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Elephantopinae (Asteraceae, Vernonieae)*

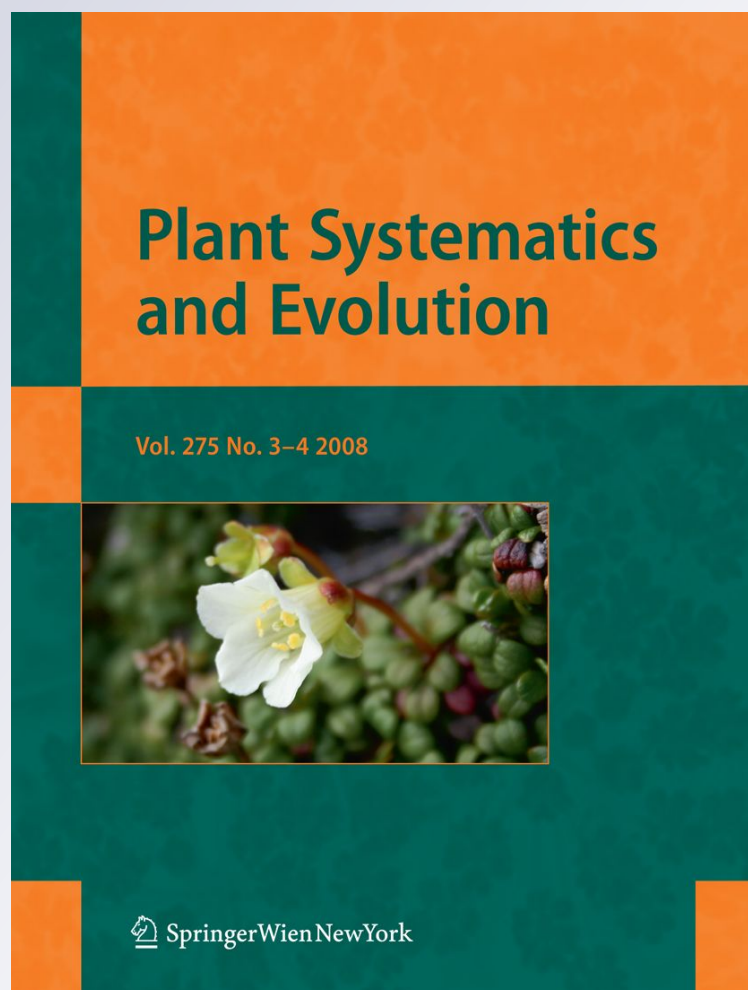
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Palynological survey of the subtribe Elephantopinae (Asteraceae, Vernoniaeae)

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Abstract Despite the taxonomic value of pollen morphology within the tribe Vernoniaeae, a detailed study of the pollen of the subtribe Elephantopinae is still lacking. The pollen morphology of ten species, representing three of the four genera of the subtribe, *Elephantopus*, *Pseudoelephantopus* and *Orthopappus*, was studied with LM, SEM, and TEM. The pollen of all the species studied was found to be echinolophate, although the differences in aperture features and both sculpture and exine structure allowed recognizing two pollen types. The species of *Elephantopus* (except for *E. elongatus*) and *Pseudoelephantopus* share the regular or more or less regular ridges pattern, the colporate condition but with the ectoapertures little developed, and the acaveate exine structure. From the sculpture and the apertures, the pollen of *Caatinganthus harleyi* was found to be similar to that of *Elephantopus* and *Pseudoelephantopus*. The pollen morphology of the monotypic *Orthopappus*, which is shared with that of *E. elongatus*, was further investigated for the first time. We found that it differs from that of the other species in having an irregular pattern of ridges, colporate condition but with a well-developed ectoapertures, and caveate exine. Additional studies of the exine structure and apertures features, coupled with molecular phylogeny, are needed to understand the evolution of pollen characters and re-evaluate the intergeneric relationships within the tribe.

Keywords Elephantopinae · Vernoniaeae · Asteraceae · Pollen morphology · LM · SEM · TEM

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Introduction

In his taxonomic treatment of Vernoniaeae, Robinson (1999) recognized the subtribe Elephantopinae comprising 3 genera and 19 species of perennial herbs. *Elephantopus* includes 16 species, *Pseudoelephantopus* 2 species, and *Orthopappus* only 1. Later, Keeley and Robinson (2009) included the genus *Caatinganthus* with two species. The subtribe is pantropical, but it extends into temperate areas in the southeastern United States (Robinson 1999). Within the tribe Vernoniaeae, the subtribe Elephantopinae is consistently recognized on the basis of the clustered heads, the corollas often zigomorphic, the tendency for a reduced or modified pappus, and the echinolophate and usually triporate pollen (Robinson 1999). Several studies have revealed that the pollen morphology is one of the most useful features for the taxonomy in the tribe Vernoniaeae (e.g., Kingham 1975; Blackmore 1986; Jeffrey 1988; Bolick and Keeley 1994; Keeley and Robinson 2009; Robinson 1999; Blackmore et al. 2009). However, the pollen studies in the subtribe Elephantopinae are scattered. Wodehouse (1928) described the pollen of *Elephantopus* as echinolophate (i.e., “with the surface thrown into ridges, anastomosing or free, provided with more or less prominent spines”). Stix (1960) also characterized as echinolophate the pollen of *Elephantopus mollis*, *E. tomentosus*, *Orthopappus angustifolius* (sub *Elephantopus angustifolius*) and *Pseudoelephantopus spicatus*. Skvarla et al. (1977), within their broad ultrastructural study on Compositae pollen, provided a SEM image of pollen of *Elephantopus carolinianus*. Robinson (1999) referred to the unusual pollen type of *Orthopappus* characterized by its separate echinate crests filling the noncolpate regions. Based on examinations with scanning electron microscopy (SEM) and transmission electron microscopy (TEM) in pollen of *Vernonia* and *Elephantopus*

caroliniana, *E. nudatus* and *E. tomentosus*, Skvarla et al. (2005) reinforced the taxonomic importance of pollen morphology in Vernoniae and emphasized the need of further studies on pollen of *Elephantopus*.

The aim of this study is to provide a detailed account of the pollen morphology of species in the subtribe Elephantopinae in order to gain more insight into the relationships within the subtribe. To achieve this goal, we used light microscopy (LM), SEM and TEM to analyze the pollen of ten species of the subtribe: *Elephantopus biflorus* (Less.) Sch. Bip., *E. elongatus* Gardn., *E. hirtiflorus* DC., *E. micropappus* Less., *E. mollis* H.B.K., *E. palustris* Gardn., *E. riparius* Gardn., *Orthopappus angustifolius* (Sw.) Gleason, *Pseudoelephantopus spicatus* (Juss.) Rohr and *P. spiralis* (Less.) Cronq. Additionally, pollen features of *Caatinganthus harleyi* H. Rob. were taken from Robinson (1999).

Materials and methods

Pollen from 25 specimens belonging to 10 species of Elephantopinae was examined. There was no material available for the remainder species of the subtribe. The specimens studied are deposited in the herbaria LP, and SI (Holmgren et al. 1990). For light microscopy (LM) pollen was acetolyzed and chlorinated according to Erdtman (1960); the slides were prepared by mounting the pollen in glycerol jelly and sealing with paraffin. Whenever possible the diameter of 20 grains was measured excluding spines. The measurements of exine thickness are based on 10 grains. For SEM, acetolyzed pollen grains were suspended in 90 % ethanol, mounted on stubs and examined using a JEOL JSM T-100 SEM. For TEM, the fresh pollen grains were fixed in 1.5 % glutaraldehyde and then buffered with 2 % OsO₄ for 2 h at room temperature. After that, they were washed for 30 min in distilled water and dehydrated in an ethanol series, finally embedded in acetone-Spurr 3:1 for 6 h and twice in Spurr for 24 h. Ultrathin sections were cut using a diamond knife fitted into a Sorvall Porter-Blum MT2-B ultramicrotome. Sections were mounted in single grids and stained with lead citrate (1 min) and uranyl acetate for 10 min. The examinations were made with a transmission electron microscopy Jeol JEM 1200 EX II from the Servicio Central de Microscopía Electrónica of the Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata.

Terminology used to describe general morphology and the exine stratification is consistent with Skvarla et al. (1977); they recognize two discrete exine layers after acetolysis treatment (Erdtman 1960): “a complex outer electron dense layer, the ektexine, composed of spines,

tectum, columellae and foot layer, and an inner electron dense single layer, the endexine.”

Specimens studied *E. biflorus*: Mendez Magalhaes 19159 (LP); Irmão Edesio 4997 (LP); Brade & Barbosa 17637 (LP). *E. elongatus*: Smith et al. 6928 (LP); Krapovickas & Cristóbal 33194 (SI). *E. hirtiflorus*: Duarte 383 (LP); Hatschbach 39416 (LP); Cutler 838 (LP). *E. micropappus*: Hatschbach 1396 (LP). Hatschbach & Haas 13968 (LP). *E. mollis*: Krapovickas, Cristóbal & Palacios 12422 (LP); Jansen & Sarandón 725 (LP); Sanane 1120 (LP). *E. palustris*: Hatschbach 34678 (LP). *E. riparius*: Hatschbach 41493 (LP). Fernald & Long 038756 (LP). *Orthopappus angustifolius*: Jansen & Sarandón 739 (LP); Maruñiak, Quarín & Schinini 618 (LP); Job 792 (LP); Cabrera & Kiesling 24942 (LP); Zuloaga & Deginani 140 (LP). *Pseudoelephantopus spicatus*: 894376 (LP); Cabrera 4127 (LP); Jorgensen 674 (LP). *P. spiralis*: Cabrera et al. 23289 (LP).

Results

General pollen morphology of Elephantopinae

Pollen grains are radially symmetrical, spheroidal and have a circular outline in both equatorial and polar view. The size (maximum diameter) is in the range 28–61 µm, *E. riparius* is the smallest and *E. hirtiflorus* the largest (Table 1). The apertures are colporate, with well- or little-developed ectoapertures (colpi). The exine is echinolophate in all species. The arrangement of ridges (lophae) may determine a quite regular pattern of pentagonal or hexagonal lacunae, or may be completely irregular with uneven

Table 1 Elephantopinae pollen measurements

Species	Maximum diameter (µm)	Exine thickness (µm)	Spine length (µm)
<i>Caatinganthus harleyi</i> ^a	c.a. 60		
<i>Elephantopus biflorus</i>	30–42	8.5–11	2
<i>E. elongatus</i>	37–44	7–8	1–2
<i>E. hirtiflorus</i>	51–61	7–10	2–6
<i>E. micropappus</i>	35–46	8–9	2–2.5
<i>E. mollis</i>	34–45	c.a. 7	2
<i>E. palustris</i>	36–46	8–10	1–2
<i>E. riparius</i>	28–36	c.a. 5	0.5–2
<i>Orthopappus angustifolius</i>	31–41	c.a. 5	1–3
<i>Pseudoelephantopus spicatus</i>	33–47	8–10	0.5–2
<i>P. spiralis</i>	37–40	8–9	1–2

^a Pollen diameter taken from Robinson (1999)

lacunae, sometimes with free ridges. The tectum is restricted to the upper surface of ridges, with perforations among spines; laterally the ridges are little perforated (Fig. 1b, d). The length of spines ranges from ca. 2 to 6 μm and may be roughly conical with rounded tip or finger-shaped (Fig. 1), they are always centrally arranged in a single row (Figs. 1, 2). The floors of lacunae are generally scabrate or scabrate-granulate (Fig. 1). The ectexine and the endexine may be separated by a reduced cavea. The endexine is generally homogeneous. The intine is thicker in apertural areas. Two morphological types, I and II, were distinguished on the basis of the

pollen surface features, lacunae pattern and the aperture features. Ultrastructural exine features such as the cavea and columellae features reinforced the characterization of pollen types.

Type I (Figs. 1, 3a–c)

LM: the pollen has a quite regular pattern of lacunae that are pentagonal or hexagonal shaped, and less frequently elongated; the lacunae number is difficult to establish. There is a subtle variation in length of spines. The ectoaperture is usually little developed. Each aperture is

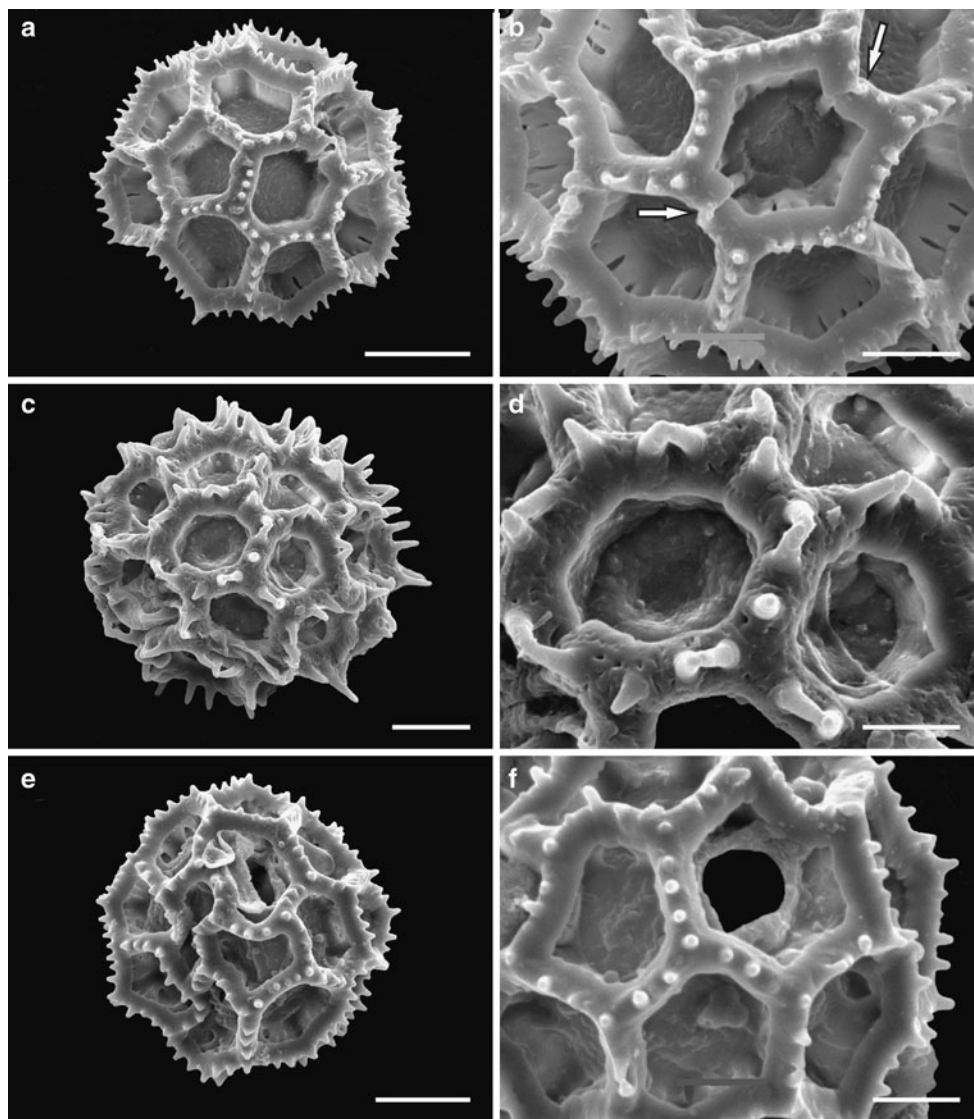


Fig. 1 SEM micrographs of type I pollen grains of Elephantopinae. **a, b** *Elephantopus biflorus*. **a** Tilted polar view of pollen grain; one of the three apertures is indicated by arrow. **b** Close-up of the aperture showing the interruptions of ridges (arrows) and columellae fused in the bases and ramified under ridges. **c, d** *E. hirtifolius*. Whole grain.

d Close-up of the pollen surface. Note the perforations of the tectum. Whole grain. **e, f** *Pseudoelephantopus spicatus*. **e** Whole grain. **f** Close-up of the lip-shaped aperture. Scale bars **a, c, e** = 10 μm ; **b, d, f** = 5 μm

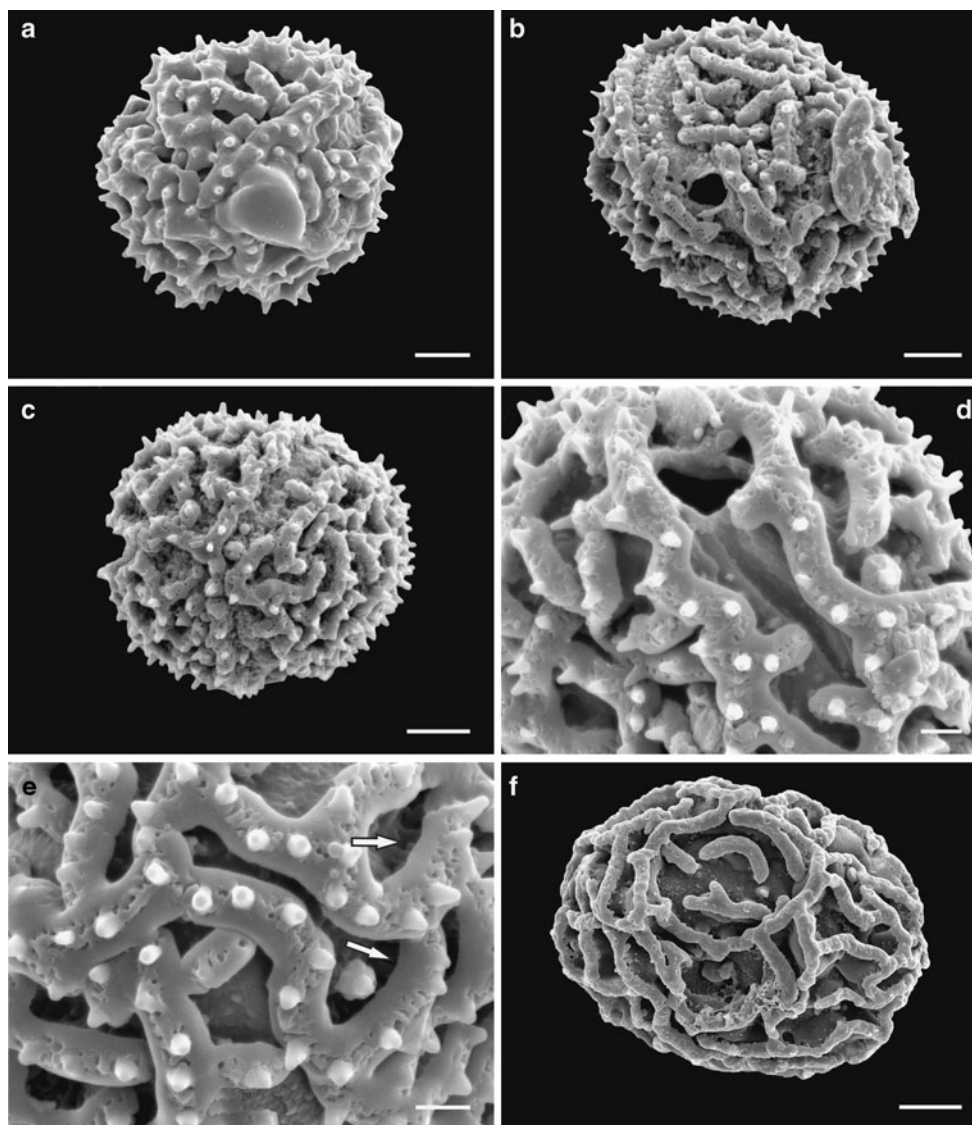


Fig. 2 SEM micrographs of type II pollen grains of Elephantopinae. **a** *Elephantopus elongatus*. Polar view. **b–e** *Orthopappus angustifolius*. **b** Tilted equatorial view of pollen grain. **c** Polar view. **d** Detail of compound apertural system surrounded by a continuous ridge. **e** Close-up of a mesocolpium region showing the intricate ridges

system of exine surface, note the thick columellae under ridges (arrows). **f** Aberrant pollen grain of *E. biflorus* (specimen Mendez Magalhães 19159 LP) showing an unusual system of ridges similar to those of *Orthopappus*. Scale bars **a–c** = 5 μ m; **d, e** = 2 μ m; **f** = 10 μ m

situated in the poral lacunae, which are scarcely differentiated in form from the rest of lacunae. The ectexine has massive columellae that are anastomosed in the bases and branched in the distal part under the tectum.

SEM: poral lacunae are connected with its neighbors through interlacunae gaps situated in two opposite ridges (Fig. 1b).

TEM: in *E. biflorus*, the endexine is approximately equal or slightly thinner than the foot layer; usually it is smooth but some areas have a heterogeneous appearance (Fig. 3a), and close the apertural area it becomes lamellate. The lamellae are organized in distinct thin stripes whose free ends are directed toward the pores (Fig. 3c). Present in

Caatinganthus harleyi, *Elephantopus biflorus*, *E. hirtifolius*, *E. micropappus*, *E. mollis*, *E. riparius*, *E. tomentosus*, *Pseudoelephantopus spicatus* and *P. spiralis*.

Remarks: in *E. biflorus*, the pollen from the specimen Mendez Magalhães 19159 (LP) presented an irregular lacunae pattern, and the surface of the ridges is spineless and contains perforations (Fig. 2f).

Type II (Figs. 2, 3d–f)

LM: the pollen has an irregular pattern of lacunae. The ectoaperture is well developed; it is long, nearly forming a syncolpus; the endoaperture is circular. These compound

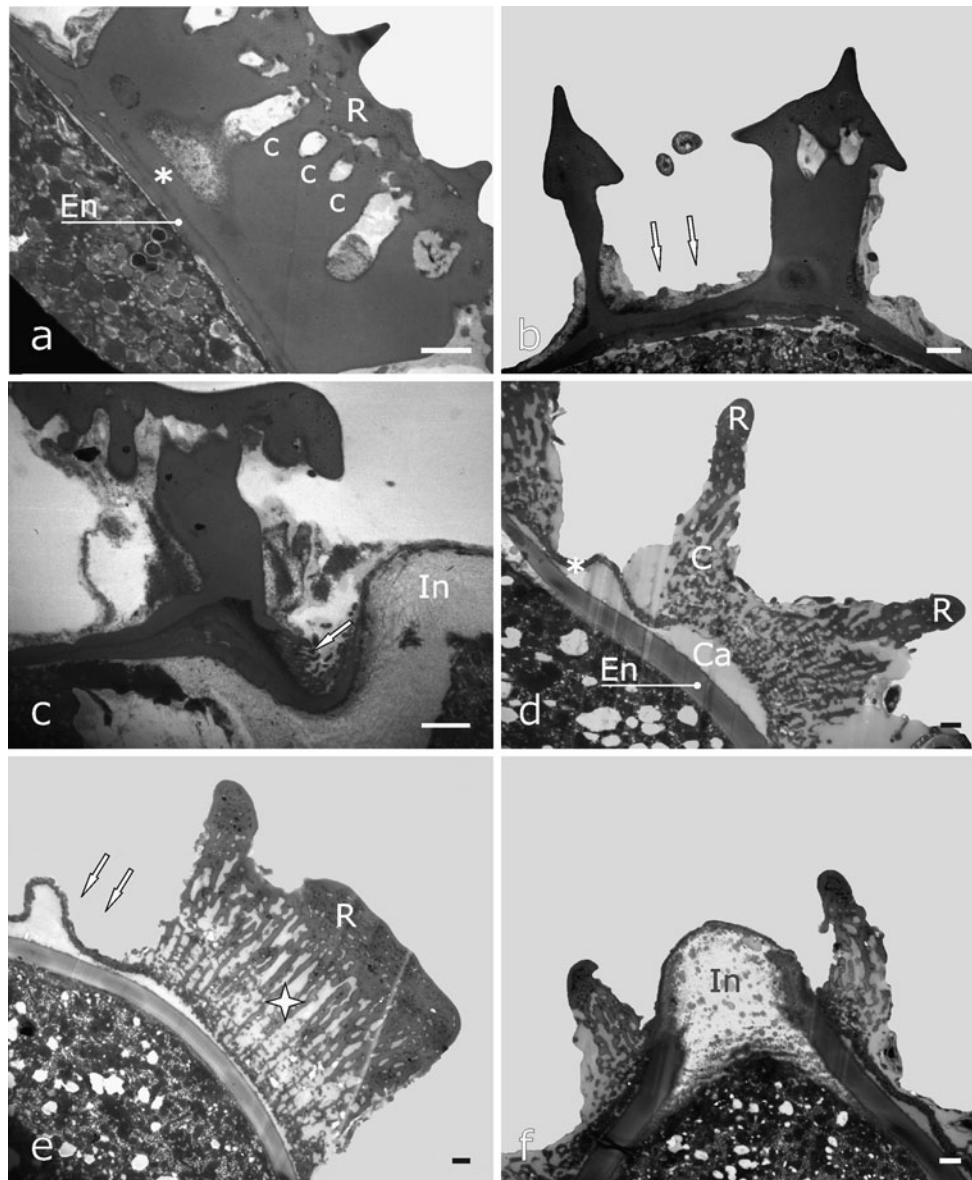


Fig. 3 TEM comparative micrographs of exine sections of pollen type I and type II of Elephantopinae. **a–c** Pollen type I. *Elephantopus biflorus*. **a** Ridge (*R*), massive columellae (*C*) fused at the base, foot layer (*asterisk*), endexine (*En*). **b** Cross-section of a ridge showing two columellae and the lacunae (*arrows*). **c** Exine section close to the aperture; note the lamellate nature of the endexine in this area (*arrow*). **d–f** Pollen type II. *Orthopappus angustifolius*. **d** Cross-

section of a ridge (*R*) showing thin columellae, caveae (*Ca*), foot layer with granular aspect (*asterisk*) and endexine (*En*). **e** Detail of exine; note the inner perforations of the ridge (*star*) and the lacunae (*arrows*). **f** Exine section perpendicular to aperture showing the ectexine, the endexine and a protruding intine (*In*). Scale bars 1 μ m

apertures may be surrounded by a more or less continuous ridge (Fig. 2b, d). The apertural membrane may be psilate (Fig. 2d) or granulated (Fig. 2b–c).

SEM: the surface of the ridges is very perforated among spines. Under the ridges, a combination of compact and columellate exine is observed (Fig. 2d).

TEM: the ectexine has thin and laterally anastomosed columellae (Fig. 3d–e); the ridge has inner perforations (Fig. 3e). The foot layer has a granular appearance; it is

separated from the endexine by a shallow cavea; in some areas the ectexine appears to be in contact with the endexine (Fig. 3d–e). The endexine is much thicker than the foot layer (Fig. 3d). Present in: *E. elongatus* and *Orthopappus angustifolius*.

Remarks: from TEM the columellae are commonly thin and laterally anastomosed (Fig. 3d–e), but on SEM some thick columellae like those of pollen type I are evident (Fig. 2e).

Discussion

Pollen morphology

We found considerable variation in the pollen morphology of the species of Elephantopinae studied. The most prominent pollen feature shared by all species is the echinolophate sculpture. The differences included mainly aperture features, sculpture pattern and exine structure. The features of the apertures are related to its development; it is clearly colpate in pollen of *Orthopappus angustifolius* and *Elephantopus elongatus* (Fig. 2), a condition that is not “obvious” in the other species of *Elephantopus* and *Pseudoelephantopus* studied, as discussed in “[Taxonomic significance](#).” On the basis of the combination of the aforementioned features, we described two pollen types. Type I comprised most species of the subtribe: *Caatinganthus harleyi*, *Elephantopus biflorus*, *E. hirtifolius*, *E. micropappus*, *E. mollis*, *E. riparius*, *E. tomentosus*, *Pseudoelephantopus spicatus* and *P. spiralis*. Under LM, the pollen of *Elephantopus* and *Pseudoelephantopus* appears to have single apertures “hidden” in the poral lacunae. Under SEM, in pollen of *Elephantopus*, the gaps located in two opposite ridges of the poral lacunae (Fig. 1b) suggest the presence of an ectoaperture (colpi). In pollen of *Pseudoelephantopus*, no gaps were observed, but the elongated shape of the aperture is reminiscent of the colporus (Fig. 1f). It is worth mentioning that different aperture types have been reported in this subtribe; three species of *Elephantopus* (*E. caroliniana*, *E. nudatus*, and *E. tomentosus*) have porate apertures (Skvarla et al. 2005), and *Caatinganthus harleyi* is regarded as having triporate to “slightly colpate” apertures (Robinson 1999). On the other hand, the pollen of Elephantopinae has been characterized as tricolpate to “subtriporate” (Keeley and Robinson 2009). Concerning the sculpture, some variation in the length of the spines exists among species, but it could be a continuous variation within the group. This pollen type is largely coincident with that of species of *Vernonia* included in the pollen type D characterized by Keeley and Jones (1979) (i.e., “echinolophate, triporate, with a discontinuous micropunctate tectum, spines generally pronounced on muri, occasionally reduced, lacunae regularly spaced, some of unequal size, germinal pores surrounded by a ridge”). However, in pollen of *Vernonia*, the microperforations cover the entire tectum surface (e.g., Keeley and Jones 1979; Skvarla et al. 2005), while in species of Elephantopinae they are commonly scarce and restricted to the surface of the ridges (Fig. 1b, d), in agreement with Skvarla et al. (2005). Type II pollen included *Elephantopus elongatus* and the monotypic genus *Orthopappus*. This type, which is very distinctive both within and outside the subtribe, is characterized by having a very irregular pattern of lacunae, tricolpate apertures,

caveate exine and infratectal thin columellae (Figs. 2, 3). The uncommon ridge system of this type has been regarded as unusual by Robinson (1999). It is interesting to note that the anomalous pollen found in one of the *E. biflorus* collections examined has an intricate ridge pattern similar to those of *Orthopappus* and *E. elongatus* (Fig. 2f). However, this unusual pattern occurs sporadically in *E. biflorus*, whereas it is normal in *Orthopappus* and *E. elongatus*, suggesting that it might have emerged as a deviation from the regular pattern present in most species of Elephantopinae. Concerning the exine structure of *O. angustifolius* pollen, examination by LM and SEM allowed obtaining little information, whereas that by TEM provided invaluable data. In this species, and probably in *E. elongatus*, the ectexine consists of a perforated tectum, a layer of anastomosed thin columellae with spongy aspect, and a thick endexine, both layers separated by a shallow cavea. Additionally, examination by SEM showed thick columellae that were randomly scattered in the ectexine; certainly, these columellae were not caught in the thin sections for TEM. Thick and ramified columellae are common in pollen of Vernonieae, as previously reported (Skvarla et al. 1977; Robinson 1999; Skvarla et al. 2005), and it was seen in Kingham (1975), Keeley and Jones (1977, 1979), Ferreira Mendonça et al. (2007), and Dematteis and Pire (2008), but their combination with a spongy structure has not been previously reported. Additional TEM examinations in a larger number of specimens are necessary to elucidate this “apparently” unusual structure. Another distinctive feature of this pollen type is the well-developed colpate aperture.

Taxonomic significance

Although the pollen of the species studied shares the echinolophate sculpture, which is common within the subtribe Elephantopinae, we found some differences at the level of the apertures and exine morphology. The most usual pollen type in the subtribe is represented by *Elephantopus* (except for *E. elongatus*), *Pseudoelephantopus*, and *Caatinganthus* (as seen in Robinson 1999). The species belonging to these three genera cannot be distinguished one from another by the features of the pollen. The cryptic apertures found in the pollen of Elephantopinae are, apparently, shared with those of species belonging to the subtribe Dipterocypselinae, which have been characterized as having “subtriporate” pollen (Keeley and Robinson 2009).

The pollen morphology of *E. elongatus* and *Orthopappus angustifolius* differs from that of the other species. Although the exine structure of *Orthopappus* pollen is apparently rare in the tribe Vernonieae, it is a repeated pattern across lophate Asteraceae pollen; it may be found in some basal Barnadesioideae (e.g., Zao et al. 2000) and in advanced Lactuceae (e.g., Tomb et al. 1974; Blackmore et al. 2009). From the literature, it is evident that, within

Vernonieae, the exine sculpture has received more attention than the exine structure. However, the exine structure in species of Elephantopinae shows quite variation in relation to that of the remaining Vernonieae. In the latter, the exine has a very perforated tectum, a spongy infratectum (occasionally columellate) supported by a layer of thick columellae, an endexine equal to or thicker than the foot layer, and the probable presence of the cavea (Blackmore et al. 2009). The structure of the exine in pollen grains of Elephantopinae species does not fit in this general characterization. In this subtribe, the tectum covers only the surface of the ridges and is perforated only among spines; on the other hand, the exine lacks the spongy, or columellate, infratectum that is typical within Vernonieae.

The utility of pollen characters in the context of molecular phylogeny still cannot be evaluated. Although a molecular phylogeny of Vernonieae exists (Keeley et al. 2007) it only included species of *Elephantopus* as representing the subtribe. However, it is worth mentioning that pollen of *Elephantopus*, and consequently pollen of *Caatinganthus* and *Pseudoelephantopus*, is considered to be derived within the broad scheme of the evolution of the pollen morphology of Asteraceae (Blackmore et al. 2009). Interestingly, the advanced pollen morphology is accompanied by extra-palynological features that are unique within Vernonieae, such as the clustered heads and the tendency for a reduced or modified pappus (Robinson 1999).

Conclusions

The pollen morphology of Elephantopinae is varied in both the exine and the apertures, and includes two pollen types. One type is represented by three of the four genera of the subtribe; the other type is unique in the subtribe and thus in the tribe Vernonieae.

The use of SEM and TEM was crucial to characterize those pollen types. It is remarkable that the apertures in this small subtribe are relatively not very stable. They appear to show a continuum of variation ranging from porate (as seen in Skvarla et al. 2005) to colporate with the ectoaperture clearly distinguishable through “slightly colporate” forms. The pollen morphology of *Orthopappus* is described in detail for the first time; its distinctive exine structure is a novelty in the tribe but not in the family Asteraceae. However, to better understand the evolution of pollen morphology and the relationships within this tribe, it would be necessary both to carry out additional studies in pollen of Vernonieae as a whole, especially on the exine structure and apertures, and to include all the genera of Elephantopinae in the molecular phylogeny.

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References

- Blackmore S (1986) The identification and taxonomic significance of lophate pollen in the Compositae. *Can J Bot* 64:3101–3112
- Blackmore S, Wortley AH, Skvarla JJ, Robinson H (2009) Evolution of pollen in Compositae. In: Funk VA, Susanna A, Stuessy T, Bayer R (eds) *Systematic, evolution and biogeography of the Compositae*. IAPT, Vienna
- Bolick M, Keeley SC (1994) Pollen morphology and classification of the Vernonieae (Compositae). *Acta Bot Gall* 141:279–284
- Dematteis M, Pire SM (2008) Pollen morphology of some species of *Vernonia* s.l. (Vernonieae, Asteraceae) from Argentina and Paraguay. *Grana* 47:117–129
- Erdtman G (1960) The acetolysis method, a revised description. *Vensk Bot Tidskr* 54:561–564
- Ferreira Mendonça CB, Esteves RL, Gonçalves-Esteves V (2007) Palinotaxonomia de espécies de *Lepidaploa* (Cass.) Cass. (Vernoniinae-Compositae) ocorrentes no Sudeste do Brasil. *Revista Brasil Bot* 30:71–88
- Holmgren PK, Holmgren NH, Barnett LC (1990) *Index herbariorum*, part 1. The herbaria of the world, 8th edn. New York Botanical Garden, Bronx
- Jeffrey C (1988) The Vernonieae in east tropica Africa: notes on Compositae. V. *Kew Bull* 43:195–277
- Keeley SC, Jones SB (1977) Taxonomic implications of external pollen morphology to *Vernonia* (Compositae) in the West Indies. *Amer J Bot* 64:576–584
- Keeley SC, Jones SB (1979) Distribution of pollen types in *Vernonia* (Vernonieae: Compositae). *Syst Bot* 43:195–202
- Keeley SC, Robinson H (2009) Vernonieae. In: Funk VA, Susanna A, Stuessy T, Bayer R (eds) *Systematic, evolution and biogeography of the Compositae*. IAPT, Vienna, pp 438–469
- Keeley SC, Forsman ZH, Chan R (2007) A phylogeny of the “evil tribe” (Vernonieae: Compositae) reveals old/new world long distance dispersal: support from separate and combined congruent datasets (*trnL-F*, *ndhF*, ITS). *Mol Phylogenet Evol* 44:89–103
- Kingham DL (1975) A study of the pollen morphology of tropical African and certain other Vernonieae (Compositae). *Kew Bull* 31:9–26
- Robinson H (1999) Generic and subtribal classification of American Vernonieae. *Smithsonian Contrib Bot* 89:1–116
- 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*. Academic, London, pp 141–248
- Skvarla JJ, De Vore M, Chissoe WF (2005) Lophate sculpturing of Vernonieae (Compositae) pollen. *Rev Palaeobot Palynol* 133:51–68
- Stix E (1960) Pollenmorphologische untersuchungen an compositen. *Grana Palynol* 2:40–104
- Tomb AS, Larson DA, Skvarla JJ (1974) Pollen morphology and detailed structure of family Compositae tribe Cichorieae. I. Subtribe Stephanomerinae. *Amer J Bot* 61:486–499
- Wodehouse RP (1928) Phylogenetic value of pollen characters. *Ann Bot* 42:891–934
- Zao Z, Skvarla JJ, DeVore M (2000) Phylogenetic implications of pollen morphology and ultrastructure in the Barnadesioideae. *Lundellia* 3:26–40