Acta Botanica Brasilica 26(1): 46-57. 2012.

Pollen morphology of the genus *Eremanthus* Less. (Vernonieae, Asteraceae)

Benoît Loeuille[1], Raquel Maria Batista Souza-Souza[2], Vanessa Holanda Righetti Abreu[2], Cláudia Barbieri Ferreira Mendonça[2] and Vania Gonçalves-Esteves[2,3]

Recebido em 2/10/2011. Aceito em 7/11/2011

RESUMO

(Morfologia polínica de espécies do gênero *Eremanthus* Less. (Vernonieae, Asteraceae)). Com a finalidade de avaliar a importância da morfologia polínica para a taxonomia de *Eremanthus* (Vernonieae, Asteraceae) em nível genérico e infragenérico e fornecer dados adicionais para a sua reconstrução filogenética, os grãos de pólen de 20 das 23 espécies do gênero foram examinados usando a microscopia de luz e eletrônica de varredura. Os grãos de pólen foram acetolisados, medidos, descritos e ilustrados sob microscópio de luz. Para a análise em microscópio eletrônico de varredura foram utilizados grãos de pólen com e/ou sem tratamento químico. As espécies apresentaram grãos de pólen isopolares, oblato-esferoidais, na maioria dos táxons, mais raramente prolato-esferoidais ou suboblatos, âmbito subtriangular, tricolporados e subechinolofados. A variação entre os caracteres quantitativos não se correlacionam com a subdivisão macromorfológica do gênero nem com os limites genéricos ou específicos.

Palavras-chave: Lychnophorinae, Compositae, taxonomia, palinologia

ABSTRACT

(Pollen morphology of the genus *Eremanthus* Less. (Vernonieae, Asteraceae)). In order to evaluate the significance of the pollen morphology for generic and infrageneric taxonomy of the genus *Eremanthus* (Vernonieae, Asteraceae), and to provide additional data for its phylogenetic reconstruction, the pollen of 20 of the 23 species of the genus was examined using light and scanning electron microscopy. Acetolysed pollen grains were measured, described, and illustrated using light microscopy, while non-acetolysed pollen grains were analyzed using scanning electron microscopy. Pollen grains of these species are isopolar, oblate-spheroidal in most of the species, more rarely prolate spheroidal or suboblate, subtriangular amb, tricolporate and subechinolophate. The variation among quantitative characters does not correlate with the macromorphological subdivision of the genus or with the generic or specific limits.

Key words: Lychnophorinae, Compositae, taxonomy, palynology

Introduction

The tribe Vernonieae Cass. (Asteraceae) contains c. 1500 species distributed mostly in the tropical parts of the world with two major centers of diversification: southeastern Brazil and the central region of Africa (Robinson 1999, 2006/2007; Keeley & Robinson 2009). The 129 genera are placed into 21 subtribes mainly defined by their inflorescence pattern, pollen morphology, chemical composition and chromosome number (Keeley & Robinson 2009). Lychnophorinae is one of the biggest subtribes of Vernonieae, and includes ca. 100 species (11 genera) from the *cerrado* and *campos rupestres* of Brazil. This subtribe is defined by the lack of enlarged nodes or sclerified cells at the base of the styles, usually the extensive presence of a pubescence of T-shaped hairs, presence of sclerified cells and lack of glands on the anther appendages (Robinson 1992, 1999, 2007; Keeley & Robinson 2009).

Eremanthus, a genus of c. 23 species, endemic to Brazil, is a typical element of the *cerrado* and *campo rupestre* floras (Keeley & Robinson 2009). Robinson (1980) excluded herbaceous elements from *Eremanthus* and MacLeish (1984, 1987) recircumscribed the genus synonymising *Vanillosmopsis* (with deciduous inner pappus setae) under *Eremanthus* (with persistent inner pappus setae) and transferring nine species from *Eremanthus* to *Vernonia*. Robinson (1999) restricted the concept of *Vernonia* to North American taxa, and therefore had to reintegrate five of the latter excluded species into *Eremanthus*—*E. crotonoides* (DC.) MacLeish, *E. leucodendron* Mattf., *E. mollis* Sch. Bip., *E. pabstii* G. M.

---

[1] Universidade de São Paulo, Instituto de Biociências, Departamento de Botânica, São Paulo, SP, Brazil
[2] Universidade Federal de Rio de Janeiro, Museu Nacional, Departamento de Botânica, Rio de Janeiro, RJ, Brazil
[3] Author for correspondence: esteves.vr@gmail.com

Barroso and *E. veadeiroensis* H. Rob.—without specific morphological investigations. The narrower concept of *Eremanthus*, i.e., including *Vanillosmopsis* but not *Paralychnophora* (MacLeish 1987, Hind 2000), is here followed (for a different point of view, see Robinson 1997, 1999, 2006/2007).

Pollen characters of Asteraceae have been shown to be particularly variable and form useful patterns in the context of phylogenies. Such patterns could be used to support hypotheses of relationships, or provide diagnostic characters for groups at different levels (Wortley *et al.* 2007, Wortley *et al.* 2008, Blackmore *et al.* 2009). Blackmore *et al.* (2009) noticed that Vernonieae provides an example where a large number of pollen characters are congruent with the relationships presented in the Asteraceae supertree (Funk *et al.* 2005). Blackmore *et al.* (2009) provide putative synapomorphies for groups, most of them concerning African clades. Vernonieae pollen grains are usually lophate or sublophate, tricolporate or triporate, with either a continuous or discontinuous punctate or micropunctate tectum, and are with or without spines (Keeley & Robinson 2009; for a detailed description see Blackmore *et al.* 2009). The large pollen diversity of the tribe has been used extensively in taxonomic delimitations at generic and subtribal levels (Jones 1979, 1981, Bolick & Keeley 1994; Keeley & Robinson 2009). Kingham (1976) created six pollen Types (I–VI) for the tribe, based on the study of 85 species (mostly African). Keeley and Jones (1977, 1979) also identified six basic Types (A–F) to which additional variations have been added (Robinson 1999). Currently, ten pollen Types are recognised for the tribes (Dematteis & Pire 2008). Using mainly the classification of Keeley and Jones, several authors have analysed and described pollen grains of Vernonieae, mostly of *Vernonia s.l.* (Keeley & Jones 1977, 1979; Jones 1979, 1981; Robinson 1987a,b,c, 1988a,b,c, 1990; Skvarla *et al.* 2005; Mendonça & Gonçalves-Esteves 2000; Mendonça *et al.* 2007a,b,c, 2009, 2010; Dematteis & Pire 2008; Angulo & Dematteis 2010).

The pollen grains of Lychnophorinae are tricolporate, echinate, sublophate with a perforated tectum continuous between colpi (Type "A") (Robinson 1992, 1999; Keeley & Robinson 2009). The endoaperture is usually lalongate (Peçanha *et al.* 2008). The Type "A" pollen is considered a reversion from more strongly lophate ancestors in the Vernonieae, but it is nevertheless one of the most common forms in the tribe and is consistent in many groups such as the Piptocarphinae, *Vernonia s.s.* and *Vernonanthura* (Robinson 1990, 1992, 1999). Robinson (1999) suggested that due to common reversion of lophate pollen to Type "A", co-occurrence in different groups of the Vernonieae may have little phylogenetic significance.

The pollen Type of *Eremanthus* was initially described by Stix (1960) (based on *E. glomerulatus* Less. and *E. polycephalus* (DC.) MacLeish) as *Lychnophora*-type, and latter called Type "A" by Keeley and Jones (1979). Kingham (1976) assigned the pollen of *E. crotonoides* (as *Vernonia crotonoides* DC.) to his category VI: grains spherical, tricolporate, micropunctate, subechinolophate tending to echinate. Peçanha *et al.* (2008) described pollen grains of *Paralychnophora bicolor* (DC.) MacLeish (as *E. bicolor* (DC.) Baker) and *E. erythropappus* (DC.) MacLeish (as *Vanillosmopsis erythropappa* (DC.) Baker). This study revealed some interesting variation of the exine pattern at the generic level: *Paralychnophora* having a sublophate exine and *Eremanthus* a subechinolophate one. Peçanha *et al.* (2008) concluded that their data do not support the inclusion of *Vanillosmopsis* in *Eremanthus* (inclusion made by MacLeish in 1987). Such conclusion however cannot be considered valid, since they actually compared pollen grains of *Paralychnophora* with *Eremanthus* subg. *Vanillosmopsis* MacLeish, and not the latter with *E.* subg. *Eremanthus* Sch. Bip. as intended.

The present study aimed to conduct a comprehensive examination of the pollen morphology in the genus *Eremanthus*, using LM and SEM, with almost complete species coverage, in order to evaluate the significance of this structure for generic and infrageneric taxonomy and to provide additional data for the phylogenetic reconstruction.

Materials and methods

Pollen grains of 20 species of *Eremanthus* were examined (see Appendix). The samples were obtained from anthers of flower buds from specimen kept at the herbaria ESA, HRB, HUEFS, IBGE, MBM, SP, SPF, UB and UEC; acronyms according to Holmgren *et al.* (1990).

The terminology used for descriptions follows Punt *et al.* (2007), taking into consideration size, form, number of apertures and the ornamentation of the sexine. For the light microscopy (LM) study, the pollen grains were photomicrographed with a Sony Cyber-shot DSC-W7 digital camera coupled with a Zeiss Axiostar Plus microscope. For scanning electron microscopy (SEM), acetolysed and non-acetolysed pollen samples were placed on aluminium stubs covered with carbon tape and sputter-coated with a thin layer of gold palladium (c. 150 Å). The samples were analysed using a ZEISS DS M960 microscope at Laboratório de Ultraestrutura Celular Hertha Meyer, Inst. de Biofísica (UFRJ) and a JEOL JSM-5800 microscope at Departamento de Invertebrados do Museu Nacional (UFRJ).

Pollen grains were prepared for light microscopy by the acetolysis method of Erdtman (1952), modified by Melhem *et al.* (2003). Measurements in equatorial view (PD= polar diameter and ED=equatorial diameter) were randomly taken on 25 pollen grains per sample. Measurements of equatorial diameter from polar view (EDPV) and apocolpus were randomly taken on 10 pollen grains distributed on, at least, three different slides.

Statistical procedures were carried out, calculating the arithmetic mean ($_X$); the standard deviation of the mean (SD$_X$), the mean deviation (S$_X$), the coefficient of variation (CV%), the confidence interval at 95% and the variation range. For the measurements of the other characteristics, such as endoapertures size, layers of exine and pollen grain diameters of comparison material, the arithmetic mean of 10 measurements were calculated randomly chosen from, at least, three different slides (Salgado-Labouriau *et al.* 1965; Salgado-Labouriau 1973).

Results

The palynological description has been organised according to the following characteristics: size, polarity, shape, apertures and exine surface. The results of the measurements are summarized in Tab. 1-3, Fig. 1-5.

Polarity, size and shape

Pollen grains are isopolar, large, medium sized only in *E. auriculatus* (Fig. 1D), *E. capitatus*, *E. erythropappus*, *E. polycephalus*, *E. seidelii* and *E. veadeiroensis*, oblate spheroidal in most species, prolate spheroidal in *E. argenteus* and *E. veadeiroensis*, suboblate in *E. uniflorus*, subtriangular amb, small polar area in most species, very small in *E. pohlii* and large in *E. argenteus* and *E. auriculatus* (Tab. 1, 2).

Apertures

Pollen grains are 3-colporate; colpus long (values range from 23.9 µm in *E. auriculatus* and *E. capitatus* to 33 µm in *E. elaeagnus*); colpus wide, width varying from 4.6 µm (*E. mattogrossensis*) to 9.1 µm and 9.6 µm (*E. elaeagnus* and *E. glomerulatus*). The endoapertures are lalongate (smallest diameter: 1.6 µm in *E. mollis*; largest one: 6.8 µm in *E. mattogrossensis*) (Tab. 3). Some species have endoapertures with a median constriction, as in *E. capitatus* (Fig. 1I), *E. crotonoides* (Fig. 2C), *E. erythropappus* (Fig. 2I), *E. graciellae* (Fig. 3E), *E. leucodendron* (Fig. 3K), *E. polycephallus* (Fig. 4H), *E. rondoniensis* (Fig. 4K), *E. uniflorus* (Fig. 5F).

Exine

The exine is thick: values range from 5.1 (*E. rondoniensis*) to 13.5 mm (*E. argenteus*). The sexine is subechinolophate, muri tall, sinuous, densely microperfurate at the base of muri and one microperfuration at the base of spine. The spines show variation in size: the longest spines were found in *E. pohlii* (12.2 µm) (Fig. 4F) and the shortest ones in *E. veadeiroensis* (4 µm) (Fig. 5H), the width of the spines ranges from 2 (*E. veadeiroensis*) to 7.4 µm (*E. incanus*). The distance between the spines varies widely, ranging from 3.4 (*E. veadeiroensis*) to 11.4, 11.7 and 11.8 mm (*E. glomerulatus*, *E. pohlii* and *E. uniflorus*, respectively). The sexine is always thicker than the nexine (Tab. 3).

Discussion

In the present study 20 species of *Eremanthus* were analysed (87% of the species), including all taxa placed by Robinson (1999) in the genus (except *Paralychnophora* species). The pollen of *Eremanthus* is isopolar, oblate spheroidal in most of the species, more rarely prolate spheroidal or suboblate, subtriangular amb, tricolporate and subechinolophate, i.e., corresponding to Type «A». Many of the quantitative characters have some variability, however the results show considerable overlap between species. Therefore, it was not possible to construct a palynological key to identify the species or to define some pollen subtypes.

The pollen shape is the only qualitative character that varies in the genus. *Eremanthus argenteus* MacLeish & H. Schumach. and *E. veadeiroensis* H. Rob. have prolate spheroidal pollen grains, the former belongs to the subg. *Eremanthus* and the latter was not included in *Eremanthus* by MacLeish (1984, 1987) because of its densely pubescent stems, loose inflorescence and a large number of florets per capitulum (8–11); these three characters are uncommon within the genus. Phylogenetic analyses based on molecular and morphological data (Loeuille 2011) have indicated that *E. veadeiroensis* is closely related to *E. elaeagnus* (Mart. ex DC.) Sch. Bip. of subg. *Pseuderemanthus*. The two species of subg. *Pseuderemanthus* (*E. elaeagnus* and *E. seidelii* MacLeish & H. Schumach.) have, nonetheless, an oblate spheroidal pollen as the majority of the species. *Eremanthus argenteus* belongs to *E.* subg. *Eremanthus* sect. *Synglomerulus* MacLeish & H. Schumach. characterised by its simple cyme synflorescence. The two others species of this section (*E. auriculatus* MacLeish & H. Schumach. and *E. cinctus* Baker) have an oblate spheroidal pollen shape, not prolate spheroidal like *E. argenteus.*

The subg. *Vanillosmopsis* is composed of eight species, six of them are included in this study: *Eremanthus capitatus* (Spreng.) MacLeish, *E. erythropappus* (DC.) MacLeish, *E. graciellae* MacLeish & H. Schumach., *E. pohlii* (Baker) MacLeish, *E. polycephalus* (DC.) MacLeish and *E. uniflorus* MacLeish & H. Schumach. No palynological characters have been found to characterise this subgenus. Based on a macromorphological analysis, Loeuille *et al.* (in prep.) suggested that *E. capitatus*, *E. graciellae* and *E. pohlii* are conspecific. The quantitative characters vary conspicuously between the three species, a variation that encompasses the subgeneric categories, *E. pohlii* having more similar pollen grains of the species of subg. *Eremanthus* than of subg. *Vanillosmopsis*.

The results of phylogenetic analyses (Loeuille 2011) have indicated that *E. crotonoides*, *E. leucodendron* and *E. pabstii* are not closely related to the genus *Eremanthus*. Again, our palynological data did not show any difference between these species and the rest of the genus.

The presence of meaningless differences in pollen between closely related species of the tribe Vernonieae has already been documented. For instance, in the small genus *Eirmocephala* H. Rob., *E. brachiata* (Bentham ex Oersted) H. Rob. has a Type «D» and *E. megaphylla* (Hieron.) H. Rob. Type «A» (Robinson 1987b) pollen. A certain degree of instability of types is also found in *Distephanus*

Table 1. Pollen characters (µm) in equatorial view of *Eremanthus* species (n = 25).

Species	PD			ED			PD/ED
	Variation range	X±SD$_x$	IC (95%)	Variation range	X±SD$_x$	IC (95%)	
E. argenteus	47.5-57.5	52.4±0.5	51.4-53.4	40.0-62.5	51.6±0.9	49.8-53.4	1.01
E. auriculatus	40.0-57.5	45.0±0.7	43.6-46.4	42.5-52.5	48.0±0.5	47.0-49.0	0.93
E. capitatus	37.5-47.5	41.6±0.5	40.6-42.6	35.0-50.0	45.8±0.6	44.6-47.0	0.90
E. cinctus	55.0-67.5	61.2±0.5	60.2-62.2	61.8-72.5	67.7±0.5	66.7-68.7	0.90
E. crotonoides	42.5-52.5	46.1+0.3	45.5-46.7	45.0-60.0	51.1+0.5	50.1-52.1	0.90
E. elaeagnus	47.5-55.5	52.5±0.3	51.9-53.1	20.0-62.5	55.9±0.5	54.9-56.9	0.93
E. erythropappus	37.5-55.0	44.8±0.7	43.4-46.2	42.5-57.5	49.7±0.8	48.1-51.3	0.90
E. glomerulatus	48.0-61.2	53.7±0.6	52.5-54.9	52.5-61.2	56.3±0.5	55.3-57.3	0.95
E. goyazensis	47.5-55.0	51.5±0.3	50.9-52.1	50.0-57.5	52.9±0.3	52.3-53.5	0.97
E. graciellae	45.0-50.0	47.1±0.3	46.4-47.8	47.5-55.0	50.6±0.4	49.8-51.4	0.93
E. incanus	42.5-55.0	47.4±0.6	46.2-48.6	47.5-57.5	51.3±0.5	50.3-52.3	0.92
E. leucodendron	47.5-55.0	51.0±0.4	50.2-51.8	52.5-62.5	56.2±0.4	55.4-57.0	0.90
E. mattogrossensis	48.8-55.0	52.2±0.4	51.4-53.0	50.0-57.5	53.5±0.4	52.7-54.3	0.97
E. mollis	50.0-60.0	56.2±0.4	55.4-57.0	55.0-65.0	61.6±0.5	60.6-62.6	0.91
E. pohlii	52.5-62.5	57.7±0.4	56.9-58.5	57.5-65.2	61.6±0.4	60.8-62.4	0.93
E. polycephalus	40.0-52.5	46.0±0.5	45.0-47.0	46.2-53.8	49.2±0.4	48.4-50.0	0.93
E. rondoniensis	52.5-62.5	57.7±0.6	56.5-58.9	57.5-67.5	61.7±0.5	60.7-62.7	0.93
E. seidelii	40.0-46.2	43.2±0.3	42.6-43.8	45.0-50.0	47.3±0.2	46.9-47.7	0.91
E. uniflorus	42.5-50.0	47.0±0.3	46.4-47.6	50.0-54.0	53.9±0.5	52.9-54.9	0.87
E. veadeiroensis	37.5-45.0	41.2±0.4	40.4-42.0	35.0-40.0	38.0±0.3	37.4-38.6	1.08

PD - polar diameter; ED – equatorial diameter; X – means; SD$_x$ - standard deviations of the mean; IC – confidence interval

Table 2. Pollen characters (µm) in polar view of *Eremanthus* species (n = 10).

Species	EDPV		Apocolpus		Polar area	
	Variation range	X	Variation range	X	PAI	Size
E. argenteus	46.25-62.5	55.8	27.5-32.5	28.5	0.51	large
E. auriculatus	45.0-50.0	47.5	25.0-27.5	25.2	0.53	large
E. capitatus	42.5-47.5	45.6	10.0-12.5	11.5	0.25	small
E. cinctus	60.0-70.0	65.8	15.0-25.0	19.5	0.29	small
E. crotonoides	47.5-52.5	51.2	20.0-25.0	23.2	0.45	small
E. elaeagnus	47.5-60.0	54.1	10.0-20.0	16.0	0.29	small
E. erythropappus	42.5-53.8	48.7	10.0-20.0	13.0	0.26	small
E. glomerulatus	47.5-60.0	53.6	12.5-20.0	17.7	0.33	small
E. goyazensis	50.0-57.5	53.0	12.5-17.5	14.2	0.26	small
E. graciellae	47.0-52.5	49.4	10.0-15.0	12.5	0.25	small
E. incanus	46.25-51.2	49.5	15.0-25.0	20.0	0.40	small
E. leucodendron	50.5-55.25	53.8	12.5-20.0	15.5	0.28	small
E. mattogrossensis	47.5-55.0	51.6	12.5-25.0	20.5	0.39	small
E. mollis	55.5-63.8	59.7	22.5-30.0	27.5	0.46	small
E. pohlii	55.0-61.2	59.6	12.5-17.5	14.7	0.24	very small
E. polycephalus	45.0-52.5	49.6	20.0-25.0	23.0	0.46	small
E. rondoniensis	56.25-62.5	59.1	15.0-25.0	18.5	0.31	small
E. seidelii	42.5-49.8	46.0	12.5-15.0	13.7	0.29	small
E. uniflorus	49.75-57.5	52.2	12.5-20.0	15.5	0.29	small
E. veadeiroensis	50.0-57.5	51.7	12.5-17.5	15.2	0.29	small

EDPV – equatorial diameter in polar view; PAI – polar area index.

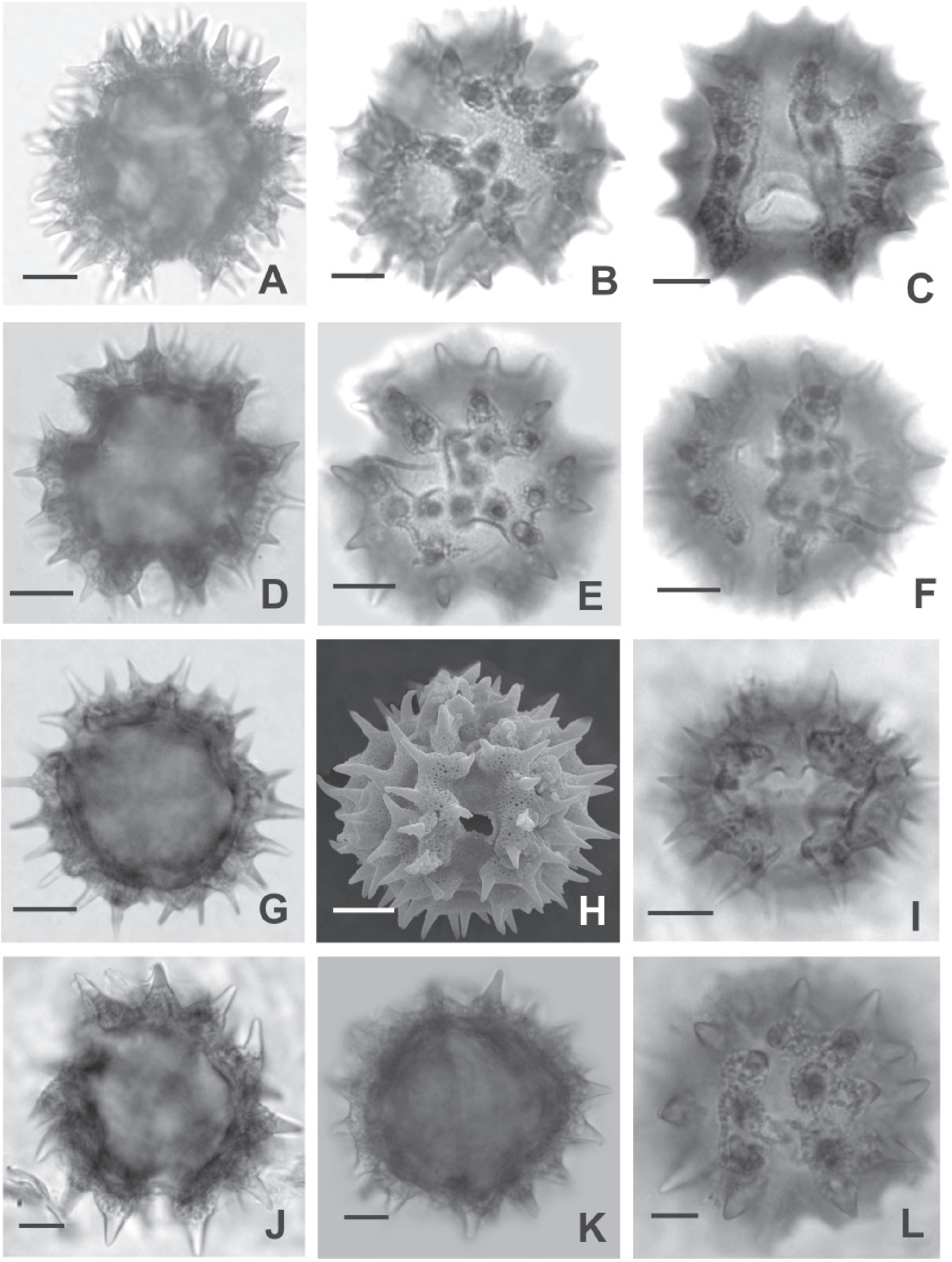

Figure 1. LM and SEM photomicrographs of the pollen grains of *Eremanthus*. A–C. *E. argenteus* – polar view: A. Cross section; B. Surface of apocolpium; C. Lateral view, aperture. D–F. *E. auriculatus* – polar view: D. Cross section; E. Surface of apocolpium; F. Equatorial view, aperture. G–I. *E. capitatus* – polar view: G. cross section; equatorial view: H. Surface of the aperture area (SEM); I. Aperture. J–L. *E. cinctus* – polar view: J. Cross section; equatorial view: K. Cross section; L. Aperture. Barras = 10 mm.

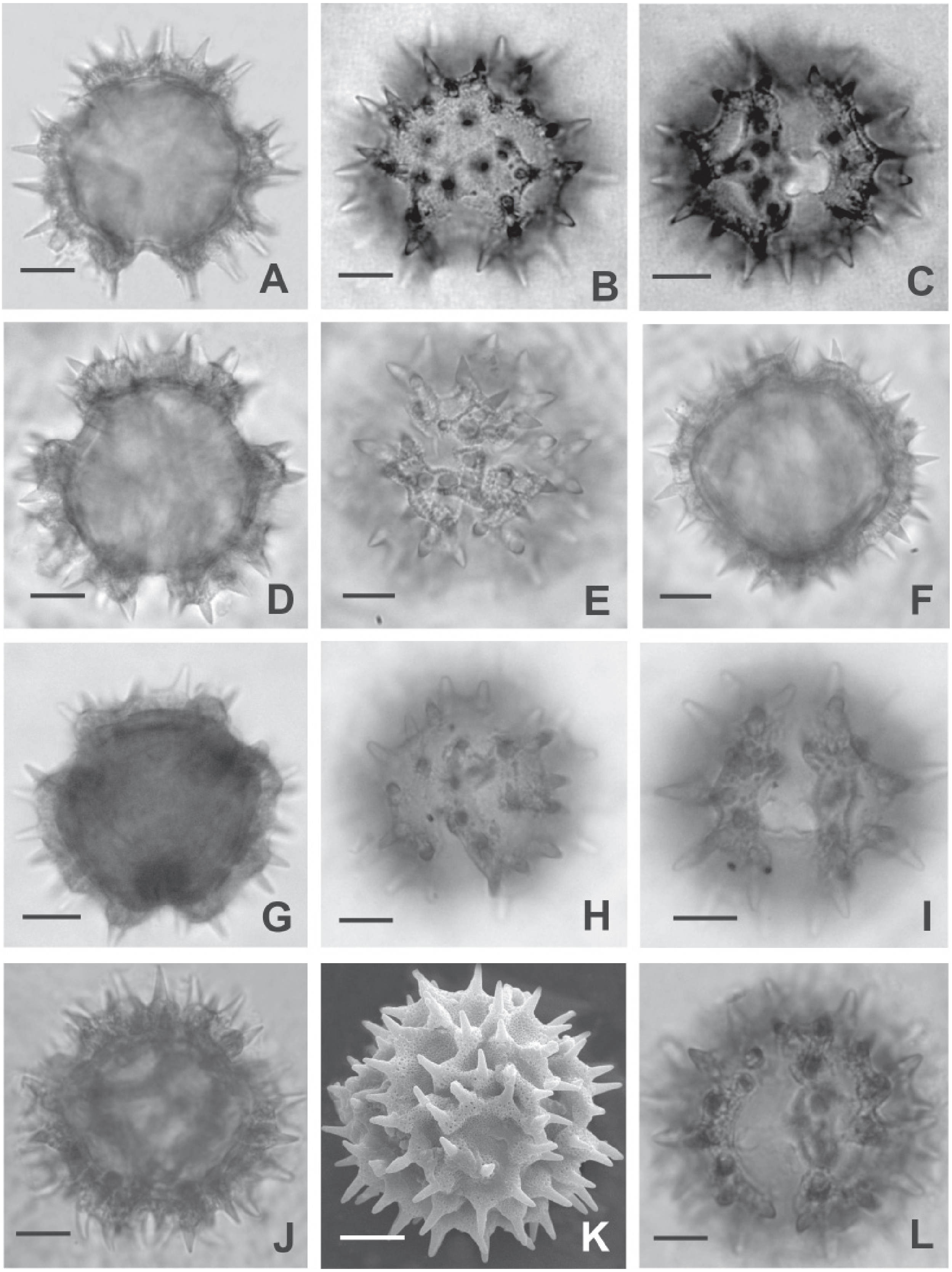

Figure 2. LM and SEM photomicrographs of the pollen grains of *Eremanthus*. A–C. *E. crotonoides* – polar view: A. Cross section; B. Surface of apocolpium; C. Lateral view, aperture. D–F. *E. elaeagnus* – polar view: D. Cross section; E. Surface of apocolpium; F. Equatorial view, cross section and aperture. G–I. *E. erythropappus* – polar view: G. Cross section; H. Surface of apocolpium; equatorial view: I. Aperture. J–L. *E. glomerulatus* – polar view: J. Cross section; equatorial view: K. Surface of mesocolpium (SEM); L. Aperture. Barras = 10 mm.

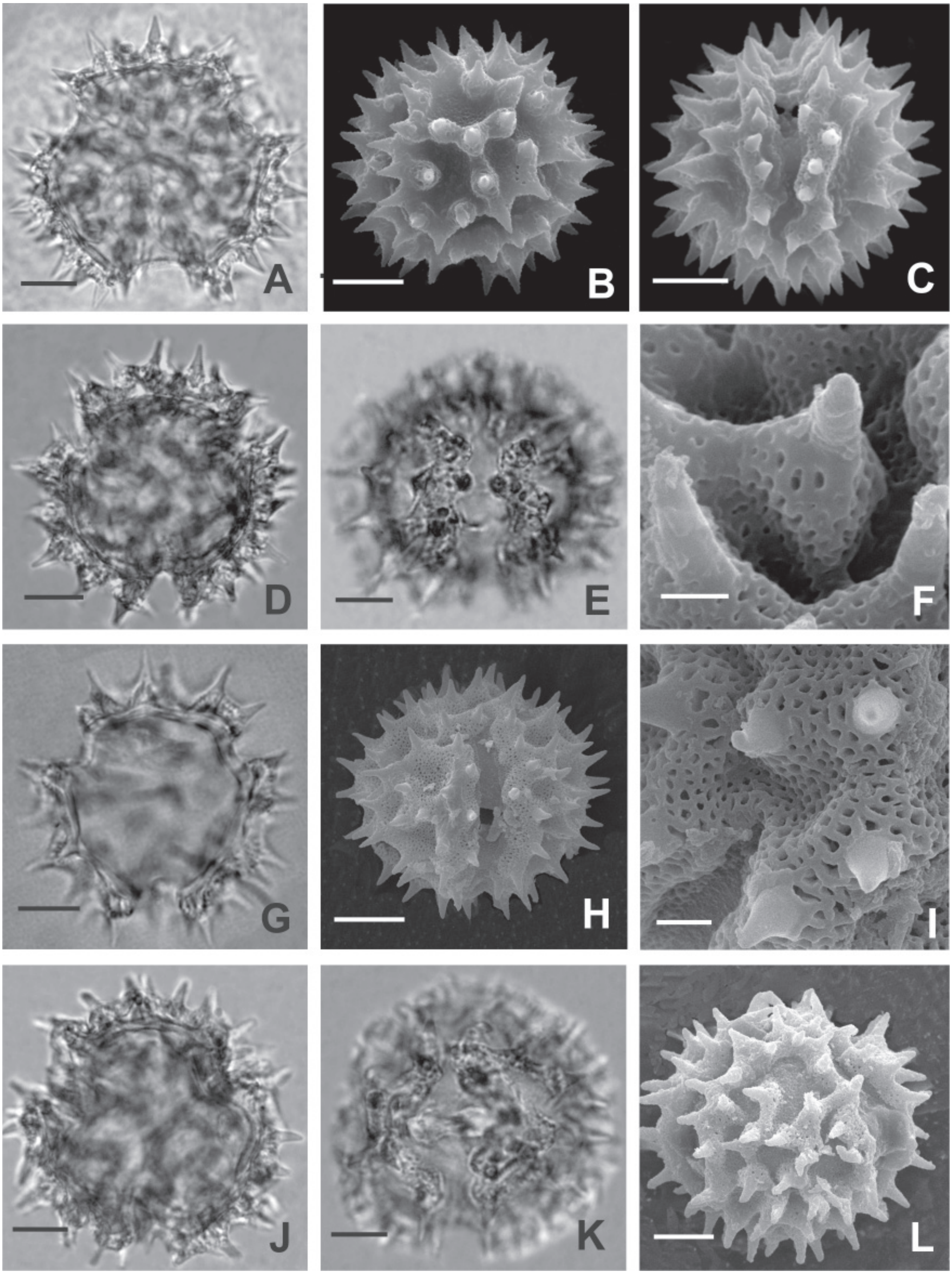

Figure 3. LM and SEM photomicrographs of the pollen grains of *Eremanthus*. A–C. *E. goyazensis* – polar view: A. Cross section; equatorial view: B. Surface of apocolpium (SEM); C. Aperture (SEM). D–F. *E. graciellae* – polar view: D. Cross section; equatorial view: E. Aperture; F. Detail of surface (SEM). G–I. *E. incanus* – polar view: G. Cross section; equatorial view: H. Aperture (SEM), I. Detail of surface (SEM). J–L. *E. leucodendron* – polar view: J. Cross section; equatorial view: K. Aperture; L. Surface of mesocolpium (SEM). Barras = 10 mm; F, I = 2 mm.

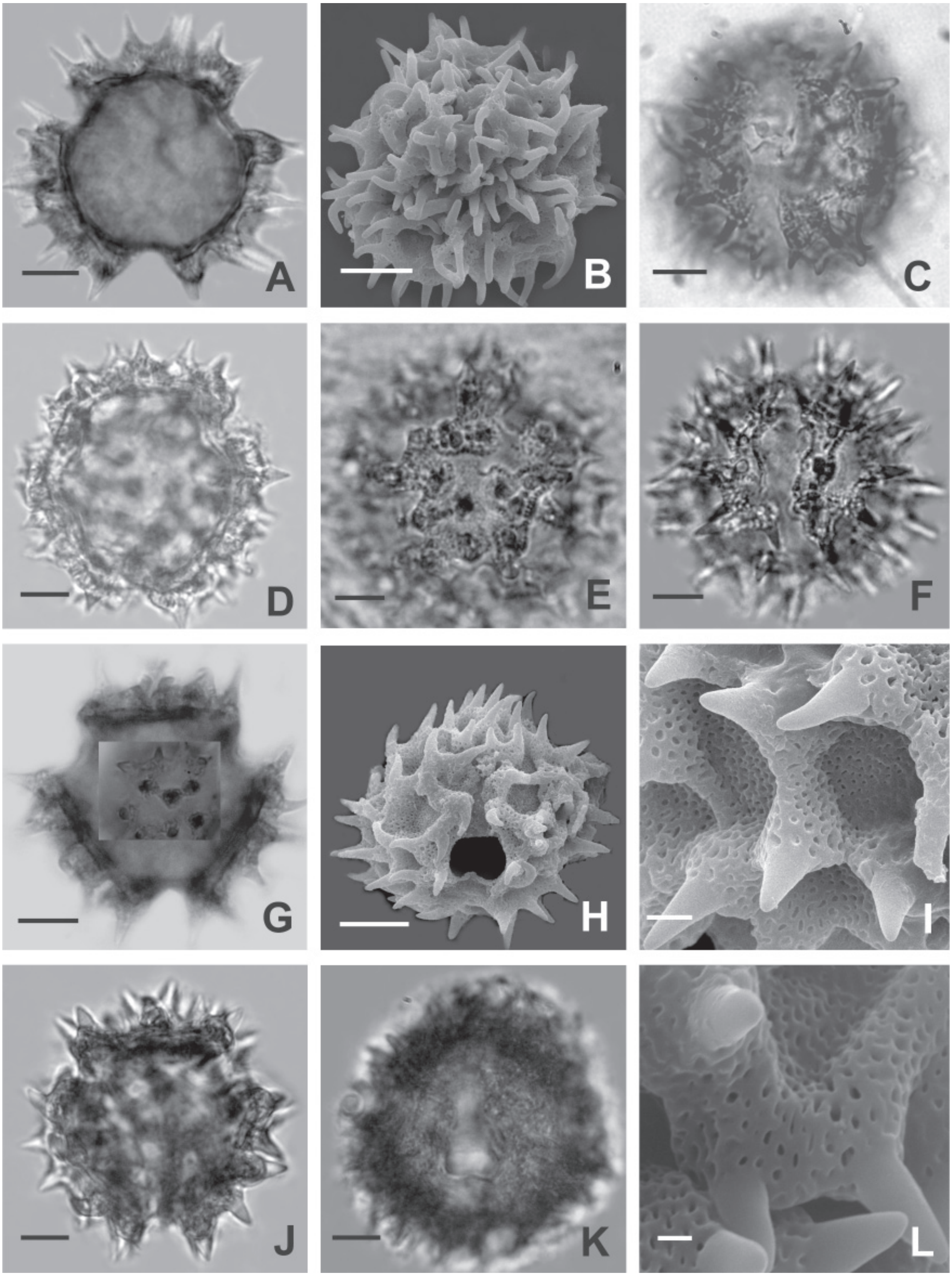

Figure 4. LM and SEM photomicrographs of the pollen grains of *Eremanthus*. A–C. *E. mattogrossensis* – polar view: A. Cross section; B. Surface of apocolpium (SEM); C. Equatorial view, aperture. D–F. *E. pohlii* – polar view: D. Cross section; E. Surface of apocolpium; F. Equatorial view, aperture. G–I. *E. polycephalus* – polar view: G. Cross section; equatorial view: H. Aperture; polar view: I. Detail of surface (SEM). J–L. *E. rondoniensis* – polar view: J. Cross section; equatorial view: K. Aperture; L. Detail of surface (SEM). Barras = 10 mm; I = 2 mm; L = 1 mm.

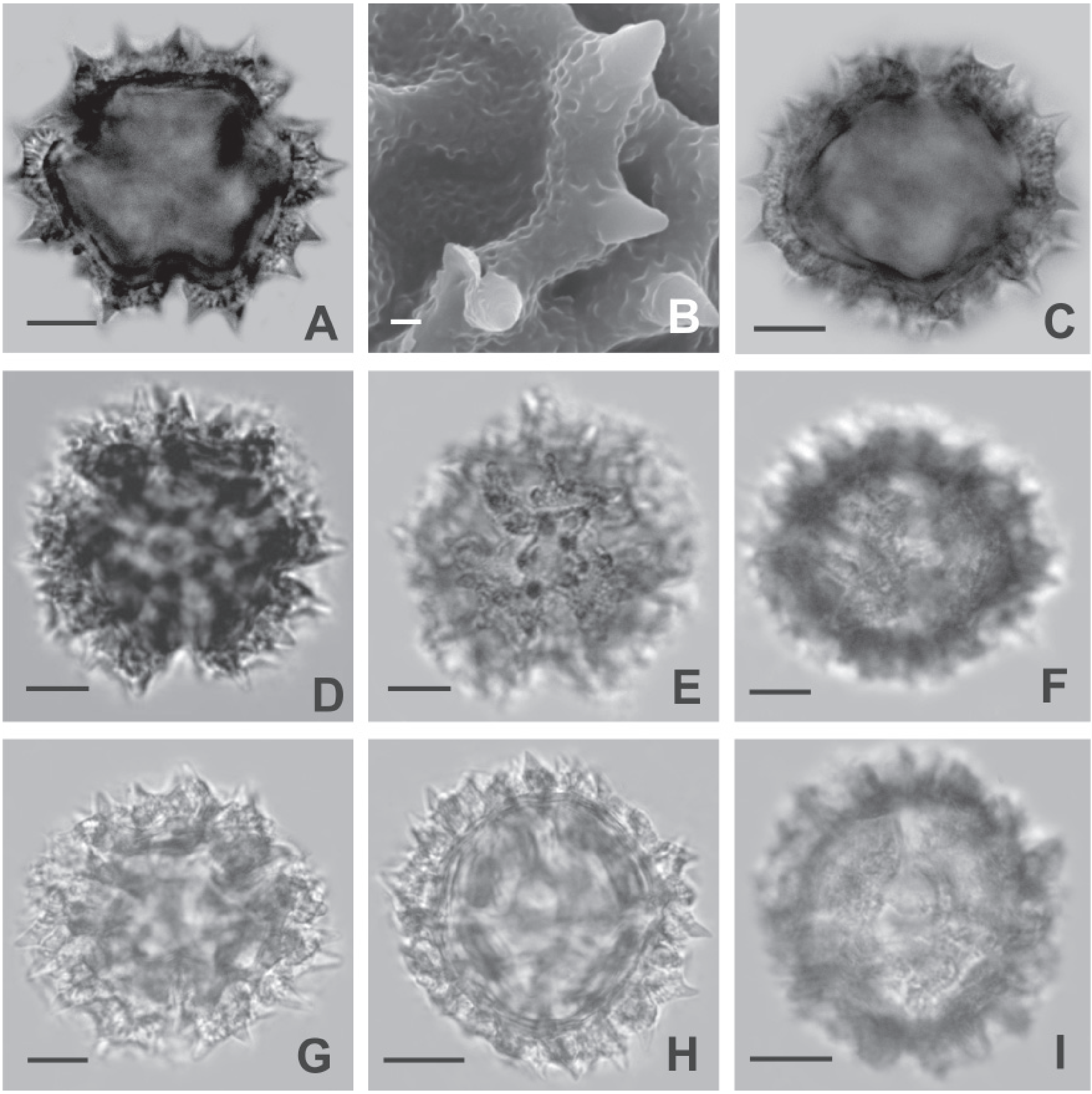

Figure 5. LM and SEM photomicrographs of the pollen grains of *Eremanthus*. A–C. *E. seidelii* – polar view: A. Cross section; B. Detail of surface (SEM); C. Equatorial view, aperture. D–F. *E. uniflorus* – polar view: D. Cross section; E. Surface of apocolpium; F. Equatorial view, aperture. G–I. *E. veadeiroensis* – polar view: G. Cross section; equatorial view: H. Cross section; I. Aperture. Barras = 10 mm.

Cass. (Robinson & Kahn 1986). The case of *Eremanthus* is slightly different because the only variation is found in the quantitative characters, which are usually more difficult to interpret. The pollen grains of the species here analysed are typically subechinolophate and not sublophate, i.e., not Type «A» *sensu* Keeley & Jones (1979) (echinate to sublophate, continuous and microperforate tectum, spines on the ridges of sublophate grains). Therefore one might consider that the *Eremanthus* species are a modified Type «A» (subechinolophate).

Blackmore (2000) emphasizes the importance of determining at which taxonomic hierarchy level the pollen data are most useful. The present study clearly demonstrates that the pollen morphology is taxonomically uninformative at the specific level for the genus *Eremanthus* and probably to a certain degree at the generic level in the subtribe Lychnophorinae. Therefore, the general idea that pollen morphology is significant in delimitating at specific and generic levels into the entire tribe Vernonieae (Angulo & Dematteis 2010) has to be rectified; the situation in some

Table 3. Pollen measurements (μm) of endoapertures and exine layers of *Eremanthus* species (n = 10).

Species	Colpus		Endoaperture		Exine layers				Spine		
	length	width	length	width	Exine	Nexine	Sexine*	Sexine**	length	width	distance***
E. argenteus	25.6	5.5	2.8	11.3	13.5	1.0	12.5	1.1	11.4	6.4	10.7
E. auriculatus	23.9	5.2	4.4	5.4	9.6	1.0	8.6	1.0	7.6	5.2	7.9
E. capitatus	23.9	5.0	4.2	5.0	10.8	1.0	9.8	1.0	8.8	4.4	8.6
E. cinctus	29.4	7.7	4.6	10.9	7.2	0.9	6.3	0.9	5.4	3.7	6.1
E. crotonoides	24.3	6.1	5.7	26.1	11.9	0.9	11.0	0.9	10.1	4.9	9.9
E. elaeagnus	33.0	9.1	4.0	14.9	12.1	1.0	11.1	1.6	9.5	6.9	10.5
E. erythropappus	28.9	7.1	5.8	7.1	12.3	1.8	10.5	2.1	8.4	5.0	8.3
E. glomerulatus	31.3	9.6	4.9	9.6	13.2	1.8	11.4	1.4	10.0	6.0	11.8
E. goyazensis	29.4	7.2	5.7	11.2	12.3	1.0	11.3	1.2	10.1	5.6	10.7
E. graciellae	28.8	6.1	4.2	9.9	11.8	1.1	10.7	1.3	9.4	5.5	10.2
E. incanus	25.5	5.2	4.1	8.7	12.5	1.2	11.3	1.2	10.3	7.4	10.7
E. leucodendron	32.1	7.3	5.9	12.4	12.6	1.1	11.5	1.2	10.3	5.9	10.7
E. mattogrossensis	28.3	4.6	6.8	7.5	10.4	1.1	9.3	1.0	8.3	4.5	7.7
E. mollis	23.2	5.3	1.6	12.5	11.0	1.0	10.0	1.0	9.0	5.4	5.9
E. pohlii	31.0	6.4	5.2	10.7	14.3	1.0	13.3	1.1	12.2	6.3	11.7
E. polycephalus	24.6	5.8	4.2	11.0	11.5	1.0	10.5	1.0	9.5	5.9	8.9
E. rondoniensis	31.2	6.7	6.1	11.7	5.1	0.9	4.2	0.9	4.3	2.8	4.0
E. seidelii	27.3	5.3	4.1	8.1	10.2	1.0	9.2	1.0	8.2	4.9	9.0
E. uniflorus	28.3	5.9	4.0	9.7	12.6	1.3	11.3	1.0	10.3	5.6	11.4
E. veadeiroensis	25.5	5.2	4.1	13.8	6.0	1.0	5.0	1.0	4.0	2.0	3.4

Sexine * – total sexine; sexine ** – sexine between spines; distance *** – distance between spines

groups (especially the *Lepidaploa* complex) could not be used as a general rule in the tribe.

The absence of variable qualitative characters and the fact that quantitative characters show a high level of homoplasy limit greatly the use of palynological data to reconstruct the phylogeny of the subtribe Lychnophorinae. Keeley & Robinson (2009) arrived at a similar conclusion for Vernonieae. Nonetheless, because Peçanha *et al.* (2008) found sublophate pollen in *Paralychnophora bicolor*, it would be valuable to analyse the pollen grains of more species of that genus and of other genera of the subtribe Lychnophorinae to evaluate how frequent the sublophate pattern occurs and if it could be used in a systematic context.

Conclusions

Pollen Type "A" is present in all the species of the genus *Eremanthus*. No qualitative variation has been found in different species and the variation of quantitative characters does not correlate with the macromorphological subdivision of the genus at the generic or specific limits. These results indicate that palynological data might not be variable enough to be relevant in the delimitation at the specific level and probably at the generic level in the subtribe Lychnophorinae.

Acknowledgements

The authors acknowledge Noêmia Rodrigues Gonçalves (Lab. de Ultraestrutura Celular do Inst. de Biofísica da Univ. Federal do Rio de Janeiro) for the technical support, and FAPERJ (Proc. E-26/110.953/09, supplies for the lab and grant for and fellowship support to the second author), CNPq (fellowship supports for the first, third and last authors), and CAPES (fellowship support to the last author) for the financial support.

Specimens investigated

Eremanthus argenteus MacLeish & H. Schumach. **BRAZIL, Goiás**, Teresina de Goiás, Chapada dos Veadeiros, Souza 24698 (ESA).

E. auriculatus MacLeish & H. Schumach. **BRAZIL, Goiás**, Alto Paraíso, Chapada dos Veadeiros. Loeuille 279 (SPF).

E. capitatus (Spreng) MacLeish. **BRAZIL: Bahia**, Salvador, Metropolitan Park Pituaçu, Teles 35 (SPF).

E. cinctus Baker. BRAZIL: Goiás, Chapadão do Céu, National Park of Emas, Batalha 3038 (SPF).

E. crotonoides Sch. Bip. **BRAZIL: Minas Gerais**, Santa Bárbara, Serra do Caraça, Pirani 338 (SPF).

E. elaeagnus (Mart. ex DC.) Sch. Bip. **BRAZIL: Minas Gerais**, Diamantina, road to Conselheiro Mata, Arbo 4385 (SPF).

E. erythropappus (DC.) MacLeish. **BRAZIL: Minas Gerais**, Datas, Morro do Coco, Mello-Silva CFCR 7997 (SPF).

E. glomerulatus Less. **BRAZIL: Bahia**, Abaíra, Catolés, Mata do Bem Querer, Ganev 271 (SPF).

E. goyazensis (Gardner) Sch. Bip. **BRAZIL: Goiás**, Alto Paraíso, Chapada dos Veadeiros, Moraes 644 (UEC).

E. graciellae MacLeish & H. Schumach. **BRAZIL: Bahia**, Correntina, Biological Reserve Fazenda Jatobá, Aparecida da Silva 1527 (UB).

E. incanus (Less.) Less. **BRAZIL: Minas Gerais**, Diamantina, Cachoeira da Sentinela, Stehmann 2683 (ESA).

E. leucodendron Mattf. **BRAZIL: Bahia**, Rio de Contas, Pico de Itabira, Harley PCD 4277 (SPF).

E. mattogrossensis Kuntze. **BRAZIL: São Paulo**, Pedregulho, Estreito, Sasaki 527 (SPF).

E. mollis Sch. Bip. **BRAZIL: Minas Gerais**, Capitólio, Represa de Furnas, Vichnewski s.n. (UEC n° 19067).

E. pohlii (Baker) MacLeish. **BRAZIL: Minas Gerais**, São Gonçalo do Abaeté, Hatschbach, G. 67936 (MBM).

E. polycephalus (DC.) MacLeish. **BRAZIL: Minas Gerais**, Grão Mogol, estrada para Virgem da Lapa, Souza 25838 (SPF).

E. rondoniensis MacLeish & H. Schumach. **BRAZIL: Mato Grosso**, Arenápolis, Chapada dos Parecis, Hatschbach 62692 (MBM).

E. seidelii MacLeish & H. Schumach. **BRAZIL: Minas Gerais**, Formiga, Schumacher 3027 (UEC).

E. uniflorus MacLeish & H. Schumach. **BRAZIL: Goiás**, Alto Paraíso, National Park Chapada dos Veadeiros, Mendonça 2246 (IBGE).

E. veadeiroensis H. Rob. **BRAZIL: Goiás**, Alto Paraíso, Chapada dos Veadeiros, King 8831 (UB).

References

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

Blackmore, S. 2000. The palynological compass: the contribution of palynology to systematics. Pp. 161-177. In Nordenstam, B. El-Ghazaly, G. & Kassas, M. (Eds.). **Plant Systematics for the 21st Century** London, Portland Press.

Blackmore, S.; Wortley, A.H.; Skvarla, J.J. & Robinson, H. 2009. Evolution of pollen in the Compositae. Pp. 101-130. In Funk, V.A.; Susanna, A.; Stuessy, T.F. & Bayer, R.J. (Eds), **Systematics, evolution and biogeography of Compositae**. Wien, IAPT.

Bolick, M.R. & Keeley, S.C. 1994. Pollen morphology and classification of the Vernonieae. **Acta Botanica Gallica 141**: 279-284.

Dematteis, M. & Pire, S.M. 2008. Pollen morphology of some species of *Vernonia s. l.* (Vernonieae, Asteraceae) from Argentina and Paraguay. **Grana 47**: 117-129.

Erdtman, G. 1952. **Pollen morphology and plant taxonomy – Angiosperms**. Stockholm, Almqvisit & Wiksel.

Funk, V.A.; Bayer, R.J.; Keeley, S.C.; Chan, R.; Watson, L.; Gemeinholzer, B.; Schilling, E.; Panero, J.L.; Baldwin, B.G.; Garcia-Jacas, N.; Susanna, A. & Jansen, R.K. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the **Compositae. Biologiske Skrifter 55**: 343-374.

Hind, D.J.N. 2000. Two new species of *Paralychnophora* (Compositae: Vernonieae) from Bahia, Brazil. **Kew Bulletin 55**: 367-379.

Holmgren, P.K.; Holmgren, N.H. & Bainett, L.G. 1990. **Index Herbariorum**. New York, New York Botanical Garden.

Jones, S.B. 1979. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World. **Rhodora 81**: 425-447.

Jones, S.B. 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the Old World. **Rhodora 83**: 59-75.

Keeley, S.C. & Jones, S.B. 1977. Taxonomic implications of external pollen morphology to *Vernonia* (Compositae) in the West Indies. **American Journal of Botany 64**: 576-584.

Keeley, S.C. & Jones, S.B. 1979. Distribution of the pollen types in *Vernonia* (Vernonieae: Asteraceae). **Systematic Botany 4**: 195-202.

Keeley, S.C. & Robinson, H. 2009. Vernonieae. In: Funk, V.A.; Susanna, A.; Stuessy, T.F.& Bayer, R.J. (Eds). **Systematics, evolution and biogeography of Compositae.** Pp. 439-469. Wien: IAPT.

Kingham, D.L. 1976. A study of the pollen morphology of tropical african and certain other Vernonieae (Compositae), **Kew Bulletin 31**: 9-26.

Loeuille, B. 2011. Towards a phylogenetic classification of Lychnophorinae (Asteraceae). PhD Thesis. São Paulo, Universidade de São Paulo.

MacLeish, N.F.F. 1984. Eight new combinations in *Vernonia* (Compositae: Vernonieae). **Systematic Botany 9**: 133-136.

MacLeish, N.F.F. 1987. Revision of *Eremanthus* (Compositae: Vernonieae). **Annals of the Missouri Botanical Garden 74**: 265-290.

Melhem, T.S.; Cruz-Barros, M.A.V.; Corrêa, A.M.S.; Makino-Watanabe, H.; Silvestre-Capelato, M.S.F. & Gonçalves-Esteves, V. 2003. Variabilidade polínica em plantas de Campos de Jordão (São Paulo, Brasil). **Boletim do Instituto de Botânica, São Paulo 16**: 9-104.

Mendonça, C.B.F. & Gonçalves-Esteves, V. 2000. Morfologia polínica de algumas espécies da tribo Vernonieae (Compositae Giseke) ocorrentes na restinga da Carapebus, Rio de Janeiro. **Hoehnea 27**: 131-142.

Mendonça, C.B.F.; Esteves, R.L. & Gonçalves-Esteves, V. 2007a. Palinotaxonomia de espécies de *Lepidaploa* (Cass.) Cass. (Vernoniinae-Compositae) ocorrentes no Sudeste do Brasil. **Revista Brasileira de Botânica 30**: 71-88.

Mendonça, C.B.F.; Gonçalves-Esteves, V.; Souza, M.A. & Esteves, R.L. 2007b. Estudio polínico de *Albertinia brasiliensis* Spreng., de las especies de *Cololobus* H. Rob., *Cyrtocymura* H. Rob. y *Dasyanthina serrata* (Less.) H. Rob. (Vernoniinae-Compositae) que ocurren en el Sudeste de Brasil. **Polibotánica 23**: 77-92.

Mendonça, C.B.F., Souza, M.A., Gonçalves-Esteves, V. & Esteves, R.L. 2007c. Palinotaxonomia de espécies de *Chrysolaena* H. Rob., *Echinocoryne* H. Rob. e *Stenocephalum* Sch. Bip. (Vernonieae-Compositae). **Acta Botanica Brasilica 21**: 627-639.

Mendonça, C.B.F.; Gonçalves-Esteves, V.; Esteves, R.L.& Nunes, A.D. 2009. Palynotaxonomy of *Vernonanthura* H. Rob. (Vernonieae, Asteraceae) species from Southeast Brazil. **Revista Brasileira de Botânica 32**: 647-662.

Mendonça, C.B.F.; Carrijo, T.T.; Esteves, R.L. & Gonçalves-Esteves, V. 2010. *Lessingianthus* (Vernonieae-Asteraceae): generic and infrageneric relationships based on pollen morphology. **Nordic Journal of Botany 28**: 1-10.

Peçanha, A.F.; Esteves, R.L. & Gonçalves-Esteves, V. 2008. Palinotaxonomia de *Albertinia brasiliensis* Spreng., *Eremanthus bicolor* (DC.) Baker e *Vanillosmopsis erythropappa* (DC.) Sch. Bip. (Compositae-Vernonieae). **Acta Botanica Brasilica 22**: 313-321.

Punt, W.; Hoen, P.P.; Blackmore, S.; Nilsson, S. & Le Thomas, A. 2007. Glossary of pollen and spore terminology. **Review of Palaeobotany and Palynology** 143:1-81

Robinson, H. 1980. Notes on the Lychnophorine genera *Chresta* and *Eremanthus* (Vernonieae: Asteraceae). **Phytologia 45**: 89-100.

Robinson, H. 1987a. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). I. The genus *Stenocephalum* Sch. Bip. **Proceedings of the Biological Society of Washington 100**: 578-583.

Robinson, H. 1987b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). II. A new genus *Echinocoryne*. **Proceedings of the Biological Society of Washington 100**: 584-589.

Robinson, H. 1987b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). III. Two new genera *Cyrtocymura* and *Eirmocephala*. **Proceedings of the Biological Society of Washington 100**: 844-855.

Robinson, H. 1988a. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). IV. The new genus *Lessingianthus*. **Proceedings of the Biological Society of Washington 101**: 929-951.

Robinson, H. 1988b. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). V. The new genus *Chrysolaena*. **Proceedings of the Biological Society of Washington 101**: 925-958.

Robinson, H. 1988c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). VI. A new genus *Aynia*. **Proceedings of the Biological Society of Washington 101**: 959-965.

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

Robinson, H. 1992. Notes on Lychnophorinae from Minas Gerais, Brazil, a synopsis of *Lychnophoriopsis* Schultz-Bip., and the new genera *Anteremanthus* and *Minasia* (Vernonieae: Asteraceae). **Proceedings of the Biological Society of Washington 105**: 640-652.

Robinson, H. 1997. The *Paralychnophora* group of *Eremanthus* (Vernonieae: Asteraceae). **Rhodora 98**: 85-93.

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

Robinson, H. 2006/2007. Tribe Vernonieae. In J. Kadereit & C. Jeffrey (Eds.), **The families and genera of vascular plants**. vol. 8. Asterales (pp. 165–192). Berlin, Springer.

Robinson, H. & Kahn, B. 1986. Trinervate leaves, yellow flowers, tailed anthers, and pollen variation in *Distephanus* Cassini. **Proceedings of the Biological Society of Washington 99**: 493-501.

Salgado-Labouriau, M.L.; Vanzolini, P.E. & Melhem, T.S. 1965. Variation of polar axes and equatorial diameters in pollen grains of two species of *Cassia*. **Grana Palynologica 6**: 166-176.

Salgado-Labouriau, M.L. 1973. **Contribuição à palinologia dos cerrados**. Rio de Janeiro, Academia Brasileira de Ciências.

Skvarla, J.J.; DeVore, M.L. & Chissoe, W.F. 2005. Lophate sculpturing of Vernonieae (Compositae) pollen. **Review of Palaeobotany and Palynology 133**: 51-68.

Stix, E. 1960. Pollenmorphologsgische untersuchungen na Compositen. **Grana Palynologica 2**: 41-114.

Wortley, A.H.; Funk, V.A.; Robinson, H.; Skvarla, J.J. & Blackmore, S. 2007. A search for pollen morphological synapomorphies to classify rogue genera in Compositae (Asteraceae). **Review of Palaeobotany and Palynology 146**: 169-181.

Wortley, A.H.; Funk, V.A. & Skvarla, J.J. 2008. Pollen and evolution of Arctotideae (Compositae). **Botanical Review 74**: 438-466.

Versão eletrônica do artigo em www.scielo.br/abb e http://www.botanica.org.br/acta/ojs