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Original Paper
Pollen morphology and its systematic value to southern South American species of *Lepidaploa* (Vernonieae: Asteraceae)

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Abstract
Palynological data have been used in Vernonieae for generic and specific delimitations, particularly in the Lepidaploinae subtribe. For this reason, pollen studies in the genus *Lepidaploa* are important to solve taxonomic conflicts. We characterized 23 species of *Lepidaploa* searching for morphological differences among themselves. We then compared the data obtained with other genera of the Lepidaploinae. The results show that the species have pollen type "C" (with polar lacuna) or "G" (without polar lacuna), oblate-spheroidal, subprolate or prolate-spheroidal, 3-colporate and equinolophate. The pollen types and shape of pollen grain are taxonomically useful. Pollen morphology is useful to distinguish species and genera of Lepidaploinae. Together with macromorphological data it is possible to delimit *Lepidaploa* and the species studied here.
Key words: Compositae, Lepidaploinae, palynology, *Vernonia*.

Resumo
Dados palinológicos são usados em Vernonieae para a delimitação de gênero e espécies, principalmente na subtribo Lepidaploinae. Por este motivo, estudos palinológicos no gênero *Lepidaploa* são importantes para solucionar conflitos taxonômicos a nível genérico e específico. Os grãos de pólen de 23 espécies de *Lepidaploa* foram caracterizados com o objetivo de buscar diferenças morfológicas entre eles. Além disso, comparamos o pólen encontrado nestas espécies com o grão de pólen de outros gêneros de Lepidaploinae. Os resultados demonstraram que as espécies apresentam pólen do tipo "C" (com lacuna polar) ou "G" (sem lacuna polar), são oblato-esferoidal, subprolato o prolato-esferoidal, 3-colporado e equinolofado. O tipo de grão de pólen e sua forma foram taxonômicamente úteis. Ambos os caracteres foram utilizados para distinguir gêneros da subtribo e as espécies de *Lepidaploa*. Juntamente com a macromorfologia os dados dos grãos de pólen permitem delimitar os gêneros e espécies estudados.
Palavras-chave: Compositae, Lepidaploinae, palinologia, *Vernonia*.

Introduction

The palynological studies are a very important tool in taxonomy allowing the differentiation of the taxonomically complex groups through the shape of pollen grains (Fazal *et al.* 2013). The size of pollen grains, types of aperture and structure of the exine have contributed with important differences in the classification of families, tribes, genera and species (Fazal *et al.* 2013).

Throughout the decades several palynological studies have been used in the Asteraceae family (Compositae) due to the taxonomic importance that pollen has for the taxa of this family (Stix 1960; Besold 1971; Kingham 1976; Skvarla *et al.* 1977;

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Keeley & Jones 1979; Blackmore 1982; Robinson & Marticorena 1986; Bremer 1994). Despite the taxonomic importance of pollen grains for Asteraceae as a whole, the type of pollen present is more important in certain tribes than in others. For example, pollen grains of the Eupatorieae tribe are very uniform and do not provide palynological data for classification at the generic level (Payne & Skvarla 1970; Sullivan 1975). In contrast, the palynological data found in the Vernonieae tribe have been successfully used in the infratribal classification (Keeley & Robinson 2009).

Currently, the pollen classification most used in Vernonieae was based on the studies of Keeley & Jones (1977, 1979) and Robinson (1990, 1992, 1999) being that in these studies, 10 pollen types (A-H, J and *Aynia-type*) were recognized for the Vernonieae tribe. The different types of pollen grain of Vernonieae and their correlation with morphological and chromosomal characters provide important taxonomic data, especially for the subtribe Lepidaploinae which includes 12 genera and about 320 species, which occur mainly in the Western Hemisphere (Keeley & Robinson 2009). Since these genera were previously part of *Vernonia* sensu lato, they are morphologically closely related, and palynology is necessary for their distinctions.

The genus *Lepidaploa* Cass. (Cass.) belongs to the subtribe Lepidaploinae and it was reestablished by Robinson (1990) from *Vernonia* s.l. using the type of indumentum, inflorescence, the number of phyllaries over number of flowers, and lophate pollen grains of the types "C", "D" and "G". The pollen types found so far in few species of *Lepidaploa* can differentiate it from most other genera found in the subtribe Lepidaploinae (Robinson 1999).

Other authors have studied the pollen types of *Lepidaploa* (Dematteis & Pire 2008, Mendonça & Gonçalves-Esteves 2000; Mendonça *et al.* 2007a). However, many species of the genus have not been studied and the pollen type of more than half of these species is unknown. In addition, in recent years several genera of the subtribe Lepidaploinae was palynologically studied (Robinson 1990, 1992, 1999; Carrijo *et al.* 2005; Dematteis 2005; Mendonça *et al.* 2007a, b; Bunwong & Chantaranothai 2008; Angulo & Dematteis 2010; Via do Pico & Dematteis 2013), and there is no recent study that presents the relationship of the *Lepidaploa* pollen types with other genera of this subtribe.

Thus, we evaluate the taxonomic value of the pollen morphology of the *Lepidaploa* species occurring in Southern South America, allowing us to compare it to other members of Lepidaploinae.

Material and Methods

We analyzed 23 species of *Lepidaploa* from Southern South America (Argentina, Bolivia, Brazil and Paraguay). Pollen preparations were made from anthers of floral buds in pre-anthesis obtained from herbarium specimens from the Instituto de Botánica del Nordeste (CTES). The source and herbarium data of the specimens analyzed are detailed in Table 1.

The pollen grains were acetolyzed according to the methodology of Erdtman (1960). For light microscopy (LM), pollen grains were mounted on glass slides using glycerine jelly and subsequently examined with a Zeiss Axioplan light microscope. Permanent preparations were deposited at the Palynological Laboratory of the Universidad Nacional del Nordeste (PAL-CTES). The polar axis (P), the equatorial diameter (E), the ratio between polar axis and equatorial diameter (P/E), the exine thickness, the pore diameter, the spine length, and the diameter of the polar lacuna were measurement in at least 30 grains per sample.

For studies with the scanning electron microscope (SEM), acetolyzed pollen grains were first washed in alcohol 96% and absolute alcohol (100%), then plated with gold-palladium and examined with a JEOL 5801 LV microscope.

The terminology used to describe the pollen morphology was that suggested by Erdtman (1966), Keeley & Jones (1977, 1979), Robinson (1990, 1992, 1999), Punt *et al.* (2007) and Hesse *et al.* (2009). For differences between pollen types found in Vernonieae, see Table 2.

To show the palynological patterns between species, the qualitative characters were coded in binary (shape of pollen grain = 1: prolate-spheroidal 2: oblate-spheroidal and type of pollen grain = 1: type C 2: type G), and for the quantitative characters (polar axis and equatorial axis) the averages were considered. The values of the exine thickness, spine length, diameter of polar lacuna and pore were not considered because they showed little variability among the analyzed specimens. A UPGMA cluster analysis (Unweighted Pair Group Method with Arithmetic Mean) was applied, based on the Gower distance index. The InfoStat program version 2018 was used for this analysis (Di Rienzo *et al.* 2018).

Table 1 – Details of the data source and herbarium specimens of *Lepidaploa* species from Southern South America analyzed.

Species	Location and Voucher specimens
Lepidaploa amambaia H. Rob.	Paraguay. Amambay, 25 km de N de J. P. Caballero, camino a Colonia Estrella. *M. Dematteis & A. Schinini 867* (CTES).
	Paraguay. Concepción, 25 km W de San Carlos del Apa, Estancia Arrecifes. *M. Dematteis et al. 3336* (CTES).
Lepidaploa argyrotricha (Sch.Bip. *ex* Baker) H. Rob.	Brasil. Paraná, Município de Bocaiúva do Sul. *E. Barbosa et al. 1012* (CTES).
Lepidaploa bakerana (Britton) H. Rob.	Bolivia. Departamento La Paz, Provincia Muñecas, antes de Marumpampa. *A. Fuentes et al. 7042* (CTES).
	Bolivia. Departamento La Paz, Provincia Nor Yungas, NNW de Coroico, Suapi 3,5 km, hacia el fín del camino. *St. G. Beck 8317* (CTES).
Lepidaploa balansae (Hieron.) H. Rob.	Argentina. Misiones, Departamento San Ignacio, acceso hacia Parque Provincial Teyú Cuaré. *H.A. Keller 8792* (CTES).
	Paraguay. Departamento Concepción, 34 km de Concepción, Ruta 5. *A. Krapovickas & C.L. Cristóbal 45131* (CTES).
Lepidaploa beckii H. Rob.	Bolivia. Departamento de La Paz, Província Murillo, Valle de Zongo, 1650 m, borde del camino. *St. G. Beck 4678* (CTES).
	Bolivia. Departamento de La Paz, Provincia Nor Yungas, cerca de Coroico. *St. G. Beck 14931* (CTES).
Lepidaploa buchtienii (Gleason) H. Rob.	Bolivia. Departamento de La Paz, Provincia Larecaja, Consata unos 34 km hacia Mapiri 15°18'S, 68°21'W, 700 msnm. *St. G. Beck 29463* (CTES).
Lepidaploa canescens (Kunth) H. Rob.	Bolivia. Departamento de La Paz, Sud Yuangas, Chulumani 1700 msnm. *St. G. Beck 12108* (CTES).
Lepidaploa chamissonis (Less.) H. Rob.	Argentina. Chaco, San Lorenzo. *A.G. Schinini* (CTES 18119).
	Paraguay. P. N. Ybycuí, *G. Schemeda 55.* (CTES).
	Brazil. Santa Catarina, Praia Laranjeiras. *A. Krapovickas & C.L. Cristóbal 38426* (CTES).
Lepidaploa cordiifolia (Kunth) H. Rob.	Bolivia. Departamento La Paz, Provincia João Bautista Saavedra, Apolo, Yurilaya, 9 km subiendo hacia Camaba. 15°11'S, 69°35'W 1300 msnm. *St. G. Beck 29172* (CTES).
Lepidaploa costata (Rusby) H. Rob.	Bolivia. Departamento La Paz, Provincia Larecaja, Consata 38,6 km hacia Mapiri 15°17'S, 68°23'W, 740 msnm. *Beck St. G. 29455* (CTES).
	Bolivia. Departamento de La Paz, Provincia Larecaja, Villaque, 2 km hacia Poroma, Vale del rio Sapucuni, 600 msnm. *St. G. Beck 28282* (CTES).
	Bolivia. Departamento de La Paz Larecajaca, 25-30 km N de Caravanito. *J.R.I. Wood & D. Wasshausen 13906* (CTES).
Lepidaploa deflexa (Rusby) H. Rob.	Bolivia. Departamento La Paz, Provincia J. Bautista Saavedra, Apolo, Yurilaya, 9 km subiendo hacia Camaba 15°11'S, 68°35'W 1300 msnm. *St. G. Beck 29174* (CTES).
	Bolivia. Departamento de La Paz, Provincia Sud Yungas, Huancané, 12 km de San Isidro, 16º22'S, 67º32'W. *St. G. Beck 24903* (CTES).
	Bolivia. Departamento La Paz, Provincia Sud Yungas, Centro Lavi, arriba de Irupana, 2300 msnm. *St. G. Beck 22758* (CTES).
Lepidaploa eriolepis (Gardner) H. Rob.	Brasil. Paraná, Município Antonina, Usina Hidrelétrica Parigot de Souza, Cota 800. *J. M. Silva & G. Hatschbach 5007* (CTES).
	Brasil. Paraná, Cerro Azul, Mato Preto. *G. Hatschbach & F.J. Zelma 49535* (MBM).

Species	Location and Voucher specimens
	Brasil. Santa Catarina, Florianópolis, Morro Costa da Lagoa. *D.B. Falkenberg 4364* (MBM).
Lepidaploa fournetii (H. Rob. & B. Kahn) H. Rob.	Bolivia. Departamento La Paz, Provincia Nor Yungas, Chuspipata 6 km, hacia Caroico 2640 m. *St. G. Beck. 13578* (CTES).
	Bolivia. Departamento La Paz, Provincia Nor Yungas, Chuspipata 6.5 km, 2550 m. *J.C. Solomon 15657* (CTES).
Lepidaploa mapirensis (Gleason) H. Rob.	Bolivia. Departamento La Paz, Provincia Nor Yungas, 0.9 km W de Chuspipata, 3100 m 16º18'S, 67°49'W. *J.C. Salomon 9656* (CTES).
	Bolivia. Departamento La Paz. Provincia Nor Yungas, 1.2 km E de Cotapata entre la ruta Unduavi y Chuspipata, 16°17'S, 67°50'W 3100 m. *J.C. Solomon 15318* (CTES).
Lepidaploa myriocephala (DC.) H. Rob.	Bolivia. Departamento de La Paz, Provincia Larecaja, Camino entre Guanay y Mapiri, 11 km N La Aguada 15°28'18"S, 67°58'18"W. *M. Dematteis 1221* (CTES).
	Bolivia. Departamento de La Paz, Provincia Franz Tamayo, Madidi, Peluchuco-Apolo, Coranara Parque Nacional Madidi. 14º46'21"S, 68º59'09"W. *A. Fuentes et al. 13068* (CTES).
Lepidaploa novarae (Cabrera) A. J. Vega & Dematt.	Argentina. Salta, Departamento Santa Victoria, Parque San Martín, entrando por la pista de aterrrizaje de Toldos, 22°18'S, 64°40'W. *O. Ahumada & J. Aguero 8365* (CTES).
	Argentina. Salta. Departamento Santa Victoria, Parque San Martín, camino de Toldos a Lipeos, a 13 km de Toldos. *Vervoorst 4581* (CTES).
Lepidaploa psilostachya (DC.) H. Rob.	Argentina. Misiones. San Ignacio, Teyú Cuaré 27°16'46"S, 55°37'37"W 147 m. *M. Dematteis et al. 4139* (CTES).
	Brasil. Santa Catarina, Tibagi, Guartelá. *L.P. Deble & A.S. de O. Deble 12020* (CTES).
Lepidaploa pseudomuricata H. Rob.	Brasil. Santa Catarina, Município Urubici, Águas Brancas. *G. Hatschbach et al. 78921* (CTES, MBM).
	Brasil. Paraná, Município de São Mateus do Sul, Usina de Xisto da Petrobrás. *O.S. Ribas et al. 6518* (CTES, MBM).
Lepidaploa remotiflora (Rich.) H. Rob.	Argentina. Corrientes, Ituzaingó, Costa del Río Paraná. *A. Krapovickas & C.L. Cristóbal 29153* (CTES).
	Bolívia. Santa Cruz, Valle Grande, 5 km de El Trigal. 18°25'56"S, 64°7'17"W 1982 m.s.n.m. *M. Dematteis 3673* (CTES).
Lepidaploa salzmannii (DC.) H. Rob.	Brasil. Paraná: Tomazina, Guaviroval, 02.IX.1998, *G. Hatschbach 68293* (CTES).
	Bolivia. Tarija, O'Connor, 8,3 km E de Entre Rios, camino a Villamontes 21°27'55"S, 64°8'57"W. 1098 msmn. *M. Dematteis 3438* (CTES).
Lepidaploa setososquamosa (Hieron.) M. B. Angulo & Dematt.	Argentina. Salta, Departamento Rosario de Lerma, Dique Las Lomitas, Ribera Oeste, 1400 m.s.m. *L.J. Novara 10877* (CTES).
	Bolivia. Santa Cruz. Chiquitos, 15 km E de Ipias. 17°59'43"S, 60°15'12"W, 402 m.s.m. *V.S. Neffa et al. 1305* (CTES).
	Paraguay. Boquerón, Parque Valle Natural, 25 km S de Filadelfia. *A. Krapovickas & C.L. Cristóbal 44197* (CTES).
Lepidaploa sordidopapposa (Hieron.) H. Rob.	Bolivia. Departamento de La Paz, Provincia Nor Yungas, entre Chuspipata y San Rafael, 16°16'S, 67°50'W, 280 msnm. *St. G. Beck 22672* (CTES).
	Bolivia. Departamento de La Paz, Provincia Nor Yungas, de la cumbre bajando 30 km hacia Chuspipata, pasando Cotapata 2980 msnm. *St. G. Beck 17717* (CTES).
Lepidaploa tarijensis (Griseb.) H. Rob.	Argentina. Salta, Departamento Gral. S. Martín, Pocitos. *A. Krapovickas et al. 19425* (CTES).

Table 2 – Types of pollen according to Keeley & Jones (1977, 1979), Robinson (1990, 1992, 1999).

Pollen type	Ornamentation	Colpus	Equatorial lacuna	Number of polar lacuna	Tectum microperforate	Spines or spinules	Bacular structure	Lacunae on the poles alignment
A	echinate to sublophate	tricolporate	absent	absent	present	present	present	×
B	echinolophate	tricolporate	present	absent	present	present	present	with colpus
C	echinolophate	tricolporate	absent	present	present	present	present	×
D	echinolophate	triporate	absent	absent	present	present	present	with colpus
E	lophate or subechinate	triporate	absent	absent	absent	usually absent	usually absent	×
F	echinolophate to lophate	triporate	absent	absent	present	present	present	×
G	echinolophate	tricolporate	absent	absent	present	present	present	with colpus
H	echinolophate	triporate	absent	absent	present	present	absent	×
J	lophate	triporate	absent	absent	present, but weak perforated	present	present, but scanty	×
Aynia-type	echinolophate	tricolporate	absent	absent	present	present	present	with intercolpus

Results

The analyzed measurements of pollen grain of the *Lepidaploa* species are listed in Table 3.

General pollen morphology (Figs. 1-6)

The pollen grains are radially symmetric, isopolar, small to medium, oblate-spheroidal, subprolate or prolate-spheroidal (P/E = 0.96–1.1), 3-colporate and equinolophate (Figs. 1-6). The colpi are long and visible in polar view, with the lophae separating or not the polar lacuna from the abporal lacunae (Fig. 1c,f,i,l,o; Fig. 2c,f,i,l,o; Fig. 3c,f,i,l,o; Fig. 4b,d,g; Fig. 5d,g,l,o; Fig. 6a,d,f,g,l,o). The polar axis ranged between 13.6 and 50.43 µm and the equatorial diameter between 14.96 and 50.56 µm. The thickness of the exine, excluding the spines, varied between 1.36 and 6.8 µm. The tectum is discontinuous and formed by lacunae surrounded by lophae. The number of lacunae may be 27, 29 or 30. The diameter of the poral lacuna oscillated between 2.72 and 13.8 µm and its shape varied between more or less regular and irregular. The tectum has a microperforate surface with spines (Figs. 1-6). The spines oscillated between 1.36 and 5.44 µm length and they have a linear distribution along the walls of the lophae. The diameter of the endoaperture (pore) ranged between 2.04 and 16.32 µm. Observations with SEM showed an exine formed by columella joined at the base by a transversal structure that separates the tectum from the floor (Figs. 5h; 6e).

The 23 species studied had Type “C” or “G” pollen, according to studies performed by Keeley & Jones (1977, 1979) and Robinson (1990, 1999). In addition, variations were found in pollen grains “G”, which will be described below.

Pollen type “C” (*L. beckii*, *L. buchtienii*, *L. canescens*, *L. chamissonis*, *L. costata*, *L. cordiifolia*, *L. deflexa*, *L. pseudomuricata* and *L. salzmannii*) (Figs. 1; 4): small to medium pollen grains, oblate-spheroidal or prolate-spheroidal (P/E = 0.97–1.07 µm), 3-colporate, equinolophate. Pollen size: P = 15.2–31.28 µm, E = 14.96–31,28 µm. Colpus with or without wall separating the poral lacunae from abporal lacunae. Exine thickness, excluding the spines, between 1.36 and 6.8 µm. Tectum discontinuous with lacunae

Table 3 – Morphological characteristics of *Lepidaploa* pollen grains measured in µm (microns). (P = polar axis; E = equatorial diameter; P/E = ratio P and E; * = pollen type "G" atypical).

Pollen type	Number of lacunae	Species	P	E	P/E	Shape P/E	Exine thickness	Spine length	Poral lacuna diameter	Pore diameter
C	29	*Lepidaploa beckii*	20.40 (22.08) 25.84	20.4 (22.57) 27.2	0.98	oblate-spheroidal	2.74 (3.4) 4.08	1.38 (2.85) 4.08	5.44 (7.21) 9.52	4.08 (8.16) 9.03
C	29	*Lepidaploa buchtienii*	15.20 (22.39) 26.10	17.34 (23.07) 25.2	0.97	oblate-spheroidal	2.83 (3.91) 5.47	1.36 (2.99) 4.05	5.42 (7.7) 8.91	2.04 (5. 46) 9.52
C	29	*Lepidaploa canescens*	20.40 (22.4) 22.12	20.4 (21. 85) 24.48	1.02	prolate-spheroidal	1.36 (3.58) 6.8	1.36 (1.58) 2.72	6.8 (7.93) 9.52	4.08 (5.71) 6.8
C	29	*Lepidaploa chamissonis*	19.40 (21.31) 25.84	19.4 (21.31) 25.48	1	prolate-spheroidal	2.72 (3.44) 6.8	1.36 (2.49) 4.08	5.44 (6.93) 9.52	4.08 (5.71) 8.16
C	29	*Lepidaploa costata*	20.40 (22.03) 27.20	19.04 (21.30) 27.2	1.03	prolate-spheroidal	2.72 (3.58) 5.44	1.36 (2.13) 4.08	2.72 (7.25) 9.52	2.72 (5.21) 6.80
C	29	*Lepidaploa deflexa*	16.32 (20.04) 23.12	14.96 (18.54) 23.12	1.08	prolate-spheroidal	2.72 (3.4) 5.44	1.36 (1.56) 2.72	2.72 (6.46) 8.16	2.72 (5.8) 6.80
C	29	*Lepidaploa pseudomuricata*	24.48 (27.51) 31. 28	20.40 (26. 56) 31.28	1.03	prolate-spheroidal	4.08 (4.83) 5.44	1.36 (2.51) 2.72	6.80 (8.93) 13.60	4.08 (5.98) 8.16
C	29	*Lepidaploa salzmannii*	21.76 (25.97) 28.56	21.76 (24.16) 28. 56	1.07	prolate-spheroidal	1.36 (3.49) 4.08	1.36 (1.43) 2.72	6.80 (8.52) 10.88	4.08 (8.16) 9.52
G*	27-30	*Lepidaploa amambaia*	27.2 (31.82) 40.8	24.48 (29.60) 38.08	1.07	oblate-spheroidal	2.72 (4.26) 6.8	1.36 (2.58) 5.44	5.44 (7.7) 10.88	5.44 (7.57) 9.52
G	27	*Lepidaploa argyrotricha*	24.48 (27.42) 32.64	20.4 (25.02) 29.92	1.09	prolate-spheroidal	2.72 (4.51) 6.8	1.36 (2.74) 4.08	5.44 (7.7) 10.88	4.08 (6.08) 6.80
G	27	*Lepidaploa bakerana*	16.32 (17.81) 20.40	16.32 (18.36) 21.76	0.97	oblate-spheroidal	2.04 (3.15) 4.08	1.36 (2.1) 2.72	4.08 (5.3) 6.8	4.08 (5.39) 6.80
G	27	*Lepidaploa balansae*	13.60 (22.39) 27.20	19.04 (23.07) 27.2	0.97	oblate-spheroidal	2.72 (3.72) 5.44	1.36 (2.88) 4.76	5.44 (7.7) 10.88	2.04 (5.46) 9.52
G	27	*Lepidaploa cordiifolia*	19.04 (20.74) 25.84	16.32 (21.21) 24.48	0.98	oblate-spheroidal	2.72 (3.65) 5.44	1.36 (3.26) 4.08	4.08 (5.94) 8.16	2.72 (4.42) 5.44

Pollen type	Number of lacunae	Species	P	E	P/E	Shape P/E	Exine thickness	Spine length	Poral lacuna diameter	Pore diameter
G	27	*Lepidaploa eriolepsis*	23.12 (26.38) 28.56	21.76 (25.57) 28.56	1.03	prolate-spheroidal	1.36 (3.09) 5.44	2.72 (3.06) 5.44	5.44 (8.4) 13.80	4.08 (6.07) 6.80
G	27	*Lepidaploa fournetii*	23.12 (26.38) 28.56	21.76 (25. 57) 28.56	1.03	prolate-spheroidal	1.36 (3.94) 5.44	2.72 (3.6) 5.44	4.55 (8.38) 13.60	4.08 (6.07) 6.80
G	27	*Lepidaploa mapirensis*	27.20 (33.23) 36. 72	25.84 (31.55) 35.36	1.05	prolate-spheroidal	2.72 (4.48) 5.44	3.4 (4.28) 5.44	6.80 (9.25) 13.60	6.80 (8.34) 10.88
G	27	*Lepidaploa myriocephala*	23.12 (27.24) 29.92	20.40 (24.71) 27.2	1.1	prolate-spheroidal	2.72 (3.72) 4.08	1.36 (2.31) 2.72	5.44 (8.01) 9.52	6.80 (7.98) 9.52
G	27	*Lepidaploa novarae*	39.78 (47.3) 50.43	42.30 (49.2) 50.56	0.96	oblate-spheroidal	4.0 (4.36) 5.4	4.0 (4.25) 5.4	8.60 (10.07) 12.20	4.08 (5.71) 6.80
G*	27-30	*Lepidaploa psilostachya*	17.68 (20.49) 23.12	17.68 (20.53) 23.12	1	prolate-spheroidal	2.72 (3.96) 5.44	1.36 (1.4) 2.04	6.80 (9.06) 12.24	5. 44 (6.53) 8.16
G*	27-29	*Lepidaploa remotiflora*	19.00 (21.26) 24.48	16.32 (20.54) 24.48	1.04	prolate-spheroidal	2.27 (3.88) 6.8	1.36 (1.41) 2.04	4.08 (9.61) 12.24	4.08 (5.76) 8.16
G	27	*Lepidaploa setososquamosa*	20.40 (24.12) 34	20.40 (23.98) 34	1.01	prolate-spheroidal	2.72 (3.69) 5.44	1.36 (1.75) 2.72	6.80 (11.2) 16.32	5.44 (6.62) 8.16
G	27	*Lepidaploa sordidopapposa*	25.84 (30.6) 38.08	20.40 (29.01) 40.80	1.05	prolate-spheroidal	2.72 (4.76) 6.8	1.36 (2.99) 5.44	6.80 (9.09) 10.88	6.8 (10.01) 16. 32
G	27	*Lepidaploa tarijensis*	23.12 (25.75) 27.20	20.40 (23.66) 27.20	1.08	prolate-spheroidal	2.72 (3.72) 5.44	1.36 (3.21) 5.44	6.80 (9.97) 13.60	5.44 (7.16) 8.16

arranged more or less regularly. Total number of lacunae 29: 3 poral, 6 abporal, 12 paraporal, 6 interporal and 2 polar. Surface of tectum densely microperforated and spiny. Spines between 1.36 and 4.08 μm long. Endoaperture lalongate, between 2.04 and 9.52 μm diameter.

Pollen type "G" (*L. amambaia*, *L. argyrotricha*, *L. bakerana*, *L. balansae*, *L. eriolepsis*, L. *fournetii*, *L. mapirensis*, *L. myriocephala*, *L. novarae*, *L. psilostachya*, *L. remotiflora*, *L. setososquamosa*, *L. sordidopapposa*, *L. tarijensis*). (Figs. 2; 3; 5; 6): small to medium pollen grains, oblate-spheroidal or prolate-spheroidal (P/E = 0.97–1.1 μm), 3-colporate; equinolophate. Pollen size P = 13.6–50.43 μm, E = 16.32–50.56 μm. Colpus with or without wall separating the poral lacunae from abporal lacunae. Exine thickness, excluding the spines, between 1.36 and 6.8 μm. Tectum discontinuous, with distribution of the lacunae in a more or less regular pattern. Total number of lacunae 27: 3 poral, 6 abporal, 12 paraporal and 6 interporal, without polar or equatorial lacunae. Tectum surface densely microperforated and spiny. Spines between 1.36 and 5.44 μm in length. Endoapertures lalongate, between 2.04 and 16.32 μm in diameter.

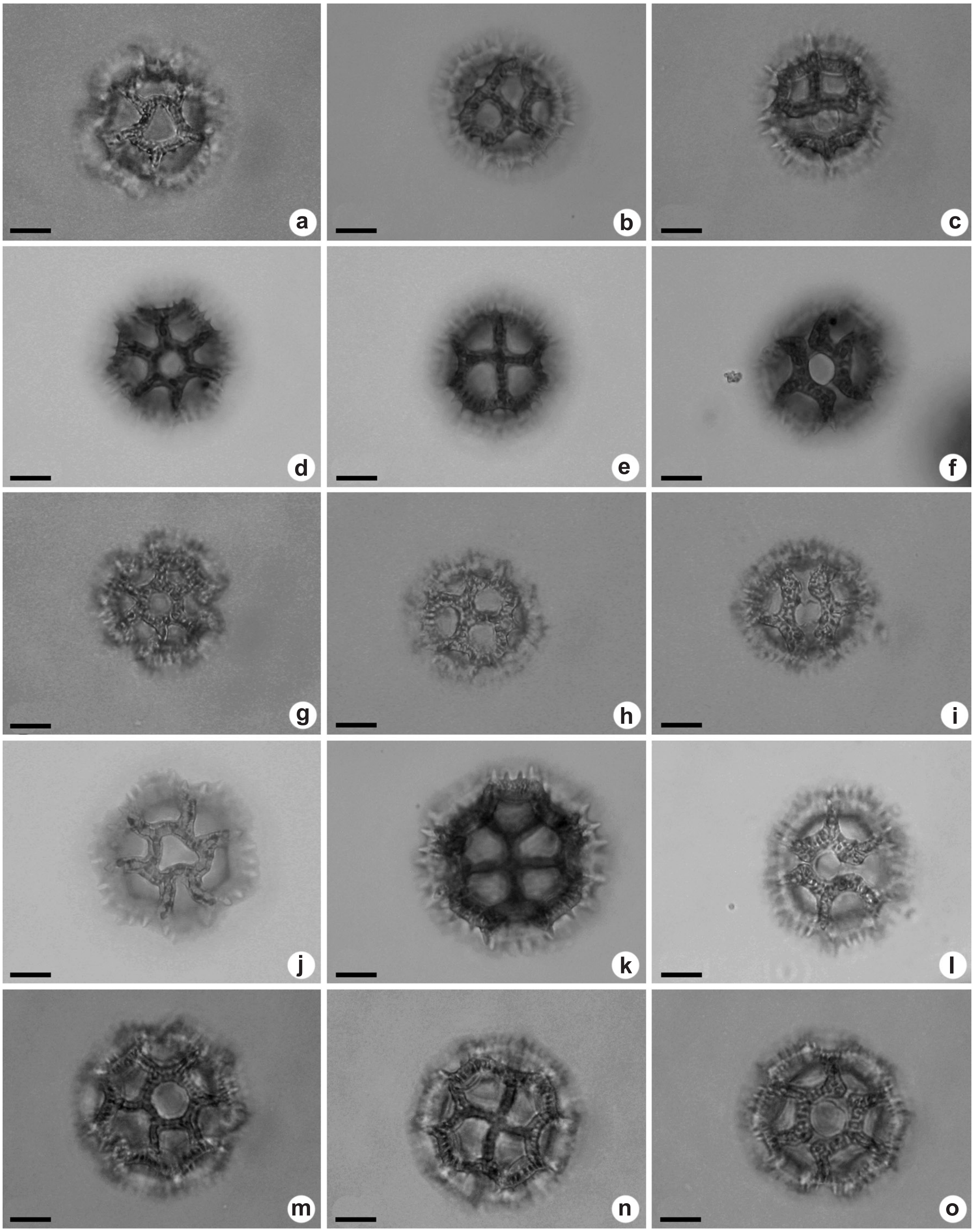

Figure 1 – a-o. Pollen type C of *Lepidaploa* (LM) – a-c. *Lepidaploa canescens* – a. polar view, polar lacunae, high focus; b. equatorial view, mesocolpium, high focus; c. equatorial view, colpus without wall separating poral lacunae from abporal lacunae, high focus; d-f. *L. chamissonis* – d. polar view, polar lacunae, high docus; e. equatorial view, mesocolpium, high focus; f. equatorial view, colpus, high focus; g-i. *L. costata* – g. polar view, polar lacunae, high focus; h. equatorial view, mesocolpium, high focus; i. equatorial view, colpus, high focus; j-l. *L. pseudomuricata* – j. polar view, polar lacunae, high focus; k. equatorial view, mesocolpium, mid focus; l. equatorial view, colpus, high focus; m-o. *L. salzmannii* – m. polar view, polar lacunae, high focus; n. equatorial view, mesocolpium, mid focus; o. equatorial view, colpus, high focus. Scales = 10 µm.

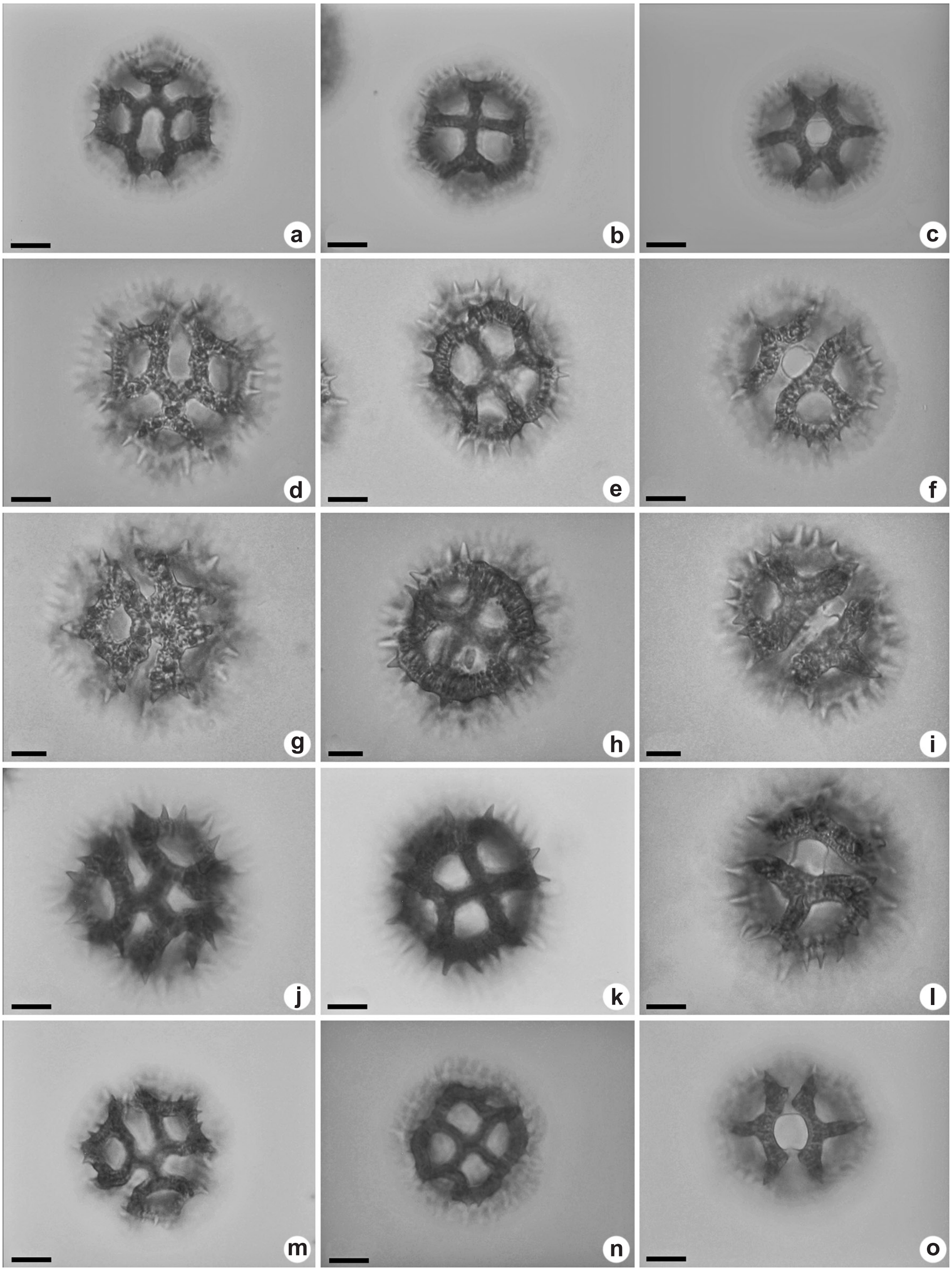

Figure 2 – a-o. Pollen type G of *Lepidaploa* (LM) – a-c. *L. amambaia* – a. polar view, mid focus; b. equatorial view, mesocolpium, mid focus; c. equatorial view, colpus, mid focus; d-f. *L. eriolepis* – d. polar view, mid focus; e. equatorial view, mesocolpium, mid focus; f. equatorial view, colpus without wall separating poral lacunae from abporal lacunae, high focus; g-i. *L. fournetii* – g. polar view, high focus; h. equatorial view, mesocolpium, mid focus; i. equatorial view, colpus, mid focus; j-l. *L. mapirensis* – j. polar view, mid focus; k. equatorial view, mesocolpium, mid focus; l. equatorial view, colpus, high focus; m-o. *L. myriocephala* – m. polar view, mid focus; n. equatorial view, mesocolpium, high focus; o. equatorial view, colpus, high focus. Scales = 10 μm.

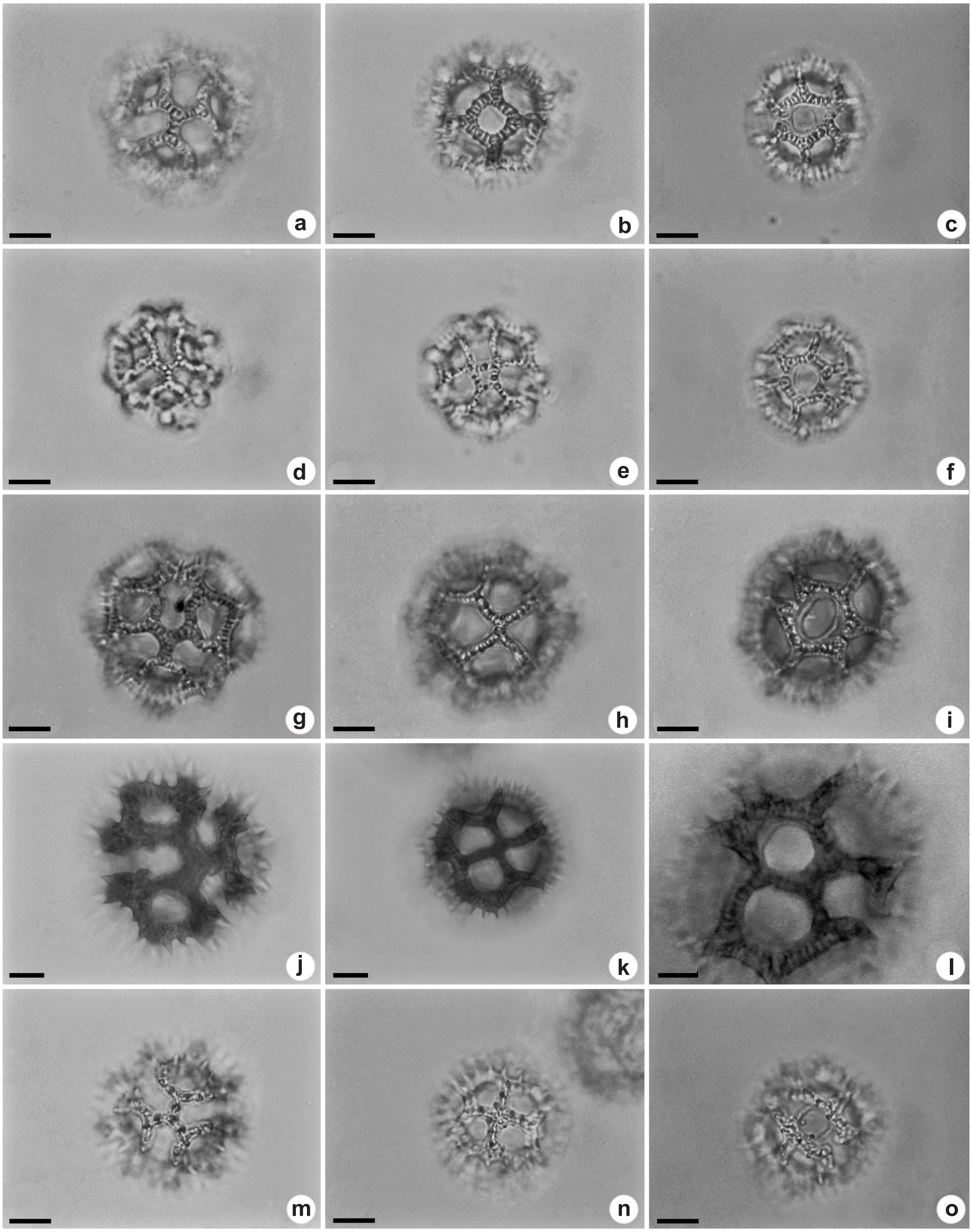

Figure 3 – a-o. Pollen type G of *Lepidaploa* (LM) – a-c. *L. psylostachya* – a. polar view, high focus; b. equatorial view, mesocolpium, high focus; c. equatorial view, colpus, high focus; d-f. *L. remotiflora* – d. polar view, high focus; e. equatorial view, mesocolpium, high focus; f. equatorial view, colpus, high focus; g-i. *L. setososquamosa* – g. polar view, high focus; h. equatorial view, mesocolpium, high focus; i. equatorial view, colpus, high focus; j-l. *L. sordidopapposa* – j. polar view, mid focus; k. equatorial view, mesocolpium, mid focus; l. equatorial view, colpus, high focus; m-o. *L. tarijensis* – m. polar view, high focus; n. equatorial view, mesocolpium, high focus; o. equatorial view, colpus, high focus. Scales = 10 µm.

Pollen type "G" atypical: in pollen type "G" a number of lacunae greater than 27 was rarely found. However, some presented a number of lacunae equal to 29 or 30. Some pollen grains of *L. remotiflora*, showed 29 lacunae due to the presence of two reduced polar lacunae (Fig. 3e). In *L. amambaia* and *L. psilostachya* pollen grains were observed with 30 lacunae, since some grains showed reduced equatorial lacunae (*L. amambaia*) (Fig. 5c) or prominent equatorial lacunae (*L. psilostachya*).

Cluster Analysis: the phenogram resulting from the UPGMA analysis is shown in (Fig. 7). The value of the cophenetic correlation (r = 0.86) coefficient indicates that the technique used is a good estimator of the relationship between the characters analyzed. The 23 species analyzed (OTUs) are grouped into two main clusters (group 1 and group 2). Group 1 is represented only by *L. novarae*, which is the only species that presented an average value of polar and equatorial axis greater than 40 µm. Group 2 is formed by species that presented an average value of polar and equatorial axis lower than 40 µm. The species in group 2 were grouped into two subgroups (2A and 2B) depending on the type of pollen. Subgroup 2A is formed by species that have pollen type "C", while subgroup 2B includes species that possess pollen type "G". Subgroup 2A is sub-divided into 2Aa, including species with prolate-spheroidal pollen grains and 2Ab with oblate-spheroidal pollen grains. Subgroup 2B is also divided according to the shape of the

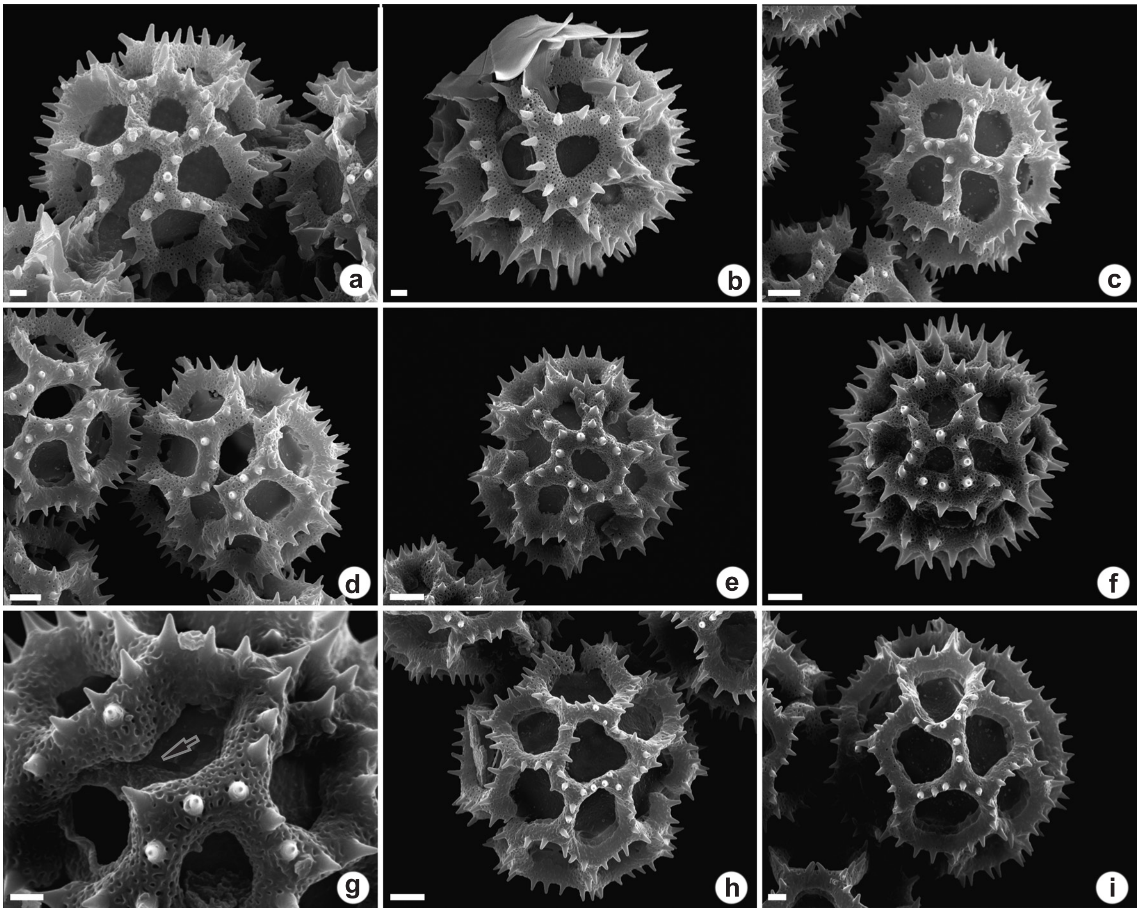

Figure 4 – a-i. Pollen type C of *Lepidaploa* (SEM) – a-b. *L. chamissonis* – a. polar view, polar lacunae; b. equatorial view, mesocolpium and colpus; c-d. *L. costata* – c. equatorial view, mesocolpium; d. equatorial view, colpus; e-g. *L. deflexa* – e. polar view, polar lacunae; f. equatorial view, mesocolpium; g. equatorial view, details of spines and colpus with small walls separating poral lacunae from the abporal lacunae (black arrow); h-i. *L. salzmannii* – h. polar view, polar lacunae; i. equatorial view, mesocolpium. Scales: a-b, g, i = 2 µm; c-f, h = 5 µm.

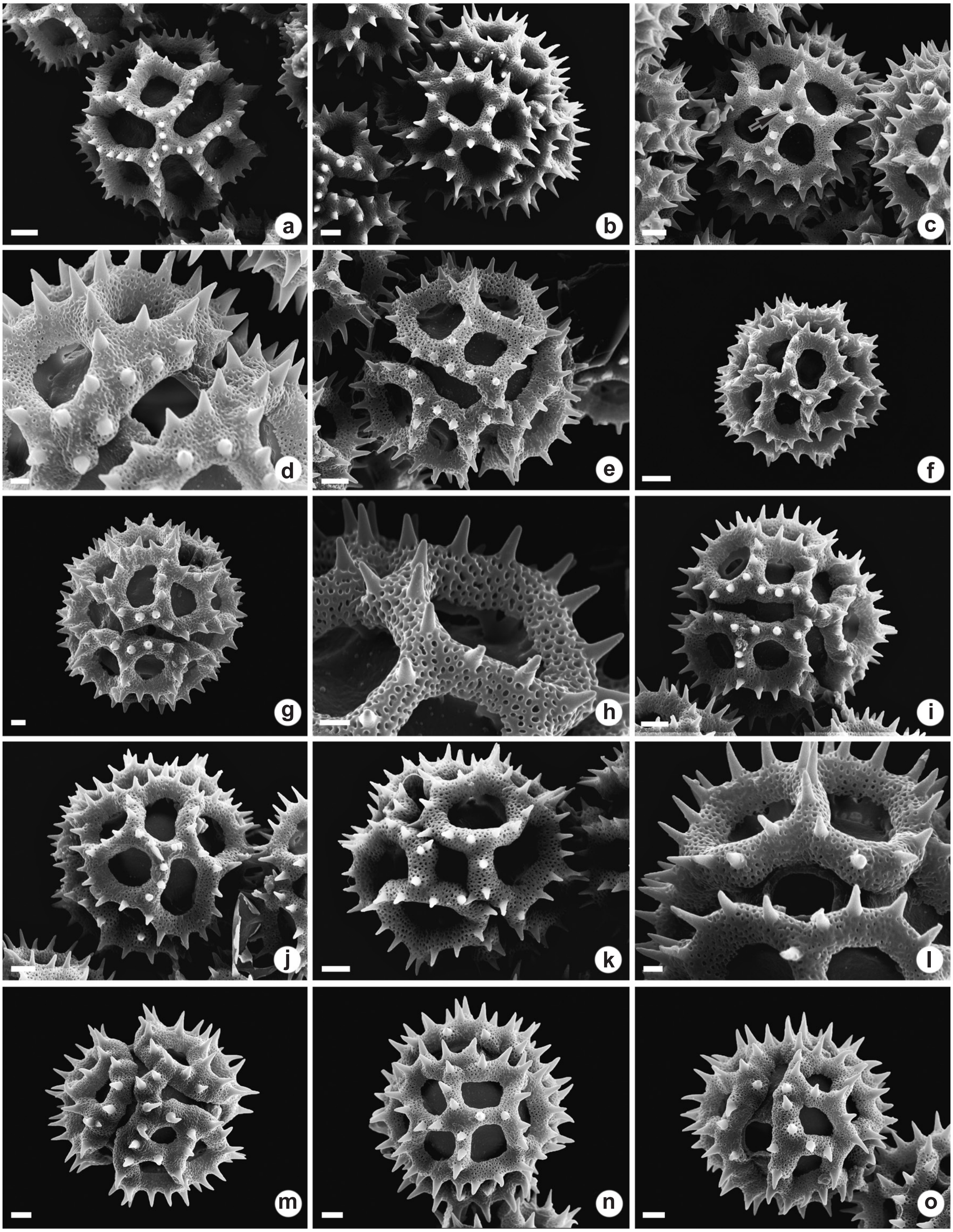

Figure 5 – a-o. Pollen type G of *Lepidaploa* (SEM) – a-d. *L. amambaia* – a. polar view; b. equatorial view, mesocolpium; c. equatorial view, mesocolpium with reduced lacunae equatorial (black arrow); d. equatorial view, details of spines and colpus; e-h. *L. bakerana* – e. polar view; f. equatorial view, mesocolpium; g. equatorial view; h. detail of tectum with spines; i-l. *L. eriolepis* – i. polar view; j. equatorial view, mesocolpium; k. equatorial view, colpus; l. equatorial view, colpus; m-o. *L. mapirensis* – m. polar view; n. equatorial view, mesocolpium; o. equatorial view, colpus. Scales: d, g-h, l = 2 µm; a-c, e-f, i-k, m-o = 5 µm.

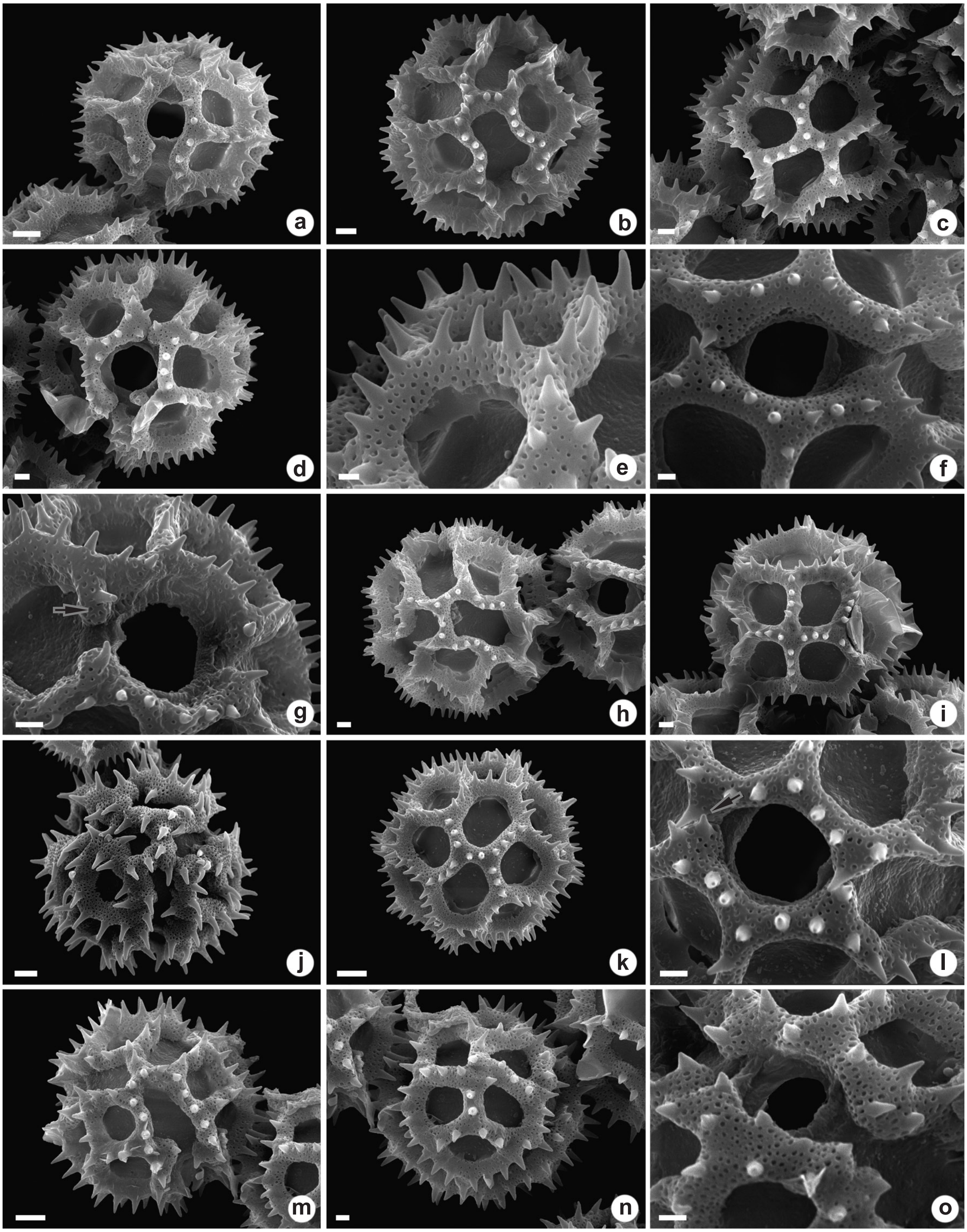

Figure 6 – a-o. Pollen type G of *Lepidaploa* (SEM) – a. *L. myriocephala* – equatorial view, colpus; b-e. *L. psilostachya* – b. polar view; c. equatorial view, mesocolpium; d. equatorial view, colpus; e. detail of tectum and spines; f. *L. remotiflora* – equatorial view, detail of colpus; g. *L. salzmannii* – equatorial view, detail of colpus evidencing the wall that separates the lophae (black arrow); h-i. *L. setososquamosa* – h. polar view; i. equatorial view, mesocolpium; j-l. *L. sordidopapposa* – j. polar view; k. equatorial view, mesocolpium; l. equatorial view, detail of wall of the colpus (black arrow); m-o. *L. tarijensis*; m. polar view; n. equatorial view, mesocolpium; o. equatorial view, colpus. Scales: e-f = 1 µm; b-d, g-i, l, n-o = 2 µm; a, j-k, m = 5 µm.

pollen grain. Subgroup 2Ba is formed by species with prolate-spheroidal pollen grains and subgroup 2Bb by species with oblate-spheroidal pollen grains. In the terminals of the phenogram it can be seen that most of the species can be differentiated from each other based on the values of the averages of the polar axis and the equatorial axis. The only species that could not be differentiated from each other by cluster analysis were *L. eriolepis* and *L. fournetii*, which have the same type and shape of pollen, in addition to the same values of polar and equatorial axis.

Discussion

Pollen morphology

All 23 species of *Lepidaploa* studied have echinolophate and tricolporate pollen grains. According to the morphological analysis, the species have variations in the aperture of the colpus and number of lacunae.

Nine species present a pollen type that coincides with the "*Vernonia cognata*" pollen type designated by Stix (1960) or with pollen type "C" designated by Keeley & Jones (1977). Pollen type "C" was also designated as characteristic of the genera *Chrysolaena* (Robinson 1988), *Stenocephalum* (Robinson 1987a), and some species of *Lepidaploa* (Robinson 1990). The characteristics that differentiate this type of pollen from the other types of pollen found in the Vernonieae tribe are the presence of polar lacuna in both poles of the pollen grain, equinolophate sexine and tricolporate colpus (Robinson 1988, 1990, 1999).

The other 14 species present a pollen morphology that coincides with pollen type "G" described by Robinson (1990). This pollen type is very similar to the "*Vernonia arenaria*" pollen type described by Stix (1960) and pollen type "D" described by Keeley & Jones (1979), but both are triporate instead tricolporate, which is a characteristic of pollen type "G (Keeley & Jones 1979; Robinson 1990).

The atypical pollen type "G" found in the species studied here was reported by Robinson (1990) for *L. psilostachya*. In this species, Robinson (1990), observed the presence of an equatorial lacuna (typical of type "B" pollen grains) in a few pollen grains. In the species studied in our work, a few pollen grains of *L. psilostachya* display a well-developed equatorial lacuna, whereas in *L. amambaia* this lacuna is reduced. Robinson (1990) suggests that the presence of equatorial lacuna in pollen type "G" may occur, but it is not a common feature in most *Lepidaploa* species. Unusually, the presence of a reduced polar lacuna (typical of pollen type "C") was seen in some pollen type "G" of *L. remotiflora*.

The variations mentioned above, although not common, were reported in other genera and species of the Vernonieae tribe. Intermediate states between pollen type "B" and "C" were found in *Lepidaploa pluvialis* (Gleason) H. Rob. and *Vernonia trinitatis* Ekman (Keeley & Jones 1977). In some populations of *Chrysolaena*, or in few grains of pollen, a reduced equatorial lacuna in pollen type "C" was observed (Via do Pico & Dematteis 2013). Finally,

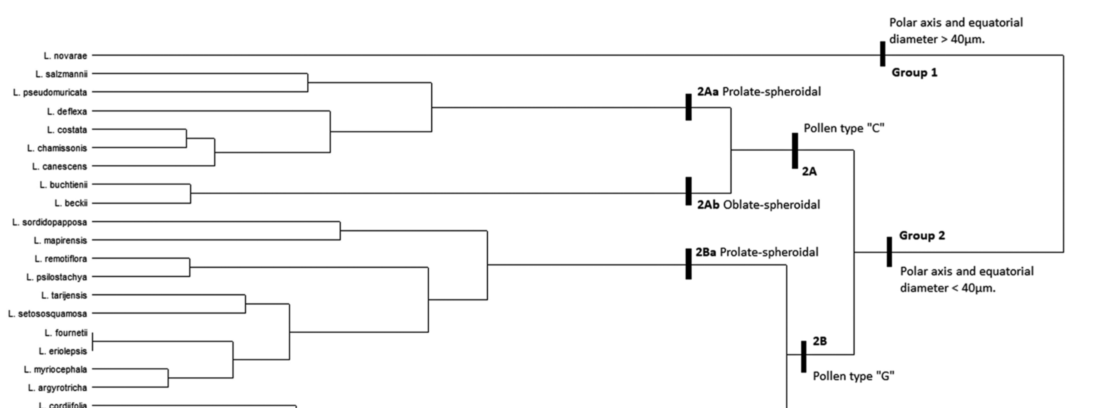

Figure 7 – Phenogram resulting from the UPGMA based on the Gower coefficient.

in the genus *Echinocoryne* H. Rob. a variation in pollen type "G" was found that presented two equatorial lacunae (Robinson 1987b, 1990). The results obtained in the analyzed species of *Lepidaploa* demonstrate that in the same species some pollen grains may present small variations (polar and equatorial lacuna in pollen type "G") which may be results of the position occupied by the lacunae in the tetrad during the formation of the pollen grain as mentioned by Robinson (1990).

Taxonomic implications

Pollen grains are one of the most important microcharacters for the segregation of genera belonging to the genus *Vernonia* s.l. (Robinson 1999) and the palynological studies made it possible to differentiate genera in the Lepidaploinae subtribe (Robinson 1999). In recent years several studies described many pollen types for the genera of the Lepidaploinae subtribe (Robinson 1987a, b, 1988, 1990, 1992, 1999; Carrijo *et al.* 2005; Mendonça *et al.* 2007a, b; Bunwong & Chantaranothai 2008; Angulo & Dematteis 2010; Via do Pico & Dematteis 2013). In Table 4, we highlight the importance of knowledge about the pollen types found in Lepidaploinae and how these pollen types contribute to the segregation of genera.

The pollen "*Aynia-type"* is present in three genera of the subtribe: *Aynia* H. Rob., *Harleya* H. Rob. and *Pseudopiptocarpha* H. Rob (Robinson 1999). This pollen type is similar to pollen type "C" described for *Lepidaploa* in our work and for other genera of Lepidaploinae, but in the "*Aynia-type"* there are three polar lacunae at each pole of the pollen grain, while a typical pollen grain type "C" possesses only one polar lacuna per pole (Robinson 1987a, 1988, 1990, 1999; Mendonça *et al.* 2007a, b; Via do Pico & Dematteis 2013).

Lessingianthus and *Mattfeldanthus* have pollen type "B" which is characterized by the presence of equatorial lacunae (Angulo & Dematteis 2010). *Lessingianthus* is the sister group of *Chrysolaena* and *Lepidaploa* (Keeley *et al*. 2007), and since these three genera are morphologically very similar, the pollinic type is very important for their distinction (Robinson 1999).

Pollen type "C" is present in all species of *Chrysolaena*, *Stenocephalum*, *Strophopappus*, and in *Lepidaploa* this pollen type is present only in some species (Robinson 1999). Although these genera and species present the same pollen type, the morphological characteristics of *Stenocephalum* and *Strophopappus* differentiate these genera from the other two. The cylindrical heads with few flowers are exclusive of *Stenocephalum* (Robinson 1987a), while the paleaceous pappus occurs only in *Strophopappus* (Esteves *et al.* 2017).

Chrysolaena and *Lepidaploa* are phylogenetically related (Keeley *et al.* 2007) and the differentiation between both genera is very complex, since there is an overlap of pollen types, although the presence of pollen type "D" or "G" is more common in *Lepidaploa* (Robinson 1999; Mendonça *et al.* 2007a). Until now, the only feature that distinguished the species of *Lepidaploa* that present pollen type "C" from *Chrysolaena* is their basic chromosome numbers, since *Chrysolaena* presents basic chromosomal number x = 10 (Via do Pico & Dematteis 2012, 2014, 2019), while the basic chromosomal number of *Lepidaploa* is x = 14, 15, 16 or 17 (Dematteis 2002; Oliveira *et al.* 2007, 2012).

Pollen type "D" and "G" that occur in *Lepidaploa* can also be found in other genera of Lepidaploinae. The morphological characteristics of the pappus, phyllaries and habit differentiate the genus *Lepidaploa* from the genera *Echinocoryne* H. Rob., *Stilpnopappus* Mart. *ex* DC., *Struchium* (L.) Kuntze and *Xipochaeta* Poepp. (Robinson 1999; Esteves & Gonçalves-Esteves 2003; Bunwong *et al.* 2014; Lorencini *et al.* 2017).

Finally, pollen type "F" found in *Caatinganthus* H. Rob. (Robinson 1999) is similar to pollen type "D" found in *Lepidaploa*. However, pollen type "F" has very short spines with a rounded apex, whereas the spines of pollen type "D" are large and have an acute apex.

In the species of *Lepidaploa* analyzed in our study there is a great similarity between pollen grains, such as the size of the polar axis, equatorial axis, thickness of the tectum, length of the spines and the diameter of the lacunae and pore. In this way, it was not possible to separate all the species studied in a taxonomic key.

Some closely related species can be differentiated by the type or form of the pollen grain that they present. *Lepidaploa argyrotricha*, is a morphologically similar species to *L. chamissonis* and *L. salzmannii*, but it can be differentiated from these other two species by the pollen type, since *L. argyrotricha* presents type "G" pollen while the other species present type "C" pollen. In turn, the species *L. amambaia* is morphologically related to the species *L. remotiflora* and *L. setososquamosa*. However, the first species differs from the others

Table 4 – Genera and pollen type of subtribe Lepidaploinae (Vernonieae, Asteraceae).

Genera	Pollen type	References
Aynia H. Rob.	*Aynia-type*	Robinson (1999)
Caatinganthus H. Rob.	F	Robinson (1999)
Chysolaena H. Rob.	C	Via do Pico & Dematteis (2013)
Echinocoryne H. Rob.	G	Robinson (1999)
Harleya Cass.	*Aynia-type*	Robinson (1999)
Lepidaploa (Cass) Cass.	C, D and G	Robinson (1990), Mendonça *et al.* (2007a[a]), this work
Lessingianthus H. Rob	B	Angulo & Dematteis (2010)
Mattfeldanthus H. Rob. & R.M. King	B	Dematteis (2005)
Pseudopiptocarpha H. Rob.	*Aynia-type*	Robinson (1999)
Stenocephalum Sch. Bip.	C	Robinson (1999), Mendonça *et al.* (2007b [a])
Stilpnopappus Mart. *ex* DC.	D	Carrijo *et al.* (2005[a])
Strophopappus DC	C	Carrijo *et al.* (2005[a])
Struchium (L.) Kuntze	D	Bunwong & Chantaranothai (2008)
Xipochaeta Poepp.	G	Robinson (1992)

[a] These studies do not use the alphabetical terminology to pollen-type adopted by Keeley & Jones (1977, 1979) and Robinson (1990, 1999). However, when analyzing pollen descriptions of Carrijo *et al.* (2005) and Mendonça *et al.* (2007a,b), we noticed correspondence between the pollen descriptions of these studies and those of Keeley & Jones (1977, 1979) and Robinson (1990, 1999).

because it presents oblate-spheroidal pollen while the others possess prolate-spheroidal pollen.

Through the UPGMA analysis it is possible to infer that the shape of the pollen grain and the type of pollen grain are the most important variables for the grouping of the taxa. However, although most species are separated in the phenogram resulting from this analysis, it should be noted that the species appear isolated from each other only because the analysis was based on the averages of the polar and equatorial axis. In Table 3, it is possible to identify the superposition that exists between the values of these two variables (polar and equatorial axis) that make it difficult to separate these species only by quantitative data.

All species studied possess pollen type "C" or "G". According to our results, the information with taxonomic value are pollen type and shape. This information is important to identify morphologically related species as in the case of *L. amambaia / L. remotiflora / L. setososquamosa* and *L. argyrotricha / L. chamissonis / L. salzmanii*. Finally, pollen type and macromorphological characteristics, when used together, can be useful to recognize most genera of Lepidaploinae, except *Chrysolaena* which is distinguished from *Lepidaploa* only by chromosome number.

Acknowledgements

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