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Original article

Pollen morphology of *Galactia* P. Browne and related genera (Papilionoideae, Leguminosae), with emphasis on Brazilian representatives

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ABSTRACT

Galactia is a pantropical genus, which is part of the Galactia clade, and together with the genera *Betencourtia, Caetangil, Cerradicola, Collaea, Lackeya, Nanogalactia,* and *Rhodopis*, it maintains a taxonomic relationship that has already been the focus of previous studies. However, the palynology of these groups has not been extensively studied, with gaps in pollen descriptions. Thus, a palynological study of 30 species belonging to *Galactia* and related genera was performed. For this purpose, pollen grains were acetolized using the standard methodology, subjected to scanning electron microscopy analysis, and then quantitatively and qualitatively evaluated. Generally, pollen grains of this genera are medium or large size, isopolar or heteropolar, 3-colporate, and may have microreticulate or reticulate exine. Pollen data for *Rhodopis* and *Nanogalactia* agree with the most recently proposed circumscription of these genera. Other genera exhibited similar pollen characteristics; however, the diameter of the lumen, associated with other pollen characteristics, proved to be important for the differentiation of the genera. Thus, the pollen morphology provided information that contributes to the description of the genera, mainly Brazilian representatives of *Galactia* and related genera.

Keywords: Diocleae, Galactia clade, palynotaxonomy, pollen grains, Brazil.

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Introduction

Galactia is a pantropical genus belonging to the Leguminosae family, with species distributed throughout the American continent (Ceolin & Miotto 2013). It is characterized by the presence of papilionate flowers with one bract and two bracteoles and lilac, red, or pink flowers (Ceolin & Miotto 2013; Nesom 2015; Queiroz *et al.* 2020). It has species whose flowers are pollinated mainly by bees (Couto *et al.* 1997; Amaral *et al.* 2013).

The estimated number of species of this genus remains controversial owing to discrepancies between studies: approximately 65 species are referenced by Burkart (1971); 50–60 species by Sede *et al.* (2003; 2008); 50 species in tropical regions by Matos *et al.* (2005), and 111 species by Nesom (2015). For Brazil, it is estimated the occurrence of seven *Galactia* species, distributed in the most biomes (Oliveira & Queiroz 2020).

Classified within the Papilionoideae subfamily and belonging to the Diocleae subtribe, *Galactia*, along with another 11 genera (*Betencourtia* A. St.-Hil.; *Bionia* Mart. ex Benth.; *Caetangil* L.P. Queiroz; *Camptosema* Hook. & Arn.; *Cerradicola* L.P. Queiroz; *Collaea* DC.; *Cratylia* Mart. ex Benth.; *Mantiquera* L.P. Queiroz; *Nanogalactia* L.P. Queiroz; *Lackeya* Fortunato, L.P. Queiroz & G.P. Lewis; and *Rhodopis* Urb.) conform to the Galactia clade, has already been the focus of previous studies owing to the presence of taxonomic uncertainty among its species (Queiroz *et al.* 2015; 2020).

Of the 12 genera within the Galactia clade, seven (*Rhodopis*, *Nanogalactia,* *Caetangil*, *Cerradicola*, *Betencourtia*, *Collaea*, and *Lackeya*) have species that previously belonged to *Galactia* and consequently are related to this genus (Queiroz *et al.* 2020). Several species belonging to these genera are distributed throughout Brazilian biomes, except those belonging to *Rhodopis* and *Lackeya*, which occur in the Greater Antilles and southeastern United States (Judd 1984; Fortunato *et al.* 1996; Queiroz *et al.* 2020).

These genera are differentiated by a set of macromorphological traits, with information on the palynology of their species being limited to few studies: Kavanagh & Ferguson (1981), Silvestre-Capelato (1993), Fortunato *et al.* (1996), and Moreti *et al.* (2007a; b). According to these studies, pollen grains of these genera are, in general, microreticulate, reticulate, prolate, oblate, and tricolporate. Nonetheless, it is possible to identify that there are gaps regarding the morphological descriptions of pollen grains belonging to these genera.

Nanogalactia, *Caetangil*, and *Cerradicola* are three new genera, in which the pollen information reported for their species, as well as for *Betencourtia* species, is the same previously reported for *Galactia*: spheroidal, isopolar, and tricolporate pollen grains with reticulate exine. Furthermore, *Rhodopis* is a genus that contains species that are characterized by having red, bird-pollinated flowers and whose palynology is little known. The remaining genera, *Collaea* and *Lackeya*, are also similar palynologically, because their species have tricolporate, isopolar, and reticulate pollen grains (Kavanagh & Ferguson 1981; Fortunato *et al.* 1996).

In addition to the lack of research focused on the palynological characterization of *Galactia* and related genera, there is a deep gap in information about species distributed in Brazil. Therefore, this research aimed to examine the pollen morphology of the Brazilian species of *Galactia* and related genera for the improvement of their taxonomy, to enable the contribution of data from these genera to Brazil as well as expanding the information about them.

Materials and methods

Floral buds of 30 species belonging to *Galactia* P. Browne and related genera were selected from the exsicate of the following herbaria: HUEFS, COL, NYBG, UEC, and LPB (Acronyms following Thiers 2017). Pollen grains were acetolized according to the technique by Erdtman's (1960). Considering the probability of collapse, pollen grains were placed in a water bath for a maximum of 1.5 minutes and then centrifuged at 2400 rpm for 10 min.

Regarding the quantitative data, 25 pollen grains were randomly measured under light microscopy in order to estimate their polar axis and equatorial diameter. The length and width of the ectoaperture, length and width of the endoaperture, thickness of nexine and sexine, size of apocolpium, diameter of the lumen, and murus width were measured using 10 randomly selected pollen grains (Table 1). Samples were photomicrographed using a Leica ICC50 W light microscope.

Pollen grains were also examined under scanning electron microscopy (SEM). Acetolyzed pollen grains were dehydrated using alcoholic or acetic series (70%, 90%, and 100%), subsequently placed on metal stubs to dry, and then coated with gold. Electron micrographs were obtained using a JSM-6390LV scanning electron microscope.

Due to the fragility of the pollen grains of some species of *Betencourtia* A. St.-Hil., *Collaea* DC., and *Galactia* when processed regularly for the analysis under SEM, and considering that some samples presented few pollen grains, a poly-L-lysine was used aiming to mitigate the encountered difficulties. Circular coverslips were cleaned with a 1% Extran® neutral solution. Then, on a Petri dish previously coated with parafilm, each coverslip was added on a drop (c. 25 μL) of 0.1% poly-L-lysine (Sigma) for 10 minutes. Afterward, the acetone containing the pollen grains was dripped onto the coated coverslip, allowing it to dry for 24 hours. After this period, the coverslips were placed on a stub, coated with gold, observed, and photographed under SEM.

The pollen terminology provided by Punt *et al.* (2007) and Halbritter *et al.* (2018) was followed. The finished slides were deposited to the pollen library of the State University of Feira de Santana.

Table 1. Morphometric characters of *Galactia* P. Browne pollen grains and related genera (Leguminosae).

Species/Voucher	P		E		Epv		P/E	PAI	Ecto	Endo	Sex	Nex	Lum	Mur
	x±Sx	R	x±Sx	R	x±Sx	R								
***Galactia* P. Browne**														
Galactia benthamiana Micheli														
Queiroz, L.P. de 12496 (HUEFS)	31,5±0,38	27,5-35,0	25,4±0,44	20,0-30,0	32,5±0,43	27,5-35,0	1,24	0,32	18,7x2,9	4,6x5,1	1,05	0,8	3,3	1,1
Lima, L.C.P. 499 (HUEFS)	33,7±0,59	27,5-40,0	24,5±0,47	20,0-30,0	--	--	1,37	--	18,3x2,5	--	1,17	0,8	3,8	1,08
Galactia glaucescens Kunth														
Lima, L.C.P. 580 (HUEFS)	36,2±0,32	32,5-40,0	29,4±0,36	25,0-32,5	35,4±0,44	32,5-40,0	1,23	0,28	21,4x2,1	3,9x5,0	0,95	1,05	4,3	1,0
Cavalcanti, T.B. 1659 (HUEFS)	31,4±0,57	27,5-37,5	25,9±0,55	22,5-32,5	32,6±0,42	27,5-35,0	1,21	0,31	17,5x2,2	4,1x4,7	1,0	1,0	3,9	1,05
Queiroz, L.P. de 10591 (HUEFS)	30,0±0,47	25,0-32,5	27,3±0,49	22,5-32,5	29,2±0,34	27,5-32,5	1,09	0,30	15,4x2,3	4,3x5,4	0,9	1,2	4,3	1,0
Galactia jussiaeana Kunth														
Oliveira, M. 3818 (HUEFS)	34,9±0,30	32,5-37,5	30,7±0,39	25,0-32,5	33,0±0,35	30,0-37,5	1,13	0,30	23,0x3,1	4,1x4,7	1,49	0,51	5,1	1,9
Queiroz, L.P. de 10153 (HUEFS)	29,1±0,31	27,5-32,5	25,1±0,33	22,5-27,5	27,9±0,27	25,0-30,0	1,15	0,33	18,5x2,2	3.9x4,1	1,05	0,95	3,3	1,1
Galactia latisiliqua Desv.														
Queiroz, L.P. de 13578 (HUEFS)	34,1±0,51	30,0-40,0	28,5±0,43	25,0-32,5	31,5±0,35	30,0-35,0	1,19	0,29	22,2x2,9	3,6x4,1	1,0	1.0	3,7	1,3
Haught 6295 (COL)	33,8±0,45	30,0-37,5	26,6±0,28	25,0-30,0	30,1±0,36	27,5-32,5	1,27	0,31	21,2x3,0	3,9x4,5	0,92	0,92	3,1	1,0
Araque & Barkley 255 (COL)	28,9±0,25	27,5-30,0	24,7±0,26	22,5-27,5	28,3±0,34	25,0-32,5	1,17	0,32	18,6x2,1	3,5x3,9	1,05	1,05	2,6	1,05
Galactia remansoana Harms														
Cardoso, D. 964 (HUEFS)	31,2±0,29	30,0-35,0	28,5±0,25	27,5-30,0	29,4±0,33	27,5-32,5	1,09	0,36	20,7x3,5	3,3x3,8	1,32	0,57	4,2	1,05
Oliveira, M.V.M. 721 (HUEFS)	26,7±0,27	25,0-30,0	23,1±0,26	20,0-25,0	24,6±0,31	20,0-27,5	1,15	0,36	13,1x2,0	3,9x4,2	0,95	1,15	3,9	1,0
Barreto, K.L. *et al.* 47 (HUEFS)	27,7±0,24	25,0-30,0	25,4±0,34	22,5-27,5	27,7±0,32	25,0-32,5	1,09	0,35	14,2x3,5	4,4x4,2	0,85	1,15	4,3	1,0
Galactia striata (Jacq.) Urb.														
Stannard, B. 2495 (HUEFS)	27,0±0,25	25,0-30,0	22,2±0,26	20,0-25,0	24,9±0,39	22,5-27,5	1,21	0,36	15,1x2,2	4,6x5,5	1,5	0,5	3,4	1,0
Nunes, E. 11583 (HUEFS)	33,4±0,28	30,0-35,0	27,0±0,32	25,0-30,0	30,8±0,40	27,5-35,0	1,23	0,31	21,0x2,0	--	1,1	0,9	3,9	1,0
Fernandes, A. 15147 (HUEFS)	29,4±0,46	25,0-37,5	23,0±0,40	20,0-25,0	28,1±0,33	25,0-32,5	1,27	0,33	16,6x1,9	--	1,2	0,7	4,3	1,1
RELATED GENERA														
***Betencourtia* A. St.-Hil.**														
Betencourtia crassifolia (Benth.) L.P. Queiroz														
Cardoso, D. 2749 (HUEFS)	35,5±0,61	30,0-42,5	30,5±0,73	25,0-37,5	33,0±0,43	30,0-37,5	1,16	0,33	20,4x2,5	3,7x5,9	1,1	0,9	4,4	1,1

Table 1. Cont.

Species/Voucher	P		E		Epv		P/E	PAI	Ecto	Endo	Sex	Nex	Lum	Mur
	x±Sx	R	x±Sx	R	x±Sx	R								
Santos, A.K.A. 1018 (HUEFS)	37,2±0,33	35,0-40,0	33,3±0,31	30,0-35,0	34,6±0,31	32,5-37,5	1,11	0,32	24,5x3,1	3,4x5,9	1,3	0,7	3,9	1,1
Betencourtia gracillima (Benth.) L.P. Queiroz														
Idrobo 2581 (COL)	33,3±0,42	30,0-37,5	26,7±0,31	25,0-30,0	31,9±0,48	27,5-35,0	1,24	0,31	19,9x2,7	4,2x5,1	1,1	0,9	2,9	1,0
Betencourtia martii (DC.) L.P. Queiroz														
Silva-Castro, M.M. 1689 (HUEFS)	31,2±0,32	30,0-35,0	27,0±0,38	22,5-30,0	30,1±0,33	27,5-32,5	1,15	0,29	18,0x3,0	3,6x3,7	1,05	0,95	3,5	1,05
Azevedo, C. 292 (HUEFS)	31,6±0,47	27,5-35,0	29,4±0,46	25,0-32,5	29,9±0,44	25,0-35,0	1,07	--	17,7x2,5	3,7x3,8	1,12	0,93	4,0	1,0
Betencourtia neesii (DC.) L.P. Queiroz														
Oliveira, R.P. 72 (HUEFS)	33,4±0,40	30,0-37,5	27,1±0,37	22,5-30,0	32,1±0,60	27,5-40,0	1,23	0,29	18,4x2,0	3,8x4,4	1,1	0,9	4,2	1,45
Baitello, J.B. 1754 (HUEFS)	33,3±0,47	30,0-37,5	28,1±0,50	22,5-32,5	33,3±0,42	30,0-37,5	1,18	0,27	16,4x2,9	3,5x4,1	1,02	0,87	3,6	1,0
Silva, G.P. 2139 (HUEFS)	31,7±0,31	30,0-35,0	27,2±0,44	22,5-32,5	--	--	1,16	--	20,2x2,1	3,4x3,5	1,1	0,9	3,9	1,1
Betencourtia scarlatina (Mart. ex Benth,) L.P. Queiroz														
Faria, J.G. 279 (HUEFS)	32,9±0,34	30,0-37,5	26,2±0,25	25,0-27,5	29,7±0,26	27,5-32,5	1,25	0,29	22,0x3,2	3,6x4,2	1,3	0,7	3,2	1,1
Snak, C. 1080 (HUEFS)	36,0±0,35	32,5-37,5	28,7±0,32	27,5-32,5	33,9±0,54	30,0-40,0	1,25	0,29	24,1x3,6	3,8x4,4	1,55	0,45	3,7	1,1
Ordones, J. 1824 (HUEFS)	33,5±0,38	30,0-37,5	26,3±0,29	25,0-30,0	--	--	1,27	--	24,0x2,1	3,4x4,2	1,15	0,85	2,3	1,2
Betencourtia stereophylla (Harms) L.P. Queiroz														
Snak, C. 616 (HUEFS)	30,3±0,46	25,0-35,0	24,3±0,36	22,5-27,5	29,5±0,40	27,5-35,0	1,24	0,28	15,8x2,5	--	1,0	1,0	3,0	1,0
Silva, U.C.S. 100 (HUEFS)	32,8±0,69	30,0-42,5	26,8±0,53	25,0-32,5	32,7±0,37	27,5-35,0	1,22	0,29	20,5x2,2	3,6x3,6	1,11	0,91	3,4	1,17
***Caetangil* L.P. Queiroz**														
Caetangil paraguariensis (Chodat & Hassl.) L.P. Queiroz														
Queiroz, L.P. de 14691 (HUEFS)	33,9±0,43	30,0-37,5	36,0±0,36	27,5-32,5	33,0±0,40	30,0-37,5	1,10	0,35	19,9x3,2	3,5x3,6	1,4	0,57	4,2	1,09
***Cerradicola* L.P. Queiroz**														
Cerradicola boavista (Vell.) L.P. Queiroz														
Sakuragui, C.M. 437 (HUEFS)	30,8±0,47	27,5-37,5	25,1±0,44	20,0-30,0	29,6±0,42	27,5-35,0	1,22	0,24	17,7x2,4	3,9x5,2	1,0	1,0	3,9	1,25
Cruz, J. 142 (HUEFS)	30,4±0,47	22,5-35,0	26,7±0,59	20,0-30,0	30,1±0,65	20,0-35,0	1,13	0,32	18,7x2,5	4,1x5,2	1,3	0,8	3,6	1,5
Silva, J.M. *et al.* 2175 (HUEFS)	39,5±0,35	37,5-42,5	31,4±0,52	27,5-35,0	37,2±0,41	32,5-40,0	1,25	0,31	23,0x2,4	5,0x5,1	0,95	0,95	2,9	1,6
Cerradicola decumbens (Benth.) L.P. Queiroz.														
Pastore, J.F.B. 4034 (HUEFS)	33,9±0,45	30,0-37,5	28,6±0,38	25,0-32,5	32,4±0,42	27,5-35,0	1,18	0,33	22,5x2,7	4,8x4,0	1,0	1,0	3,5	1,9

Table 1. Cont.

Species/Voucher	P		E		Epv		P/E	PAI	Ecto	Endo	Sex	Nex	Lum	Mur
	x±Sx	R	x±Sx	R	x±Sx	R								
Sampaio, A.B.306 (HUEFS)	32,6±0,54	27,5-37,5	27,7±0,47	22,5-32,5	32,3±0,53	27,5-40,0	1,17	0,33	19,7x2,1	--	1,32	0,68	3,1	1,7
Natividade, P.C. 23 (HUEFS)	30,9±0,51	27,5-35,0	25,6±0,71	17,5-32,5	31,2±0,57	27,5-37,5	1,20	0,31	17,9x2,5	5,0x3,8	1,24	0,76	3,9	1,5
Cerradicola diversifolia (Benth.) L.P. Queiroz														
Queiroz, L.P. de 10432 (HUEFS)	37,3±0,57	32,5-42,5	30,9±0,55	25,0-35,0	38,5±0,55	32,5-45,0	1,20	0,30	21,3x3,1	5,7x4,4	1,0	1,0	4,1	1,4
Queiroz, L.P. 10326 (HUEFS)	43,2±0,49	37,5-47,5	36,0±0,61	30,0-40,0	41,8±0,7	35,0-47,5	1,20	0,25	22,8x2,6	4,1x3,7	1,02	0,88	6,8	1,15
Cerradicola douradensis (Taub.) L.P. Queiroz														
Cavalcanti, T.B. 1943 (HUEFS)	33,6±0,45	30,0-37,5	27,1±0,34	25,0-30,0	34,4±0,43	30,0-37,5	1,23	0,31	19,9x2,0	3,8x3,9	1,0	1,0	3,3	1,1
Cardoso, D. 2590 HUEFS)	40,5±0,47	35,0-45,0	29,0±0,62	25,0-35,0	38,0±0,47	32,5-42,5	1,39	0,27	19,4x2,0	--	1,07	1,07	3,6	1,0
Cerradicola elliptica (Desv) L.P. Queiroz.														
Queiroz, L.P. de 10340 (HUEFS)	32,6±0,33	30,0-35,0	27,3±0,24	25,0-30,0	31,8±0,51	27,5-37,5	1,19	--	22,6x2,5	3,8x3,9	0,95	1,05	2,9	1,0
Snak, C. 1010 (HUEFS)	32,7±0,32	30,0-37,5	27,1±0,34	22,5-30,0	30,2±0,37	25,0-35,0	1,20	--	19,3x3,6	4,2x3,9	1,3	0,7	3,6	1,02
Schultze-Kraft, R. s/n (HUEFS)	37,1±0,31	35,0-40,0	29,2±0,37	25,0-32,5	33,0±0,57	27,5-40,0	1,27	--	23,5x4,0	4,1x4,9	0,9	1,1	3,4	1,05
Cerradicola eriosematoides (Harms) L.P. Queiroz														
Paula-Souza, J. 3861 (HUEFS)	31,9±0,50	27,5-37,5	28,2±0,42	25,0-32,5	32,2±0,36	27,5-35,0	1,13	0,34	18,9x2,4	3,9x4,2	1,3	0,67	3,7	1,05
Machado, M. 137 (HUEFS)	32,9±0,37	30,0-37,5	28,1±0,46	25,0-35,0	33,1±0,29	30,0-35,0	1,17	0,34	18,4x2,2	--	1,04	0,56	3,8	1,15
Queiroz, L.P. de 14199 (HUEFS)	32,3±0,57	25,0-37,5	27,6±0,69	20,0-35,0	30,5±0,57	25,0-37,5	1,17	0,26	16,7x2,8	--	1,05	1,0	4,8	1,2
Cerradicola grewiifolia (Benth.) L.P. Queiroz														
Paiva, V.F. *et al.* 139 (HUEFS)	34,5±0,38	30,0-37,5	29,7±0,33	27,5-32,5	35,0±0,59	30,0-40,0	1,16	0,25	20,5x2,6	3,9x5,0	1,4	1,4	4,3	1,1
Silva, G.P. 1845 (HUEFS)	35,1±0,42	30,0-37,5	27,6±0,39	25,0-32,5	34,2±0,45	30,0-40,0	1,27	0,30	19,6x3,2	3,3x3,8	1,0	1,0	4,1	1,4
França, F. 4632 (HUEFS)	32,7±0,40	30,0-35,0	33,5±0,43	30,0-37,5	33,8±0,35	30,0-37,5	0,97	0,32	20,2x4,3	3,6x4,6	1,2	0,8	7,1	1,3
Cerradicola heringeri (Burkart) L.P. Queiroz														
Araujo, L. 80 (HUEFS)	31,6±0,53	27,5-37,5	26,7±0,51	22,5-32,5	30,5±0,54	25,0-35,0	1,18	--	19,7x2,8	--	1,4	1,4	3,3	1,1
Silva, A. 7266 (HUEFS)	39,0±0,52	32,5-42,5	29,7±0,56	22,5-35,0	38,9±0,52	32,5-42,5	1,31	--	22,7x2,5	3,2x3,5	1,4	1,4	4,6	1,05
Romero, R. *et al.* 5192 (UEC)	36,2±0,35	32,5-40,0	30,2±0,43	27,5-35,0	33,8±0,58	30,0-40,0	1,19	--	21,9x2,1	3,3x4,1	1,0	1,0	3,6	1,1
Cerradicola longifolia (Benth.) L.P. Queiroz														
Queiroz, L.P. de 10403 (HUEFS)	37,0±0,47	30,0-40,0	31,6±0,35	30,0-35,0	34,5±0,5	30,0-40,0	1,17	--	20,8x2,5	2,9x4,1	1,5	1,5	4,5	1,1
Cerradicola peduncularis (Benth.) L.P. Queiroz														

Table 1. Cont.

Species/Voucher	P		E		Epv		P/E	PAI	Ecto	Endo	Sex	Nex	Lum	Mur
	x±Sx	R	x±Sx	R	x±Sx	R								
Cavalcanti, T.B. *et al.* 821 (HUEFS)	36,9±0,68	30,0-42,5	29,8±0,61	22,5-35,0	36,4±0,57	30,0-42,5	1,23	0,24	22,7x1,9	--	1,0	1,0	3,6	1,05
Walter, B.M.T. 3871 (HUEFS)	34,5±0,54	30,0-37,5	29,5±0,57	25,0-35,0	35,5±0,54	30,0-40,0	1,16	--	18,0x2,6	3,4x3,3	0,9	1,1	3,5	1,0
***Collaea* DC.**														
Collaea speciosa (Loisel.) DC.														
Vargas, I.L. 1733 (LPB)	31,3±0,38	27,5-35,0	28,0±0,25	25,0-30,0	30,3±0,46	25,0-35,0	1,11	0,35	19,4x3,1	3,2x3,3	1,06	1,03	2,0	1,0
Lewis, M. 881758 (LPB)	39,8±0,32	37,5-42,5	31,8±0,42	27,5-35,0	36,6±0,57	32,5-42,5	1,25	0,41	27,5x3,2	3,2x3,2	1,2	0,85	2,3	1,0
Collaea stenophylla (Hook. & Arn.)														
Bianchini, R.S. 1206 (HUEFS)	24,8±0,32	22,5-27,5	21,0±0,32	17,5-25,0	24,7±0,36	22,5-27,5	1,18	0,34	15,2x2,3	--	1,15	0,85	1,8	--
Giulietti, A.M. 13583 (HUEFS)	25,8±0,27	22,5-27,5	22,2±0,46	20,0-27,5	24,3±0,30	22,5-27,5	1,16	--	16,1x3,0	3,7x3,3	1,32	0,68	2,5	1,0
***Lackeya* Fortunato, L.P. Queiroz & G.P. Lewis**														
Lackeya viridiflora (Rose) L.P. Queiroz														
Téllez, V.O. 792 (HUEFS)	28,6±0,29	27,5-32,5	27,4±0,17	25,0-30,0	28,7±0,38	25,0-32,5	1,04	--	18,5x3,0	3,3x3,3	1,43	0,58	3,6	1,02
Lackeya multiflora (Torr. & A.Gray) Fortunato, L.P. Queiroz & G.P. Lewis														
Gwaltney, J.R. s/n (HUEFS)	34,8±0,35	32,5-37,5	28,4±0,37	22,5-32,5	34,5±0,57	30,0-40,0	1,22	0,37	20,9x2,6	4,1x3,4	1,15	1,05	4,8	1,05
Bryson, C.T. 23759	37,3±0,37	32,5-40,0	28,6±0,29	25,0-30,0	37,8±0,60	32,5-42,5	1,30	0,35	24,9x2,8	4,5x3,8	1,1	1,1	5,3	1,5
***Nanogalactia* L.P. Queiroz**														
Nanogalactia heterophylla (Gillies ex Hook. & Arn.) L.P. Queiroz														
Gonçalves s.n. (COL)	35,3±0,36	30,0-40,0	30,2±0,40	27,5-35,0	36,6±0,35	35,0-40,0	1,16	0,28	20,8x2,2	3,9x4,3	1,1	0,9	3,6	2,38
Nanogalactia pretiosa (Burkart)L.P. Queiroz														
Queiroz, L.P. de 12463 (HUEFS)	32,6±0,44	27,5-35,0	27,8±0,48	25,0-32,5	34,1±0,24	32,5-35,0	1,17	0,31	17,1x2,4	3,0x3,2	1,0	1,0	3,3	1,3
Poliquesi, C.B. 68 (HUEFS)	38,8±0,72	32,5-47,5	29,7±0,66	22,5-35,0	38,1±0,61	32,5-42,5	1,30	0,32	20,4x2,2	--	1,4	1,4	4,6	1,9
***Rhodopis* Urb.**														
Rhodopis volubilis (Willd.) L.P. Queiroz														
Heller, A.A. 632 (NYBG)	--	--	--	--	56,0±0,52	50,0-62,5	--	0,37	--	--	1,8	1,25	--	--
Shafer, J.A. 3387 (NYBG)	--	--	--	--	50,9±0,61	45,0-57,5	--	0,40	--	--	1,75	1,25	--	--
Shafer, J.A. 3227 (NYBG)	--	--	--	--	53,0±0,52	47,5-57,5	--	0,38	--	--	1,8	1,2	--	--

P= Polar axis; E= Equatorial diameter; Epv= Equatorial diameter in polar view; x= Arithme tic mean; Sx= Standard deviation; R= Range; PAI= Polar area index; Ecto= Length and width of the ectoaperture; Endo= Length and width of endoaperture; Sex=Sexine; Nex=Nexine, Lum= Lumen; Mur= Murus width. *n<25 measurements. Measurements in μm.

Principal Component Analysis (PCA)

PCA employing the Past.3.22 (2018) program was performed using six metric variables for the analysis of ANOVA (following Souza *et al.* (2014)). The data were obtained from the arithmetic means (x) of the morphometric analyzes of the pollen grains, which were subjected to PCA own transformation: which consists of the linear combination of the original variables (*karhunnen-Loéve* transformation). The six variables were as follows: P = Polar axis, E = Equatorial diameter in equatorial view, Epv = Equatorial diameter in polar view, P/E = Polar axis/ Equatorial diameter ratio, Lumen = Lumen diameter, Murus = Murus width.

Results

General description

The pollen grains of *Galactia* and related genera, in general, are in monads, isopolar or heteropolar commonly medium-size but can be small or large, are 3-colporate or parasyncolpate, and are angulaperturate, varying from subtriangular, triangular to circular amb. The most common shape observed was subprolate; however, oblate spheroidal, prolate spheroidal, and prolate pollen grains were also observed (Table 1-2; Figures 1-4).

All species have pollen with a long ectoaperture, and the colpus may be equatorially constricted, varying in length (Fig. 1A, C, L; 2A, C, F; 4O, P, Q). One *Collaea* species (*Co. speciosa*) reached the highest value for ectoaperture length (27.5 μm). However, the other species and consequently their respective genera also frequently showed similarly high ectoaperture length values, e.g., 24.9 μm (*Lackeya*), 24.5 μm (*Betencourtia*), 23.5 μm (*Cerradicola*), 23.0 μm (*Galactia*), and 20.8 μm (*Nanogalactia*). The lowest values for ectoaperture length belonged to one species of *Galactia* (14.2 μm), *Betencourtia* (15.8 μm), and *Collaea* (16.1 μm). The endoaperture is frequently lalongate and may be circular or elliptical and difficult to visualize (Fig. 1A, C, L, M; 2A, M; 3C, J, K). The details of all values measured for the ectoaperture and endoaperture are shown in Table 1.

The exine has a microreticulate or reticulate sculpture, and it can be heterobrochate (Fig. 1-I; Fig. 2-G, O; Fig. 3-H). The lumina decreased in size near the apertural region in most species (Fig. 1N; Fig. 2K; Fig. 3N). The details of the reticulation of some species (belonging to different genera) were also variable (Figure 4 R-U). These details helped determine the differences in the lumina diameter. The species belonging to *Cerradicola* showed the highest values of the lumen diameter (2.9–7.1 μm), followed by *Lackeya* (3.6–5.3 μm), *Galactia* (2.6–5.1 μm), *Nanogalactia* (3.3–4.6 μm), and *Betencourtia* (2.3–4.4 μm). The species belonging to *Collaea* showed the lowest values (1.8–2.5 μm).

It is important to highlight that *Nanogalactia* has the highest values for murus width (1.3–2.38 μm), whereas other genera had a low murus width: *Galactia* and *Cerradicola* (1.0–1.9 μm), *Betencourtia* (1.0–1.45 μm), *Lackeya* (1.02–1.5 μm), and *Collaea* (1.0 μm) (Table 1).

Genera description

Galactia P. Browne (Fig. 1)

Analyzed species: *G. benthamiana* Micheli, *G. glaucescens* Kunth, *G. jussiaeana* Kunth, *G. latisiliqua* Desv., *G. remansoana* Harms, and *G. striata* (Jacq.) Urb.

Pollen grains are in monads, medium size, isopolar, subprolate, less frequently prolate spheroidal (*G. glaucescens* and *G. jussiaeana*) and prolate (*G. benthamiana*); angulaperturate; they had circular, subtriangular to triangular amb (Table 2; Fig. 1F, K, N). Long ectoaperture, narrow in most of the species was observed. Psilate or microreticulate margo (Fig. 1D, J, O); psilate apertural membrane, except in *G. remansoana* and *G. striata* that had granules (Fig. 1M, O); and colpus equatorially constricted (Fig. 4P, Q). We also observed a lalongate endoaperture, being little evident in *G. latisiliqua* and *G. benthamiana* (Fig. 1A, C, H, L). Reticulate exine, heterobrochate with an angular lumina that reduced in size near the apertural region (Fig. 1I, N, O). In *G. jussiaeana*, the reticulate can be incomplete (Fig. 4R). Anastomosate and little width murus were observed. Under SEM, a bireticulate exine was observed, except in *G. jussiaeana*, whose exine was reticulate (Fig. 1B, E, G, O). The murus of the reticulum was psilate in all species, except *G. glaucescens*, whose murus had perforations (Fig. 1E). Sexine and nexine were of equal thickness, or the sexine was thicker than nexine (Table 2).

Related genera

Betencourtia A. St.-Hil. (Fig. 2A-I)

Analyzed species: *Be. crassifolia* (Benth.) L.P. Queiroz, *Be. gracillima* (Benth.) L.P. Queiroz, *Be. martii* (DC.) L.P. Queiroz, *Be. neesii* (DC.) L.P. Queiroz, *Be. scarlatina* (Mart. ex Benth,) L.P. Queiroz, and *Be. stereophylla* (Harms) L.P. Queiroz

Pollen grains are in monads, medium size, isopolar, subprolate, less frequently prolate-spheroidal (*Be. crassifolia* and *Be. martii*), 3-colporate, angulaperturate, costate in *Be. martii* (Fig. 2D), with circular to triangular amb (Table 2; Fig. 2E, K). We observed a long ectoaperture, ending at the polar region in *Be. martii*, *Be. scarlatina*, *Be. crassifolia*, and *Be. neessi*. In these three last species, it seems that colpus apices break near to the polar area (Figure 2A, F), whereas in the other species, the colpus ended running toward the poles of the pollen grain (Figure 2H). We also observed differentiated microreticulate margo and a psilate apertural membrane (Figure 2C, I). Colpus equatorially constricted (Figure 2F); and lalongate, circular, or elliptical endoaperture (Fig. 2A). Reticulate exine, heterobrochate;

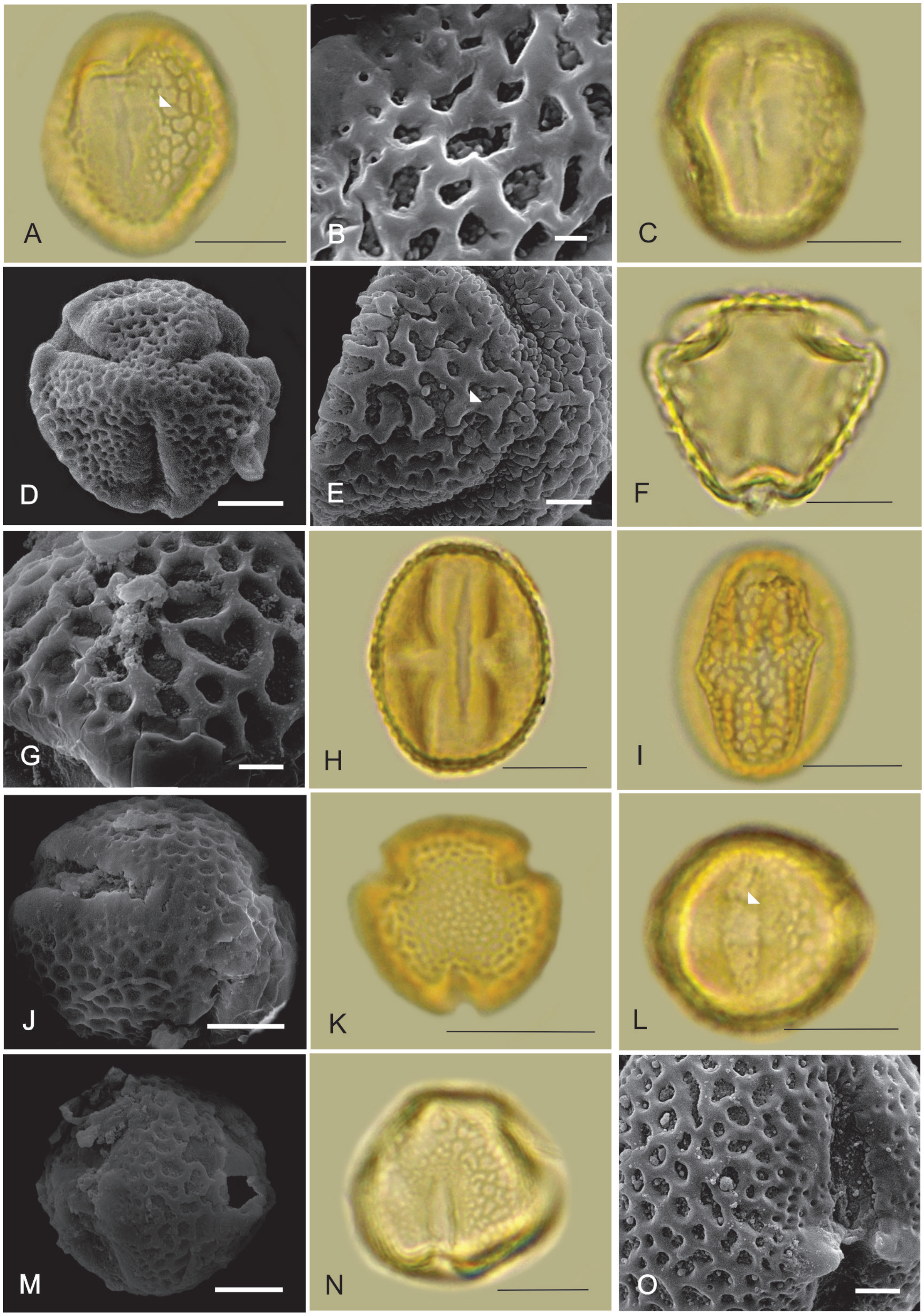

Figure 1. Pollen grains of *Galactia* P. Browne (Leguminosae) **A - O.** *Galactia*: **A – B**; *G. benthamiana:* **A.** equatorial view; **B.** Surface (SEM); **C - E.** *G. glaucescens:* **C.** Equatorial view, **D.** Polar view (SEM), **E.** Surface (SEM); **F - G.** *G. jussiaeana:* **F.** Polar view, **G.** Surface (SEM); **H - K.** *G. latisiliqua*: **H - I.** Light section and surface, respectively, **J.** Apocolpium (SEM), K. Polar view; **L - M.** *G. remansoana:* equatorial view **L.** light microscopic, endoaperture detail, **M.** SEM; **N - O.** *G. striata:* **N.** Polar view, **O.** Exine detail at apertural zone (SEM). Scales: 10 µm (A, C, D, F, H, I, K, L, N); 6 µm (J, M); 4 µm (E, G, O); 1 µm (B).

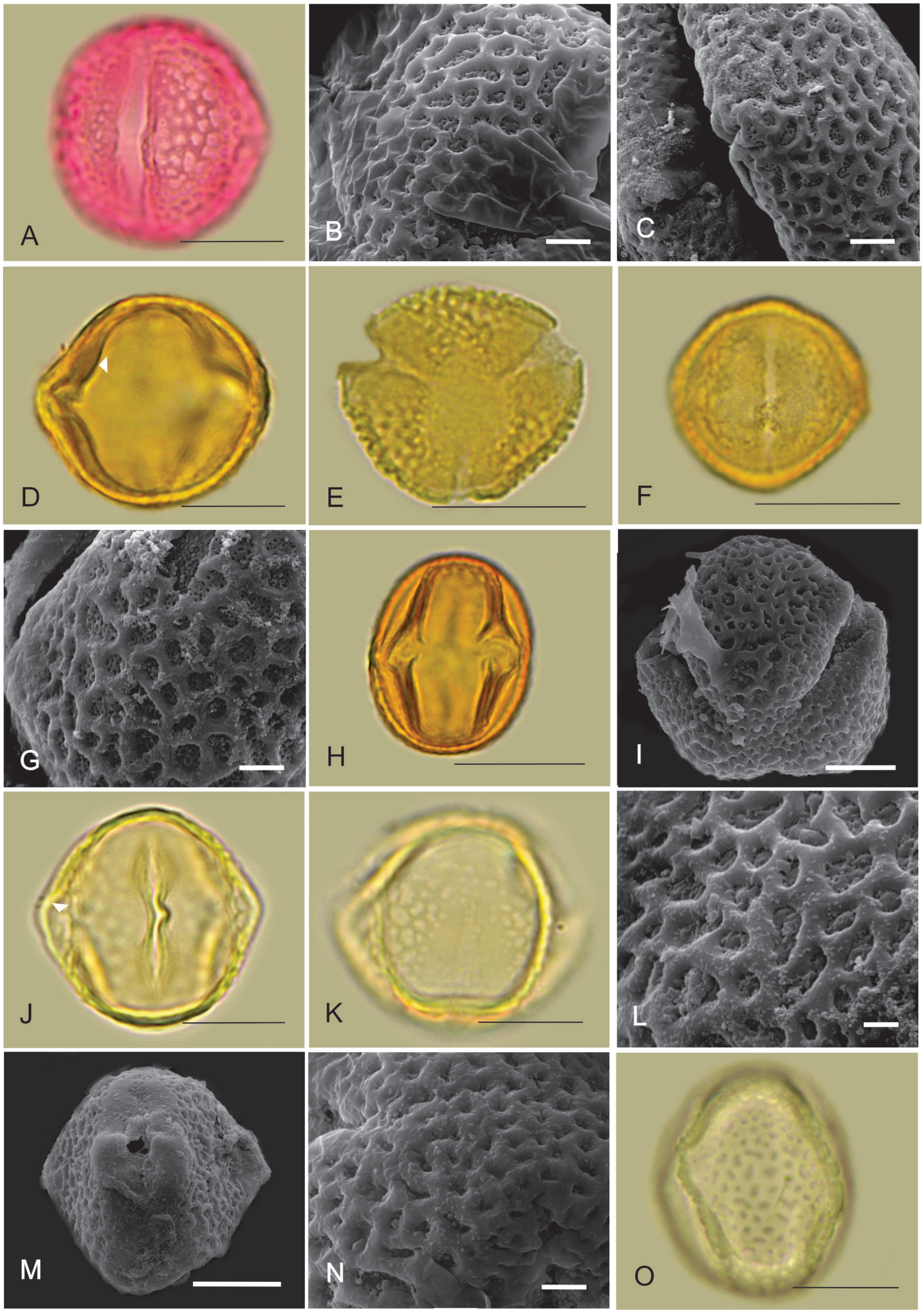

Figure 2. Pollen grains of *Betencourtia* A.St.-Hil., *Caetangil* L.P. Queiroz and *Cerradicola* L.P. Queiroz (Leguminosae). **A - I.** *Betencourtia*: **A - B.** *Be. crassifolia*, **A.** Equatorial view, ectoaperture length detail (safranine stained), **B.** Surface (SEM); **C.** *Be. gracillima*, surface (SEM); **D.** *Be. martii*, equatorial view, costa detail (light section); **E - F.** *Be. neesii*, **E.** polar view, **F.** equatorial view; **G - H.** *Be. scarlatina*, **G.** surface (SEM), **H.** equatorial view; **I.** *Be. stereophylla*, polar view (SEM); **J - M.** *Caetangil*: **J - M.** *Ca. paraguariensis*, **J.** equatorial view, notice the fastigium; **K.** polar view, **L.** Surface (SEM), **M.** equatorial view (SEM); **N - O.** *Cerradicola*: **N - O.** *Ce. boavista*, **N.** surface (SEM), **O.** equatorial view. Scales: 10 µm (A, D, E, F, H, J, K, M, O); 6 µm (I); 4 µm (B, C, G, N); 1 µm (L).

with an isodiametric or lengthened lumina (Fig. 2B, C, I; 4T). Anastomosate or straight at angles and little width murus (Fig. 2G). Under SEM, we observed a bireticulate exine (Fig. 2B, C, G), with granules at the lumen center in *Be. stereophylla* (Fig. 2I). We also observed pollen with psilate suprareticulum murus, the width of which was low in all species, except in *Be. gracillima*, wherein the murus width was slightly elevated (Fig. 2C). The sexine was thicker than the nexine in all species (Table 2).

Caetangil L.P. Queiroz (Fig. 2J-M)

Analyzed species: *Ca. paraguariensis* (Chodat & Hassl.) L.P. Queiroz

Pollen grains are in monads, medium size, prolate spheroidal, isopolar, 3-colporate, and angulaperturate (Table 2). Triangular amb was observed with sides being slightly convex (Fig. 2K). Long ectoaperture, ending at the polar region; psilate margo and apertural membrane with granules of small size were observed (Fig. 2J, M). In addition, pollens had a circular endoaperture (Figure 2M) and presence of fastigium (Fig. 2J). Reticulate exine, heterobrochate, and polygonal lumina, along with anastomosate and a slightly width murus (Fig. 2K). Under SEM, a reticulate perforate exine, with a psilate and low suprareticulum murus were observed (Fig. 2L). The sexine was thicker than the nexine (Table 2).

Cerradicola L.P. Queiroz (Fig. 2N-O, 3A-K)

Analyzed species: *Ce. boavista* (Vell.) L.P. Queiroz, *Ce. decumbens* (Benth.) L.P. Queiroz, *Ce. douradensis* (Taub.) L.P. Queiroz, *Ce. elliptica* (Desv) L.P. Queiroz, *Ce. eriosematoides* (Harms) L.P. Queiroz, *Ce. grewiifolia* (Benth.) L.P. Queiroz, *Ce. heringeri* (Burkart) L.P. Queiroz, *Ce. peduncularis* (Benth.) L.P. Queiroz, *Ce. diversifolia* (Benth.) L.P. Queiroz, and *Ce. longifolia* (Benth.) L.P. Queiroz

Pollen grains are in monads, medium size, mostly subprolate, also being oblate spheroidal, prolate spheroidal, and prolate, isopolar, and less frequently heteropolar (*Ce. elliptica*, *Ce. decumbens*, *Ce. heringeri*, *Ce. longifolia*) (Fig. 3A, D; Table 2). 3-colporates, angulaperturate, circular amb, less frequently varying from subtriangular to triangular with straight sides (Fig. 3G, K); costate in *Ce. eriosematoides* and *Ce. grewiifolia* (Fig. 3F). Long ectoaperture were observed, in all species. (Psilate margo in *Ce. decumbens*, *Ce. grewiifolia*, *Ce. diversifolia, Ce. longifolia* and *Ce. eriosematoides*, and microreticulate margo in the remaining species (Fig. 3B, C, J, M). Psilate apertural membrane, except in *Ce. grewiifolia* and *Ce. decumbens*, which had granules (Fig. 3B, G, J). Lalongate endoaperture, not well evident under light microscopy (Fig. 3A, D). The colpus could be equatorially constricted (Fig. 4O). A reticulate exine, heterobrochate were noted (Fig. 2N, O; Fig. 3H; 4S). We also observed polyhedral lumina, with larger and spaced between them in *Ce. diversifolia*, *Ce. grewiifolia*, and *Ce. heringeri* but close spaces in *Ce. elliptica* (Fig. 3C, E, H). An incomplete reticulum was observed in *Ce. heringeri* and *Ce. grewiifolia* (Fig. 3H; 4S). Anastomosate and little width murus were also observed. Under SEM, a bireticulate exine was observed, sometimes having granules in the lumen of *Ce. heringeri* and *Ce. longifolia* (Fig. 3B, E, I, J). A high and psilate suprareticulum murus was observed. In *Ce. elliptica* is possible to visualize the columellae under the suprareticulum murus (Fig. 3E). The thickness of the sexine and nexine was variable (Table 2).

Collaea DC. (Fig. 3L-P)

Analyzed species: *Co. speciosa* (Loisel.) DC. and *Co. stenophylla* (Hook. & Arn.) Benth.

Pollen grains are in monads, small (*Co. stenophylla*) and medium size (*Co. speciosa*), isopolar, subprolate (Table 2), 3-colporates, angulaperturate, and costate in *Co. stenophylla* (Fig. 3L); subtriangular to circular amb (Fig. 3N). Long ectoaperture, a microreticulate margo and a psilate apertural membrane (Fig. 3M, P) were observed. The colpus was equatorially constricted. Reticulate exine, small and polygonal lumina (Fig. 3M, P; Fig. 4U). Anastomosate and little width murus were observed. Under SEM, a bireticulate exine and low and psilate suprareticulum murus were observed (Fig. 3M, O, P). The sexine was slightly thicker than the nexine (Table 2).

Lackeya Fortunato, L.P. Queiroz & G.P. Lewis (Fig. 4A-D)

Analyzed species: *L. multiflora* (Torr. & A.Gray) Fortunato, L.P. Queiroz & G.P. Lewis, and *L. viridiflora* (Rose) L.P. Queiroz

Pollen grains are in monads, medium size, subprolate, isopolar (*L. multiflora,* Fig. 4A), prolate spheroidal, heteropolar (*L. viridiflora* Fig. 4D), 3-colporate, angulaperturate and costate. Furthermore, triangular amb with straight sides in *L. viridiflora* and plano-convex in *L. multiflora* was observed (Fig. 4C). Long ectoaperture, microreticulate margo, and psilate apertural membrane. Lalongate endoaperture was not well evident under light microscopy. We also observed a reticulate exine, heterobrochate, with a circular lumina in *L. viridiflora* and irregular shapes in *L. multiflora*. In the latter, the reticulum would be incomplete (Fig. 4B). Anastomosate and small width murus were observed. Under SEM, a bireticulate exine with a psilate and low suprareticulum murus was found (Fig. 4B, D). The sexine was thicker than the nexine in *L. viridiflora*, and the sexine and nexine were equally thick in *L. multiflora* (Table 2).

Nanogalactia L.P. Queiroz (Fig. 4E-I)

Analyzed species: *N. pretiosa* (Burkart) L.P. Queiroz and *N. heterophylla* (Gillies ex Hook. & Arn.) L.P. Queiroz

Pollen grains are in monads, medium size, isopolar, subprolate, 3-colporate, with circular amb (Table 2).

Table 2. Morphopalynological traits of *Galactia* P. Browne species (Leguminosae).

Species/Section	Size	Shape	Polar area	Amb	Apertural type	Exine
***Galactia* P. Brownie**						
Galactia benthamiana	M	SP/P	Small	Circular	3-colporate	S<N
Galactia glaucescens	M	PE/SP	Small	Subtriangular	3-colporate	S<N
Galactia jussiaeana	M	PE	Small	Subtriangular to triangular	3-colporate	S<N
Galactia latisiliqua	M	SP	Small	Subtriangular to circular	3-colporate	S=N
Galactia remansoana	M	PE/SP	Small	Subtriangular	3-colporate	S<N
Galactia striata	M	SP	Small	Circular	3-colporate	S>N
RELATED GENERA						
***Betencourtia* A. St.-Hil.**						
Betencourtia crassifolia	M	PE/SP	Small	Subtriangular to circular	3-colporate	S>N
Betencourtia gracillima	M	SP	Small	Circular	3-colporate	S>N
Betencourtia martii	M	PE/SP	Small	Circular	3-colporate	S>N
Betencourtia neesii	M	SP	Small	Circular	3-colporate	S>N
Betencourtia scarlatina	M	SP	Small	Triangular	3-colporate	S>N
Betencourtia stereophylla	M	SP	Small	Circular	3-colporate	S>N
***Caetangil* L.P. Queiroz**						
Caetangil paraguariensis	M	PE	Small	Triangular	3-colporate	S>N
***Cerradicola* L.P. Queiroz**						
Cerradicola boavista	M	PE/SP	Small	Subtriangular to circular	3-colporate	S>N
Cerradicola decumbens	M	SP	Small	Subtriangular to circular	3-colporate	S>N
Cerradicola diversifolia	M	SP	Small	Circular	3-colporate	S>N
Cerradicola douradensis	M	SP/P	Small	Circular	3-colporate	S=N
Cerradicola elliptica	M	SP	--	Subtriangular	3-colporate	S<N
Cerradicola eriosematoides	M	PE/SP	Small	Circular	3-colporate	S>N
Cerradicola grewiifolia	M	OE/SP	S mall	Subtriangular to circular	3-colporate	S=N
Cerradicola heringeri	M	SP	--	Triangular to subtriangular	3-colporate	S=N
Cerradicola longifolia	M	SP	--	Triangular	3-colporate	S=N
Cerradicola peduncularis	M	SP/P	Small	Circular	3-colporate	S=N
***Collaea* DC.**						
Collaea stenophylla	S	SP	Small	Subtriangular to circular	3-colporate	S>N
Collaea speciosa	M	PE/SP	Small	Subtriangular	3-colporate	S>N
***Lackeya* Fortunato, L.P. Queiroz & G.P. Lewis**						
Lackeya viridiflora	M	PE	--	Triangular	3-colporate	S>N
Lackeya multiflora	M	SP	Small	Triangular	3-colporate	S=N
***Nanogalactia* L.P. Queiroz**						
Nanogalactia heterophylla	M	SP	Small	Circular	3-colporate	S>N
Nanogalactia pretiosa	M	SP	Small	Circular	3-colporate	S=N
***Rhodopis* Urb.**						
Rhodopis volubilis	L	--	Small	Triangular	parasyncolpate	S>N

S=Small; M= Medium; L=Large; OS= Oblate-spheroidal; PS= Prolate-spheroidal; SP= Subprolate; P= Prolate; S=Sexine; N=Nexine.

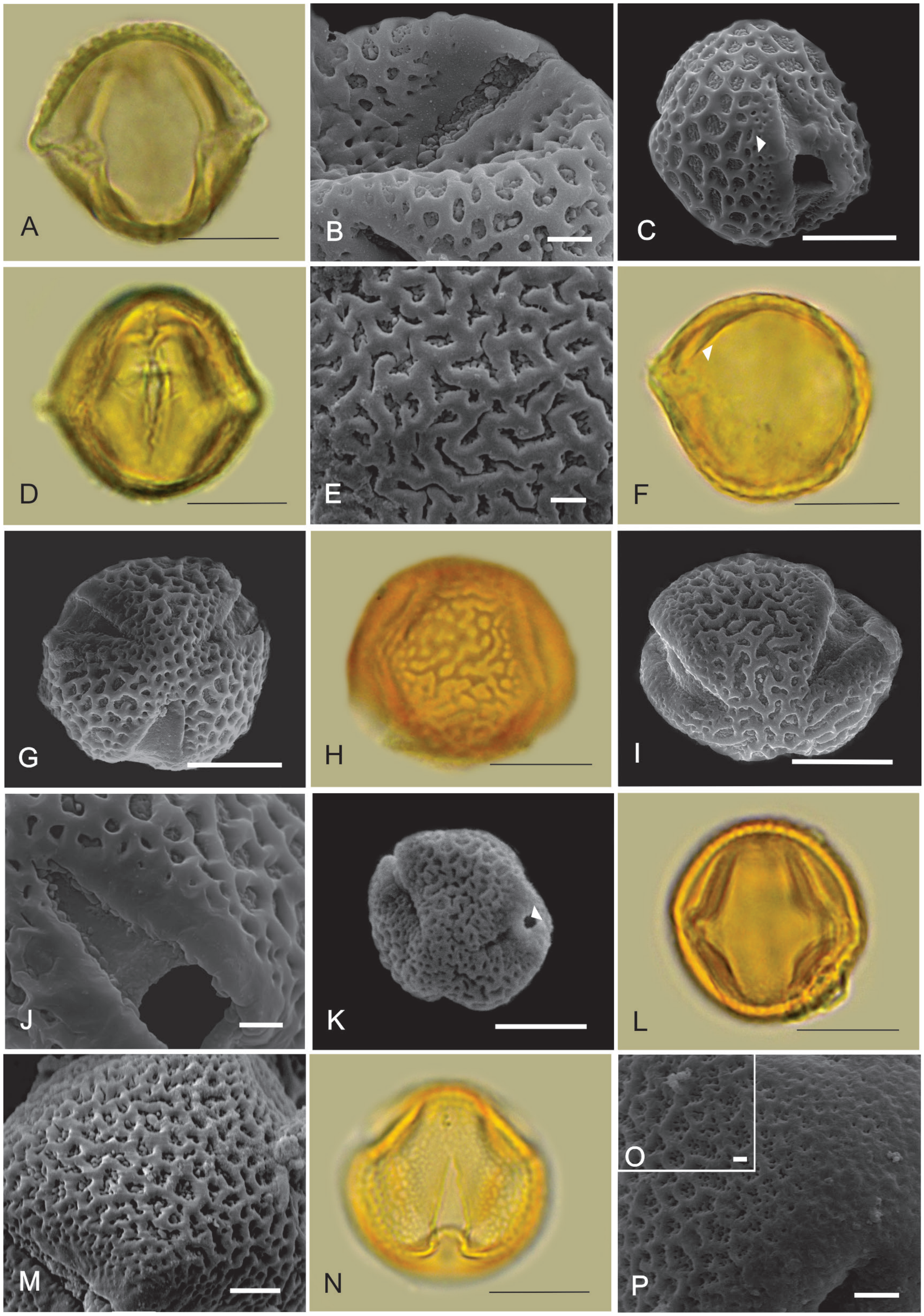

Figure 3. Pollen grains of *Cerradicola* L.P. Queiroz and *Collaea* DC. (Leguminosae). **A - K.** *Cerradicola*: **A - B.** *Ce. decumbens*, **A.** equatorial view, **B.** Surface in the apertural zone, see psilate margo (SEM); **C.** *Ce. diversifolia*, equatorial view, notice psilate apertural membrane (SEM); **D - E.** *Ce. elliptica*, **D.** equatorial view, **E.** Surface (SEM); **F - G.** *Ce. eriosematoides*, **F.** equatorial view, costa detail, **G.** polar view (SEM); **H.** *Ce. grewiifolia*, equatorial view, exine evidence; **I.** *Ce. heringeri*, polar view (SEM); **J.** *Ce. longifolia*, apertural detail, notice margo and membrane (SEM); **K.** *Ce. peduncularis*, polar view, endoaperture detail (SEM). **L - P.** *Collaea*: **L - M.** *Co. stenophylla*, **L.** Equatorial view, **M.** Surface (SEM); **N - P.** *Co. speciosa*, **N.** Polar view; **O - P.** Surface (SEM). Scales: 10 µm (A, C, D, F-I, K, L, N); 4 µm (B, J, M, P); 1 µm (E, O).

We found a long ectoaperture, psilate margo and psilate apertural membrane in *N. pretiosa* and granulate in *N. heterophylla* (Fig. 4G, H). Circular, small, not evident endoaperture in *N. pretiosa*. A reticulate exine with anastomosate muri was observed. Very wide murus was found (Fig. 4E, F, I). Under SEM, the exine was bireticulate, making it possible to observe the width of the murus. Psilate and low suprareticulum murus (Fig. 4H, I). The sexine was thicker than the nexine in *N. heterophylla*, and the sexine and nexine were equally thick in *N. pretiosa* (Table 2).

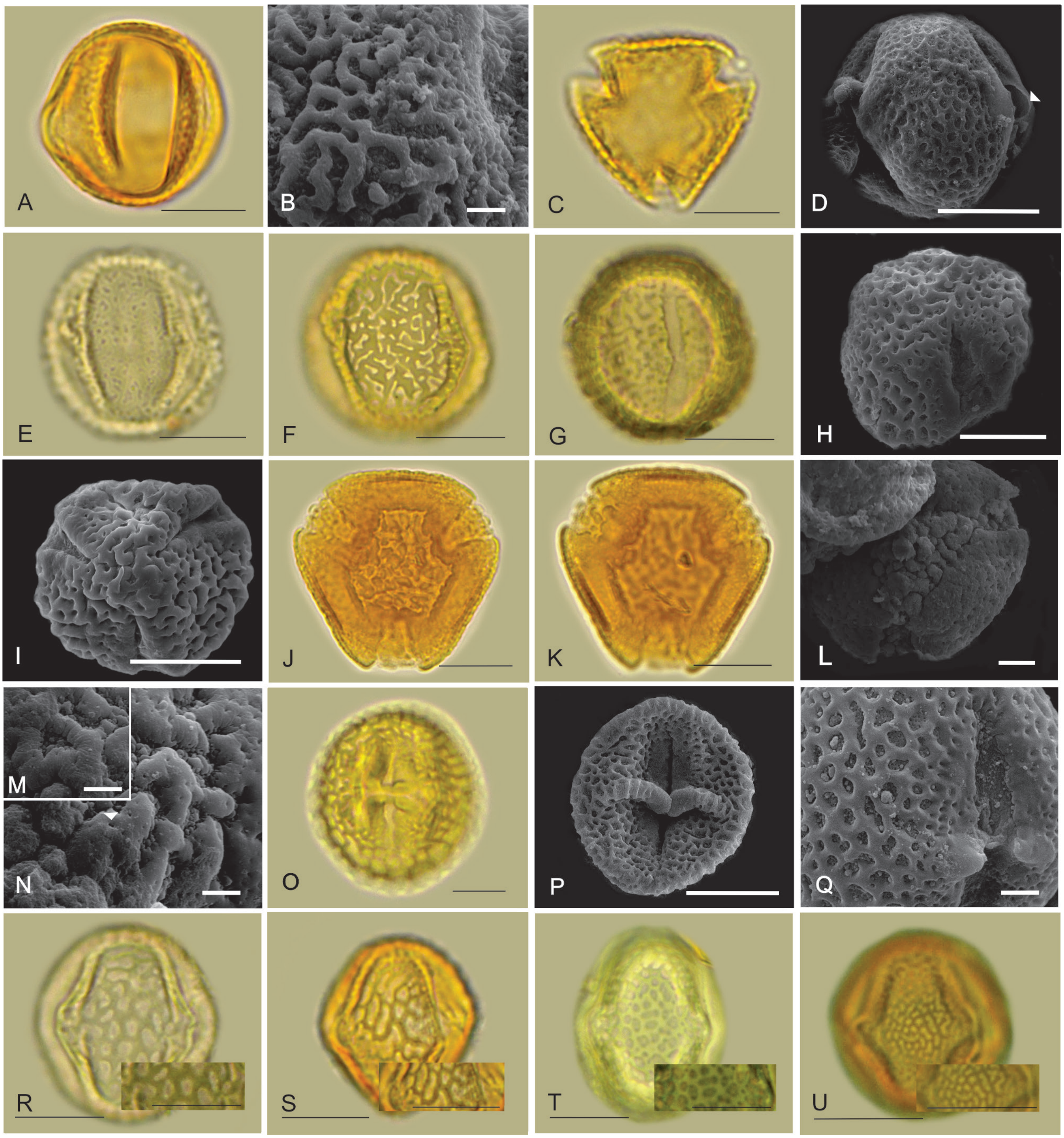

Figure 4. Pollen grains of *Lackeya* Fortunato, L.P. Queiroz & G.P. Lewis, *Nanogalactia* L.P. Queiroz, and *Rhodopis* Urb. (Leguminosae). **A - D.** *Lackeya*: **A - B.** *L. multiflora*, **A.** Equatorial view, **B.** Surface (SEM); **C - D.** *L. viridiflora*, **C.** Polar view, **D.** Equatorial view, endoaperture detail (SEM). **E - I.** *Nanogalactia*: **E - H.** *N. heterophylla*, **E - F.** Equatorial view, exine detail (LO) **G.** Equatorial view, see aperture, **H.** Equatorial view (SEM) **I.** *N. pretiosa*, Polar view (SEM). **J - N.** *Rhodopis volubilis*, **J.** Polar view (LO); **K.** Polar view; **L.** Polar view (SEM); **M-N.** Details of the surface (SEM), **M.** plica, **N.** perforation. **O - P.** Colpus constriction: **O.** *Ce. eriosematoides*, **P.** *G. glaucescens*, **Q.** *G. striata*. **R - U.** Pollen grains, and detail of the reticulation: **R.** *Galactia jussiaeana*; **S.** *Ce. heringeri*; **T.** *Be. crassifolia*; **U.** *Co. stenophylla*. Scales: 10 µm (A, C - L, O, P, R - U); 4 µm (B, N, P, Q); 1 µm (M).

Rhodopis Urb. (Fig. 4J-N)

Analyzed species: *R. volubilis* (Willd.) L.P. Queiroz

Pollen grains are in large size monads. In this species, pollen grains are disposed mainly in polar view (Fig. 4J, K). Further, pollens were 3-aperturate, angulaperturate, parasyncolpate, with triangular amb having straight sides. Apertural membrane with granules of different sizes (Fig. 4L). A microreticulate exine, and areolate apocolpium with an irregular murus were found (Fig. 4J, K). Under SEM, microreticulate exine with the murus sparsely perforated was observed. Apocolpium areolate with the murus plicate laterally and mesocolpium perforate (Fig. 4L, M, N). The sexine was thicker than the nexine (Table 2).

The quantitative data of measurements of the pollen grains are shown in table 1.

*Pollen key of **Galactia** P. Browne and related genera*

1. Pollen grains in medium size, 3-colporate 2

1'. Pollen grains in large size, parasyncolpate .... *Rhodopis*

2. Pollen grains isopolar 3

2'. Pollen grains heteropolar .... *Cerradicola* (*Ce. elliptica*; *Ce. decumbens*, *Ce. heringri* and *Ce. longifolia*) and *Lackeya* (*L. viridiflora*)

3. Aperture with fastigium .... *Caetangil*

3'. Aperture without fastigium 4

4. Pollen grains with a reticulate exine and thin murus (1.0–1.9 µm) 5

4'. Pollen grains with a reticulate exine and very wide murus (1.3–2.38 µm) .... *Nanogalactia*

5. Pollen grains with broad lumina diameter (ranging from 2.6–7.1 µm) 6

5'. Pollen grains with small lumina, not exceeding 1.8–2.5 µm diameter .... *Collaea*

6. Psilate apertural membrane (under SEM) 7

6'. Granulate apertural membrane (under SEM) .... *Galactia* (*G. remansoana* and *G. striata*) and *Cerradicola* (*Ce. grewiifolia* and *Ce. decumbens*)

7. Bireticulate exine with perforate muri (under SEM) .... *Galactia* (*G. galucescens*)

7'. Bireticulate exine with no perforations on muri (under SEM) 8

8. Exine with an incomplete reticulum .... *Galactia* (*G. jussiaeana*; *G. heringeri*), *Cerradicola* (*Ce. grewiifolia*), and *Lackeya* (*L. multiflora*)

8'. Exine with a complete reticulum .... *Galactia* (other species), *Lackeya* (*L. viridiflora*), *Betencourtia* and *Cerradicola* (other species)

Principal Component Analysis (PCA)

In the PCA, the first three components explained 81% of the total variations. The first component explained 43.97%, and it was represented by the polar axis in the equatorial view. Furthermore, the second component explained 22.67% of the analysis, showing the equatorial diameter in the equatorial view as the principal valor. Finally, the third component explained 14.77%, being represented by the equatorial diameter in the polar view (Table 3).

Table 3. Cumulative variance and eigenvectors of principal component analysis (PCA) carried out using palynological variables of *Galactia* P. Browne species and related genera.

PC	Eigenvalue	% variance
1	2.52008	43.97
2	1.29972	22.677
3	0.846495	14.77
4	0.559454	9.7613
5	0.485553	8.4719
6	0.0200374	0.34961

According to the biplot, *Rhodopis volubilis* showed the highest values related to axis number three (equatorial diameter in polar view), contributing to the differentiation of this species and consequently of its genus. On the other hand, the equatorial diameter in the equatorial view and lumina diameter were highly important in the segregation of *Ce. diversifolia* and *Ce. grewiifolia*. Furthermore, *Co. stenophylla* showed negative values associated with all axes, followed by *G. remansoana*, *G. striata*, and *G. latisiliqua*. The polar axis in equatorial view and P/E ratio had the highest weight for the segregation of *Ce. douradensis* and *N. pretiosa*. All the remaining species showed negative and positive components values, which difficult their discrimination (Figure 5).

Discussion

Galactia, *Cerradicola*, and *Betencourtia* were the genera with the largest number of analyzed species. These genera shared pollen traits that were like each other; thus, pollen grains showed the same size, polar area index, and exine ornamentation (medium size, small PAI-Polar Area Index, and heterobrochate reticulate exine, respectively). Nonetheless, even while exhibiting similar traits, it was possible to identify differences between them. In *Betencourtia*, the most evident pollen traits were pollen grains with sexine thicker than nexine in all species analyzed, a reticulate exine with lumina not exceeding 4.4 µm diameter (*Be. crassifolia*), and murus not exceeding 1.45 µm width (*Be. neessi*). On the other hand, pollen grains of *Cerradicola* showed the largest lumina diameter value (7.1 µm in *Ce. grewiifolia*) compared to the other analyzed species. In *Galactia*, the largest lumen diameter registered was 5.1 µm, and murus width did not exceed 1.9 µm (*G. jussiaeana*).

Most pollen traits reported for these three genera, such as size, variation in the shape of pollen grains, exine ornamentation, and lumina diameter range corroborate the research of Kavanagh & Ferguson (1981). Following these authors, the pollen type associated with these species (Type B(ii) = *Galactia*) was the trait that corresponded, in several ways, to the typical pollen type of Papilionoideae.

Pollen data registered for *Be. martii* corroborate the results reported by Da Luz *et al.* (2013) regarding size, polarity, type and number of apertures, and exine ornamentation. Nevertheless, the shape and amb were divergent because circular amb and subprolate shape were observed for the pollen grains analyzed in this study, in contrast to the triangular amb and oblate shape reported by Da Luz *et al.* (2013) for *Be. martii* pollen grains. The shape heteromorphism in pollen grains of the genus in which this species was previously classified (*Galactia*) has already been reported by Melhem (1971) and Silvestre-Capelato (1993).

Moreti *et al.* (2007a; b) described the pollen morphology of two *Galactia* species: *G. glaucescens* and *G. striata*. Their results differed from ours in some aspects, such as the exine ornamentation of these species.

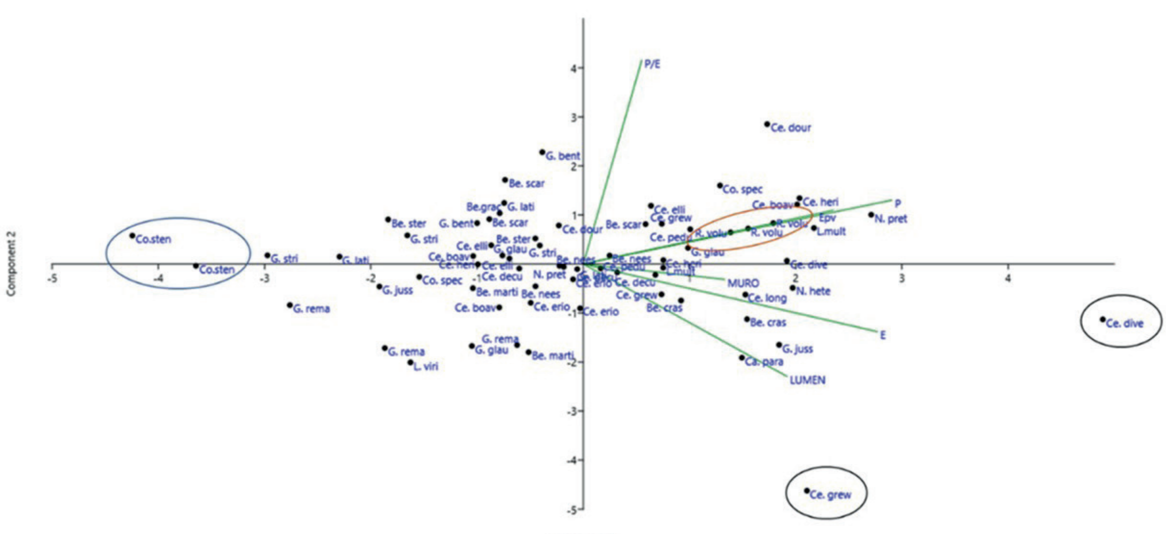

Figure 5. Principal component analysis biplot performed with the metric values of the variables of the *Galactia* species and related genera (Papilionoideae, Leguminosae); P = Polar axis in equatorial view; E = Equatorial diameter in equatorial view; Epv = Equatorial diameter in polar view; P/E= Polar axis/equatorial diameter ratio; Lumen; Murus. G. bent= *G. benthamiana*; G. glau= *G. glaucescens*; G. juss= *G. jussiaeana*; G. lati= *G. latisiliqua*; G. rema= *G. remansoana*; G. stri= *G. striata*; Be. cras= *Be. crassifolia*; Be. grac= *Be. gracillima*; Be. mart= *Be. martii*; Be. nees= *Be. neesii*; Be. scar; *Be. scarlatina*; Be. ster= *Be. stereophylla*; Ca. para= *Ca. paraguariensis*; Ce. boav= *Ce. boavista*; Ce. decum= *Ce. decumbens*; Ce. dive= *Ce. diversifolia*; Ce. dour= *Ce. douradensis*; Ce. elli= *Ce. elliptica*; Ce. erio= *Ce. eriosematoides*; Ce. grew= *Ce. grewiifolia*; Ce. heri= *Ce. heringeri*; Ce. long= *Ce. longifolia*; Ce. pedu= *Ce. peduncularis*; Co spec= *Co. speciosa*; Co. sten= *Co. stenophylla*; L. viri= *L. virififlora*; L. mult= *L. multiflora*; N. hete= *N. heterophylla*; N. pret= *N. pretiosa*; R. volu= *R. volubilis*. Blue circle= *Co. stenophylla*; Red circle = *R. volubilis*; Black circles= *Ce. grewiifolia* e *Ce. diversifolia*.

According to these authors, the exine ornamentation in these species has a microreticulate pattern, whereas in our study it has been classified as reticulate. The limited previous studies that describe the palynological morphology of *G. striata* (Kavanagh & Ferguson 1981; Buril *et al.* 2011), have reported the exine ornamentation as reticulate, as we described here.

Heteropolar pollen grains were observed in *Ce. elliptica*, *Ce. decumbens*, *Ce. heringeri*, *Ce. longifolia*, and *L. viridiflora*. In palynological descriptions focused on the genus in which *Ce. elliptica* was previously included (*Camptosema* Hook. & Arn), Kavanagh & Ferguson (1981) and Melhem (1971) reported heteropolar pollen grains for some of its species (*Campt. coccineum* Benth., *Campt. tomentosum* Benth. and *Campt. pedicellatum* Benth.). Such statements indicated a possible heteropolarity for this genus, however, Makino (1978) and Silvestre-Capelato (1993) explained that heteropolarity is not a characteristic trait of this group. Pollen data for *Ce. decumbens*, *Ce. heringeri*, *Ce. longifolia*, and *L. viridiflora* registered isopolar pollen grains (Kavanagh & Ferguson 1981).

The species of the genera *Rhodopis* and *Lackeya* are genera whose species are not distributed in Brazil. Notably, *Rhodopis* species have pollen grains with the most distinctive traits among the genera related to *Galactia*. Pollen grains in this group are large, with a microreticulate exine with perforate muri, and its apocolpium region has a width and anastomosate murus. On the other hand, *Lackeya* species have pollen grains whose traits are similar to those found in *Galactia* (medium size, subprolate, isopolar, 3-colporate, and reticulate).

Pollen data regarding *Lackeya* reported in this study are in concordance with those reported by Kavanagh & Ferguson (1981) and Fortunato *et al.* (1996); however, our data differ from that of the latter for the polar axis and equatorial diameter values. In the pollen analysis of *Lackeya* performed by Fortunato *et al.* (1996), it was not possible to segregate *Lackeya* from *Galactia* based on pollen traits. Furthermore, these authors reported that there are intermediate palynological traits between these two genera.

Different from *Galactia* – which presents flowers with different colors and are pollinated by bees, the flowers of *Rhodopis* species are red and bird-pollinated (Judd 1984; Queiroz *et al.* 2020). The research focused on differences in wall sculpture and stratification influenced by pollination or pollinators in Papilionoideae have been previously addressed by Ferguson & Skvarla (1982) and Ferguson (1984).

Regarding *Collaea*, pollen grains exhibit a reticulate exine pattern and the smallest lumina diameter among all analyzed species (not exceeding 2.5 µm in *Co. stenophylla*). Our palynological descriptions for this group corroborate those reported by Kavanagh & Ferguson (1981) and Silvestre-Capelato (1993) in terms of the ornamentation pattern and lumen diameter and shape. According to Moreti *et al.* (2007a; b) the exine in pollen grains of *Co. speciosa* is reported as microreticulate, which is different from our study that revealed a reticulate exine. Although the results are conflicting, it is observed that pollen grains in *Collaea* have an exine with a small reticulum, once that the more extensive literature focused on this genus reported lumen with a diameter of 2-3 µm (Kavanagh & Ferguson 1981).

Caetangil is a new genus described by Queiroz *et al.* (2020) that includes two species. In this study, the pollen grains of one species, *Ca. paraguariensis,* were analyzed. This species shows a notable trait that is not seen in other pollen grains, namely, the presence of fastigium. Pollen grains of *Ca. paraguariensis* have pollen traits that are similar to those described for the typical pollen type of Papilionoideae and Diocleae tribe.

Variation in pollen colpi of all species analyzed here was frequently registered. Gupta & Gupta (1979) previously reported variations in the colpus constriction of some species belonging to Leguminosae (e.g., in the genus *Crotalaria* L.). On the other hand, Soares *et al.* (2020) considered the absence or presence of constriction in pollen grains, along with other palynological traits, to differentiate two legume species from Cerrado. In this study, these constrictions were important for the determination of constricted colpus frequency and to determine how these constrictions prevented the viewing of the endoapertures.

Principal components analysis

Through PCA, it was possible to differentiate *Rhodopis* from the remaining genera considering the equatorial diameter in polar view values. Our results corroborate the segregation of this group considering its qualitative descriptions (microreticulate exine and areoles at the apocolpium). In *Ce. diversifolia* and *Ce. grewiifolia*, the data associated with lumen diameter was highlighted. The *Cerradicola* species analyzed in this study were separated in an artificial palynological key by having the highest lumen diameter, associated with other palynological traits. *Co. stenophylla* was the only species that presented small size pollen grains, corroborating the negative values regarding the polar axis and equatorial diameter in the equatorial view. Although, *G. remansoana*, *G. striata*, and *G. latisiliqua* also showed negative values in these axes, these species have medium size pollen grains. PCA contributed to the separation of *Rhodopis*, as well as offered data about values of importance for the differentiation of one *Collaea* and two *Cerradicola* species. The remaining axis values were similar between all species.

Brief taxonomic approach

Phylogenetic data provided by Queiroz *et al.* (2015), indicated *Galactia* as a polyphyletic genus, composed of species of other genera. However, Queiroz *et al.* (2020) recently proposed a new phylogeny that indicated *Galactia* as a more homogeneous genus by providing discriminative characters that offered a better resolution for this group.

In addition, these authors highlighted the genera related to *Galactia* and those comparatives. The palynology in these groups has already revealed species belonging to the same genus that have different pollen types (Kavanagh & Ferguson 1981). Thus, species of *Galactia* and other genera may be clustered in their pollen subtype having similar palynology or may be clustered in different pollen subtypes.

Although the macromorphology of *Galactia* is more homogeneous, palynological characteristics are common between *Galactia*, *Betencourtia*, *Cerradicola*, *Lackeya*, and *Collaea*. Morphological pollen traits of species belonging to these genera resemble the more comprehensive pollen type of *Galactia* described by Kavanagh & Ferguson (1981), who reported pollen grains with a thin exine and reticulate tectum. Nevertheless, it is important to point out that some species of these genera were clustered in different pollen subtypes since palynological differences justified their segregation. The artificial palynological key elaborated here gathered a set of pollen traits that were more evident and remarkable for each genus or species.

This division with the pollen key was carried out using, mainly, the values of the diameters of the lumen and width of the murus, which were significant to determine the highest and lowest values between the species and their respective genera. Thus, it was possible to make a junction with the other observed pollen characteristics to obtain a separation (when possible). This association proved to be an important value in distinguishing the groups studied.

In *Galactia*, palynological traits were common between species of this group, except for *G. glaucescens*. Pollen grains in this species presented spaced perforations on the suprareticulum murus, an exclusive trait that was not found in any other *Galactia* species or most parts of the related genera. Murus perforations were also reported in *Rhodopis* in this study. Nevertheless, this genus presented its characteristic pollen morphology due to the presence of microreticulate exine and areolate apocolpium, being different from the other complementary traits present in *G. glaucescens*. Such palynological evidence reinforces the taxonomic/phylogenetic uncertainties of *G. glaucescens* previously reported by Queiroz *et al.* (2020).

In *Nanogalactia*, a reticulum with a very large width and anastomosate murus were observed. This set of traits regarding the exine pollen grains presented in *Nanogalactia* were not observed in the other genera analyzed here. In previous studies, *N. pretiosa* and *N. heterophylla* were placed within *Galactia* (Burkart 1971; Sede *et al.* 2008), and macromorphological data already indicated similarities between these two species (Ceolin 2011). This group is currently taxonomically discriminated by a set of macromorphological characters, namely, the inflorescence and its herbaceous habit (Queiroz *et al.* 2020), and the palynological morphology, indicated here, was in concordance with that division.

In general, *Galactia* and most parts of the related genera exhibited low pollen morphology variation, except *Rhodopis* and *Nanogalactia* that showed more distinctive palynology.

Galactia and its related genera presented some different palynological characteristics, however, *Lackeya* was similar to *Galactia*. On the other hand, *Rhodopis* has discriminative palynological traits when compared to *Galactia* and the remaining genera such as parasyncolpate pollen grains with microreticulate exine.

Palynological data corroborate the segregation of the *Nanogalactia*. Its species were grouped within *Galactia*; nonetheless, phylogenetic studies evidenced a different position in agreement with its pollen morphology, since pollen grains from this species were different when compared to pollen grains of *Galactia* and related genera.

Betencourtia, *Cerradicola*, *Collaea*, and *Caetangil* presented palynological traits similar to those of *Galactia*; however, their pollen morphology varied in some features. Such differences combined with macromorphological data can be useful in the taxonomy of these groups.

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