Original Paper

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

Danilo Marques¹,³,⁶, Gisela Mariel Via do Pico¹,⁴, Jimi Naoki Nakajima² & Massimiliano Dematteis¹,⁵

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-esférico, subprolate o prolate-esférico, 3-colporado e equinolofado. O tipo de grão de pólen e sua forma foram taxonomicamente 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;...
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 Vernonia 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 Vernonia 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 other genera found in the subtribe Lepidaploinae (Robinson 1999).

Other authors have studied the pollen types of *Lepidaploa* (Dematteis & Pire 2008, Mendoça & Gonçalves-Esteves 2000; Mendoça 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; Mendoça 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 Botânica 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 fin 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 La Paz, Provincia 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, Provincia Sud Yungas, 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 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, 16°22′S, 67°32′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                                                                 |
|---------------------------------|-----------------------------------------------------------------------------------------------|
| *Lepidaploa fournetii* (H. Rob. & B. Kahn) H. Rob. | Brasil. Santa Catarina, Florianópolis, Morro Costa da Lagoa. *D.B. Falkenberg* 4364 (MBM). Bolivia. Departamento La Paz, Provincia Nor Yungas, Chusipata 6 km, hacia Caroico 2640 m. *St. G. Beck.* 13578 (CTES). Bolivia. Departamento La Paz, Provincia Nor Yungas, Chusipata 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 Chusipata, 3100 m 16º18’S, 67º49’W. *J.C. Solomon* 9656 (CTES). Bolivia. Departamento La Paz, Provincia Nor Yungas, 1.2 km E de Cotapata entre la ruta Unduavi y Chusipata, 16º17’S, 67º50’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 15º28’18”S, 67º58’18”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. | Argentinia. Salta, Departamento Santa Victoria, Parque San Martín, entrando por la pista de aterrizaje de Toldos, 22º18’S, 64º40’W. *O. Ahumada & J. Aguero* 8365 (CTES). Argentinia. 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. | Argentinia. Misiones. San Ignacio, Teyú Cuaré 27º16’46”S, 55º37’37”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, Municipio Urubici, Águas Brancas. *G. Hachtsbach et al.* 78921 (CTES, MBM). Brasil. Paraná, Municipio de São Mateus do Sul, Usina de Xisto da Petrobrás. *O.S. Ribas et al.* 6518 (CTES, MBM). |
| *Lepidaploa remotiflora* (Rich.) H. Rob. | Argentinia. Corrientes, Ituzaingó, Costa del Río Paraná. *A. Krapovickas & C.L. Cristóbal* 29153 (CTES). Bolivia. Santa Cruz, Valle Grande, 5 km de El Trigal. 18º25’56”S, 64º7’17”W 1982 m.s.m.m. *M. Dematteis* 3673 (CTES). |
| *Lepidaploa salzmannii* (DC.) H. Rob. | Brasil. Paraná: Tomazina, Guaviroval, 02.IX.1998, 64º7’57”S, 58º9’05”W. 1098 m.s.m. *M. Dematteis* 3438 (CTES). Bolivia. Tarija, O'Connor, 8,3 km E de Entre Rios, camino a Villamontes 21º27’55”S, 64º8’57”W. *M. Dematteis* 1305 (CTES). |
| *Lepidaploa setososquamosa* (Hieron.) M. B. Angulo & Dematt. | Argentinia. Salta, Departamento Rosario de Lerma, Dique Las Lomitas, Ribera Oeste, 1400 m.s.m. *L.J. Novara* 10877 (CTES). Bolívia. Santa Cruz. Chiquitos, 15 km E de Ipias, 17º59’43”S, 60º15’12”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. | Bolívia. Departamento de La Paz, Provincia Nor Yungas, entre Chusipata y San Rafael, 16º16’S, 67º50’W, 280 m.s.m.m. *St. G. Beck* 22672 (CTES). Bolívia. Departamento de La Paz, Provincia Nor Yungas, de la cumbre bajando 30 km hacia Chusipata, pasando Cotapata 2980 m.s.m. *St. G. Beck* 17717 (CTES). |
| *Lepidaploa tarijensis* (Griseb.) H. Rob. | Argentinia. Salta, Departamento Gral. S. Martín, Pocitos. *A. Krapovickas et al.* 19425 (CTES). Paraguayan. Boquerón, Parque Valle Natural, 25 km S de Filadelfia. *A. Krapovickas & C.L. Cristóbal* 44197 (CTES). Paraguayan. Boquerón, Parque Valle Natural, 25 km S de Filadelfia. *A. Krapovickas & C.L. Cristóbal* 44197 (CTES). Paraguayan. Boquerón, Parque Valle Natural, 25 km S de Filadelfia. *A. Krapovickas & C.L. Cristóbal* 44197 (CTES). |
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 1.36 and 5.44 μm length and they have a linear distribution along the walls of the lophae. The diameter of the endoaperature (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, 1992, 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. cordifolia*, *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 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 | × |
| C           | echinolophate | tricolporate | absent | present | present | present | present | × |
| D           | echinolophate | triporate | absent | absent | present | usually absent | usually absent | × |
| E           | lophate or subechinate | triporate | absent | absent | present | present | present | × |
| 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, but scanty | present | × |
| Aynia-type  | echinolophate | tricolporate | absent | absent | present | present | present | with intercolpus |

Rodriguésia 72: e01412019. 2021
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) | 20.4     | 0.98     | oblate-| spheroidal| 2.74           | (3.4)       | 5.44                  | 4.08          |
|             |                   | 25.84         | 27.2     |          |         |           | 4.08           | (2.85)      | 9.52                  | 9.03          |
| C 29        | Lepidaploa buchienii | 15.20 (22.39)| 17.34    | 0.97     | oblate-| spheroidal| 2.83           | (3.91)      | 5.42                  | 2.04          |
|             |                   | 26.10         | 25.2     |          |         |           | 5.47           | 4.05        | 8.91                  | 9.52          |
| C 29        | Lepidaploa canescens | 20.40 (22.4) | 20.4     | 1.02     | prolate-| spheroidal| 1.36           | (1.58)      | 6.8                   | 4.08          |
|             |                   | 22.12         | 24.48    |          |         |           | 6.8            | 2.72        | 9.52                  | 6.8           |
| C 29        | Lepidaploa chamissonis | 19.40 (21.31)| 19.4     | 1        | prolate-| spheroidal| 2.72           | (2.49)      | 5.44                  | 4.08          |
|             |                   | 25.84         | 25.48    |          |         |           | 6.8            | 4.08        | 9.52                  | 8.16          |
| C 29        | Lepidaploa costata | 20.40 (22.03)| 19.04    | 1.03     | prolate-| spheroidal| 2.72           | (2.13)      | 7.25                  | 5.21          |
|             |                   | 27.20         | 27.2     |          |         |           | 5.44           | 4.08        | 9.52                  | 6.8           |
| C 29        | Lepidaploa deflexa | 16.32 (20.04)| 14.96    | 1.08     | prolate-| spheroidal| 2.72           | (1.56)      | 6.46                  | 5.8           |
|             |                   | 23.12         | 23.12    |          |         |           | 5.44           | 2.72        | 8.16                  | 6.8           |
| C 29        | Lepidaploa pseudomuricata | 24.48 (27.51)| 20.40    | 1.03     | prolate-| spheroidal| 4.08           | (2.51)      | 8.93                  | 5.98          |
|             |                   | 31.28         | 31.28    |          |         |           | 5.44           | 2.72        | 13.60                 | 8.16          |
| C 29        | Lepidaploa salzmannii | 21.76 (25.97)| 21.76    | 1.07     | prolate-| spheroidal| 1.36           | (1.43)      | 8.52                  | 8.16          |
|             |                   | 28.56         | 28.56    |          |         |           | 4.08           | 2.72        | 10.88                 | 9.52          |
| G* 27-30    | Lepidaploa amambia | 27.2 (31.82)  | 24.48    | 1.07     | oblate-| spheroidal| 2.72           | (2.58)      | 7.7                   | 7.57          |
|             |                   | 40.8          | 38.08    |          |         |           | 6.8            | 5.44        | 10.88                 | 9.52          |
| G 27        | Lepidaploa argyrotricha | 24.48 (27.42)| 20.4     | 1.09     | prolate-| spheroidal| 2.72           | (2.74)      | 7.7                   | 6.08          |
|             |                   | 32.64         | 29.92    |          |         |           | 6.8            | 4.08        | 10.88                 | 6.8           |
| G 27        | Lepidaploa bakerana | 16.32 (17.81)| 16.32    | 0.97     | oblate-| spheroidal| 2.04           | (2.1)       | 5.3                   | 5.39          |
|             |                   | 20.40         | 21.76    |          |         |           | 4.08           | 2.72        | 6.8                   | 6.8           |
| G 27        | Lepidaploa balansae | 13.60 (22.39)| 19.04    | 0.97     | oblate-| spheroidal| 2.72           | (2.88)      | 7.7                   | 5.46          |
|             |                   | 27.20         | 27.2     |          |         |           | 5.44           | 4.76        | 10.88                 | 9.52          |
| G 27        | Lepidaploa cordifolia | 19.04 (20.74)| 16.32    | 0.98     | oblate-| spheroidal| 2.72           | (3.26)      | 5.94                  | 4.42          |
|             |                   | 25.84         | 24.48    |          |         |           | 5.44           | 4.08        | 8.16                  | 5.44          |
Pollen of species of Lepidaploa

| 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  | 21.76  | 1.03  | prolate-spheroidal | 1.36           | (3.09)      | 2.72                  | 5.44         | 4.08                |
|             |                   |                          | (26.38)| (25.57)|       |            | (3.06)        |             | (8.4)                 | (6.07)       |                     |
|             |                   |                          | 28.56  | 28.56  |       |            | 5.44           |             | 13.80                 | 6.80         |                     |
| G           | 27                | Lepidaploa fournietii    | 23.12  | 21.76  | 1.03  | prolate-spheroidal | 1.36           | (3.94)      | 2.72                  | 5.44         | 4.08                |
|             |                   |                          | (26.38)| (25.57)|       |            | (3.6)         |             | (8.38)                | (6.07)       |                     |
|             |                   |                          | 28.56  | 28.56  |       |            | 5.44           |             | 13.60                 | 6.80         |                     |
| G           | 27                | Lepidaploa mapirensis    | 27.20  | 25.84  | 1.05  | prolate-spheroidal | 2.72           | (4.48)      | 3.4                   | 6.80         | 6.80                |
|             |                   |                          | (33.23)| (31.55)|       |            | (4.28)        |             | (9.25)                | (8.34)       |                     |
|             |                   |                          | 36.72  | 35.36  |       |            | 5.44           |             | 13.60                 | 10.88        |                     |
| G           | 27                | Lepidaploa myrioccephala| 23.12  | 20.40  | 1.1   | prolate-spheroidal | 2.72           | (3.72)      | 1.36                  | 5.44         | 6.80                |
|             |                   |                          | (27.24)| (24.71)|       |            | (2.31)        |             | (8.01)                | (7.98)       |                     |
|             |                   |                          | 29.92  | 27.2   |       |            | 4.08           |             | 9.52                  | 9.52         |                     |
| G           | 27                | Lepidaploa novarae       | 39.78  | 42.30  | 0.96  | oblate-spheroidal | 4.0            | (4.36)      | 4.0                   | 8.60         | 4.08                |
|             |                   |                          | (47.3) | (49.2) |       |            | (4.25)        |             | (10.07)               | (5.71)       |                     |
|             |                   |                          | 50.43  | 50.56  |       |            | 5.4            |             | 12.20                 | 6.80         |                     |
| G*          | 27-30              | Lepidaploa psilostachya  | 17.68  | 17.68  | 1     | prolate-spheroidal | 2.72           | (3.96)      | 1.36                  | 6.80         | 5.44                |
|             |                   |                          | (20.49)| (20.53)|       |            | (1.4)         |             | (9.06)                | (6.53)       |                     |
|             |                   |                          | 23.12  | 23.12  |       |            | 5.44           |             | 12.24                 | 8.16         |                     |
| G*          | 27-29              | Lepidaploa remotiflora   | 19.00  | 16.32  | 1.04  | prolate-spheroidal | 2.27           | (3.88)      | 1.36                  | 4.08         | 4.08                |
|             |                   |                          | (21.26)| (20.54)|       |            | (1.41)        |             | (9.61)                | (5.76)       |                     |
|             |                   |                          | 24.48  | 24.48  |       |            | 6.8            |             | 12.24                 | 8.16         |                     |
| G           | 27                | Lepidaploa setososquamosa| 20.40  | 20.40  | 1.01  | prolate-spheroidal | 2.72           | (3.69)      | 1.36                  | 6.80         | 5.44                |
|             |                   |                          | (24.12)| (23.98)|       |            | (1.75)        |             | (11.2)                | (6.62)       |                     |
|             |                   |                          | 34     | 34     |       |            | 5.44           |             | 16.32                 | 8.16         |                     |
| G           | 27                | Lepidaploa sordidopapposa| 25.84  | 20.40  | 1.05  | prolate-spheroidal | 2.72           | (4.76)      | 1.36                  | 6.80         | 6.8                 |
|             |                   |                          | (30.6) | (29.01)|       |            | (2.99)        |             | (9.09)                | (10.01)      |                     |
|             |                   |                          | 38.08  | 40.80  |       |            | 6.8            |             | 10.88                 | 16.32        |                     |
| G           | 27                | Lepidaploa tarijensis    | 23.12  | 20.40  | 1.08  | prolate-spheroidal | 2.72           | (3.72)      | 1.36                  | 6.80         | 5.44                |
|             |                   |                          | (25.75)| (23.66)|       |            | (3.21)        |             | (9.97)                | (7.16)       |                     |
|             |                   |                          | 27.20  | 27.20  |       |            | 5.44           |             | 13.60                 | 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.

Pollentype "G" (L. amambaia, L. argyrotricha, L. bakerana, L. balansae, L. eriolepsis, L. fournietii, L. mapirensis, L. myrioccephala, 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 focus; 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. fournietii* – 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. amambiaia* and *L. psilostachya* pollen grains were observed with 30 lacunae, since some grains showed reduced equatorial lacunae (*L. amambiaia*) (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 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 \( \mu \)m. Group 2 is formed by species that presented an average value of polar and equatorial axis lower than 40 \( \mu \)m. 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 characters analyzed.

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 \( \mu \)m; c-f, h = 5 \( \mu \)m.
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. mapiensis* – 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. fournetti*, 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.

Rodriguésia 72: e01412019. 2021
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 & Chantaranonthai 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 *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., *Stilnopappus* Mart. ex DC., *Struchium* (L.) Kuntze and *Xipochaeta* Poopp. (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. salzmanni*, 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
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

This work was supported by grants from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

### References

Angulo MB & Dematteis M (2010) Pollen morphology of the South American genus Lessingianthus (Vernonieae, Asteraceae) and its taxonomic implications. Grana 49: 12-25.

Besold B (1971) Pollen morphologischen Untersuchungen an Inuleen (Angianthinae, Relhaniinae, Arthrixiinae). Dissertationes Botanicae 14: 1-72.

Blackmore S (1982) A functional interpretation of Lactuceae (Compositae) pollen. Plant Systematic and Evolution 141: 153-168.

Bremer K (1994) Asteraceae: cladistics & classification. Timber Press, Portland. 752p.

Bunwong S & Chantaranothai P (2008) Pollen morphology of the tribe Vernonieae (Compositae).
in Thailand. The Natural History Journal of Chulalongkorn University 8: 45-55.
Bunwong S, Chantaranothai P & Sterling CK (2014) Revisions and key to the Vernonieae (Compositae) of Thailand. PhytoKeys 37: 25-101.
Carrijo TT, Mendonça CBF, Esteves RL & Gonçalves-Estevess V (2005) Palinotaxonomic analysis of species of Stilpnopappus Mart. ex DC. e Strophopappus DC. (Compositae). Hoehnea 32: 259-268.
Dematteis M (2002) Cytotaxonomic analysis of South American species of Vernonia (Vernoniae: Asteraeae). Botanical Journal of the Linnean Society 139: 401-408.
Dematteis M (2005) Revisión de Mattfeldanthus, un género de Vernonieae (Asteraceae) endémico del Nordeste de Brasil. Bonplandia 17: 73-81.
Dematteis M & Pire SM (2008) Pollen morphology of some species of Vernonia sensu lato (Vernoniae, Asteraceae) from Argentina and Paraguay. Grana 47: 117-129.
Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M & Robledo CW (2018) Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. Available at <http://www.infostat.com.ar>. Access on 4 May 2018.
Erdtman G (1960) The acetolysis method. A revised description. Svensk Botanisk Tidskrift 54: 561-564.
Erdtman G (1966) Pollen morphology and plant taxonomy. Angiosperms: an introduction to Palynology. Hafner Publishing Company, New York.
Esteves RL & Gonçalves-Estevess V (2003) Redelimitação de Stilpnopappus Mart. ex DC. (Vernoniae-Asteraeae). Bradea 9: 77-92.
Esteves RL, Loueuille B, Nakajima JN, Marques D, Soares P, Esteves-Gonçalves V, Mendonça C & Dematteis M (2017) Tribo Vernonieae Cass. In: Roque N, Magalhães AT & JN Nakajima (eds.) A família Asteraceae no Brasil, classificação e diversidade. EDUFBA, Salvador. Pp. 101-118.
Fazal H, Ahmad N & Abassi BH (2013) Identification, characterization, and palynology of high-valued medicinal plants. The Scientific World Journal 2013: 1-9.
Hesse M, Halbritter H, Zetter R, Weber M, Buchner R, Frosch-Radivo A & Ulrich S (2009) Pollen terminology: an illustrated handbook. Springer, New York. 483p.
Keeley SC & Jones SB (1977) Taxonomic implications of external pollen morphology to Vernonia (Compositae) in the West Indies. American Journal of Botany 64: 576-584.
Keeley SC & Jones SB (1979) Distribution of the pollen types in Vernonia (Vernoniae: Asteraeae). Systematic Botany 4: 195-202.
Keeley SC, Forsman ZH & Chan R (2007) A phylogeny of the “evil tribe” (Vernoniae: Compositae) reveals Old/New World long distance dispersal: support from separate and combined congruent datasets (trnL-F, ndhF, ITS). Molecular Phylogenetics and Evolution 44: 89-103.
Keeley SC & Robinson H (2009) Vernonieae. In: Funk VA, Susanna A, Stuessy TF & Bayer RJ (eds.) Systematics, evolution and biogeography of Compositae. International Association for Plant Taxonomists, Vienna. Pp. 439-469.
Kingham DL (1976) A study of the pollen morphology of tropical African and certain other Vernonieae (Compositae). Kew Bulletin 31: 9-26.
Lorencini TS, Okano RMC, Gonçalves APS & Nakajima JN (2017) Estudos taxonômicos do gênero Echinocoryne H. Rob. (Asteraceae, Vernonieae) no Brasil. Iheringia 72: 16-32.
Mendonça CBF & Gonçalves-Estevess V (2000) Morfologia polínica de algumas espécies da tribo Vernonieae (Compositae Giseke) ocorrentes na restenga de Carapebus, Rio de Janeiro. Hoehnea 27: 31-142.
Mendonça CBF, Esteves RL & Gonçalves-Estevess V (2007a) Palinotaxonomia de espécies de Lepidaploa (Cass.) Cass. (Vernoniae-Compositae) ocorrentes no sudeste do Brasil. Revista Brasileira de Botânica 30: 71-78.
Mendonça CBF, Souza MA, Gonçalves-Estevess V & Esteves RL (2007b) Palinotaxonomia de espécies de Chrysoalaena H. Rob., Echinocoryne H. Rob. e Stenocephalum Sch. Bip. (Vernoniae-Compositae) ocorrentes no sudeste do Brasil. Acta Botanica Brasilia 21: 627-639.
Oliveira VM, Forni-Martins ER & Semir J (2007) Cytotaxonomy of species of Vernonia, section Lepidaploa, group Axilliflorae (Asteraceae, Vernonieae). Botanical Journal of the Linnean Society 154: 99-108.
Oliveira VM, Semir J & Forni-Martins ER (2012) Chromosome Numbers and Karyotypes of Species of Vernonia sect. Lepidaploa (Asteraceae: Vernonieae). Folia Geobotanica 47: 93-103.
Payne WW & Skvarla JJ (1970) Electron microscope study of Ambrosia pollen (Compositae: Ambrosieae). Grana 10: 89-100.
Punt W, Hoen PP, Blackmore S, Nilsson S & Le Thomas A (2007) Glossary of pollen and spore terminology. Review of Paleobotany and Palynology 143: 1-81.
Robinson H (1987a) Studies of the Lepidaploa complex (Vernoniae: Asteraeae). I. The genus Stenocephalum Sch. Bip. Proceedings of The Biological Society of Washington 100: 578-583.
Robinson H (1987b) Studies of the Lepidaploa complex (Vernoniae: Asteraeae). II. A new genus, Echinocoryne. Proceedings of The Biological Society of Washington 100: 584-589.
Robinson H (1988) Studies in the Lepidaploa complex (Vernoniae: Asteraeae). V. The new genus
Chrysolaena. Proceedings of The Biological Society of Washington 100: 952-958.

Robinson H (1990) Studies in the Lepidaploa complex (Vernonieae: Asteraceae). VII. The genus Lepidaploa. Proceedings of The Biological Society of Washington 103: 464-498.

Robinson H (1992) The Asteraceae of the Guianas, III: Vernonieae and restoration of the genus Xiphochaeta. Rhodora 94: 348-361.

Robinson H (1999) Generic and subtribal classification of American Vernonieae. Smithsonian Contributions to Botany 89: 1-116.

Robinson H & Marticorena C (1986) A palynological study of the Liabeae (Asteraceae). Smithsonian Contributions to Botany 64: 1-50.

Skvarla JJ, Turner BL, Patel VC & Tomb AS (1977) Pollen morphology in the Compositae and in morphologically related families. In: Heywood VH, Harborne JB & Turner BL (eds.) The Biology and Chemistry of the Compositae. Vol. 1. Academic Press, London. Pp. 141-248.

Stix E (1960) Pollen morphologische Untersuchungen an Compositen. Grana Palynologica 2: 41-104.

Sullivan VI (1975) Pollen and pollination in the genus Eupatorium (Compositae). Canadian Journal of Botany 53: 582-589.

Via do Pico GM & Dematteis M (2012) Chromosome number, meiotic behavior and pollen fertility of six species of Chrysolaena (Vernonieae, Asteraceae). Caryologia 65: 176-181.

Via do Pico GM & Dematteis M (2013) Taxonomic implications from the pollen morphology in the genus Chrysolaena (Vernonieae, Asteraceae). Palynology 37: 177-188.

Via do Pico GM & Dematteis M (2014) Cytotaxonomy of two species of genus Chrysolaena H. Robinson, 1988 (Vernonieae, Asteraceae) from Northeast Paraguay. Comparative Cytogenetics 8: 125-137.

Via do Pico GM, Pérez YJ, Angulo MB & Dematteis M (2019) Cytotaxonomy and geographic distribution of cytotypes of species of the South American genus Chrysolaena (Vernonieae, Asteraceae). Journal of Systematic and Evolution 57: 451-467.