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Palynological study of heterostylous species of *Melochia* L. (Byttinerioideae-Malvaceae) occurring in Bahia, Brazil

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ABSTRACT

Melochia L. species are morphologically characterized by a pentacarpelar gynoecium with free papillose styles at the apex, whereas some are connate. The genus comprises about 60 species, with 22 occurring in Brazil. We analyzed pollen grains from 12 heterostylous species occurring in the State of Bahia to contribute to the palynology of the *Melochia* Group, including *Melochia betonicifolia* A. St.-Hil., *M. caracasana* Jacq., *M. chamaedrys* A. St.-Hil., *M. hirsuta* Cav., *M. illicoides* K. Schum., *M. parvifolia* Kunth, *M. pilosa* (Mill.) Fawc. & Rendle, *M. pyramidata* L., *M. spicata* (L.) Fryxell, *M. splendens* A. St.-Hil. & Naudin, *M. tomentosa* L., and *M. villosa* Fawc. & Rendle. Pollen grains were provided from specimens deposited at the CEPEC, HUEFS, and SP herbaria. The floral morphs of all specimens had been previously studied with a stereomicroscope. Acetolyzed pollen grains were investigated by light microscopy, and non-acetolyzed pollen grains were observed by scanning and transmission electron microscopy. It was confirmed in two pollen types of the two floral morphs: (1) the longistylous morph was characterized as medium sized; prolate spheroidal; 3-colporate, with ectoapertures comparatively larger, endoaperture lalongate; reticulate-perforate; exine ultrastructure with nexine differentiated into endexine and a foot layer (*M. pyramidata*) or undifferentiated (*M. betonicifolia*); a 4-stratified sexine may also occur; (2) the brevistylous morph showed medium to large-sized pollen grains; oblate spheroidal; 3(4)-colporate, ectoaperture short, endoaperture lalongate; microechinate and echinate; semitectum perforate and microreticulate-rugulate (*M. betonicifolia*); *M. pyramidata* wall ultrastructure with nexine showing "internal foramina." Pollen dimorphism was confirmed in the genus due to heterostyly. The type and number of apertures were not as useful as exine ornamentation to characterize and distinguish the pollen grains.

1. Introduction

The genus *Melochia* L. consists of approximately 60 species that are widespread in tropical and subtropical regions but most species are confined to the Americas. Twenty-two species are found in Brazil, three of them are endemics (Goldberg, 1967; Dorr and Barnett, 1989; Esteves, 2010).

Melochia is included within the Malvaceae family and the Byttnerioideae subfamily, because their flowers have five stamens and no or reduced staminodes (Bayer et al., 1999). The genus belongs to the Hermannieae tribe, which is morphologically recognized by five antipetal stamens and plane petals (Dorr and Barnett, 1989). According to Goldberg (1967), *Melochia* is mainly characterized by a pentacarpelar gynoecium and by the five free styles that are partially connate and papillose at the apex.

The Americas hold most species within this genus; therefore, some of the samples of the relevant taxonomic studies were extracted from that continent. For example, Brizicky (1966) and Dorr and Barnett (1989) studied North American species; Robyns and Cuatrecasas (1964) and Faife-Cabrera et al. (2014) investigated Central American species; and Fernández and Grande (2007), Cristóbal (2007), and Rondón (2007a, 2007b, 2009) collected South American species. To date, the most well-known floristic survey in Brazil was of the traditional Sterculiaceae family, such as those of Cristóbal (1983) for the Flora of Santa Catarina State; Cristóbal and Tressens (1986) and Cristóbal et al. (1995) for the Flora of Bahia State; Esteves (1986) for the Flora of Minas Gerais State; Vicentini and Silva (1999) for the Amazon Forest; and Cruz (2007) for the Flora of São Paulo State.

Heterostyly in *Melochia* was studied by Martin (1966), who observed a self-incompatibility system related to non-germination of pollen grains and restricted pollen tube growth to the stigma and style. Heterostyly is a genetically established floral heteromorphism that occurs in at least 24 flowering plant families. Heterostyly is related to pollen dimorphism within species, mainly regarding size and ornamentation of the exine. This trait is remarkably characteristic of *Melochia* and is shared only by the genus *Waltheria* in the Malvaceae family (Ganders, 1979).

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Palynological studies that considered the influence of heterostyly on pollen grain morphological characters have been included to *Melochia* taxonomy. Pollen grains with different aperture length dimensions and exine ornamentation can be found within the same species, but it depends on the floral morphs analyzed (Dorr and Barnet, 1989; Saba et al., 2004; Faife-Cabrera et al., 2014). Several authors, such as Erdtman (1952), Sharma (1970), Melhem et al. (1976), Palácios-Chávez et al. (1990), Roubik and Moreno (1991), Miranda et al. (1992), and Saba and Santos (2000; 2003) described palynologically species of *Melochia*; however, they did not mention that pollen dimorphism is derived from heterostyly. Moreover, these studies were predominantly performed using light microscopy (LM), making it difficult to clearly visualize all of the morphological characters of the pollen. A few authors have used scanning electron microscopy (SEM), and some studies have used transmission electron microscopy (TEM) to study Malvaceae. TEM allows detailed visualization of the pollen grain surface and stratification of the exine.

Thus, in this study, we characterized pollen morphology from heterostylous *Melochia* spp. occurring in the State of Bahia, Brazil.

2. Material and methods

Based on a literature review (Saba and Santos, 2003; Cruz, 2007; Esteves, 2010) and the CEPEC (Centro de Pesquisa do Cacau), HUEFS (Universidade Estadual de Feira de Santana), and SP (Instituto de Botânica de São Paulo) herbaria databases (acronyms according to Thiers, 2014), we selected 26 specimens belonging to 12 *Melochia* heterostylous species occurring in the State of Bahia. We used additional specimens from other states when necessary and selected specimens identified by Malvaceae taxonomic experts when possible. Pollen grains were collected from at least four different specimens of each species whenever possible. Mature floral buds of all specimens were studied under LM to determine the floral morphs. Only the brevistylous flowers of some species, such as *M. caracasana*, *M. chamaedrys*, *M. hirsuta*, *M. illicoides*, and *M. splendens*, were studied due to an insufficient number of longistylous flower samples in the herbaria.

LM were performed under a Zeiss Axioskop 2 microscope (Jena, Germany) in the Palynology Laboratory of the Universidade do Estado da Bahia, *Campus* VII. The pollen grains were prepared using an acetolysis protocol (Erdtman, 1960) from anthers belonging to more than one flower of each specimen. The acetolyzed material was mounted between a slide and a coverslip, immersed in glycerin jelly, and sealed with hot paraffin.

The main morphometric parameters (equatorial and polar diameters) were measured in 25 pollen grains, when possible, and the remaining parameters (aperture diameter and exine, sexine, and nexine thicknesses) were measured in 10 randomly selected pollen grains using an ocular micrometer.

Quantitative results were statistically analyzed by calculating the arithmetic average, standard deviation, standard deviation of the average, coefficient of variation, and the 95% confidence intervals for the pollen parameter measurements with a sample size of 25. The other measurements had a sample size of 10, and only the arithmetic average was calculated.

The pollen grains were acetolyzed, washed, and dehydrated for 10 min each in an ascending ethanol series (50, 70, 90, and 100%) for the SEM pollen surface analysis. Absolute alcohol containing the pollen grains was dripped directly over a SEM stub (specimen holder), dried completely, coated using gold evaporation under high vacuum, and the pollen grains were qualitatively analyzed using a JEOL 6390LV microscope (Tokyo, Japan) at the Electron Microscopy Platform of Centro de Pesquisas Gonçalo Moniz-FIOCRUZ.

The TEM analysis was also performed at FIOCRUZ. All non-acetolyzed material was fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer solution for 2 h. The samples were washed in sodium cacodylate buffer and post-fixed in 1% osmium tetroxide, 0.8% potassium

Plate I. Pollen grains of *Melochia* L. (see on page 194)

1-4 *Melochia betonicifolia* - Longistylous morph: [Castro et al. 1286 (HUEFS)] — 1. equatorial view, aperture detail and costa detail (arrow); 2. polar view (SEM); 3-A. exine surface (SEM); 3-B**.** detail of the exine in a sectioned pollen grain (SEM); [Santos, V.J. et al. 466 (HUEFS)] — 4. wall structure in transversal section (TEM).

5–9 *M. betonicifolia* — brevistylous morph: [Rapini, A. et al. 1202 (HUEFS)] — 5. polar view, fastígio in evidence (arrow); 6. equatorial view, aperture detail, costa detail (arrow); [Queiroz, L.P. and N. S. Nascimento 4662 (HUEFS)] — 7. equatorial view (SEM); 8-A. exine surface showing undulating tectum (SEM); 8-B. exine surface (SEM); 9. detail of the exine in a sectioned pollen grain (SEM).

10–12 *M. caracasana* — brevistylous morph: [Carneiro-Torres, D.S. s.n. (HUEFS -98288)] — 10. equatorial view, aperture detail, costa detail (arrow); 11. polar view (SEM); 12-A. exine surface (SEM). 12-B. Detail of the exine in a sectioned pollen grain (SEM).

13–15 *M. chamaedrys* — brevistylous morph: [W. A. Archer and A. Gehrt s.n. (SP-36416)] — 13. polar view, fastigium in evidence (arrow); 14. equatorial view, aperture detail, costa detail (arrow); 15-A. exine surface (SEM); 15-B. Detail of the exine in a sectioned pollen grain (SEM). (N = nexine; 1 = sexine 1; 2 = sexine 2; 3 = sexine 3; 4 = sexine 4).

Plate II. Pollen grains of *Melochia* L. (see on page 195)

1–4 *M. hirsuta* — brevistylous morph: [R. M. Harley 15776 (CEPEC)] — 1. polar view, fastigium in evidence (arrow); 2-A. equatorial view, aperture detail; 2-B. costa detail; 3. polar view (SEM); 4. exine surface (SEM).

5–7 *M. illicoides* — brevistylous morph: [Queiroz, L. P. 6770 (HUEFS)] — 5. equatorial view, aperture detail; 6. LO analysis; 7. exine surface (SEM).

8–11 *M. parvifolia* — longistylous morph: [R. M. Harley 21650 (CEPEC)] — 8. polar view, fastigium in evidence (arrow); 9. equatorial view, aperture detail, costa detail (arrow); 10. polar view (SEM); 11. exine surface (SEM).

12–15 *M. parvifolia* — brevistylous morph: [Saunders, J. and Carvalho, A. M. 3086 (CEPEC)] — 12. polar view, fastigium in evidence (arrow); 13-A. equatorial view, aperture detail; 13-B. costa detail; 14. exine surface (SEM); 15. detail of the exine in a fragmented pollen grain (SEM).

Plate III. Pollen grains of *Melochia* L. (see on page 196)

1–3 *M. pilosa* — longistylous morph: [Lee, E. P. et al. 4871 (CEPEC)] — 1-A. equatorial view, aperture detail; 1-B. costa detail; 2. polar view (SEM); 3. exine surface (SEM).

4–6 *M. pilosa* — brevistylous morph: [Ribas O. S. 1235 (SP)] — 4. polar view; 5. LO analysis; 6. equatorial view, aperture detail and costa detail (arrow).

7–10 *M. pyramidata* — longistylous morph: [Harley, R. M. 2933 (HUEFS)] — 7. equatorial view, aperture detail and costa detail (arrow); 8. equatorial view (SEM); 9. exine surface (SEM); 10-A. wall structure in transversal section (TEM); 10-B. aperture region (TEM).

11–15 *M. pyramidata* — brevistylous morph: [Melo, E. et al. 2759 (HUEFS)] — 11. polar view, 4-colporate pollen grain; 12. equatorial view, aperture detail and costa detail (arrow); 13. polar view, 3-colporate pollen grain (SEM); 14. exine surface (SEM); 15. wall structure in transversal section, arrow pointing a perforation, arrowheads pointing internal foramina (TEM). (N = nexine; T = tectum; C = columella; E = echinae; FL = foot layer; EN = endexine; IN = intine).

Plate IV. Pollen grains of *Melochia* L. (see on page 197)

1–4 *M. spicata* — longistylous morph: [Dias T. A. B et al. 376 (HUEFS)] — 1. polar view, fastigium in evidence (arrow); 2-A. equatorial view, aperture detail; 2-B. costa detail; 3. equatorial view (SEM); 4. exine surface (SEM).

5–9 *M. spicata* — brevistylous morph: [Noblick L. R. et al. 2120 (HUEFS)] — 5. polar view, fastigium in evidence (arrow); 6-A. equatorial view, aperture detail; 6-B. costa detail; 7. polar view (SEM); 8. equatorial view (SEM); 9-A. exine surface (SEM). 9-B. Detail of the exine in a fragmented pollen grain (SEM).

10–15 *M. splendens* — brevistylous morph: [França, F. 3266 (HUEFS)] — 10. polar view, fastigium in evidence (arrow); 11. equatorial view, aperture detail and costa detail (arrow); 12. equatorial view (SEM); 13. colporus detail (SEM); 14. exine surface (SEM). 15. Detail of the exine in a fragmented pollen grain (SEM).

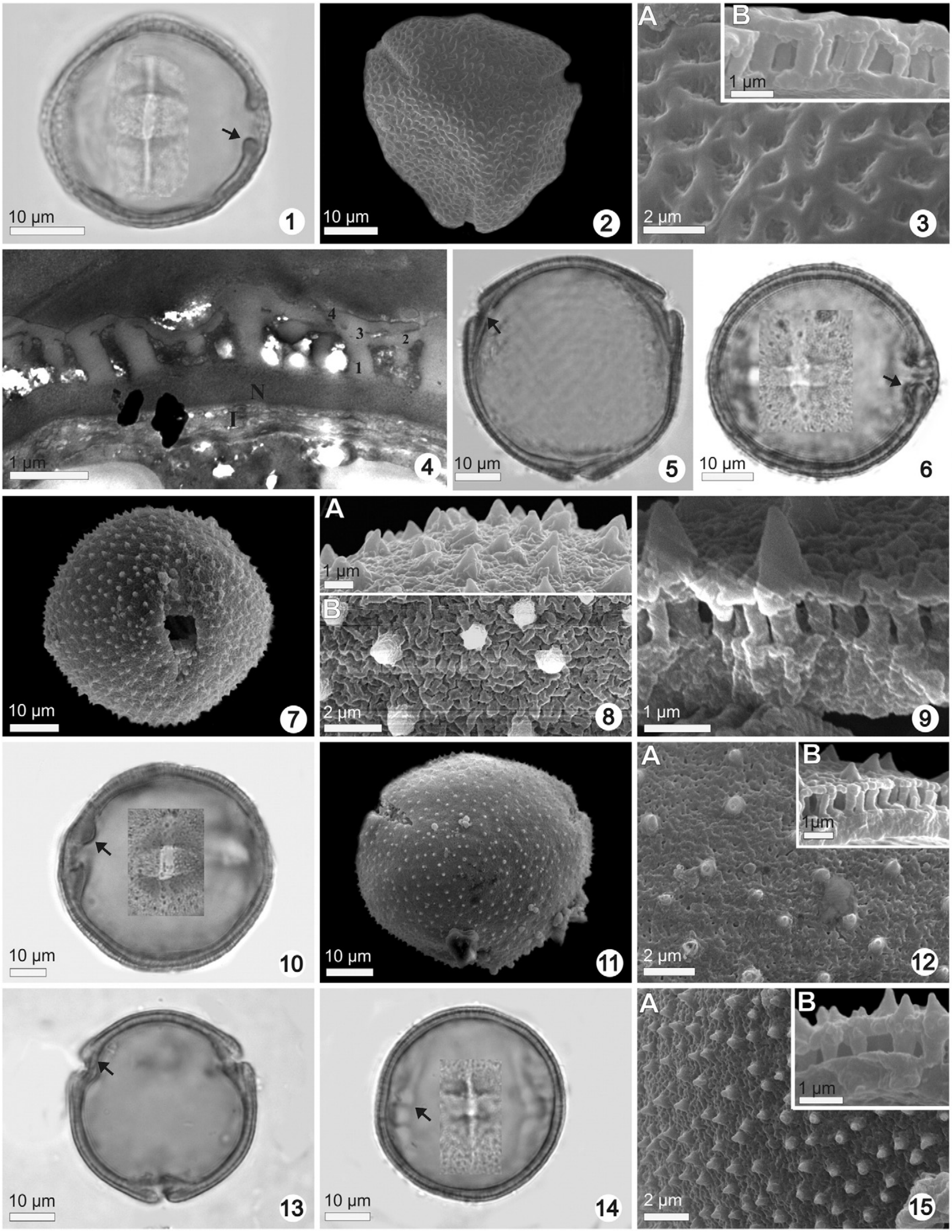


Plate I (*caption on page 193*).

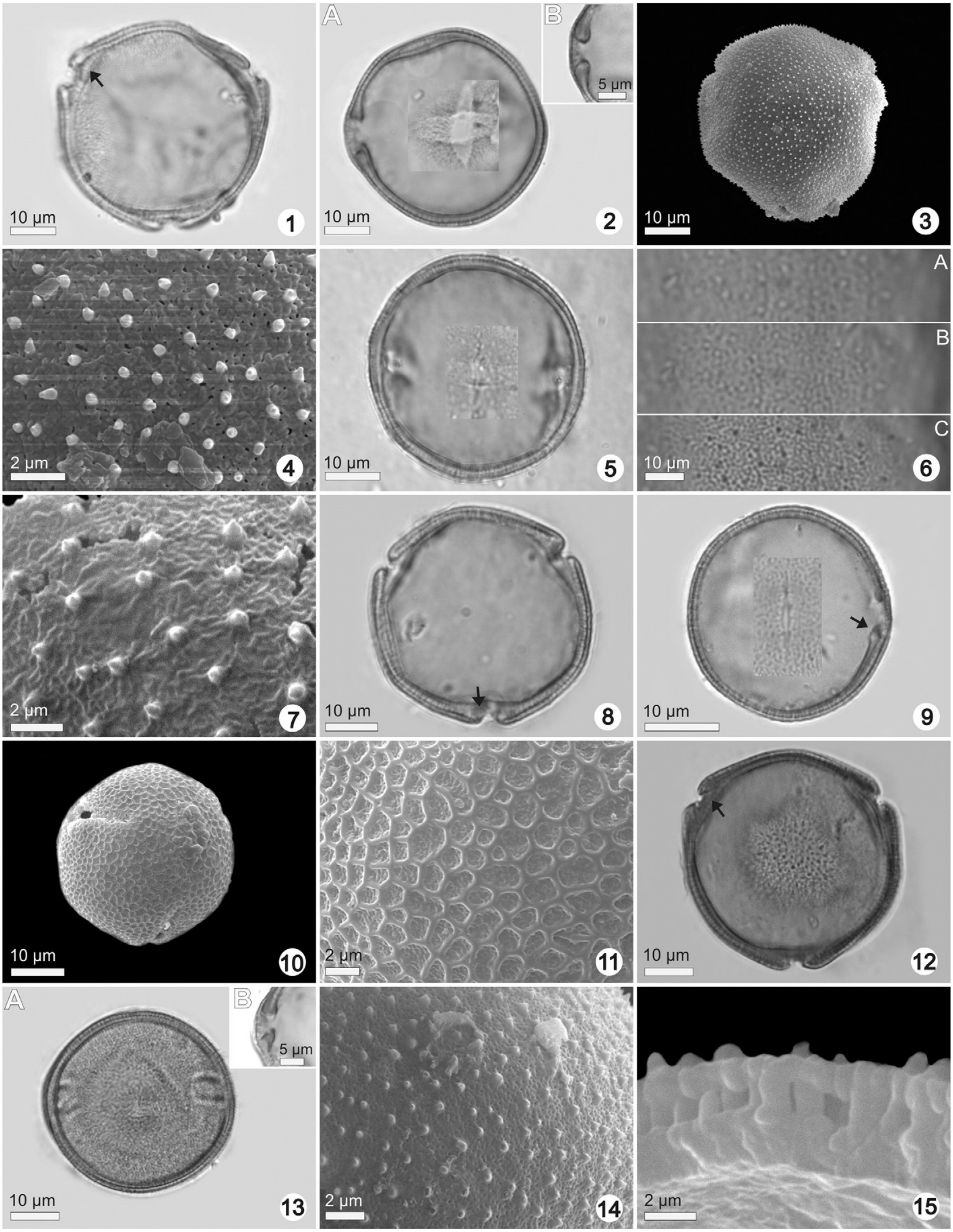


Plate II (*caption on page 193*).

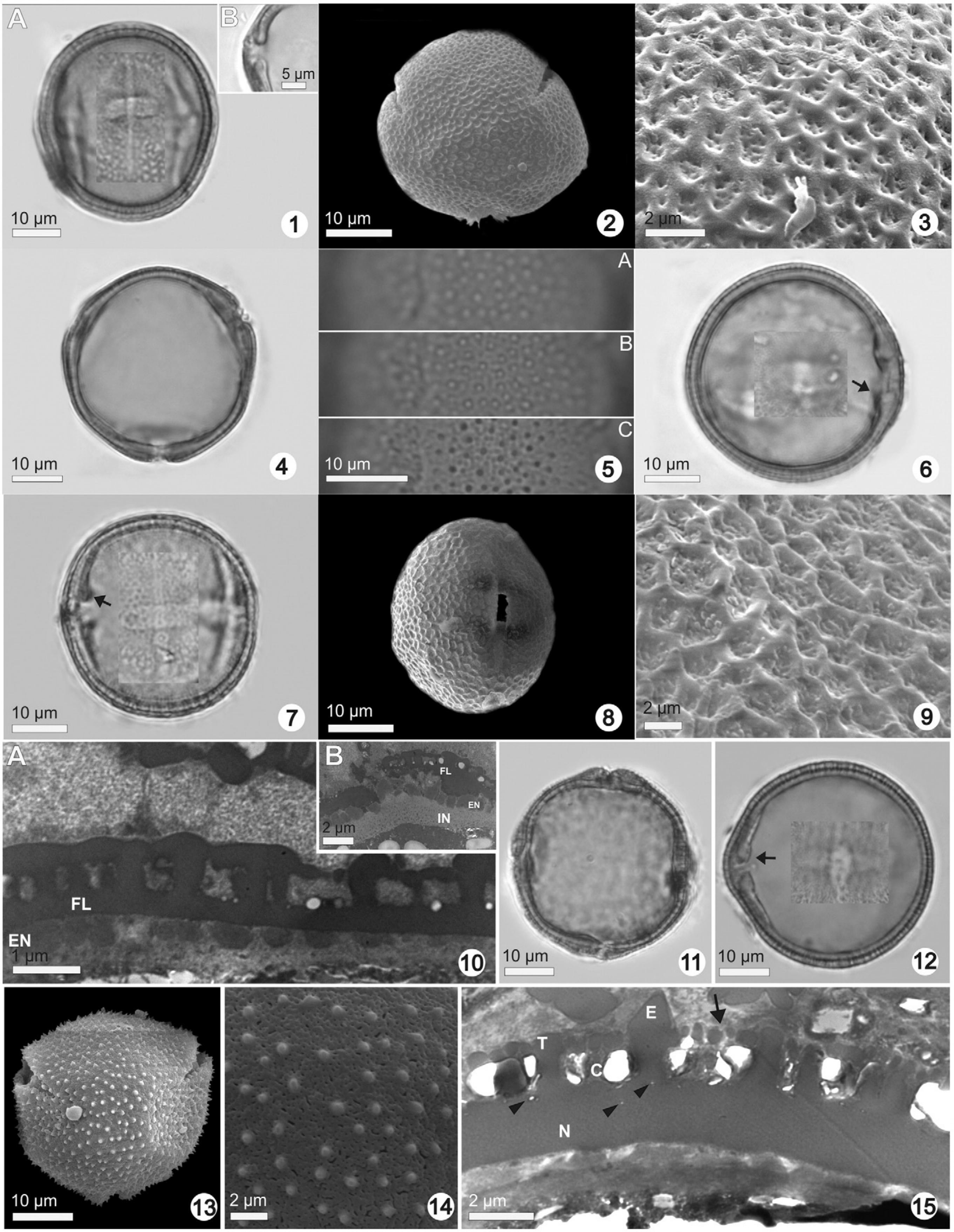


Plate III (*caption on page 193*).

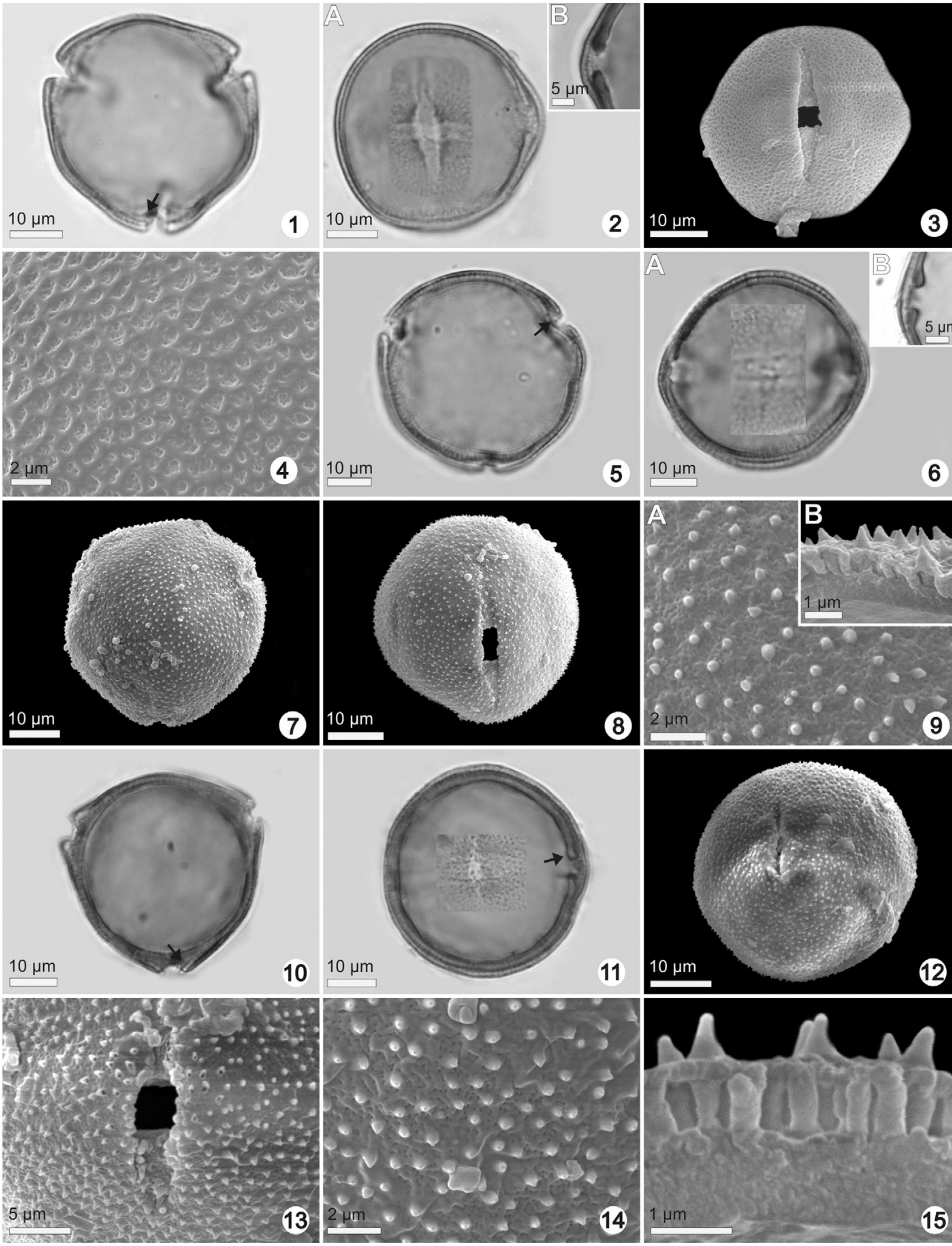


Plate IV (*caption on page 193*).

ferricyanide, and 5 mM calcium chloride in sodium cacodylate buffer for 1 h and 30 min. The pollen grains were re-washed and dehydrated in an ascending acetone series (30, 50, 70, 90, and 100%). The last wash was performed with absolute super dry acetone and repeated three times. Embedment occurred among the samples in Epon resin at room temperature, and 70 nm blocks were cut on an ultramicrotome (Ultracut E; Leica Microsystems, Buffalo Grove, IL, USA). The blocks were posteriorly contrasted in 7% uranyl acetate and lead citrate. The samples were analyzed under a Zeiss EM 109 microscope.

SEM and TEM micrographs were taken of all materials. We adopted the palynological terminology used by Hesse et al. (2009) for the ultrastructural analyses and that by Punt et al. (2007) and Erdtman (1952) for the remaining analyses.

3. Results

Two pollen types were recognized and grouped as species based on exine ornamentation. The pollen grains studied are illustrated in Plates I, II, III, IV and IV. Morphometric data are shown on Table 1, and the morphological characters are shown in Tables 2 and 3.

3.1. Reticulate type-longistylous morph

3.1.1. Light microscopy

The pollen grains were medium sized, isopolar, prolate spheroidal, amb circular, and less often triangular (*M. betonicifolia* and *M. spicata*). Three-zonocolporate, angulaperturate (*M. betonicifolia* and *M. spicata*), and exine reticulate-perforate.

The ectoapertures were short (Table 1; Plate II: 24; Plate III: 7–8; Plate IV: 3; Plate V: 1, 3, 10, 11), usually narrow (Plate I: 1; Plate II: 9, Plate III: 1-A) or slightly wide (*M. spicata* – Plate IV: 2-A), with an irregular contour in *M. spicata*; apex often acute or slightly rounded (*M. pyramidata* – Plate III: 7; and *M. spicata*).

The endoapertures were elongate; height and width varied within species; the upper and lower margins varied from parallel to concave, being rectangular (Plate III: 2-A) or elliptic shaped (Plate V: 10), respectively. Both morphs usually occurred on the same species. The lateral extremities of *M. pilosa* and *M. pyramidata* were visible and rounded (Plate III: 1-A and 7, respectively). Costa were observed on the pollen grains of all species, whereas a fastigium was found only in *M. parvifolia* (Plate II: 8), *M. spicata* (Plate III: 1) and *M. villosa* (Plate V: 9).

The sexine was always thicker than the nexine (Table 1; Plate I: 3-B; Plate V: 4-B), except in *M. parvifolia* in which the sexine was as thick as the nexine. Reticulum often had homogeneous (Plate I: 2–3-A; Plate II: 10–11; Plate III: 3; Plate IV: 3–4) or heterogeneous lumina related to size (*M. pyramidata* – Plate III: 9; and *M. tomentosa* – Plate V: 4-A). These generally measured > 1 μm in diameter, but those < 1 μm occurred in *M. pilosa*, *M. spicata*, and *M. villosa*.

The muri were simplicolumellate, continuous, and straight (Plate I: 2–3-A; Plate II: 10–11; Plate III: 3, Plate IV: 3–4) but discontinuous layers were found in *M. villosa* (Plate V: 12); usually measuring < 1 μm in thickness. Columellae were distinct, with different lengths and had a slightly undulating semitectum in the optical section (Plate I: 3-B and Plate V: 4-B).

3.1.2. Scanning and transmission electron microscopy

SEM confirmed the exine ornamentation characters and provided a more detailed description of the reticulum, which has lower muri (*M. pilosa*, *M. pyramidata*, and *M. spicata*) or slightly higher but narrower in *M. parvifolia* (Plate II: 11). The lumina possessed densely distributed perforations in most species or more sparsely on *M. pyramidata* (Plate III: 9).

Pollen grain wall ultrastructure of two species was investigated under TEM. The pollen grain wall of *M. betonicifolia* (Plate I: 4) consisted of a continuous and compact nexine (foot layer and endexine are inconspicuous), with thick columellae, heterogeneous in size and thickness (sexine 1); discontinuous infratectum (sexine 2); very thin columellae located just above and sparsely distributed and sometimes inconspicuous (sexine 3); and sustaining a continuous supratectum, wider than infratectum, with few perforations (sexine 4). In contrast, *M. pyramidata* (Plate III: 10) pollen grains consisted of a nexine with a continuous foot layer and a discontinuous and compact endexine. The sexine was formed by long and homogeneously sized columellae, and the semitectum was sparsely perforated with muriform enlargements.

3.2. Echinate type-brevistylous morph

3.2.1. Light microscopy

The pollen grains were medium to large-sized (*M. betonicifolia*, *M. caracasana*, *M. illicoides* and *M. pyramidata*), isopolar, oblate spheroidal to prolate spheroidal, spheroidal only in *M. splendens* and *M. tomentosa*, amb circular. 3-(4)-zonocolporate angulaperturate, and exine microechinate and echinate.

The ectoapertures were short to very short (*M. hirsuta*, *M. pilosa* and *M. splendens* – Table 1), usually wide (Plate I: 6–7, 10; Plate II: 2-A; Plate III: 6, 12; Plate V: 6), with an irregular contour in *M. betonicifolia* (Plate I: 6), *M. chamaedrys* (Plate I: 14), *M. hirsuta* (Plate II: 2-A), *M. parvifolia* (Plate II: 13-A) and *M. splendens* (Plate IV: 11). The aperture membrane was always ornamented with echinae, which had an acute apex in all species.

The endoapertures were lalongate (Table 1 and 3), with varying heights and widths among species and upper and lower concave or parallel margins. Lateral ends were rounded (*M. tomentosa* – Plate V: 13) or elliptic (*M. pyramidata* – Plate III: 12) when visible. Costa was present in all species, whereas a fastigium was observed only in *M. caracasana*, *M. pilosa*, *M. pyramidata*, and *M. villosa*.

Sexine was thicker than nexine in most species (Table 1; Plate I: 9, 15-B; Plate IV: 9, 15; Plate V: 8-B). Sexine was less thick than nexine in *M. caracasana*, *M. illicoides*, *M. parvifolia*, *M. pyramidata*, and *M. spicata*. Equally thick sexine and nexine were found only in *M. spicata*. The supratectum elements included microechinae and less commonly echinae, with the largest occurring in *M. tomentosa* (Plate V: 8-B). Echinae were cone-shaped and pointed and densely distributed over the pollen grain surface. The way in which the echinae were distributed between species varied from distantly distributed (in *M. caracasana*) to < 1 μm (*M. spicata* and *M. villosa* – Plate V: 14–15).

3.2.2. Scanning and transmission electron microscopy

M. betonicifolia pollen grains showed a microreticulate-rugulate semitectum under SEM (Plate I: 8), whereas those of other species showed a perforate semitectum (Table 3). We also examined other supratectum elements similar to granules (but not identified) from all species under LM, which were also densely distributed over the pollen grain surface (Plate II: 6; Plate III: 5). These elements were determined to be undulations on the supratectum under SEM. All species had an apertural membrane ornamented with sparse echinae.

Among all brevistylous morphs, only *M. pyramidata* (Plate III: 15) had pollen grains examined under TEM. We found a thick nexine in this taxon without a clear distinction between the endexine and foot layer, besides "internal circular foramina." The sexine was composed of short and heterogeneous columellae, which were wider at the base of echinae, with a densely perforated semitectum.

4. Discussion

Our results support literature data on pollen dimorphism associated with heterostyly in *Melochia*; the pollen grains from the brevistylous morphs were comparatively larger and had an echinate exine, whereas pollen grains from the longistylous morphs had a reticulate exine (Dorr

Table 1
Morphometric characters of pollen grains of heterostylous species of *Melochia* L.

Species/Specimen	PD		ED		EDp		P/E	Ecto	Endo	PAI	Sex	Nex	Lum	E.H.	I.D.
	$\bar{x} \pm S_{\bar{x}}$	Fv	$\bar{x} \pm S_{\bar{x}}$	Fv	$\bar{x} \pm S_{\bar{x}}$	Fv									
Melochia betonicifolia															
Santos V. J. *et al.* 466 (HUEFS) (L)	42.3 ± 0.9	37.5–45.0	40.7 ± 0.8	35.0–42.5	42.2 ± 0.9	37.5–47.5	1.03	27.2 × 2.0	6.0 × 11.6	0.56	1.7	0.7	1.6	–	–
Castro *et al.* 1286 (HUEFS) (L)	43.0 ± 1.0	37.5–47.5	41.2 ± 1.1	37.5–47.5	41.7 ± 0.8	37.5–45.0	1.04	30.5 × 1.1	6.8 × 8.6	0.64	2.0	0.8	2.3	–	–
Rapini, A. *et al.* 1202 (HUEFS) (B)	48.5 ± 1.4	37.5–55.0	51.5 ± 1.5	40.0–57.5	50.7 ± 1.3	45.0–57.5	0.94	22.4 × 3.8	4.4 × 9.0	0.68	1.2	1.8	–	1.0	3.1
Harley, R. M. 54076 (HUEFS) (B)	48.2 ± 1.2	42.5–50.0	48.4 ± 1.4	40.0–57.5	45.8 ± 1.0	42.5–50.0	0.99	22.5 × 3.0	6.5 × 10.0	0.68	1.2	1.1	–	1.0	3.5
M. caracasana															
Carneiro-Torres D. S. 376 (HUEFS) (B)	54.0*	50.0–62.5	56.5*	50.0–65.0	54.1*	45.0–57.5	0.95	28.0 × 4.4	6.4 × 10.0	0.64	1.9	1.0	–	1.0	3.8
M. chamaedrys															
Archer, W. A. & Gehrt. (SP–36416) (B)	42.1 ± 1.1	35.0–45.0	42.3 ± 0.8	37.5–45.0	42.1 ± 0.8	37.5–45.0	0.99	24.1 × 2.3	5.5 × 11.0	0.72	1.0	1.4	–	<1.0	1.5
M. hirsuta															
Harley, R. M. 15776 (CEPEC) (B)	44.4 ± 0.9	40.0–47.5	44.5 ± 0.7	40.0–47.5	43.3 ± 1.0	37.5–47.5	0.99	18.9 × 4.0	6.7 × 14.0	0.80	1.1	1.2	–	<1.0	1.1
M. illicoides															
Queiroz, L. P. 6770 (HUEFS) (B)	50.0*	45.0–52.5	49.0*	47.5–50.0	47.0*	42.5–50.0	1.02	20.2 × 2.7	5.0 × 9.0	0.65	2.0	1.2	–	1.1	3.5
M. parvifolia															
Harley, R. M. 21650 (CEPEC) (L)	41.4*	37.5–47.5	38.2*	35.0–42.5	39.5*	37.5–42.5	1.08	22.9 × 1.4	6.7 × 5.8	0.63	1.8	1.0	2.3	–	–
França, F. 3254 (HUEFS) (L)	44.6 ± 0.6	42.5–47.5	42.0 ± 0.5	40.0–45.0	41.7 ± 0.7	40.0–45.5	1.06	21.4 × 2.4	6.7 × 8.8	0.65	1.1	1.1	1.0	–	–
Saunders, J. 3086 (CEPEC) (B)	44.5 ± 0.9	40.0–50.0	46.1 ± 1.0	40.0–50.0	45.4 ± 1.1	42.5–50.0	0.95	16.5 × 2.7	5.3 × 10.0	0.71	1.5	1.1	–	<1.0	1.0
M. pilosa															
Lee, E. P. *et al.* 4871 (CEPEC) (L)	32.7 ± 0.7	30.0–35–0	29.0 ± 2.0	27.5–32.5	31.0 ± 0.6	27.5–32.5	1.12	20.3 × 1.5	4.4 × 10.0	0.61	1.3	0.9	<1.0	–	–
Ribas O. S. 1235 (SP) (B)	39.9 ± 0.9	35.0–45.0	40.9 ± 0.7	37.5–45.0	38.8*	32.5–45.0	0.97	15.6 × 4.6	6.6 × 15.0	0.77	1.1	1.3	–	<1.0	2.2
M. pyramidata															
Harley, R. M. 2933 (HUEFS) (L)	34.2 ± 1.7	30.0–42.5	30.2 ± 1.0	27.5–37.5	30.0*	30.0–30.0	1.13	21.5 × 1.8	5.4 × 8.0	0.65	1.5	0.6	1.8	–	–
Melo, E. *et al.* 2759 (HUEFS) (B)	38.8 ± 0.7	35.0–42.5	39.8 ± 0.6	37.5–45.0	39.7 ± 0.6	37.5–42.5	0.97	16.5 × 3.7	4.0 × 7.0	0.64	1.0	1.5	–	<1.0	1.6
Ribeiro, T. *et al.* 30 (HUEFS) (B)	54.7*	45.0–65.0	53.5*	47.5–60.0	50.0*	35.0–60.0	1.02	17.5 × 3.7	7.2 × 10.2	0.77	1.5	1.1	–	<1.0	1.6
M. spicata															
Dias T. A. B. *et al.* 376. (HUEFS) (L)	43.4 ± 0.9	37.5–47.5	41.2 ± 0.6	40.0–45.0	41.4 ± 0.7	37.5–45.0	1.05	25.6 × 4.4	3.9 × 11.9	0.53	1.1	1.0	<1.0	–	–
Noblick L. R. *et al.* 2120 (HUEFS) (B)	45.4 ± 0.9	42.5–50.0	46.3 ± 0.9	42.5–50.0	45.9 ± 1.0	42.5–50.0	0.98	20.4 × 2.5	4.5 × 14.4	0.75	1.1	1.1	–	<1.0	<1.0
Ganev W. 2755 (HUEFS) (B)	39.4 ± 0.6	37.5–42.5	41.1 ± 0.7	37.5–45.0	41.6 ± 0.7	40.0–45.0	0.95	21.5 × 4.5	6.0 × 13.0	0.65	1.4	0.9	–	<1.0	<1.0
M. splendens															
França, F. 3266 (HUEFS) (B)	42.1 ± 1.2	37.5–47.5	41.8 ± 1.3	37.5–47.5	42.6*	37.5–50.0	1.00	14.6 × 3.6	4.7 × 7.0	0.76	1.1	1.4	–	<1.0	1.0
M. tomentosa															
Carvalho, A. M. 595 (CEPEC) (L)	44.9 ± 1.2	40.0–52.5	40.0 ± 0.7	37.5–42.5	41.3*	40.0–45.0	1.12	22.0 × 1.3	7.6 × 8.4	0.63	_	_	1.7	–	–
Guedes, M. L. *et al.* 7310 (CEPEC) (L)	40.0 ± 0.8	35.0–45.0	38.5 ± 0.8	35.0–42.5	39.0*	35.0–45.0	1.03	19.6 × 2.1	5.5 × 7.0	0.73	1.5	1.0	1.3	–	–
Mori S. A. *et al.* 11202 (CEPEC) (B)	42.6*	37.5–50.0	42.6*	37.5–50.0	40.7*	37.5–45.0	1.00	17.9 × 2.8	5.3 × 9.4	0.65	1.1	1.2	–	1.3	2.3
M. villosa															
Mori, S. A. 12256 (CEPEC) (L)	38.3 ± 0.9	32.5–42.5	36.0 ± 0.5	35.0–40.0	37.1*	35.0–40.0	1.06	24.0 × 1.3	5.4 × 11.0	0.61	1.3	1.0	<1.0	–	–
Carvalho & Gatti 830 (CEPEC) (B)	43.5 ± 1.0	40.0–50.0	42.7 ± 0.9	37.5–47.5	41.0*	37.5–45.0	1.01	17.2 × 2.7	5.3 × 11.5	0.73	1.2	1.5	–	<1.0	<1.0
Hatschbach G. 48010 (CEPEC) (B)	37.8 ± 1.0	32.5–42.5	38.3 ± 1.2	32.5–45.0	38.8 ± 1.4	30.0–47.5	0.98	14.0 × 1.1	3.5 × 9.1	0.73	1.1	1.3	–	<1.0	<1.0

Note: (L) = longistylous morph; (B) = brevistylous morph; PD = polar diameter; ED = equatorial diameter; EDp = equatorial diameter in polar view; Ecto = length × width of the ectoaperture; Endo = height × width of the endoaperture; PAI = polar area index; Sex = sexine; Nex = nexine; Lum = lumina diameter; E.H. = echinae height; I.D. = interspinal distance; *$n < 25$; measures in μm and indexes in absolute numbers.

Table 2
Morphological characters of pollen grains of *Melochia* L. species — longistylous morph.

Species	Size	v	Colporus					Exine ornamentation (SEM and LM)
			No.	Ectoaperture	Endoaperture	Costa	Fastigium	
Melochia betonicifolia	M	PS	3	Short, narrow, apexes acute	Lalongate: elliptical	+	−	Reticulate; homogeneous and irregular lumina; semitectum slightly undulating
M. parvifolia	M	PS	3	Short, narrow, apexes acute	Lalongate: rectangular to elliptical	+	+	Reticulate; homogeneous and circular lumina; semitectum slightly undulating
M. pilosa	M	PS	3	Short, narrow, apexes acute	Lalongate: elliptical	+	−	Reticulate; homogeneous and circular lumina; semitectum non-undulating
M. pyramidata	M	PS	3	Short, narrow, apexes acute	Lalongate: rectangular to elliptical	+	−	Reticulate; heterogeneous and irregular lumina; semitectum slightly undulating
M. spicata	M	PS	3	Short, wide, apexes acute	Lalongate: rectangular to elliptical	+	+	Reticulate; homogeneous and irregular lumina; semitectum non-undulating
M. tomentosa	M	PS	3	Short, narrow, apexes acute	Lalongate: elliptic to circular	+	−	Reticulate; heterogeneous and irregular lumina; semitectum slightly undulating
M. villosa	M	PS	3	Short, narrow, apexes acute	Lalongate: rectangular to elliptical	+	+	Reticulate; homogeneous and irregular lumina; semitectum slightly undulating

Note: M = medium sized; PS = prolate spheroidal; [+] present; [−] absent.

and Barret, 1989; Miranda et al., 1992; Saba and Santos, 2003; Saba et al., 2004; Faife-Carbrera et al., 2014).

Medium-sized pollen grains were the most common among the species studied, corroborating the literature (Erdtman, 1952; Palacios-Chávez et al., 1990; Miranda et al., 1992; Saba and Santos, 2003; Saba et al., 2004; Faife-Cabrera et al., 2014). Large-sized pollen grains occurred only in the brevistylous morphs of *Melochia betonicifolia*, *M. caracasana*, *M. illicoides*, and *M. pyramidata*, a character also observed by Miranda et al. (1992) and Saba et al. (2004).

Oblate spheroidal shaped pollen grains were the most common among the brevistylous morphs, whereas only prolate spheroidal shapes were found in longistylous morphs, which agreed with the literature (Miranda et al., 1992; Saba and Santos, 2003; Saba et al., 2004). However, Miranda et al. (1992) found prolate spheroidal pollen grains on brevistylous morphs of *M. villosa*. We also found spherical pollen grains on brevistylous morphs of *M. splendens* and *M. tomentosa.* The same pattern was observed by Palacios-Chávez et al. (1990) on *M. tomentosa*, whereas Erdtman (1952) described spherical pollen grains on longistylous morphs of *M. hirsuta* and *M. tomentosa*.

The 3-colporate type aperture was common among the pollen types studied, confirming literature data on this character (Erdtman, 1952; Sharma, 1970; Melhem et al., 1976; Dorr and Barret, 1989;

Table 3
Morphological characters of pollen grains of *Melochia* L. species — Brevistylous morph.

Species	Size	Shape	Colporus					Exine ornamentation (SEM e LM)
			No.	Ectoaperture	Endoaperture	Costa	Fastigium	
Melochia betonicifolia	M to L	OS	3	Short, wide, apex acute	Lalongate: rectangular to elliptical	+	+	Echinate-microreticulate-rugulate (SEM); echinae sparsely distributed;
M. caracasana	L	OS	3	Short, wide, apex acute	Lalongate: elliptical	+	−	Echinate-perforate (SEM); echinae sparsely distributed;
M. chamaedrys	M	OS	3	Short, narrow, apex acute	Lalongate: rectangular to elliptical	+	+	Microechinate-perforate (SEM); micro echinae densely distributed;
M. hirsuta	M	OS	3	Very short, wide, apex acute	Lalongate: rectangular to elliptical	+	+	Microechinate-perforate (SEM); micro echinae densely distributed;
M. illicoides	L	PS	3	Short, narrow, apex acute	Lalongate: rectangular	−	−	Echinate-perforate (SEM); echinae sparsely distributed;
M. parvifolia	M	OS	3	Short, narrow, apex acute	Lalongate: elliptical	+	+	Microechinate-perforate (SEM); micro echinae densely distributed;
M. pilosa	M	OS	3	Very short, wide, apex acute	Lalongate: elliptical	+	−	Microechinate; micro echinae densely distributed;
M. pyramidata	M to L	OS	3(4)	Short to very short, wide, apex acute	Lalongate: elliptical	+	−	Microechinate-perforate (SEM); microechinae densely distributed;
M. spicata	M	OS	3(4)	Short, narrow to wide, apex acute	Lalongate: elliptical	+	+	Microechinate-perforate (SEM); microechinae densely distributed;
M. splendens	M	S	3	Very short, wide, apex acute	Lalongate: rectangular to elliptical	+	+	Microechinate-perforate (SEM); microechinae densely distributed;
M. tomentosa	M	S	3	Short, wide, apex acute	Lalongate: elliptical	+	+	Echinate-perforate (SEM); echinae densely distributed;
M. villosa	M	OS-SP	3	Short, narrow, apex acute	Lalongate: rectangular to elliptical	+	−	Microechinate-perforate (SEM); microechinae densely distributed;

Note: L = large sized; M = medium sized; OS = oblate spheroidal; PS = prolate spheroidal; S = spheroidal; SP = subprolate; [+] present; [−] absent.

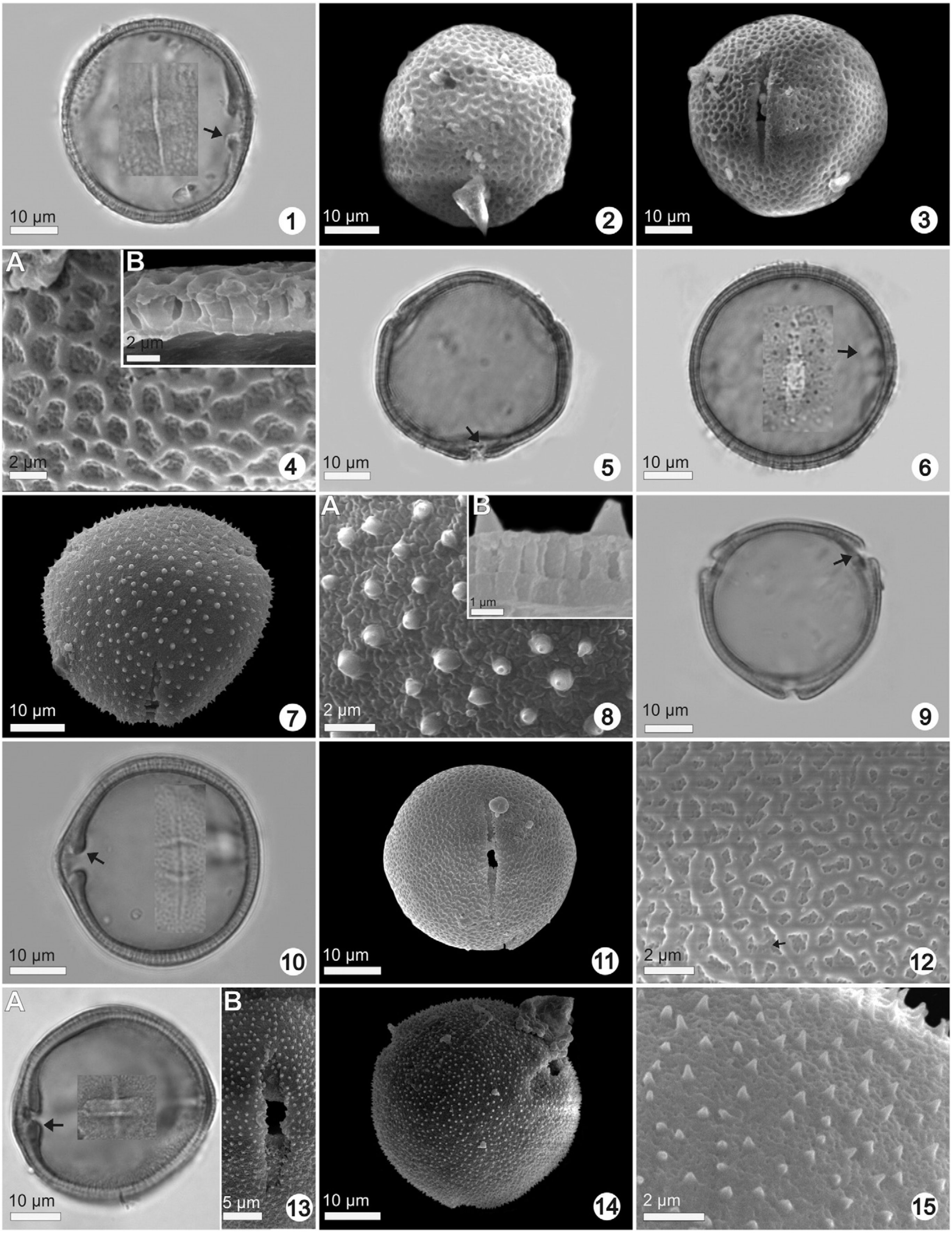
Plate V. Pollen grains of *Melochia* L.

1–4 *M. tomentosa* — longistylous morph: [Carvalho, A. M. 595 (CEPEC)] — 1. equatorial view, aperture detail and costa detail (arrow); 2. polar view (SEM); 3. equatorial view (SEM); 4-A. exine surface (SEM). 4-B. Detail of the exine in a fragmented pollen grain (SEM).

5–8 *M. tomentosa* — brevistylous morph: [Mori S. A. et al. 11202 (CEPEC)] — 5. polar view, fastigium in evidence (arrow); 6. equatorial view, aperture detail and costa detail (arrow); 7. polar view (SEM); 8-A. exine surface (SEM). 8-B. Detail of the exine in a fragmented pollen grain (SEM).

9–12 *M. villosa* — longistylous morph: [Mori, S. A. 12256 (CEPEC)] — 9. polar view, fastigium in evidence (arrow); 10. equatorial view, aperture detail and costa detail (arrow); 11. polar view (SEM); 12. exine surface (SEM), detail of the a discontinuous murus (arrow).

13–15 *M. villosa* — brevistylous morph: [Carvalho A. M. and Gatti, J. 830 (CEPEC)] — 13-A. equatorial view, aperture detail and costa detail (arrow); 13-B. Detail of the colporus (SEM); 14. polar view (SEM); 15. exine surface (SEM).


10 µm
1
10 µm
2
10 µm
3
A
B
2 µm
2 µm
4
10 µm
5
10 µm
6
10 µm
7
A
B
1 µm
2 µm
8
10 µm
9
10 µm
10
10 µm
11
2 µm
12
A
B
10 µm
5 µm
13
10 µm
14
2 µm
15

Palacios-Chávez et al., 1990; Saba and Santos, 2003; Saba et al., 2004; Faife-Cabrera et al., 2014). Parasyncolpate pollen grains, as described by Roubik and Moreno (1991) for some *Melochia* species, were not observed on any of the taxa studied. Another contradiction is the description of colpate pollen grains on *M. betonicifolia* as described by Miranda et al. (1992). Heteromorphic variations related to the number of apertures occurred in the brevistylous morphs of the two species, with four colpi found in 29.4% of *M. pyramidata* pollen grains but only 4% of *M. spicata* pollen grains. Saba et al. (2004) also observed the same pattern in *M. pyramidata*; however, this variation was observed in *M. spicata* longistylous morphs.

The sizes of the ectoapertures varied among the different floral morphs, and the largest were detected on pollen grains from longistylous morphs. Saba et al. (2004) observed this difference only in *M. spicata* and *M. tomentosa*, whereas the opposite was seen in *M. pyramidata*. Therefore, it is clear that the dimensions of the colpi on pollen grains vary highly within the same *Melochia* species, as observed by Palacios-Chávez et al. (1990), Miranda et al. (1992), and Saba et al. (2004). Palacio-Chávez et al. (1990) reported a scabrate aperture membrane on *M. tomentosa* (brevistylous flowers) under LM, whereas Saba et al. (2004) described ectoapertures with an irregular contour and an apertural membrane ornamented with sparse microechinae on *M. spicata* and *M. tomentosa* brevistylous morphs under SEM. We found the same pattern under SEM.

Endoapertures were always lalongate with different heights and widths, and did not correlate between the floral morphs. Their shapes were described as elliptic or rectangular herein, following Saba et al. (2004). It is clear that this character varies within the same species. The occurrence of a fastigium was common in most of the species studied, including both floral morphs, but most authors who have examined this genus did not detect this character. Saba et al. (2004) recorded a fastigium on the pollen grains of *M. betonicifolia*, *M. pyramidata*, and *M. tomentosa* brevistylous morphs. We found no fastigium in either *M. pyramidata* floral morph. A costa was frequently seen on the study specimens but was not on *M. illicoides* (brevistylous flowers). A costa has only been found on the *M. spicata* longistylous morph by Saba and Santos (2003).

The exines on the brevistylous morphs were usually thicker, although their thickness was similar among the *M. betonicifolia* and *M. pilosa* floral morphs. Saba et al. (2004) also observed thicker exines on brevistylous morphs. The sexine was always thicker than the nexine on longistylous morphs, and the opposite pattern was seen on the brevistylous morphs, which was similar with the literature (Dorr and Barret, 1989; Saba et al., 2004).

Overall, our data agree with the literature regarding exine ornamentation (Saba and Santos, 2003; Saba et al., 2004; Faife-Carbrera et al., 2014); however, Saba et al. (2004) described a suprareticulate exine in the genus, which contrasts with our interpretation. The *Melochia* genus includes a species with no records of heteromorphic ornamentation, as reported by Dorr and Barret (1989) for *Melochia* sect. *Physodium*.

The size, shape, and diameter of the lumina among reticulate pollen grains were used as informative characters to distinguish *Melochia* species. Most species had lumina >1 μm, which were homogeneous in size but irregular in shape. Similar data were reported by Saba et al. (2004) for *M. betonicifolia*, *M. spicata*, and *M. tomentosa*, diverging only for *M. pyramidata*, which was described as homobrochate. In contrast, Saba and Santos (2003) described *M. spicata* as microreticulate under LM, instead of reticulate as in our study. Saba et al. (2004) observed the same characters seen here for *M. betonicifolia* and *M. pyramidata*.

The brevistylous pollen grains had an echinate exine, with an elevated semitectum like grains, but mostly inconspicuous under LM. Saba et al. (2004) did not report these elements, whereas Palacios-Chávez et al. (1990) described a perforated semitectum in *M. tomentosa*. Furthermore, Faife-Carbrera et al. (2014) reported verrucate pollen grains in brevistylous morphs of *M. parvifolia*, *M. pyramidata*, *M. tomentosa*, and *M. villosa* under SEM, which disagrees with our data. The distribution of echinae over the pollen grain surface was also an important character in our study. They were mostly densely distributed, although differences in interspinal measures were detected. These echinae were described as homogeneously distributed by Saba et al. (2004). Those authors described *M. betonicifolia* and *M. tomentosa* as microechinate, whereas we found echinae >1 μm. The same pattern was observed by Palacios-Chávez (1990) in *M. tomentosa*.

Saba et al. (2004) shared some of the species studied with our work (*M. spicata* and *M. tomentosa*). They reported similar results as our study, although they highlighted different echinae characters. *Melochia* pollen grain wall ultrastructure is reported here for the first time.

5. Conclusion

Melochia L. had highly variable pollen morphology among the specimens studied, due to heterostyly, including pollen grain size, shape, ectoaperture length, and exine ornamentation, which were helpful for distinguishing the two floral morphs.

Some characters we described varied more among specimens than descriptions in previous studies; thus, they are of little taxonomic relevance. For example, the qualitative characters of the ectoaperture and endoaperture were not useful to distinguish species, although they differed among the floral morphs.

Exine ornamentation was the most consistent character for recognizing *Melochia* L. sp. Among the brevistylous morphs, semitectum ornamentation and interspinal distance were principal features characterizing the pollen grains. The differences among the longistylous morphs were restricted to dimensions of the reticulum lumina and perforation density.

The study of pollen grain ultrastructure revealed reliable characters for differentiating the longistylous morphs of *M. betonicifolia* and *M. pyramidata*, based on the nexine foot layer, differentiation of the endexine, and sexine stratification.

This study provides important information for future studies regarding *Melochia* spp. Our results must be verified with a greater number of specimens.

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