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Palynotaxonomy of Brazilian species of Passifloraceae *sensu stricto*

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ABSTRACT

This study aims to expand knowledge of the pollen morphology of Passifloraceae and contribute to the taxonomic delimitation of the group by morphologically characterizing pollen grains of species that occur in the Brazilian state of Bahia. Thirty-six species occur in the state, one of the genus *Mitostemma* (*M. glaziovii*) and 35 of the genus *Passiflora*. Pollen samples were acetolysed, measured, and described using light and scanning electron microscopy. The results group the studied species into four pollen types based mainly on aperture type and number, opercular variation, and the presence/absence of ornamentation elements inside the lumina of the reticulum: Pollen type I - species belonging to the subgenera *Astrophea* and *Deidamioides*; pollen type II - subgenus *Decaloba*; pollen type III - subgenus *Passiflora*; and pollen type IV - *M. glaziovii*, with pollen characteristics that separate it from the other species analyzed. The results reinforce the recognition of three subgenera of *Passiflora*. Morphopalynologically the species have very similar pollen types except for those of the subgenus *Deidamioides*, which are quite diverse and thus included in another pollen type. The results reveal the importance of pollen grains for the taxonomic study of Passifloraceae.

Keywords: Brazil, *Mitostemma*, *Passiflora*, palynology, pollen morphology, taxonomy

Introduction

Passifloraceae *sensu stricto* comprises 16 genera and more than 630 species distributed in tropical and subtropical regions. Its greatest diversity is in the Neotropical region, where there are about 576 species (Ocampo & d'Eeckenbrugge 2017). Four genera occur in Brazil, including 154 native and cultivated species: *Ancistrotryrsus*, *Dilkea*, *Mitostemma*, and *Passiflora* (Nunes & Queiroz 2006; Souza & Lorenzi 2008; Bernacci *et al*. 2015). *Passiflora* is the most economically important genus (Sacco 1980; Cervi 2005) due to the use of its fruits as food, its adaptability to cultivation as an ornamental plant, and its medicinal properties (Killip 1938; Bernacci *et al*. 2003). Recent studies in the state of Bahia revealed the presence of the genus *Passiflora*, represented by 43 taxa, and the genus *Mycostemma*, with only one species, *M. glaziovii* (Bernacci *et al*. 2015).

Mitostemma has only three recognized species: *M. glaziovii*, *M. brevifilis* and *M. jenmanii*. *Passiflora* is currently represented by about 520 species (Ulmer & MacDougal 2004), with predominance in the Neotropical region (Killip 1938). Killip (1938) and Escobar (1989) subdivided the genus *Passiflora* into 23 subgenera. Only four subgenera are recognized by a more recent grouping proposed by Feuillet & MacDougal (2003 [2004]) based exclusively on morphological and ecological traits: *Astrophea*, *Deidamioides*, *Decaloba*, and *Passiflora*. These subgenera were partial or totally corroborated by recent phylogenetic work using molecular markers (Muschner *et al.* 2003; Yockteng & Nadot

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2004; Muschner 2005; Hansen *et al*. 2006; Zamberlan 2007; Krosnick *et al.* 2013). *Passiflora*, *Decaloba,* and *Astrophea* were strongly supported by several analyses carried out by Muschner *et al.* (2003), Muschner (2005) and Zamberlan (2007), while *Deidamioides* was accepted as valid only by Hansen *et al.* (2006), and considered polyphyletic by other authors (Muschner *et al.* 2003; Yockteng & Nadot 2004; Krosnick *et al*. 2006; Muschner 2005; Nunes 2009, Zamberlan 2007).

The study of pollen grains of species of Passifloraceae, mainly of the genus *Passiflora*, has long aroused the interest of several palynologists. Mohl (1834) presented the pollen morphology of species of *Passiflora*, highlighting shape and ornamentation as good taxonomic characters. These observations were supported by further studies conducted by Fischer (1890) and Erdtman (1952), who indicated striking pollen characteristics among species of *Passiflora*. Subsequently, Presting (1965) conducted a detailed study of the pollen grains of 153 species of the family Passifloraceae, of which 106 belonged to the genus *Passiflora*. This author traced the phylogeny of this group based on pollen grain morphology and the classification of Killip (1938).

Studies dealing with the pollen morphology of Brazilian species of Passifloraceae have evidenced their apertural diversity and provided important contributions to describing pollen morphology of the family. They also highlighted problems found in the interpretations of structures and nomenclature (Carreira 1977; Roubik & Moreno 1991; Palacios-Chávez 1991; Melhem *et al.* 2003; Milward-de-Azevedo *et al*. 2004; 2010; 2014; Dettke & Santos 2009; Evaldt *et al.* 2011; Verdasca *et al.* 2013; Mezzonato-Pires *et al*. 2015a; b; 2017; 2018; Borges & Milward-de-Azevedo 2017; Soares *et al*. 2018).

Among such studies, Dettke & Santos (2009), using several microscopy techniques, performed detailed studies of the apertural types of species of *Passiflora*. These authors discussed the most controversial nomenclature issues in the literature of this group, and contributed significantly to uniformity of palynological terms related to Passifloraceae.

The present work aims to analyze the pollen morphology of species of Passifloraceae occurring in the state of Bahia, Brazil, to contribute to the taxonomic delimitation of species and increase knowledge of pollen morphology of the family.

Materials and methods

Thirty-five species of the genus *Passiflora* and one species of the genus *Mitostemma* (*M. glaziovii*) were selected for study based on the survey carried out by Nunes (2009). The species of *Passiflora* belong to the subgenera *Astrophea* (two species), *Deidamioides* (three species), *Decaloba* (eight species) and *Passiflora* (22 species).

Poliniferous material was obtained from specimens deposited in the main herbaria in the state of Bahia, namely ALCB, CEPEC, HRB and HUEFS, as well as in herbaria of other states, namely IPA and JPB, to obtain additional material (acronyms according to Thiers *et al.* 2013). More than one specimen was analyzed for each species whenever possible.

The following is the material examined ordered by subgenus: **Subg. *Astrophea*** (Ohwi) Rchb.: *Passiflora mansoi* (Mart.) Mast. **BRAZIL. Mato Grosso:** Xavantina, 21/X/1968, M.J.C. Sidney 1470 (JPB). *P. rhamnifolia* Mast. **- Bahia:** Palmeiras, 31/XII/2007, A. Rapini 1426 (HUEFS); Palmeiras, 30/XII/1994, M.L.Guedes *et al.* 1507 (HUEFS). **Subg. *Decaloba*** (DC.) Rchb.: *P. capsularis* L. **- Bahia:** Ilhéus, 5/V/198, J.L. Hage & H.S. Brito 645 (HRB); Ilhéus, s.d., J.L. Hage *et al*. 2142 (CEPEC). *P. jiboiaensis* M.L. Milward-de-Azevedo **- Bahia:** Serra da Jibóia, 19/XI/2000, J.C. Carvalho-Sobrinho *et al.* 40 (HUEFS); *P. misera* Kunth **- Bahia:** Ibiraba (=Icatu), 24/II/1997, L.P. Queiroz 4832 (HUEFS); Nilo Peçanha, 5/5/2000, R.P. Oliveira *et al.* 534 (HUEFS); *P. organensis* Gardner **- Bahia:** Cairu, Ilha de Tinharé, Mata do Sertão, 28/X/1996, M.L. Guedes & M. Acioly 4786 (ALCB); *P. pohlii* Mast. **Mato Grosso:** Nova Xavantina, Margem do rio das Mortes até o rio Areiões. 13/X/1968, A.M. Giulietti 493 (IPA); *P. rubra* L. **- Bahia:** Canavieiras, 27/XII/2005, T.S. Nunes 1428 (HUEFS). *P. saxicola* Gontsch **- Bahia:** Xique-Xique, 13/1X/1990, A. Freire-Fierro *et al.* 1931 (HUEFS); *P. suberosa* L. **- Bahia:** Mundo Novo, 11/III/1999, E.de Melo *et al.* 2781 (HUEFS); Cravolândia, 29/V/1994, E. de Melo & F. França 1048 (HUEFS). **Subg. *Deidamioides*** (Harms) Killip: *P. contracta* Vitta - **Bahia:** Maraú, 30/XII/1999, D.S.Carneiro-Torres & J.F.Torres, 189 (HUEFS); Entre Rios, 16/IV/2000, E.B. Miranda-Silva *et al.* 400 (HUEFS); *P. igrapiunensis* T.S.Nunes & L.P.Queiroz **- Bahia:** Igrapiúna, 18/XII/2002, M.L. Guedes 9294 (ALCB - Holótipo); *P. timboënsis* T.S.Nunes & L.P.Queiroz **- Bahia:** Amargosa, 18/XI/2007, A.M. Amorin 7027 (CEPEC - Holótipo). **Subg. *Passiflora*** L.: **Bahia:** *Passiflora alata* Curtis **- Bahia:** Rio de Contas, Área de controle da Caraíba Metais, 1/XII/1982, L.R. Noblick 2252 (HUEFS); Caminho para Jiló, estrada Rio de Contas, 28/III/1998, T.S.N. Sena 38 (HUEFS). *P. amethystina* J.C.Mikan **- Bahia:** Uruçuca, 21/VI/1970, T.S.dos Santos s/n (UFPR 13069); Itajuípe, 28/III/1998, R.S. Pinheiro 1305 (CEPEC); Buerarema, 10/VII/1964, C.M. Magalhães 57 (CEPEC). *P. bahiensis* Klotzsch **- Bahia:** Itaberaba, 14/VII/2006, L.P. de Queiroz de 12235 (HUEFS). *P. cacao* Bernacci & M. M.Souza **- Bahia:** Entre Rios, 26/XII/2014, A.V. Popovkin 1661 (HUEFS). *P. caerulea* L. - **Paraná:** Curitiba, 14/I/1986, J. Cordeiro & J.M. Silva 216 (HUEFS). *P. cincinnata* Mast. **- Bahia:** Serra Preta, 1/VII/2000, R.C.M.S. Araújo 01 (HUEFS); Cachoeira, 1/III/1992, M.C. Ferreira 475 (HUEFS). *P. clathrata* Mast. **- Bahia:** Cachoeira, VI/1990, Grupo Pedra do Cavalo 256 (HRB). *P. edmundoi* Sacco **- Bahia:** Catolés, 27/XI/1999, A.S. Conceição & G.L. Campos 438 (HUEFS); Senhor do Bonfim, 28/VII/2005, T.S.Nunes 1237 (HUEFS); *P. edulis* Sims. **- Bahia:** Salvador, 31/X/1995, A.O. França 01 (ALCB); Ilhéus,

08/II/1999, N.R.S. Santos & L.S.S. Martins 82 (HUEFS). *P. foetida* L. - **Bahia:** Serra Preta, 1/4/200, R.C.M.S. Araújo 03 (HUEFS); Castro Alves, 30/VII/1994, C.A.L. Carvalho 56 (HUEFS). *P. lueltzelburgii* Harms. - **Bahia:** Morro do Chapéu, 17/XI/1999, E. de Melo *et al.* 3159 (HUEFS); Araci, 20/2/2000, A.M. Giulietti. & R.M. Harley 1710 (HUEFS); *P. miersii* Mast. **São Paulo:** São Paulo, 5/XI/1989, L.P. de Queiroz 2214 (HUEFS). *P. mucronata* Lam. - **Bahia:** Ilhéus, 15/I/1990, A.M. de Carvalho 2731 (CEPEC); Cairu, Morro de São Paulo, 25/X/1996, M.L. Guedes & M. Acioly 4760 (ALCB). *P. mucugeana* T.S.Nunes & L.P.Queiroz - **Bahia:** Estrada para Capão do Correia, 15/II/2002, T.S. Nunes *et al.* 847 (HUEFS); *P. nitida* Kunth. - **Bahia:** Barra do Choça, 03/III/1978, S.A. Mori *et al.* 9398 (CEPEC). *P. odontophylla* Harms. - **Bahia:** Eunápolis, s.d., R.P. Belém *et al.* 2627 (CEPEC). *P. recurva* Mast. - **Bahia:** Gentio do Ouro, 25/IX/1999, E. Miranda-Silva *et al.* 238 (HUEFS); Morro do Chapéu, 18/XI/1999, E. de Melo 3178 (HUEFS). *P. setacea* DC. - **Bahia:** Lençóis, 20/XI/1986, L.P. de Queiroz *et al.* 1321 (HUEFS). *P. silvestris* Mast. - **Bahia:** Entre Rios, 14/V/2014, A.V. Popovkin 1714 (HUEFS). *P. trintae* Sacco. - **Bahia:** Barra do Choça, 30/XII/1997, R.M. Harley *et al.* 20197 (CEPEC); Vitória da Conquista, 4/III/1978, S.A. Mori *et al.* 9416 (CEPEC). *P. villosa* Vell. - **Bahia:** Ibicoara, 16/II/2002, T.S. Nunes 889 (HUEFS); *P. watsoniana* Mast. - **Bahia:** Castro Alves, 7/V/1993, L.P. de Queiroz *et al.* 3163 (HUEFS); Santa Terezinha, 18/III/1995, F. França *et al.* 1098 (HUEFS); *Mitostemma glaziovii* Mast. – **BRASIL. Espírito Santo:** Linhares, 19/VIII/2007, T.S.Nunes, 1813 (HUEFS).

For observation using light microscopy (LM), pollen samples were acetolysed following the method of Erdtman (1960). Pollen grains were mounted between slides and coverslips with glycerinated gelatin and measured, described, and photomicrographed (LM). Polar diameter (PD), equatorial diameter (ED) in equatorial view and equatorial diameter in polar view (EDpv) were measured for 25 randomly-selected pollen grains, whenever possible. Ten measurements were taken for the diameters of pseudopercula, opercula and mesocolpia, as well as for the greatest width of pontopercula, and exine layers (sexine and nexine). For heteromorphic species, only pollen grains with six apertures were measured because they were the majority in all samples.

For SEM analysis, acetolysed pollen grains were submitted to an ascending hydroethanolic series, dripped directly onto the specimen hold, and covered by a thin layer of gold (ca. three minutes). The assembly was observed and electromicrographed using a LEO 1430 VP microscope.

Quantitative results were treated statistically by calculating the arithmetic mean , the standard deviation of the sample, the standard deviation of the mean (S, and the coefficient of variability (CV %) with a confidence interval of 95 % for parameters with a sample size of 25; only the arithmetic mean was calculated for measurements with a sample size of ten. The examined slides were deposited in the pollen collection of the Laboratório de Micromorfologia Vegetal (LAMIV) of the Departmento de Ciências Biológicas of the Universidade Estadual de Feira de Santana. The adopted terminology was based on the palynological nomenclature of Punt *et al.* (2007).

Results

Analysis of species of the genera *Mitostemma* and *Passiflora* established four pollen types according to the aperture number and type, opercular morphology, and presence/absence of elements within lumina. Subtypes were established to group species that exhibited variation, in any of the mentioned characters, within established types. The main analyzed characters of pollen morphology are shown in Tables 1-3 and illustrated in Figures 1-3.

Pollen Type I. 6-colporate pollen grains with pontopercula forming a tri-radiate structure, reticulum lumina not ornamented to slightly or densely granulate (Fig. 1 A-C).

Subtype I.1: Pollen grains with deep lumina, not ornamented or slightly granulate. Species: *P. mansoi* and *P. rhamnifolia* (subgenus *Astrophea*) (Fig. 2A-C), and *P. timboënsis* (subgenus *Deidamioides*) (Fig. 2D-E).

Subtype I.2: Pollen grains with shallow lumina, densely granulate. Species: *P. contracta* and *P. igrapiunensis* (subgenus *Deidamioides*) (Fig. 2F-H).

Pollen grains medium (*P. mansoi* and *P. rhamnifolia)* to large-sized (other species), isopolar, prolate spheroidal, subtriangular to subcircular, 6-colporate, exine reticulate. Ectoapertures paired, narrow and tapered at ends, not fused in the apocolpium (Fig. 2A); three linear endoapertures with rounded ends for each pair of proximal ectoapertures, but difficult to visualize; protruding pontopercula in equatorial region strongly fused to apocolpium forming a tri-radiate structure (Fig. 1A-C). Exine reticulate, heterobrochate with perforation in apocolpium region (*P. rhamnifolia*); deep lumina not ornamented (*P. rhamnifolia*), deep lumina slightly granulate (*P. mansoi* and *P. timboënsis*), shallow lumina densely granulate (*P. contracta* and *P. igrapiunensis*); muri continuous (or interrupted in *P. timboënsis* - Fig. 2E), psilate, sinuous and simplicolumellate.

Pollen Type II. 6-12-colporate pollen grains with (pont-) opercula, reticulum lumina granulate or not ornamented (Fig. 1D-E).

Subtype II.1: 6-colporate pollen grains with six opercula on six individual endoapertures and six mesocolpia. Species: *P. jiboiaensis*, *P. misera*, *P. pohlii*, *P. saxicola* and *P. suberosa* (subgenus *Decaloba*) (Fig. 3A).

Subtype II.2: 12-colporate pollen grains with six opercula between a pair of endoapertures, with three pontopercula and three pseudopercula. Species: *P. capsularis*, *P. organensis*, *P. rubra* (subgenus *Decaloba*) (Fig. 3B-C).

Pollen grains medium-sized, isopolar, oblate-spheroidal to prolate-spheroidal, amb subcircular to subtriangular, colporate, exine reticulate. Long ectoapertures, long endoapertures with imprecise contours. Subtype 1 has pollen grains with six functional opercula (Fig. 1D) on six individual endoapertures, which are difficult to visualize, intercalating six mesocolpia (Fig. 3A), and possible partial fusion of ectoapertures in the apocolpium, especially in *P. misera* and *P. suberosa* (Fig. 3A). Subtype 2 has pollen grains with six non-functional opercula between a pair of endoapertures interspersed by three pseudopercula and three pontopercula (Figs. 1E, 3B) that extend and fuse in the apocolpium region. Exine reticulate, heterobrochate; lumina granulate or not ornamented (*P. suberosa*); muri smooth, tall, sinuous, continuous simplicolumellate (Fig. 3C).

Table 1. Measurements (in µm) of pollen grains of species of Passifloraceae. TYPE I. PD = polar diameter, ED = equatorial diameter, EDpv = equatorial diameter in polar view, $\bar{x}$ = arithmetic mean, $S_{\bar{x}}$ = standard deviation of the mean, FV = range, P/E = polar/equatorial diameter ratio [n = 25], Pt = length of pontoperculum in equatorial view, Mes = width x length of mesocolpium, SEX = sexine, NEX = nexine [n = 10] [n* = 25].

Genus/ Subgenus Species / Specimens	PD		ED		EDpv		P/E	Pt	Mes	SEX	NEX
	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV					
Passiflora L.											
Subg. *Astrophea* (DC.) Mast.											
P. mansoi											
M.J. Sidney 1470	58.5±0.8	67.5-50.0	52.7±1.1	37.5-62.0	53.5±0.8	47.5-60.0	1.15	3.9	19.0-6.0	2.0	1.5
P. rhamnifolia											
A. Rapini 1426	36.8±0.3	27.5-40.0	38.9±0.8	32.5-47.5	37.5±0.4	32.5-49.0	1.10	4.0	17.0-5.0	1.9	1.0
M.L. Guedes *et al* 1507	34.6±0.7	27.5-40.0	30.9±0.7	25.0-35.0	29.5±0.6	27.5-35.0	0.95	4.3	15.0-5.0	2.0	1.0
Subg. *Deidamioides* (DC.) Mast.											
P. contracta											
D.S. Carneiro-Torres & J.F. Torres 189	63.0±0.4	60.0-67.5	62.1±0.7	57.5-67.5	64.2±0.7	69.0-70.0	1.01	5.9	16.0-10.0	2.0	1.5
E.B. Miranda-Silva *et at*. 400	61.7±1.5	42.5-75.0	63.6±1.4	47.5-75.0	62.6±0.7	57.5-67.5	0.97	7.3	20.0-15.0	1.8	1.3
P. igrapiunensis											
M.L.Guedes 9294	71.3±1.5	47.5-82.5	67.8±1.5	60.0-71.8	*71.8	62.5-75.0	1.05	13.0	17.0-12.5	2.9	1.1
P. timboënsis											
A.Amorim 7027	68.8±0.9	65.0–75.0	63.6±1.2	55.0-70.0	*67.5	60.0-70.0	1.08	13.5	18.0-14.0	2.4	2.1

Table 2. Measurements (in µm) of pollen grains of species of Passifloraceae. TYPE II. PD = polar diameter, ED = equatorial diameter, EDpv = equatorial diameter in polar view, $\bar{x}$ = arithmetic mean, $S_{\bar{x}}$ = standard deviation of the mean, FV = range, P/E = polar/equatorial diameter ratio [n = 25], Pt = length of pontoperculum in equatorial view, Mes = width x length of mesocolpium, Ps = width pseudoperculum, Op = width operculum, SEX = sexine, NEX = nexine [n = 10] [n* = 25].

Genus/ Subgenus Species / Specimens	PD		ED		EDpv		P/E	Pt	Mes	Ps	Op	SEX	NEX
	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV							
Passiflora L.													
Subg. *Decaloba* (DC.) Mast.													
P. capsularis													
JL. Hage & H.S. Brito 645	54.8±1.3	50.0-62.5	57.4±0.44	50.0-52.5	56.4±0.6	52.5-62.5	0.95	4.1	–	13.0-7.0	10.0-4.0	3.6	2.0
J.L.Hage *et al* 2142	56.0±0.5	62.5-50.0	58.3±0.5	50.0-72.5	59.0±0.7	55.0-67.5	0.96	4.2	–	12.0-7.5	10.0-5.0	2.4	2.1
P. jibooianensis													
J.C. Carvalho-Sobrinho *et al*. 40	48.3±0.4	42.5-50.0	42.0±0.4	42.5-50.0	47.6±0.4	45.0-50.0	1.15	3.6	13.5-5.0	–	10.5-4.0	1.8	1.2
P. misera													
Oliveira. R.P. *et al*. 534	39.4±0.6	35.1-45.1	34.3±0.5	30.1-37.5	36.3±0.4	32.5-40.1	1.14	–	13.0-5.0	–	9.5-3.5	2.5	2.1
L.P. Queiroz 4832	44.2±0.4	40.0-50.0	41.7±0.5	37.5-50.0	40.7±0.6	35.0-47.5	1.05	–	12.5-5.0	–	9.0-4.0	2.2	2.0
P. organensis													
M.L. Guedes & M. Acioly 4786	45.5±0.5	40.0-55.5	46.9±0.9	37.5-57.5	49.3±1.3	37.5-72.5	0.96	5.0	–	11.0-9.0	12.0-5.0	2.0	2.7
P. pohlii													
A. Giulietti 493	44.4±1.3	37.5-50.0	37.3±1.6	30.0-45.0	*40.2	35.0-45.0	1.19	–	9.2-4.0	–	10.0-3.5	3.5	1.8
P. rubra													
T. S. Nunes 1428	50.3±0.7	47.5-53.5	46.5±1.1	42.5-50.0	48.5±1.3	45.0-55.0	1.08	5.0	-	15.0-4.0	9.0-5.0	3.0	2.0
P. saxicola													
A. Freire-Frieirro *et al* 1931	45.5±0.5	40.0-50.0	41.4±0.3	40.0-45.0	42.3±0.4	37.5-47.5	1.10	–	12.0-4.0	–	7.5-3.5	1.9	1.0
P. suberosa													
E.de Melo *et al*. 2781	41.6±0.4	37.5-45.5	42.0±0.5	35.0-45.0	43.6±0.8	40.0-47.5	0.99	–	15.0-5.0	–	6.5-3.0	1.5	1.0
E. de Melo & F. França 1048	43.2±1.2	35.0-52.5	45.7±0.7	42.5-55.0	48.5±0.6	42.5-52.5	0.92	–	14.0-4.5	–	5.6-3.0	1.3	1.0

Table 3. Measurements (in μm) of pollen grains of species of Passifloraceae. TYPE III and IV. PD = polar diameter, ED = equatorial diameter, (EDpv) = equatorial diameter in polar view, $\overline{x}$ = arithmetic mean, $S_{\overline{x}}$ = standard deviation of the mean, FV = range, P/E= polar/equatorial diameter ratio [n=25], Pt = length of pontoperculum in equatorial view, Ps = width pseudoperculum, SEX = sexine, NEX = nexine [n = 10] [* n<25].

Genus/ Subgenus Species / Specimens	PD		ED		EDpv		Pt	Ps	SEX	NEX
	$\overline{x} \pm S_{\overline{x}}$	FV	$\overline{x} \pm S_{\overline{x}}$	FV	$\overline{x} \pm S_{\overline{x}}$	FV				
Passiflora L.										
Subg. *Passiflora* L.										
P. alata										
L.R. Noblick 2252	–	–	–	–	64.7±0.7	56.5–70.0	6.4	14.9-10.9	4.7	3.8
P. amethystina										
T.S. dos Santos s/n	–	–	–	–	53.2±0.3	45.0–60.0	5.0	12.0-10.0	5.0	3.7
R.S. Pinheiro 1103	–	–	–	–	53.5±0.8	47.5–62.5	4.1	13.0-12.0	4.5	3.7
C.M.Magalhães 57	–	–	–	–	63.9±1.1	55.0-75.0	6.6	15.6-12.2	4.3	4.2
P. bahiensis										
L.P.de Queiroz 12235	–	–	–	–	70.7±3.3	50.0-80.0	5.0	21.0-20.0	4.0	3.0
P. cacao										
A.V. Popovkin 1661	–	–	–	–	61.7±5.0	50.0–67.2	6.0	12.5-9.4	3.1	3.9
P. caerulea										
J. Cordeiro & J.M. Silva 216	–	–	–	–	62.0±1.1	50.0–75.0	6.3	15.6-13.8	4.2	2.5
P. cincinnata										
R.C.M. Araújo 01	–	–	–	–	77.0±1.5	62.0– 92.5	5.0	19.1-16.0	5.2	6.2
M.C. Ferreira 475	–	–	–	–	71.9±1.1	25.0-32.0	5.9	21.3-18.1	4.5	5.4
P. clathrata										
Grupo Pedra do Cavalo 256	76.0±1.5	62.5-90.0	70.0±0.7	62.5-77.5	74.0±1.5	57.5- 87.5	7.8	23.0-18.2	5.7	4.6
P. edmundoi										
A.S. Conceição. & Campos. G.L. 438	–	–	–	–	58.9±0.5	52.5-65.0	4.5	14.3-11.9	3.5	3.0
T.S. Nunes 1237	–	–	–	–	65.4±4.0	55.0– 85.0	5.0	20.0-16.0	3.3	3.0
P. edulis										
A.O. França 01	–	–	–	–	66.2±0.9	57.0–75.0	5.2	17.9-14.7	4.3	5.2
N.R.S. Santos & L.S.S. Martins 82	–	–	–	–	69.2±0.9	62.5–80.0	3.8	16.2-12.9	4.5	4.7
P. foetida										
R.C.M.S. Araújo 03	61.3±1.3	52.5-75.0	69.0±0.5	65.0-75.0	72.9±0.88	65.0– 8.0	4.4	20.4-17.3	5.2	4.0
C.A.L. Carvalho 56	64.6± 0.7	57.5-75.0	63.9±0.8	57.5-70.0	71.1±0.8	62.5-77.0	7.8	18.7-16.9	4.7	4.6
P. lueltzelburgii										
E. de Melo *et al.* 3159	–	–	–	–	66.8±0.7	60.0–5.0	4.6	17.5-14.6	3.5	2.9
A.M. Giulietti & R.M. Harley 1710	–	–	–	–	74.8±1.0	50.0–67.0	4.6	13.6-10.8	3.4	3.3
P. miersii										
L.P. de Queiroz 2214	–	–	–	–	59.6±0.8	52.5–65.0	5.0	15.9-15.1	2.9	3.7
P. mucronata										
A.M. de Carvalho 2731	–	–	–	–	76.2±1.5	52.5–87.5	5.0	18.8-14.3	3.7	2.7
M.L. Guedes & M, Acioly 4760	–	–	–	–	72.4±1.3	62.5-92.5	5.1	20.7-18.7	2.9	3.9
P. mucugeana										
T.S. Nunes *et al.* 847	–	–	–	–	59.0±06	47.5– 5.0	6.4	14.1-11.2	4.6	2.5
P. nitida										
S.A. Mori *et al.* 9398	–	–	–	–	93.2±1.6	80.0-110.0	10.6	22.3-20.6	7.1	6.3
P. odontophylla										
R.P. Belém *et al.* 2627	–	–	–	–	77.3±1.5	62.5- 90.0	5.5	18.7-16.3	5.0	4.0
P. recurva										
E. Miranda-Silva *et al.* 238	–	–	–	–	74.0±0.8	67.5-77.5	4.8	17.5-15.1	3.0	4.4
E. de Melo *et al.* 3178	–	–	–	–	56.8±0.9	50.0–65.0	4.9	14.0-12.7	2.4	3.0
P. setacea										
L.P. de Queiroz *et al.* 1321	–	–	–	–	83.6±1.2	75,0–95.0	6.3	21.7-19.5	2.8	3.8
P. silvestres										
A.V. Popovkin 1714	–	–	–	–	63.7±1.3	60.0- 70.0	6.5	17.1-13.1	3.0	2.0
P. trintae										
R.M. Harley *et al.* 20197	–	–	–	–	59,3±1,1	55.0–65.0	2.4	17.5-14.2	3.6	1.8
S.A. Mori *et al.* 9416	–	–	–	–	60,8±0,7	52,5–50,0)	3,6	16.5-14.1	3.3	2.8

Table 3. Cont.

Genus/ Subgenus Species / Specimens	PD		ED		EDpv		Pt	Ps	SEX	NEX
	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV	$\bar{x} \pm S_{\bar{x}}$	FV				
P. villosa										
T.S. Nunes 889	–	–	–	–	77.8±2.0	60.1– 97.6	5.0	14.6-12.9	4.8	4.8
P. watsoniana										
L.P. de Queiroz *et al.* 3163	–	–	–	–	70.0±1.9	62.5– 77.5	5.0	15.3-13.4	4.0	3.2
F. França *et al.* 1098	–	–	–	–	72.4±0.9	70.0– 77.5	4.8	15.5-12.7	3.5	3.4
Mitostemma Mast.										
Mitostemma glaziovii										
T.S. Nunes 1813	*66.2	55.0-80.0	*62.7	52.5-75.0	72.7±0.9	55.0-85.0	–	20.0-18.0	3.5	1.0

Pollen Type III. 6-(8-10-12)-(panto)syncolpate pollen grains with pontopercula, reticulum lumina with bacula and granules in the interior (subgenus *Passiflora*) (Fig. 1F-G).

Subtype III.1: 6-syncolpate pollen grains, isopolar, monomorphic as to the number of openings, presence of 3-pseudopercula and 3-pontopercula. Species: *Passiflora alata*, *P. amethystina*, *P. bahiensis*, *P. cacao*, *P. caerulea*, *P. clathrate*, *P. edulis*, *P. foetida*, *P. miersii*, *P. mucronata*, *P. mucugeana*, *P. nitida*, *P. odontophylla*, *P. recurve*, *P. setacea*, *P. silvestris* and *P. trintae* (Fig. 3D-E).

Subtype III.2: 6-(8-10-12)-(panto)syncolpate pollen grains, isopolar to apolar, heteromorphic as to the number of apertures, presence of 3(4-5-6)-pseudopercula. Species: *P. cincinnata*, *P. edmundoi*, *P. luetzelburgii*, all 6-(8)-syncolpate with 3-(4)-pseudopecula; *P. villosa*, 6-(12)-pantosyncolpate with 3-(6)-pseudopercula; and *P. watsoniana*, (6)-8-10-12-pantosyncolpate with (3)-4-5-6 pseudopercula (Fig. 1G).

Pollen grains medium to large-sized, isopolar to apolar, spheroidal oblate to prolate-spheroidal, amb subcircular to subtriangular, colporate, exine reticulate. Subtype 1 has each pair of ectoapertures joined longitudinally at the ends forming a ring around the elliptic pseudopercula (Fig. 1F, 3D, F); pontopercula wide (Tab. 3), fused in the apocolpium region. Subtype 2 has each pair of ectoapertures joined longitudinally forming a ring around the elliptic pseudopercula (Fig. 1G) and enveloped by mesocolpia. Exine reticulate, heterobrochate; lumina with bacula and granules in the interior; muri smooth, tall, continuous, rather sinuous (Fig. 3E) and simplicolumellate.

Pollen Type IV. 3-colporate pollen grains, opercular formations absent, reticulum lumina not ornamented (Fig. 1H).

Species: *Mitostemma glaziovii* (Fig. 3G-I).

Pollen grains large-sized, isopolar, prolate-spheroidal, 3-colporate; exine reticulate. Large, long, tapered ectoapertures, not fused to apocolpium (Fig. 3H); endoapertures with rounded ends. Exine reticulate, perforated, heterobrochate; lumina granulate; muri smooth, tall, sinuous, continuous and simplicolumellated (Fig. 3I).

Discussion

The data presented here for the species of Passifloraceae occurring in Bahia reveal very complex and diversified pollen grains with regard to aperture number and type, ornamentation elements of the exine, and opercular variation. This diversity allowed grouping the species into pollen types and subtypes, which, with some exceptions, correspond to the classification proposed by Feuillet & MacDougal (2003 [2004]) with the four subgenera *Astrophea*, *Deidamioides*, *Decaloba,* and *Passiflora*.

Pollen data were found in the literature for *P. contracta*, *P. igrapiunensis* and *P. timboënsis* (*Deidamioides*) (Nunes 2009). This author included these species in the same pollen type according to the morphological characteristics of their pollen grains. They were described as 6-colporate and reticulate with many free bacula in lumina. In the present study, granules were found to be the element of ornamentation of the exine, with *P. torboënsis* being described as slightly granular and *P. contracta* and *P. igrapiunensis* as having densely granular lumina. Nunes (2009) does not mention the presence of interrupted muri, as observed in the present study for the pollen grains of *P. timboënsis*. Muschner *et al.* (2003), Yockteng & Nadot (2004), Muschner (2005), Zamberlan (2007) and Nunes (2009) all pointed out that phylogenetic studies indicate that *Deidamioides* is polyphyletic.

Thus, the species of *Deidamioides* mentioned above were included in the same pollen type of *Astrophea* because it they have similar aperture characteristics to the species of this subgenus. Such similarities include being 6-colporate and having three endoapertures associated with two paired ectoapertures that are not fused with the apocolpium, forming, along with the pontopercula, a tri-radiate structure in polar view. Some of these characters have been previously described for species of *Astrophea* (Araújo & Santos 2004; Dettke & Santos 2009; Verdasca *et al.* 2013; Mezzonato-Pires *et al.* 2015a; 2017).

Pollen grains of *P. mansoi* were described here as having lumina ornamented with rare granules and muri without perforations, while the pollen grains of *P. rhamnifolia* were described as lacking ornamentation but having perforations in the apocolpium region. These results partially corroborate Mezzonato-Pires *et al.* (2015a),

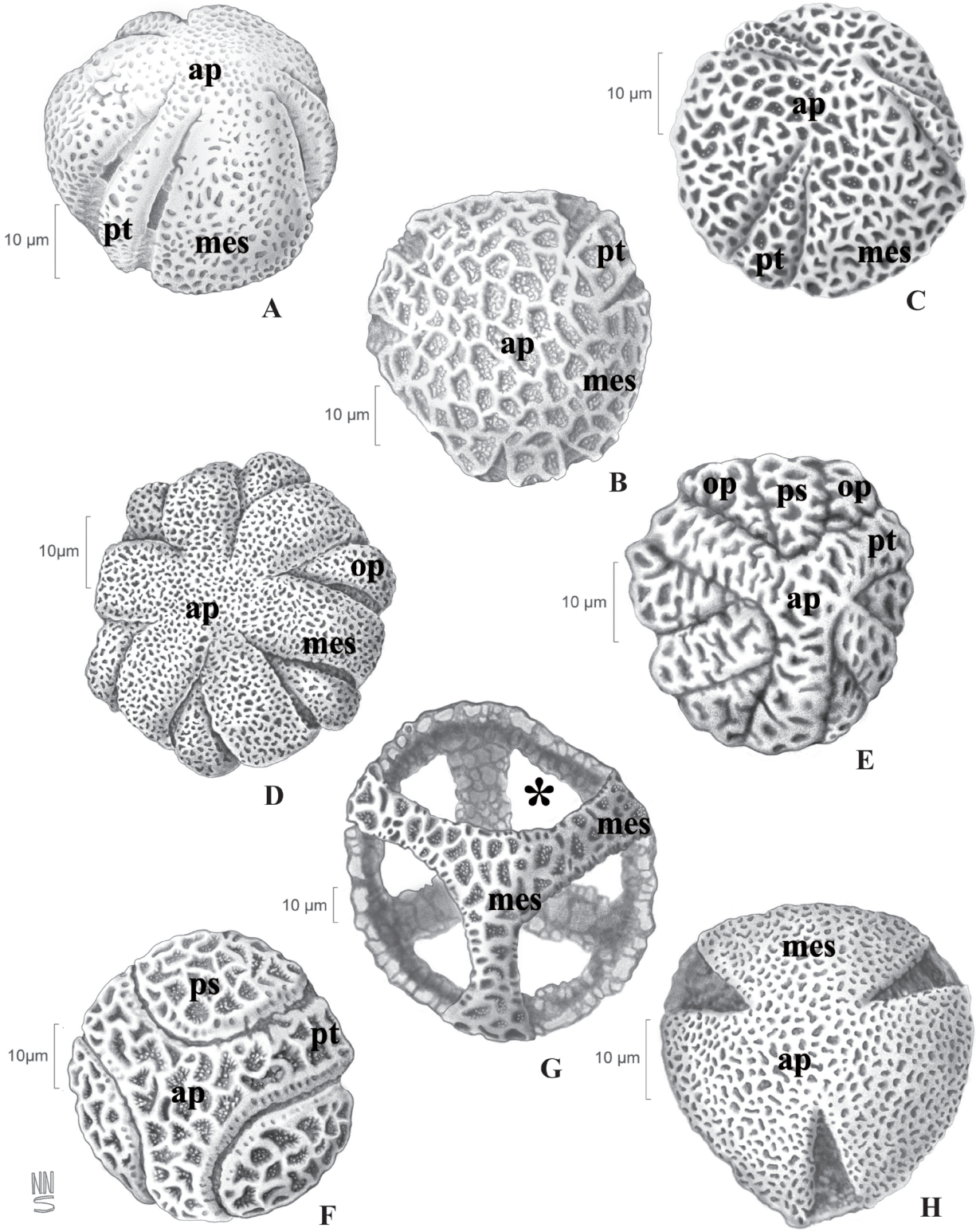

Figure 1. Illustrations of pollen grains representative of pollinic types of species of Passifloraceae. Type I: **A.** *P. rhamnifolia* Mast., **B.** *P. contracta* Vitta and C. *P. timboënsis* T.S. Nunes & L.P.Queiroz; Type II: **D.** *P. suberosa* L., **E.** *P. organensis* Grdner; Type III: **F.** *P. caerulea* L., **G.** *P. villosa* Mast.; Type IV: **H.** *Mitostemma glaziovii* Mast. (ap = apocolpus; mes = mesocolpium; pt = pontoperculum; ps = pseudoperculum; op = operculum). Drawn by Natanael Nascimento.

disagreeing in the denomination of the ornamentation element of the exine. These authors describe the presence of bacula within lumina of the reticulum and perforations of the muri in both species.

For the studied specimens, the presence of granules as the ornamentation element of the exine was constant for the pollen types that included the subgenus *Astrophea* and *Deidamioides* (pollen type I - without ornamentation in *P. rhamnifolia*) and *Decaloba* (pollen type II - without ornamentation only in *P. suberosa*). However, pollen type III, which contains species of the subgenus *Passiflora*, has the dense and concomitant presence of bacula and granules in the lumina of the reticulum. Soares *et al*. (2018) interpreted the presence of these elements in the ornamentation of the exine as a mechanism against dehydration, especially during pollination, since species of *Passiflora* have a large apertural area.

Erdtman (1952) mentioned pollen grains with lumina containing small bacula or granules for the genus *Passiflora*. Presting (1965), Milward-de-Azevedo *et al*. (2004; 2010;

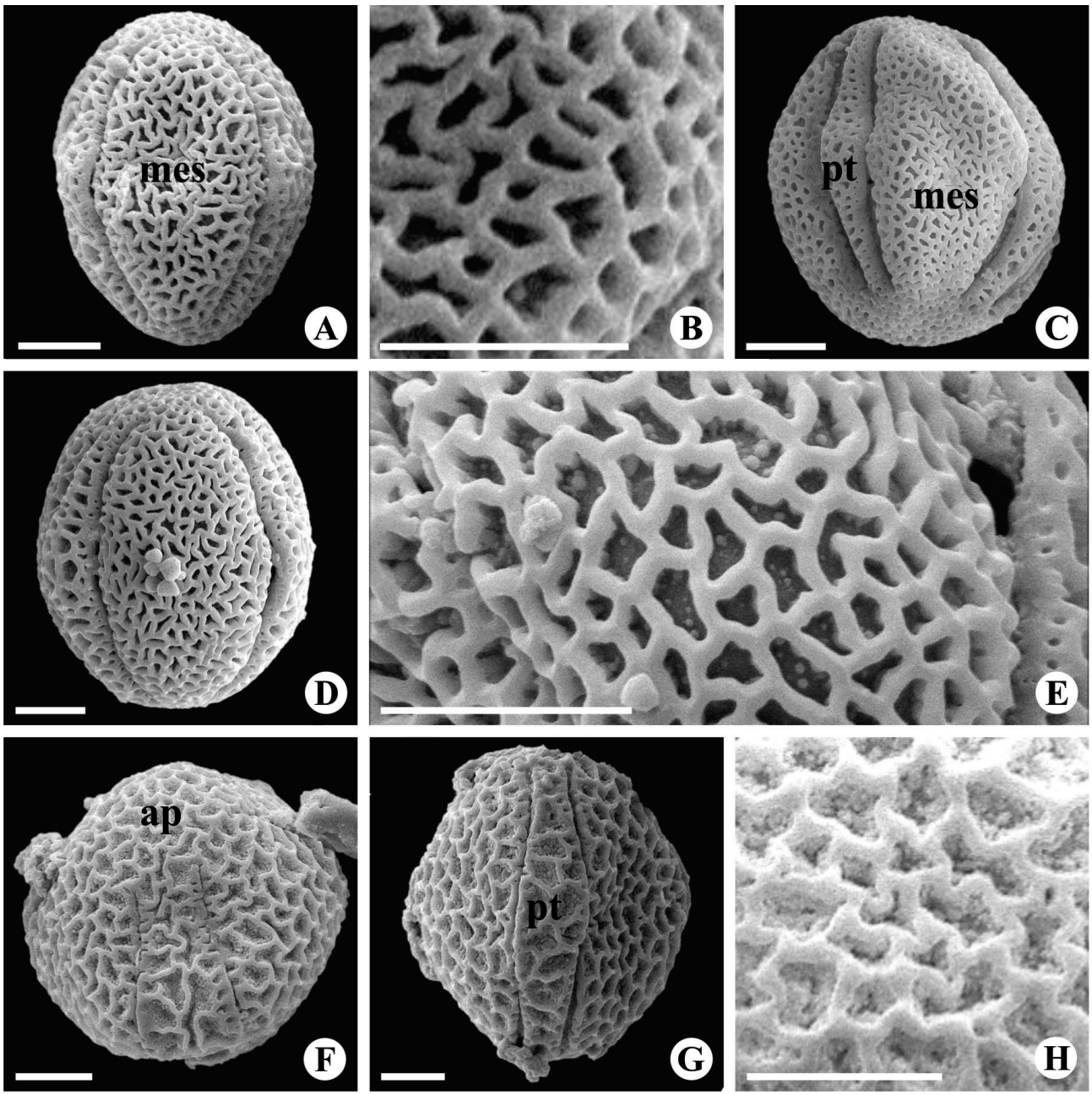

Figure 2. Electromicrographs of pollen grains of Passifloraceae. **A-B.** *P. mansoi* (Mart.) Mast.: **A.** Equatorial view, **B.** Surface; **C.** *P. rhamnifolia* Mast.: Equatorial view; **D-E**. *P. timboënsis* T.S. Nunes & L.P.Queiroz: **D.** Equatorial view, **E.** Surface detail; **F.** *P. contracta* Vitta. Equatorial view; **G-H.** *P. igrapiunensis* T.S. Nunes & L.P.Queiroz: **G.** Equatorial view, **H.** Surface. (ap = apocolpus; mes = mesocolpium; pt = pontoperculum). Bar = 10 μm.

2014), Dettke & Santos (2011), Evaldt *et al*. (2011) and Soares *et al*. (2018) also referred to the presence of bacula in lumina of the pollen grains of *Passiflora*. Mezzonato-Pires *et al*. (2015a; 2017) described the occurrence of spines, bacula, and pila as ornamentation elements in the lumina of species of *Astrophea*, but did not mention the presence of granules as observed in the present study. Verdasca *et al*. (2013) reported bacula for species of the genus *Passiflora* occurring in the state of São Paulo. It is possible that the various techniques used by researchers did not allow clear visualization of these structures, which in turn compromised nomenclatural uniformity for the group.

Of the pollen types mentioned above, pollen type II, which is represented by species of the subgenus *Decaloba* (*P. jiboiaensis*, *P. misera*, *P. pohlii*, *P. saxicola* and *P. suberosa* of subtype 1; and *P. capsularis*, *P. organensis* and *P. rubra* of subtype 2), may be the most controversial with regard to nomenclature and the identification of opercular structures of the pollen grains of the genus *Passiflora* (Presting 1965; Milward-de-Azevedo *et al*. 2004; 2010; 2014; Araújo & Santos

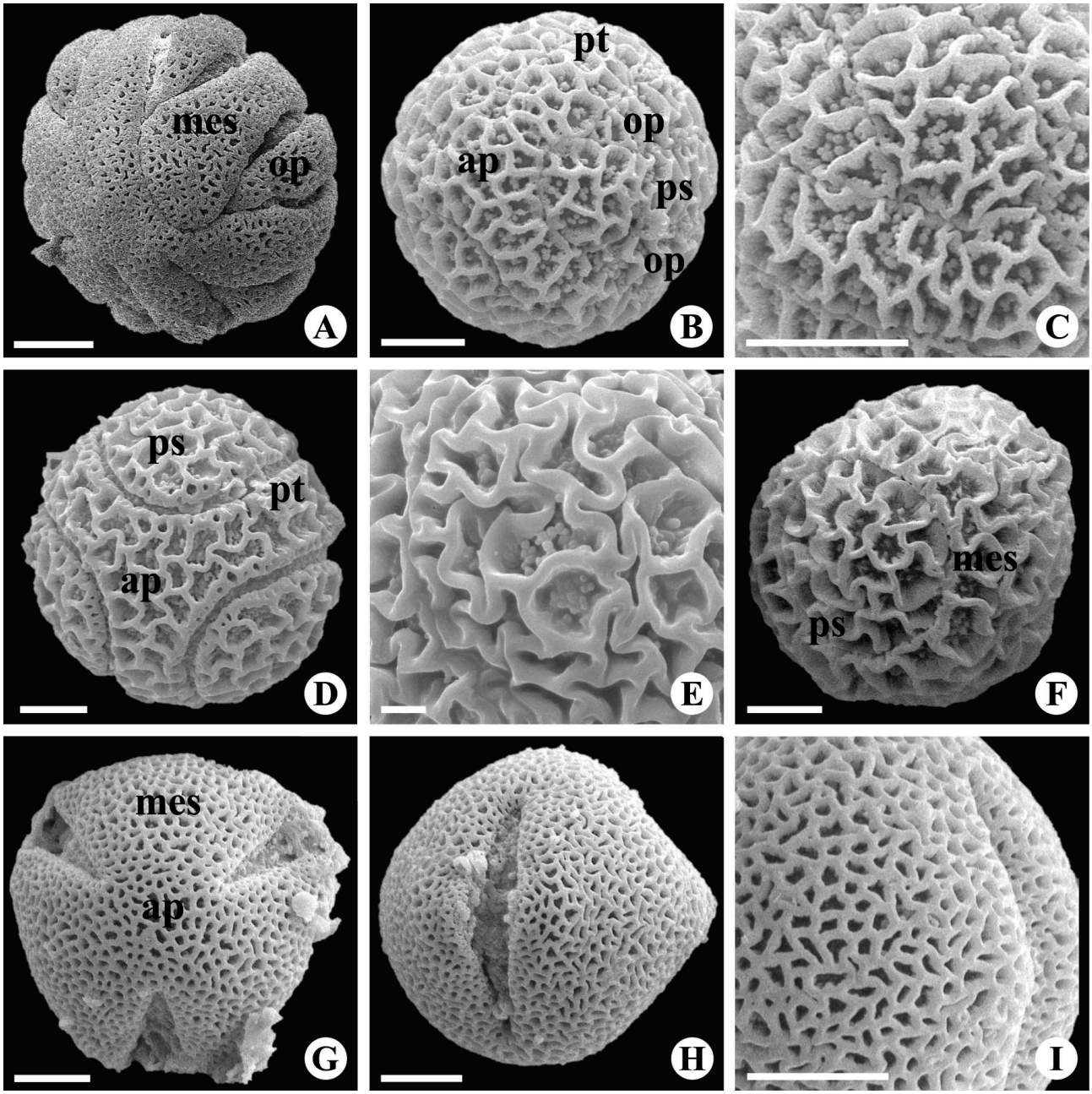

Figure 3. Electromicrographs of pollen grains of Passifloraceae. **A.** *P. suberosa L.*: General view; **B-C.** *P. capsularis* L.: **B.** General view, **C.** Surface detail; **D.** *P. caerulea* L.: Polar view; **E.** *P. mucugeana* T.S.Nunes & L.P.Queiroz: Surface detail; **F.** *P. watsoniana* Mast.: General view; **G–I**. *Mitostemma glaziovii* Mast.: **G.** Polar view, **H.** Equatorial view, **I.** Surface detail. (ap = apocolpus; mes = mesocolpium; op = operculum; pt = pontoperculum; ps = pseudoperculum). Bar = 10 µm.

2004; Evaldt *et al*. 2011; Borges & Milward-de-Azevedo 2017). This controversy stems from the interpretation of Presting's theory (1965). As cited by Dettke & Santos (2009), there is conflict with the definition of aperture used by Punt *et al*. (2007) and difficulty in observing apertural structures using light and scanning electron microscopy, particularly with pollen treated by acetolysis.

Thus, for pollen type II, species that were 6-colporate (subtype 1) or 12-colporate (subtype 2) were grouped based on variation in opercular patterns that differ in constitution, form and function; a characteristic that, in this study, was important for separating taxa. According to Dettke & Santos (2009), the presence of opercula is a peculiar characteristic shared by species of the subgenus *Decaloba*, the monophyly of which is strongly supported by various phylogenetic analyses (Muschner *et al.* 2003; Muschner 2005; Zamberlan 2007).

Subtype 1 grouped pollen grains with six ectoapertures and six individual endoapertures, located under six opercula classified as functional (Wodehouse 1935, adopted by Punt *et al.* 2007 and Dettke & Santos 2009). Morphologically, the pollen grains of the species included in this subtype were observed to have six opercula intercalated by six mesocolpia, without apparent pontopercula, adopting the naming given by Dettke & Santos (2009) for pollen grains of *P. misera* and *P. suberosa*, similar to the present study. According to these authors, identifying pontopercula in these pollen grains is difficult because there is no differentiation in mesocolpium width.

In the present study, the pollen grains of *P. misera* and *P. suberosa* were described as 6-colporate, corroborating the results of Dettke & Santos (2009), Evaldt *et al*. (2011), and Borges & Milward-de-Azevedo (2017). However, specialized literature of the group presents divergent data. Pollen grains of both species are described as 12-colpate by Amela-Garcia *et al*. (2002) and 6-colpate by Araújo & Santos (2004), 12-colporate for *P. misera* (Milward-de-Azevedo *et al*. 2004; 2010; Mezzonato-Pires *et al*. (2015b) and 12-colpate for *P. suberosa* (Milward-de-Azevedo *et al*. 2004; 2010; Soares *et al*. 2018).

The pollen grains of *P. pohlii* were described herein as 6-colporate, corroborating Milward-de-Azevedo *et al*. (2010), but disagreeing with Presting (1965) and Milward-de-Azevedo *et al.* (2004), who described it as 12-colporate. The pollen grains described herein as 6-colporate for *P. jiboiaensis* and *P. saxicola* diverge partially from Milward-de-Azevedo *et al.* (2010), who considered them to be 6- and 12-colporate, respectively.

Subtype 2 groups the species *P. capsularis*, *P. organensis* and *P. rubra*, which have 12-colporate pollen grains with 12 individual endoapertures, one on each side of the six non-functional opercula. The position of endoapertures forces the opercular structure to remain attached to the rest of the exine, thus keeping it attached to the pollen unit (Dettke & Santos 2009) even after acetolysis, as observed in the species analyzed in the present study.

Pollen grains of *P. capsularis* and *P. organensis* were described herein as 12-colporate, diverging from the works of Evaldt *et al.* (2011), who described 6-colporate pollen grains for *P. organensis*. Borges *et al.* (2017) and Milward-de-Azevedo *et al.* (2010) described 12-colpate pollen grains for *P. capsularis*. The results found here for both species agree with the findings of other studies involving them (Presting 1965; Milward-de-Azevedo *et al*. 2004; Dettke & Santos 2009). The pollen grains of *P. rubra* were also described herein as 12-colporate, which is in agreement with Milward-de-Azevedo *et al*. (2010; 2014) and Soares *et al*. (2018).

The great majority of species belonging to the family Passifloraceae in Bahia belong to the subgenus *Passiflora*. This subgenus contains approximately 63 % of the species in the present study, all of which are included in pollen type III, which is circumscribed palynologically by aperture number and type (6-syncolpate in monomorphic species with constant apertures, and 6-8-10-12-syncolpate in heteromorphic species with grains of pantocolpate pollen), the presence of the pseudopercula and/or pontopercula, and characteristics of exine ornamentation (large reticulum with many granules and/or bacula in lumina). Although commonalities were found in the findings of classical and contemporary studies of Passifloraceae (Erdtman 1952; Presting 1965; Spirlet 1965; Larson 1966; Huynh 1972; Palacios-Chávez *et al*. 1991; Roubik & Moreno 1991; Melhem *et al*. 2003; Araújo & Santos 2004; Barrios *et al.* 2005; Dettke & Santos 2009; Evaldt *et al*. 2011; Verdasca *et al.* 2013; Borges & Milward-de-Azevedo 2017; Soares *et al*. 2018), they, with some exceptions, differed in nomenclature and interpretation of apertural structures.

Thus, for species with 6-syncolpate pollen grains (with constant aperture number - subtype 1), the term 'pontoperculum' describes a narrower equatorial area between two apertures fused in the apocolpium. Generally, each ectoaperture that borders a pontoperculum merges with another aperture of the neighboring pair, at both poles, to form a ring around the structure between the apertures. This was referred to herein as 'pseudoperculum' based on Dettke & Santos (2009). The process of acetolysis breaks the apertural membrane that keeps pseudopercula attached to the pollen unit, thus releasing them in most species.

However, in species that do not have a constant apertural number, such as species of subtype 2 with pantoaperture pollen grains, unlike that observed for subtype 1, the individualization of the pontopercular structure becomes difficult due to the large amount of pseudopercula formed throughout the extension of the pollen. To reduce confusion generated in the interpretation of the structure, Dettke & Santos (2009) proposed the term 'mesocolpium' for all regions among pseudopercula when they are evenly distributed throughout the pollen grain, as observed in heteromorphic species in the present study.

Heteromorphic specimens of the same species vary in apertural number, but with a predominance of the 6-aperturate

condition. The presence of apertural heteromorphism was previously mentioned by Presting (1965), Roubik & Moreno (1991), Araújo & Santos (2004), Dettke & Santos (2009), Evaldt *et al.* (2011) and Verdasca *et al.* (2013).

Data in the literature on the subgenus *Passiflora* reveal a large number of morphological variants in relation to the apertural number of species. Analyzing species of Passifloraceae that occur in the state of Rio Grande do Sul, Evaldt *et al.* (2011) reported the pantoaperturate condition for *P. actinia* (6-8), *P. elegans* (6-10), *P. foetida* (6-14), *P. tenuifila* (6-10), and *P. eichleriana* (6-14) (all pantosyncolpate); and the monomorphic condition, as for apertural number, for *P. alata, P. amethystina, P. caerulea* and *P. edulis* (all 6-syncolpate). Of the species referred to as heteromorphic, only *P. foetida* occurs in Bahia, and was found herein to be 6-syncolpate (as also described by Soares *et al*. 2018). These results differ from those found by Evaldt *et al.* (2011) for species of Rio Grande do Sul.

Verdasca *et al.* (2013) reported heteromorphism in apertural number for *P. edulis* [6-(8-10)], *P. jilekii* [8-(10-12)], *P. miersii* [8-(10-12)], *P. porophylla* [(10-12)-14], *P. sidaefolia* [(10-12)-14], and *P. villosa* [(10-12)-14]. Of these, only the pollen grains of *P. edulis* and *P. villosa* were analyzed herein, with divergent results regarding the number of apertures. Thus, the pollen grains of *P. edulis* were described herein as monomorphic, 6-syncolpate, similar to the results of Spirlet (1965), Dettke & Santos (2009), Evaldt *et al.* (2011), Borges & Milward-de-Azevedo (2017), and Soares *et al*. (2018). The pollen grains of *P. villosa* were described here as 6-(12) pantosyncolpate, as reported by Araújo & Santos (2004) for species of *Passiflora* from Chapada Diamantina in Bahia.

Other species of the subgenus *Passiflora* (*P. amethystina, P. galbana, P. mucronata* and *P. setácea*), characterized in this work as 6-syncolpate, had their pollen grains described by other researchers as having six apertures (Araújo & Santos 2004; Dettke & Santos 2009; Evaldt *et al.* 2011; Mezzonato-Pires *et al*. 2015b; Borges & Milward-de-Azevedo 2017; Soares *et al*. 2018), however, there were disagreements as to aperture type. In contrast, the pollen grains of *P. cincinnata* and *P. edmundoi*, described herein as 6-(8)-syncolpate, were characterized by Verdasca *et al.* (2013) and Soares *et al.* (2018) as 6-syncolpate and without apertural heteromorphism. Hansen *et al.* (2006), considered the subgenus *Passiflora* to be monophyletic based on several morphological attributes, among them pollen grains with three pairs of apertures and reticulate ornamentation.

Pollen grains of *Passiflora* have characters that differentiate them from those of *Mitostemma*, which is included in pollen type IV. Morphopolinic data for *Mitostemma glaziovii*, the only representative of the genus in Bahia, were not found in the literature, and so its pollen was described here for the first time. The results revealed simpler aperture characteristics for *M. glaziovii* than for species of the genus *Passiflora*, with 3-colporate pollen grains without apertural pairing, without opercular variation, and without ornamentation elements in the reduced lumina of the reticulum, all of which are pollen attributes that individualize the species *M. glaziovii* within the proposed subdivision. Mezzonato-Pires *et al*. (2019) analyzed pollen grains of three different genera of Passifloraceae than those studied here and found *Crossostemma* and *Schlechterina* to have 3-colporate pollen grains and *Adenia* to have 4-colporate (rarely 3-4-colporate) pollen grains, further revealing the diversity aperture number for the family.

According to Presting (1965), apertural evolution in the family Passifloraceae began with 3-colporate pollen grains, which in turn evolved opercula over the apertures, yielding the derived pollen grains with apertures characteristic of *Passiflora*, as represented herein by the subgenera *Astrophea, Deidamioides, Decaloba* and *Passiflora*. Accordingly, this allows the inference that, palynologically, *M. glaziovii* is more primitive than the analyzed species of the subgenus *Passiflora* from Bahia.

The palynological data analyzed here corroborate the recognition of three subgenera for *Passiflora* — *Astrophea, Decaloba,* and *Passiflora* — with similar pollen morphology among species in their respective pollen types. However, the subgenus *Deidamioides* is an exception because it possesses species with quite diverse pollen morphologies, but shares the same pollen type with species of the subgenus *Astrophea*.

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