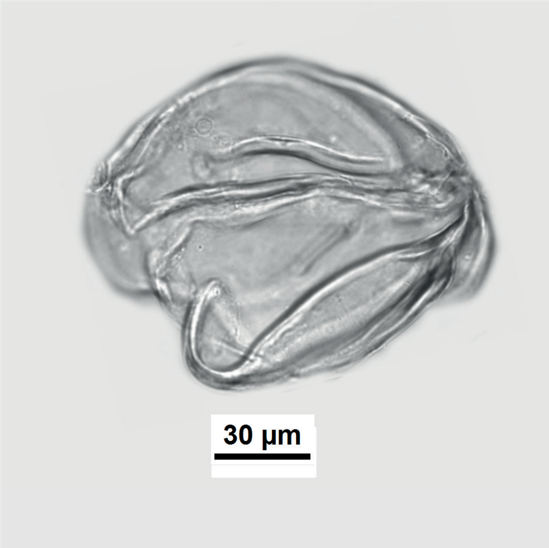


Xylopia brasiliensis Spreng.
331 – ICN 2745
Subspheroidal - Inaperturate - Scabrate
P $\bar{x}$= 49 µm   EQ $\bar{x}$= 59 µm
Polyad diameters $\bar{x}$= 100 µm x 200 µm: second plane

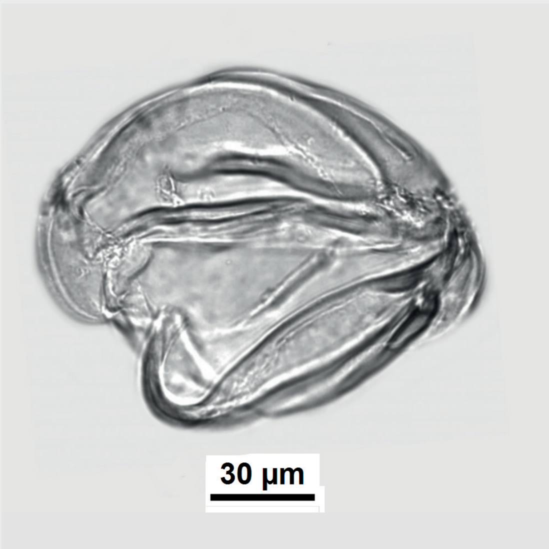


Xylopia brasiliensis Spreng.
331 – ICN 2745
Subspheroidal - Inaperturate - Scabrate
P $\bar{x}$= 49 µm   EQ $\bar{x}$= 59 µm
Polyad diameters $\bar{x}$= 100 µm x 200 µm: third plane

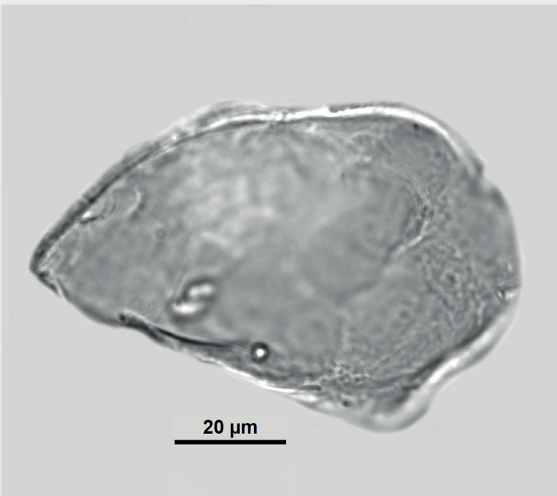
Annonaceae



Xylopia grandiflora A. St.-Hil.
332 – ICN 42284
Oblate - Inaperturate - Scabrate
P $\bar{x}$= 52 µm EQ $\bar{x}$= 76 µm
Tetrad diameters $\bar{x}$= 97 µm x 116 µm: first plane
Note: Characteristic loose tetrads

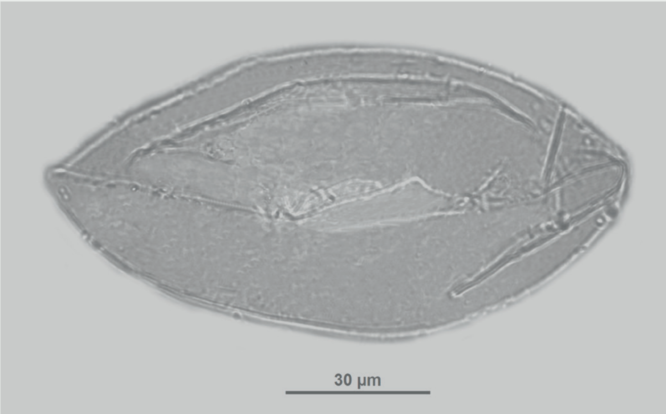


Xylopia grandiflora A. St.-Hil.
332 – ICN 42284
Oblate - Inaperturate - Scabrate
P $\bar{x}$= 52 µm EQ $\bar{x}$= 76 µm
Tetrad diameters $\bar{x}$= 97 µm x 116 µm: second plane
Note: Characteristic loose tetrads

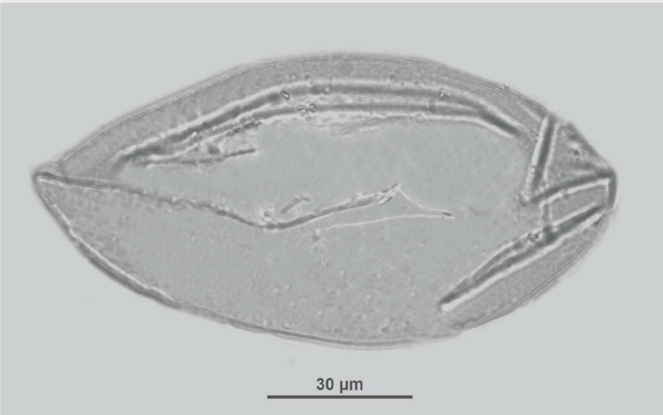


Xylopia grandiflora A. St.-Hil.
332 – ICN 42284
Equatorial view - Pollen grain
Oblate - Inaperturate - Scabrate
P $\bar{x}$= 52 µm EQ $\bar{x}$= 76 µm

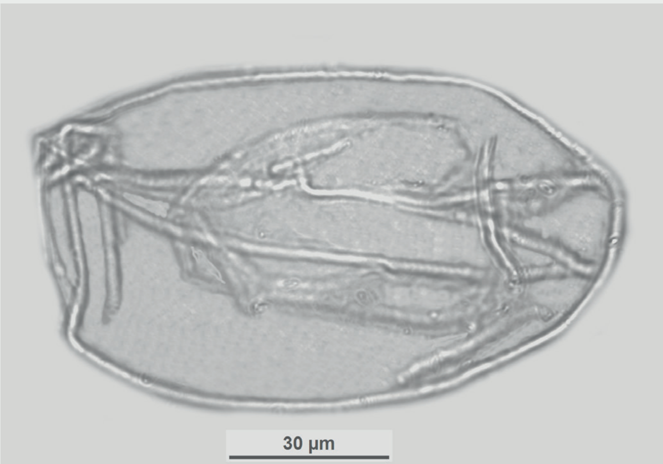
Magnoliaceae



Magnolia ovata (A. St.-Hill.) Spreng
926 – ICN 1627
Equatorial view: first plane
Peroblate – Anasulcate - Psilate
P $\bar{x}$= 63 µm   EQ $\bar{x}$= 139 µm
Note: Large grains, delicate wall with irregular folds after acetolysis.



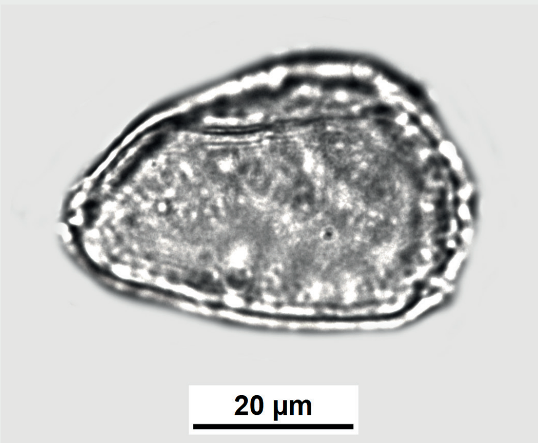
Magnolia ovata (A. St.-Hill.) Spreng
926 – ICN 1627
Equatorial view: second plane
Peroblate – Anasulcate - Psilate
P $\bar{x}$= 63 µm   EQ $\bar{x}$= 139 µm
Note: Large grains, delicate wall with irregular folds after acetolysis.



Magnolia ovata (A. St.-Hill.) Spreng
926 – ICN 1627
Polar view Distal face
Peroblate – Anasulcate - Psilate
P $\bar{x}$= 63 µm   EQ $\bar{x}$= 139 µm
Note: Large grains, delicate wall with irregular folds after acetolysis.

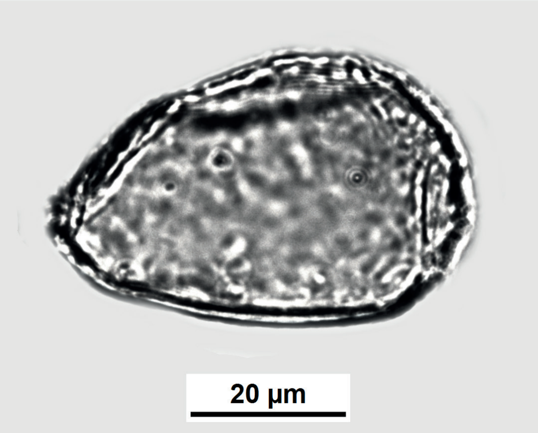
Magnoliaceae

Michelia fuscata (Andrews) Blume
698 – ICN 5062
Equatorial view: first plane
Oblate – Anasulcate - Reticulate
P $\overline{x}$= 22 µm   EQ $\overline{x}$= 30 µm

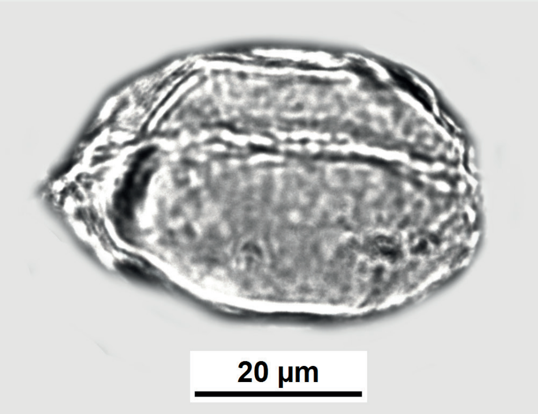


Michelia fuscata (Andrews) Blume
698 – ICN 5062
Equatorial view: second plane
Oblate – Anasulcate - Reticulate
P $\overline{x}$= 22 µm   EQ $\overline{x}$= 30 µm

Magnoliaceae

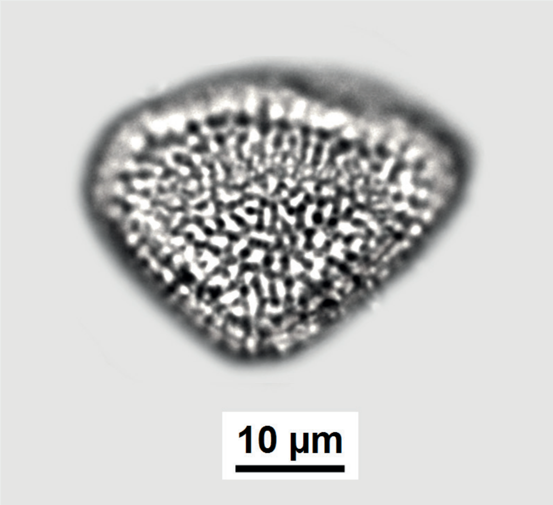


Michelia fuscata (Andrews) Blume
698 – ICN 5062
Equatorial view: third plane
Oblate – Anasulcate - Reticulate
P $\bar{x}$= 22 µm   EQ $\bar{x}$= 30 µm

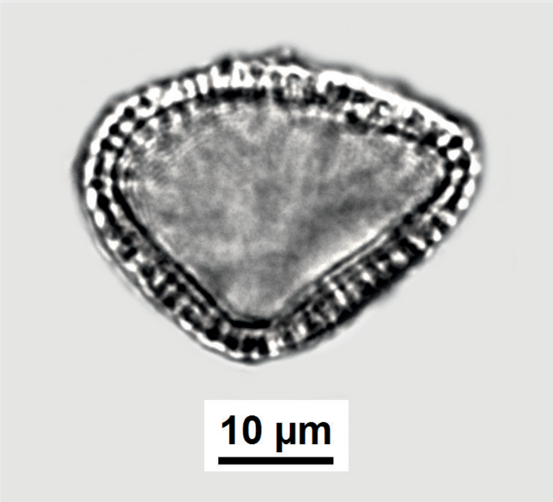


Michelia fuscata (Andrews) Blume
698 – ICN 5062
Polar view Distal face
Oblate – Anasulcate - Reticulate
P $\bar{x}$= 22 µm   EQ $\bar{x}$= 30 µm

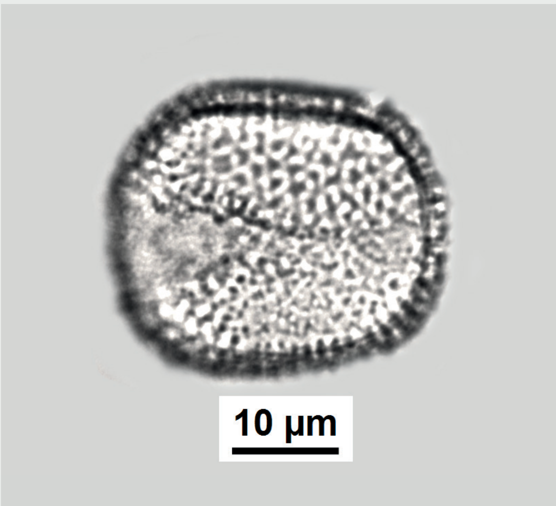
Myristicaceae



Bicuiba oleifera (Shott) W.J. de Wilde
732 – ICN 1851
Equatorial view: first plane
Oblate – Anasulcate - Rugulate
P $\bar{x}$= 24 µm   EQ $\bar{x}$= 33 µm



Bicuiba oleifera (Shott) W.J. de Wilde
732 – ICN 1851
Equatorial view: second plane
Oblate – Anasulcate - Rugulate
P $\bar{x}$= 24 µm   EQ $\bar{x}$= 33 µm



Bicuiba oleifera (Shott) W.J. de Wilde
732 – ICN 1851
Polar view Distal face
Oblate – Anasulcate - Rugulate
P $\bar{x}$= 24 µm   EQ $\bar{x}$= 33 µm

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