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Pollen morphology of some species of *Vernonia s. l.* (Vernonieae, Asteraceae) from Argentina and Paraguay

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Abstract

Pollen morphology is widely used in taxonomic treatments of tribe Vernonieae, and differences in exine structure and aperture form have been described for many species within the genera comprising the tribe. However, in recent years a number of new species have been described and, in the present paper, we describe in detail the pollen of 24 species of the tribe which are either endemic or uncommon to certain regions of Argentina or of Paraguay. The pollen of these species are radially symmetrical and more or less spheroidal, 3-colporate or, in one species, 3-porate; the exine may be tectate or semitectate and microperforate, with echinate lophae or, in the 3-porate example, psilate lophae. Using a range of characteristics related to size, shape, wall thickness, apertures and tectum surface morphology, five of the six pollen types previously described for tribe Vernonieae, and a subtype, are recognized. Our results support the usefulness of pollen morphology in helping to determine the taxonomic position of species within tribe Vernonieae.

Keywords: *Taxonomy, classification, tricolporate, triporate, lacunae, lophae,* Vernonia s. l.

The Vernonieae Cass. (Asteraceae) are a pantropical tribe of 89 genera which are concentrated around two major centers of diversification: the central region of the African continent and southern Brazil. Most of the species are included in *Vernonia* Schreb. which is by far the largest genus of the tribe with about 1 100 species. *Vernonia* shows considerable variation in habit, ranging from small, scapose herbs to large trees (Bremer, 1994).

The most characteristic feature of the Vernonieae is found in the styles, which are slender with filiform, pilose branches and an upper style shaft bearing long sweeping hairs (Robinson, 1999). The pollen of the tribe also has very characteristic morphology: the tectum consists of a pattern of lophae (crests or ridges of tectum) and lacunae (cf. very wide deep lumina) or deep depressions in the tectum continuous with the lophae (Wodehouse, 1928; Skvarla et al., 1979). The lophae in many species of the tribe are spinose and, the spines are either disposed on the central ridge of the lophae (echinolophate) or, arranged in groups in a more or less reticulate pattern (subechinolophate). Less frequently there are species of Vernonieae where the lophate pollen lacks spines, instead, although the lophae form a reticulate pattern, they are narrow and smooth ridged (psilolophate). Between species, Vernonieae pollen is also variable in aperture form, with both tricolporate and triporate forms (Stix, 1960; Kingham, 1976; Keeley & Jones, 1979; Blackmore, 1986).

The first descriptions of Vernonieae pollen morphology were those of Steetz (1864), followed by those of Fischer (1890). More detailed descriptions of the main pollen forms which occur *Vernonia* were provided by Wodehouse (1928), who described the distribution of 'crests' and lacunae in different pollen forms in Compositae, and also established a terminology which has become the basis for the description of the unusual and characteristic pollen morphology found in a wide number of species in the family. Kingham (1976) used scanning electron microscopy to describe the surface patterns of the tropical African species of the tribe, and found a

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range of different pollen forms, most of which were exclusive to sections or groups. The pollen types used to describe unique combinations of pollen characteristics observed in tribe Vernonieae date initially from Keeley and Jones (1979). Later Robinson (1992) described several additional characteristics special to Vernonieae. So far a total of ten pollen types have been recognized for the tribe; some of these are restricted to Old World species, while others are distinctive for Central and South American taxa (Jones, 1979, 1981; Robinson, 1999).

Pollen morphology constitutes one of the most useful suites of characters for taxonomic studies in tribe Vernonieae, and a correlation between pollen data and the classification of the West Indian species of *Vernonia* has already been demonstrated by Keeley and Jones (1977). Based on the variation in pollen surface morphology, Jones (1979) proposed a new infrageneric classification for the American members of *Vernonia*. Segregation of different sections and subsections of *Vernonia* to new genera was realized by Robinson (1988, 1989); in several cases the re-circumscription was based on pollen type. The most recent classification of the New World Vernonieae, proposed by Robinson (1999) is supported by a number of different features including external vegetative morphology, chromosomes, chemical composition and, importantly, pollen morphology.

Furthermore, the pollen types described for the tribe have been shown to correlate, in several cases, to other characters of taxonomic relevance, for example, chromosome number (Dematteis & Robinson, 1997; Dematteis & Salgado, 2001; Dematteis, 2002) or arrangement of the capitula (floral heads) (Robinson, 1999). In Vernonieae it has been noted (Robinson, 1992) that the species with tricolporate pollen generally have the base chromosome number of $x=17$, while the species with triporate pollen have chromosome base numbers of $x=8$, $x=9$, $x=10$, $x=11$ or $x=13$.

The surface morphology of Vernonieae pollen has been examined in a considerable number of genera and species because of its relevance to the taxonomy (Cabrera, 1944; Stix, 1960; Smith, 1969; Jones, 1970, 1979, 1981; Skvarla et al., 1977, 2005; Keeley & Jones, 1977, 1979; Bolick, 1983; Isawumi et al., 1996; Robinson, 1999; Dematteis & Salgado, 2001; Dematteis, 2003). In the last few years further new species of *Vernonia* have been described (Cabrera & Dematteis, 1999; Dematteis, 2000, 2003; Cristóbal & Dematteis, 2002) as these pollen has not been described in detail. There are also some species of Vernonieae which are relatively uncommon or narrowly distributed endemics, known from only one or a few populations (Jones, 1977; Robinson, 1999; Dematteis, 2006; Cabrera & Dematteis, 2008). The taxonomic position of almost all these species has yet to be established within the tribe, and their pollen morphology has not been described.

The purpose of our study has been to examine the pollen of 24 recently described species of *Vernonia* from Argentina and from Paraguay, and to consider their possible taxonomic positions within the genus based on pollen characteristics.

Material and methods

Pollen samples were obtained by removing one or two florets from herbarium specimens of each species. Voucher specimens are mainly deposited in the Herbarium of the Instituto de Botánica del Nordeste (CTES). The sources of the specimens examined are detailed in the Appendix where the taxa are grouped alphabetically by country of origin (Argentina or Paraguay). Pollen data are summarized in Table I. It should be noted that because the taxonomic position within tribe Vernonieae is, for several of the taxa/collections, uncertain or in need of review, all species examined in this study are considered to belong to *Vernonia sensu lato* for the time being.

The pollen was acetolysed according to Erdtman (1960). For light microscopy (LM) the pollen samples were mounted in glycerol jelly on glass slides and then examined with a Zeiss Axioplan microscope. Permanent slides were deposited at the Palynological Laboratory of the Universidad Nacional del Nordeste (PAL-CTES). Pollen measurement data were calculated from at least 30 grains per sample.

For scanning electron microscopy (SEM) acetolysed pollen grains were first washed in 96° alcohol, followed by a further wash in absolute alcohol. The samples were then air dried in Petri dishes and subsequently sputtered with gold palladium prior to observation using a JEOL 5800 LV scanning electron microscope. The terminology used for pollen grain description follows terms accepted in Punt et al. (1994, 2006, and 2007). The quantitative and qualitative characters used to define the pollen types we describe are summarized in Table I.

Results

General pollen morphology

Pollen grains are radially symmetric, oblate spheroidal, spheroidal or prolate spheroidal (P/E

Table I. *Vernonia* pollen, summary data for species examined and pollen types distinguished (A–D; see column 13). All measures (Columns: 4, 5, 8–12) in µm; mean values in brackets. Country of origin (Column 2): **A** – Argentina, **P** – Paraguay.

Taxa	Country of origin	Collector	Polar axis (P)	Equatorial diameter (E)	P/E	Shape	Colpus length	Pore diameter	Exine thickness	Spine length	Lacuna diameter	Pollen type
1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
V. chaquensis	**P**	Schinini et al. 28183	40.3 (43.7) 46.8	37.7 (42.3) 46.8	1.04	prolate-spheroidal	21.0–25.0	7.0–8.0 × 7.5–9.5	2.6 (4.2) 6.5	3.9 (4.5) 5.2	–	A
	A	Schulz 13696	39.0 (42.4) 45.5	39.0 (41.9) 45.5	1.01	prolate–spheroidal	21.0–25.0	7.5–8.0 × 7.5–11.0	2.6 (4.2) 5.2	3.9 (5.1) 6.5	–	A
V. cichoriiflora	**P**	Krapovickas & Cristóbal 34263	47.0 (51.0) 54.9	41.2 (48.8) 52.9	1.05	prolate-spheroidal	23.0–25.8	6.8–10.0 × 6.8–10.0	3.9 (4.8) 6.5	2.4 (3.1) 4.0	–	A
V. cupularis	**A**	Montes s. n.	40.3 (43.0) 46.8	40.3 (43.2) 46.8	1.00	spheroidal	24.0–25.5	8.0–8.5 × 9.0–9.8	2.6 (3.4) 3.9	4.0 (5.2) 6.4	–	A
	A	Schwindt 1071	40.3 (45.1) 52.0	39.0 (45.4) 50.7	1.00	spheroidal	24.8–25.5	8.0–8.5 × 9.0–9.8	2.6 (3.8) 5.2	4.8 (6.1) 8.0	–	A
V. lipeoensis	**A**	Cabrera et al. 23971	32.5 (36.7) 40.3	32.5 (36.3) 39.0	0.99	oblate-spheroidal	21.5–27.0	6.8–10.0 × 6.8–10.0	2.4 (3.4) 4.0	4.8 (5.7) 7.2	–	A
V. schulziana	**A**	Schulz 3757	35.1 (39.1) 44.2	36.4 (39.8) 44.2	1.07	prolate-spheroidal	23.0–25.0	7.0–8.0 × 7.0–9.5	2.6 (4.0) 5.2	2.4 (3.5) 4.0	–	A
	A	Schulz 921	35.1 (39.3) 44.2	36.4 (39.4) 42.9	0.98	oblate-spheroidal	23.0–25.0	6.8–8.0 × 6.8–8.6	3.9 (4.0) 5.2	4.0 (4.2) 4.8	–	A
V. novarae	**A**	Vervoorst & Legname 4581	33.8 (37.7) 40.3	33.8 (37.4) 42.9	1.01	prolate-spheroidal	33.0–42.0	5.0–6.0 × 5.5–7.0	2.6 (3.7) 5.2	2.4 (3.5) 4.0	5.2 (6.0) 7.8	Aa
	A	Ahumada & Aguero 8177	35.1 (39.3) 44.2	33.8 (37.9) 41.6	1.02	prolate-spheroidal	34.0–43.0	5.0–6.0 × 5.5–7.0	2.6 (3.9) 5.2	2.4 (3.7) 4.8	5.2 (6.3) 7.8	Aa
V. bellula	**P**	Fernández Casas & Molero 5989	56.8 (62.2) 66.6	52.9 (60.5) 66.6	1.04	prolate-spheroidal	56.0–65.8	3.5–4.0 × 3.5–4.0	5.2 (8.6) 11.7	3.2 (4.1) 4.8	9.1 (12.9) 15.6	B
V. centauropsidea	**A**	Hilgert 2031	52.9 (58.2) 64.7	49.0 (54.9) 60.8	1.06	prolate-spheroidal	52.0–64.0	3.5–4.9 × 4.2–4.9	6.5 (7.4) 9.1	4.0 (4.4) 4.8	9.6 (12.0) 15.2	B
V. correntina	**A**	Schinini & Ahumada 13895	58.8 (62.5) 66.6	51.0 (61.8) 66.6	1.01	prolate-spheroidal	57.5–65.5	6.0–6.8 × 9.0–10.0	7.8 (10.1) 13.0	1.6 (2.2) 2.4	13.0 (13.8) 16.9	B
V. hassleriana	**P**	Montes 7161	51.0 (55.2) 60.8	49.0 (55.2) 60.8	0.95	oblate-spheroidal	50.0–60.0	3.5–6.8 × 3.5–8.6	5.2 (6.9) 9.1	3.2 (4.0) 4.8	8.8 (11.2) 12.8	B
V. hystricosa	**P**	Dematteis et al. 905	58.8 (63.1) 66.6	56.8 (61.8) 66.6	1.00	spheroidal	58.0–65.5	8.6–10.0 × 10.0–13.7	5.2 (7.1) 9.1	3.2 (4.4) 4.8	10.4 (13.1) 15.6	B
	P	Dematteis et al. 911	64.7 (70.3) 78.4	64.7 (68.7) 74.5	1.02	prolate-spheroidal	63.8–77.5	8.0–10.0 × 9.5–13.7	5.2 (7.1) 9.1	2.4 (3.2) 4.0	11.7 (14.4) 18.2	B
V. lanata	**P**	Schinini 2211	49.4 (52.8) 59.8	48.1 (51.6) 54.6	1.03	prolate-spheroidal	48.0–59.0	8.6–10.0 × 8.6–12.0	5.2 (6.9) 9.1	2.4 (2.9) 3.2	7.8 (9.6) 11.7	B
	P	Schinini 2633	48.1 (51.7) 54.6	45.5 (51.8) 61.1	1.02	prolate-spheroidal	47.3–53.0	8.6–10.0 × 8.6–12.5	5.2 (7.1) 9.1	2.4 (2.7) 3.2	9.1 (11.1) 14.3	B

Table I. Continued.

Taxa	Country of origin	Collector	Polar axis (P)	Equatorial diameter (E)	P/E	Shape	Colpus length	Pore diameter	Exine thickness	Spine length	Lacuna diameter	Pollen type
1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
V. parvifolia	**P**	Bordas 1257	52.0 (54.7) 57.2	50.7 (52.8) 54.6	1.04	prolate-spheroidal	51.0–56.0	8.6–10.3 × 8.6–10.3	5.2 (7.4) 9.1	3.2 (3.8) 4.0	10.4 (12.3) 16.0	B
	P	Bordas 4397	52.0 (55.3) 58.5	50.7 (53.5) 57.2	1.04	prolate-spheroidal	51.0–57.0	8.0–10.3 × 8.3–10.3	5.2 (7.8) 10.4	3.6 (4.0) 4.4	9.6 (11.2) 13.6	B
	P	Schinini 2783	54.6 (57.2) 59.8	50.7 (55.0) 59.8	1.04	prolate-spheroidal	53.5–59.0	8.6–10.0 × 8.6–10.0	6.5 (8.0) 9.1	4.0 (4.4) 5.6	9.6 (11.4) 13.6	B
V. platyphylla	**P**	Dematteis & Schinini 865	50.7 (54.5) 58.5	49.4 (53.6) 58.5	1.04	prolate-spheroidal	49.5–57.5	6.8–10.0 × 8.6–12.0	5.2 (6.8) 9.1	3.2 (4.0) 4.8	7.8 (10.1) 13.0	B
V. profusa	**P**	Schinini 30440	58.5 (70.7) 75.4	59.8 (66.7) 75.4	1.01	prolate-spheroidal	57.3–74.0	6.0–6.8 × 9.0–12.0	6.4 (9.1) 12.0	3.2 (4.2) 5.6	9.1 (13.4) 15.6	B
V. ramellae	**P**	Hassler 6674	58.8 (65.0) 72.5	54.9 (60.9) 66.6	1.03	prolate-spheroidal	57.8–71.5	8.6–9.0 × 8.6–10.0	7.8 (10.3) 13.0	3.2 (3.6) 4.0	10.4 (13.9) 16.9	B
V. spicata	**A**	Schulz 7185	42.9 (45.2) 48.1	40.3 (44.3) 46.8	1.00	spheroidal	41.5–47.0	7.0–8.2 × 9.0–10.0	3.9 (5.0) 7.8	2.4 (2.8) 4.0	6.5 (9.6) 13.0	B
V. teyucuarensis	**A**	Dematteis 476	58.8 (64.7) 68.6	58.8 (62.3) 66.6	1.02	prolate-spheroidal	57.5–67.8	6.8–8.4 × 7.0–8.4	5.2 (7.8) 11.7	3.2 (3.8) 4.8	10.4 (12.91) 5.6	B
	A	Dematteis 515	62.7 (69.0) 74.5	58.8 (66.8) 72.5	1.04	prolate-spheroidal	62.0–73.0	7.0–8.4 × 7.0–8.4	6.5 (9.0) 11.7	3.2 (3.7) 4.8	10.4 (13.61) 9.5	B
V. valenzuelae	**P**	Fiebrig 859	45.1 (52.7) 58.8	41.2 (49.1) 54.9	1.03	prolate-spheroidal	44.0–58.0	6.0–6.8 × 6.0–7.3	5.2 (6.6) 7.8	2.6 (3.7) 5.2	7.2 (9.11) 10.4	B
	P	Schinini & Dematteis 33467	39.0 (42.0)45.5	39.0 (41.7) 44.2	1.01	prolate-spheroidal	38.0–44.5	6.0–6.8 × 6.3–7.5	3.9 (4.6) 6.5	2.4 (2.8) 4.0	8.0 (10.2) 12.8	B
V. hystrix	**P**	Dematteis & Schinini 852	40.3 (44.3) 46.8	40.3 (43.5) 46.8	0.97	oblate-spheroidal	39.0–45.0	8.0–8.6 × 10.0–12.0	3.9 (4.7) 6.5	3.2 (4.0) 4.8	8.0 (9.3) 12.0	C
	P	Schinini et al. 35505	44.2 (46.9) 50.7	42.9 (45.6) 49.4	0.99	oblate-spheroidal	43.0–49.0	8.0–8.6 × 10.0–12.5	3.9 (5.2) 6.5	3.2 (4.1) 4.8	8.0 (9.9) 12.8	C
Var *propinqua* var *canescens*	**P**	Dematteis 888	47.0 (50.4) 54.9	47.0 (50.9) 52.9	1.06	prolate-spheroidal	46.0–54.0	8.6–10.0 × 10.0–13.7	5.2 (6.7) 9.1	2.4 (2.6) 3.2	7.8 (10.5) 13.0	C
	P	Schinini & Dematteis 33530	52.0 (55.4) 58.5	50.7 (54.1) 58.5	0.99	oblate-spheroidal	52.0–56.8	8.0–10.0 × 9.5–13.7	5.2 (6.9) 9.1	1.6 (2.7) 4.0	7.8 (10.9) 14.3	C
V. setososquamosa	**A**	Novara 10877	41.6 (44.4) 48.1	39.0 (42.3) 46.8	0.93	oblate-spheroidal	40.0–44.0	8.0–8.3 × 9.0–11.0	3.9 (5.1) 6.5	2.4 (3.1) 4.0	9.6 (10.8) 12.0	C
	A	Spegazzini & Girola s. n.	40.3 (42.0) 44.2	39.0 (41.9) 44.2	1.05	prolate-spheroidal	39.0–43.0	8.0–8.4 × 9.0–10.0	3.9 (5.1) 6.5	1.6 (2.6) 3.2	8.0 (10.1)12.0	C
V. amambaia	**P**	Dematteis & Schinini 867	37.7 (41.0) 45.5	37.7 (40.0) 42.9	1.03	prolate-spheroidal	37.0–44.5	8.0–8.6 × 10.0–12.0	2.6 (4.2) 6.5	2.4 (3.0) 3.6	8.0 (9.8) 12.0	D
V. brunneri	**P**	Brunner 1720	49.4 (51.9) 54.6	45.5 (50.8) 54.6	1.02	prolate-spheroidal	–	6.0–8.5 × 6.0–8.5	6.5 (7.8) 9.1	–	7.8 (11.0) 15.6	E

0.93–1.07) and either, 3-colporate or 3-porate; equatorial outline subcircular to circular, polar outline rounded triangular, or subcircular to circular. Colpus length, the distance between the polar extremes of the abporal lacunae, ranges from 15–25 μm (long=15–20 μm, very long=>20 μm); the abporal lacunae have interrupted interlacunar lophae at the interfaces with the poral lacuna. Pori lalongate, often slightly constricted in the central region (Figure 2B) or almost circular. Pollen size, polar length (P): ranges from 32.5–78.4 μm, equatorial width (E); ranges from 32.5–75.4 μm; exine thickness, excluding spines, 2.4–13.0 μm; sexine: 1.5–12.0 μm, notably wider than nexine: 0.5–1.0 μm. Tectum either continuous, comprising lophae (crests or ridges) surrounding depressions (Figure 2A, B) or discontinuous comprising lophae surrounding lacunae (Figures 2C–F, 3A–F), the upper surface of the nexine is visible in the bases of the lacunae; the outline of the lacunae may be more or less regular (Figures 1E–O, 2E, 3A, C, E, 4) or notably irregular (Figures 1A–D, 2A, C). The tectum surface is usually densely microperforate and spinose, spines 2–6 μm long (Figures 2A–F, 3A–D, 4) or, less commonly, imperforate and psilate (Figures 1N, O, 3E, F).

Five pollen types and one subtype are recognized following the six pollen types of Keeley and Jones (1979): pollen types B, C and D are distinguished particularly by the lacunae pattern and the presence or absence of the central equatorial or central polar lacunae (see Figure 4A–C). The pollen types are described below in order of the least to the most specialized (Bolick & Keeley, 1994).

Type A (Figures 1A, B, 2A, B)

Pollen grains oblate spheroidal, spheroidal or prolate spheroidal (P/E 0.98–1.07), 3-colporate, subechinolophate. Colpi long: between 15–20 μm, pori lalongate. Pollen size, P: 32.5 (42.5) 54.9 μm, E: 32.5 (42.1) 52.9 μm. Exine thickness, excluding spines, 2.4–6.5 μm. Tectum continuous, comprising lophae surrounding depressions (Figure 2A, B); outline of depressions irregular (Figure 2A). Tectum surface densely microperforate and spinose, spine length 2.4–8.0 μm, apices acute, with the exception of *V. schulziana* which has spines with rounded apices.

Species included: *V. chaquensis, V. cichoriiflora, V. cupularis, V. lipeoensis, V. schulziana*

Subtype Aa (Figures 1C, D, 2C, D)

Pollen grains prolate spheroidal (P/E 1.01–1.02), 3-colporate, echinolophate. Colpi very long: 33–43 μm (notably longer than in pollen type A), with the apices visible on the polar face, pori lalongate to circular. Pollen size, P: 33.8 (38.5) 42.9 μm, E: 33.8 (37.6) 42.2 μm. Exine thickness, excluding spines, 2.6–5.2 μm. Tectum discontinuous, comprising lacunae surrounded by lophae (Figure 2C); outline of lacunae irregular (Figure 2C); number of mesocolpial lacunae variable. Tectum surface densely microperforate and spinose, spine length 2.4–4.8 μm, apices acute.

Species included: *V. novarae*

Type B (Figures 1E–G, 2E, F, 4Ai–iii)

Pollen grains oblate spheroidal, spheroidal or prolate spheroidal (P/E 0.98–1.06), 3-colporate, echinolophate. Colpi very long: 44–77 μm, with apices visible in polar view, the colpi interrupt the lophae that separate the poral lacuna from the abporal lacunae (Figure 4Aiii); pori subcircular or, sometimes, lalongate. Pollen size, P: 40.3 (57.5) 78.4 μm, E 39 (56.5) 75.4 μm. Exine thickness, excluding spines, 3.9–13.0 μm. Tectum discontinuous (Figure 2E), comprising lacunae surrounded by lophae (Figure 2E, F); outline of lacunae more or less regular; total number of lacunae 30 (Figure 4Ai–iii): 3 poral, 6 abporal, 3 equatorial (central mesocolpium), 12 paraporal and 6 interpolar, polar lacunae absent. Tectum surface densely microperforate and spinose, spines with a linear distribution along the ridges of the lophae, spine length: 1.6–5.6 μm, apices acute, with the exception of *V. hystricosa* which has rounded apices.

Species included: *V. bellula, V. centauropsidea, V. correntina, V. hassleriana, V. hystricosa, V. lanata, V. parvifolia, V. platyphylla, V. profusa, V. ramellae, V. spicata, V. teyucuarensis, V. valenzuelae*

Type C (Figures 1K–M, 3A, B, 4Bi–iii)

Pollen grains oblate spheroidal, prolate or prolate spheroidal (P/E 0.97–1.06); 3-colporate, echinolophate. Colpi long: 39–56.8 μm, the colpi interrupt the lophae that separate the poral lacuna from the abporal lacunae (Figure 4Biii); pori lalongate to subcircular. Pollen size, P: 40.3 (49.25) 58.5 μm, E: 37.7 (46.4) 52.9 μm. Exine thickness, excluding spines, 3.9–9.1 μm. Tectum discontinuous (Figure 3A), comprising lacunae surrounded by lophae (Figure 3B); outline of lacunae more or less regular; total number of lacunae 29 (Figure 4Bi–iii): 3 poral, 6 abporal, 12 paraporal, 6 interporal and 2 polar or, rarely, 4 polar lacunae (two at each pole) have been recorded, equatorial lacunae absent. Tectum surface densely microperforate and spinose, spines with a linear distribution along the

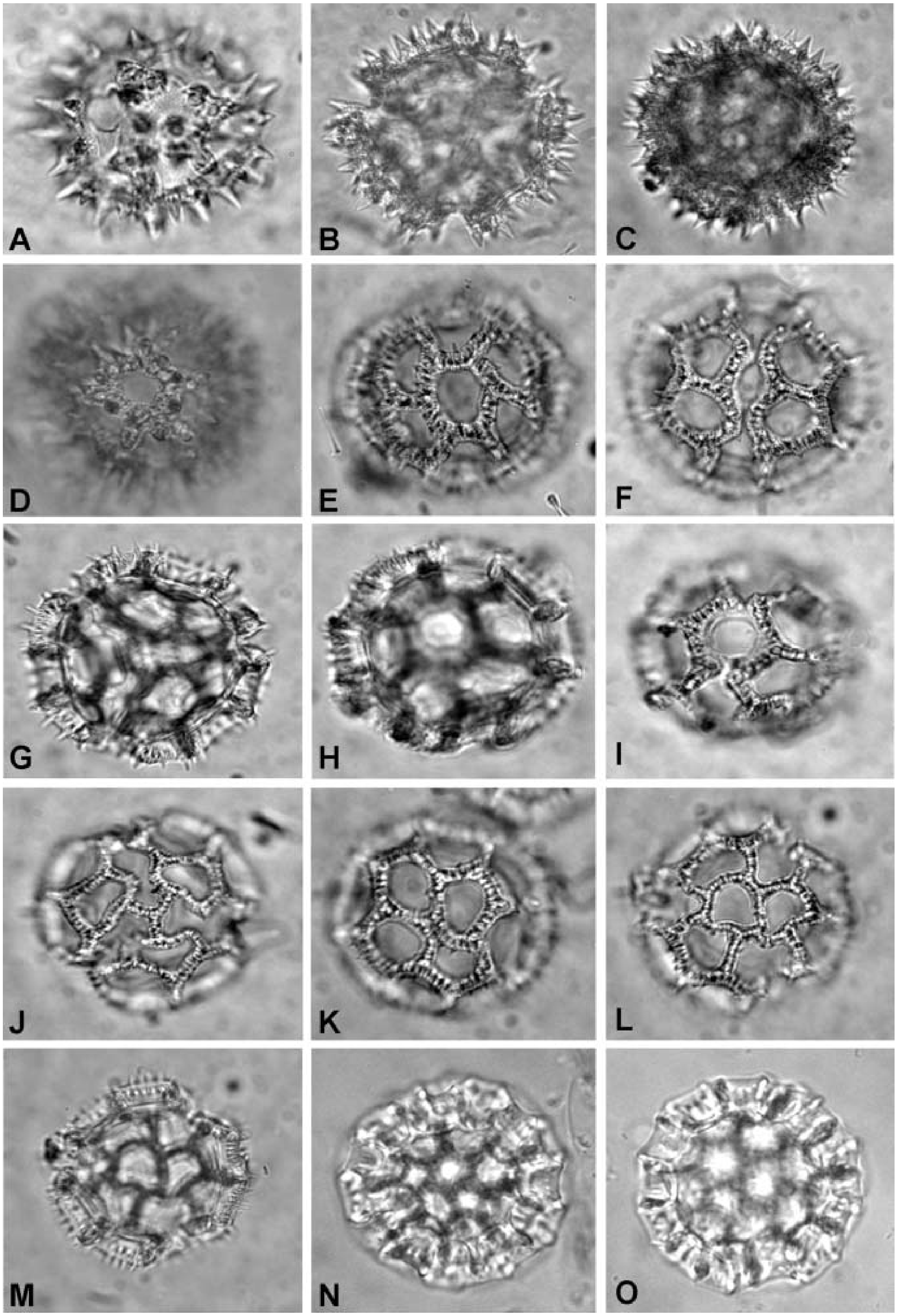

Figure 1. Pollen of *Vernonia* (LM). **A, B**. Pollen Type A – *V. cupularis*. Montes s. n.: **(A)** Slightly tilted equatorial view, showing aperture (left); **(B)** Polar view. **C, D**. Pollen Type A, subtype Aa – *V. novarae*. Vervoorst & Legname 4581: **(C)** Equatorial view; **(D)** Polar view, high focus. **E–G**. Pollen Type B – *V. spicata*. Schultz 7185: **(E)** equatorial view, mesocolpium; **(F)** Equatorial view showing aperture; **(G)** Polar view. **H–J**. Pollen Type D – *V. amambaia*. Dematteis & Schinini 867: **(H)** Equatorial view, aperture mid-low focus; **(I)** Equatorial view, aperture high focus; **(J)** Polar view. **K–M**. Type C – *V. propinqua* var. *canescens*. Dematteis 888: **(K)** Equatorial view; **(L)** polar view, high focus; **(M)** Polar view, mid focus. **N, O**. Pollen Type E – *V. brunneri*. Brunner 1720: **(N)** Polar view; **(O)** Equatorial view. [All images × 1000].

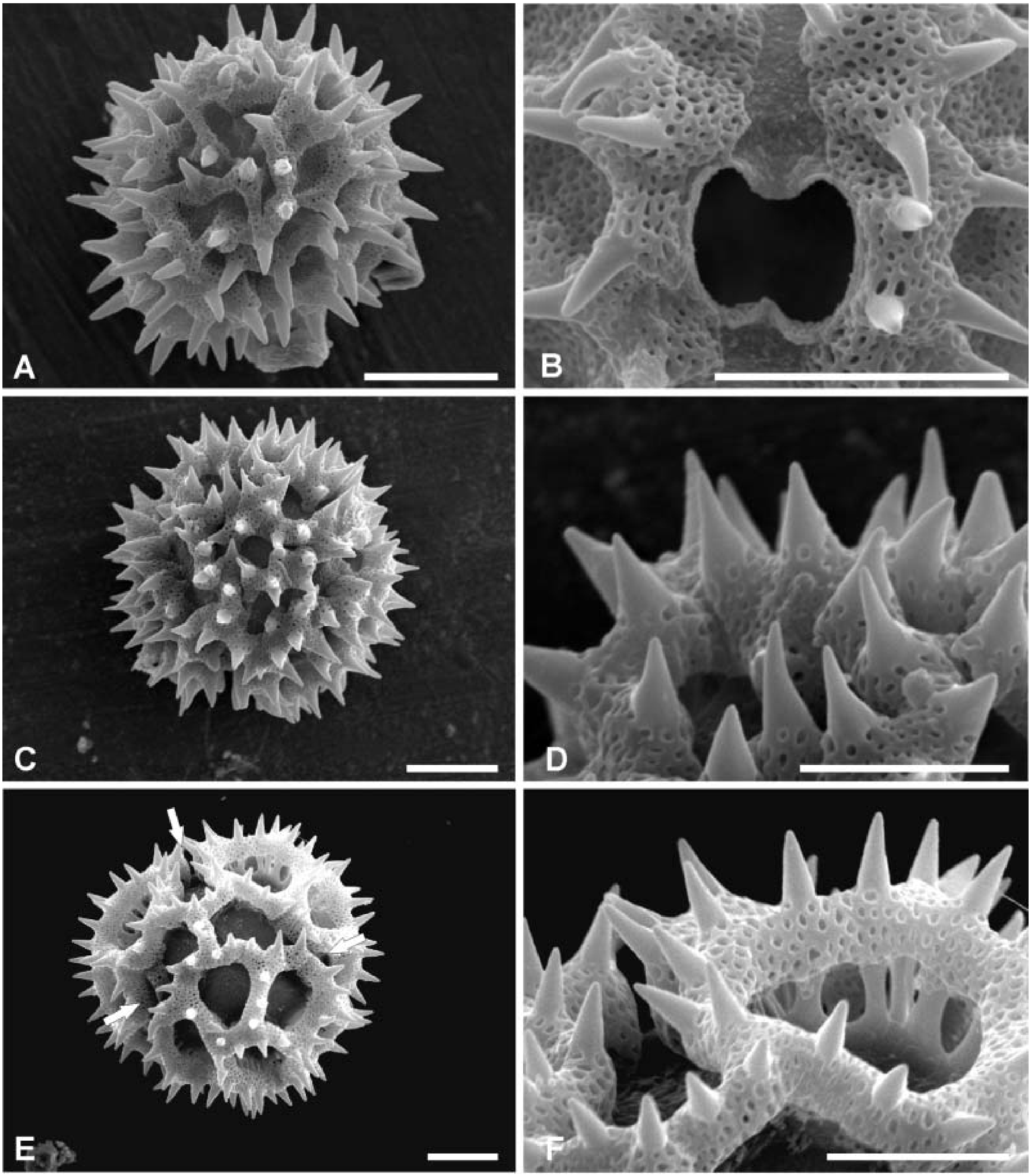

Figure 2. Pollen of *Vernonia*, Types A and B (SEM). **A, B**. Pollen Type A – *V. lipeoensis*. Cabrera et al. 23971: **(A)** Equatorial view, mesocolpium; **(B)** Close up of porus. **C, D**. Pollen Type Aa – *V. novarae*. Vervoorst & Legname 4581: **(C)** Equatorial view, mesocolpium; **(D)** Detail of spines. **E, F**. Pollen Type B – *V. centauropsidea*. Hilgert 2031: **(E)** Polar view showing the colpi (*arrow*) and the absence of polar lacuna; **(F)** Detail of lacunae and spines. Scale bars – 10 µm.

ridges of the lophae, spine length: 1.6–4.8 µm, apices acute.

Species included: *V. hystrix, V. propinqua* var. *canescens, V. setososquamosa*

Type D (Figures 1H–J, 3C, D, 4Ci–iii)

Pollen grains prolate spheroidal (P/E 1.01–1.03); 3-colporate, echinolophate. Colpi very long:

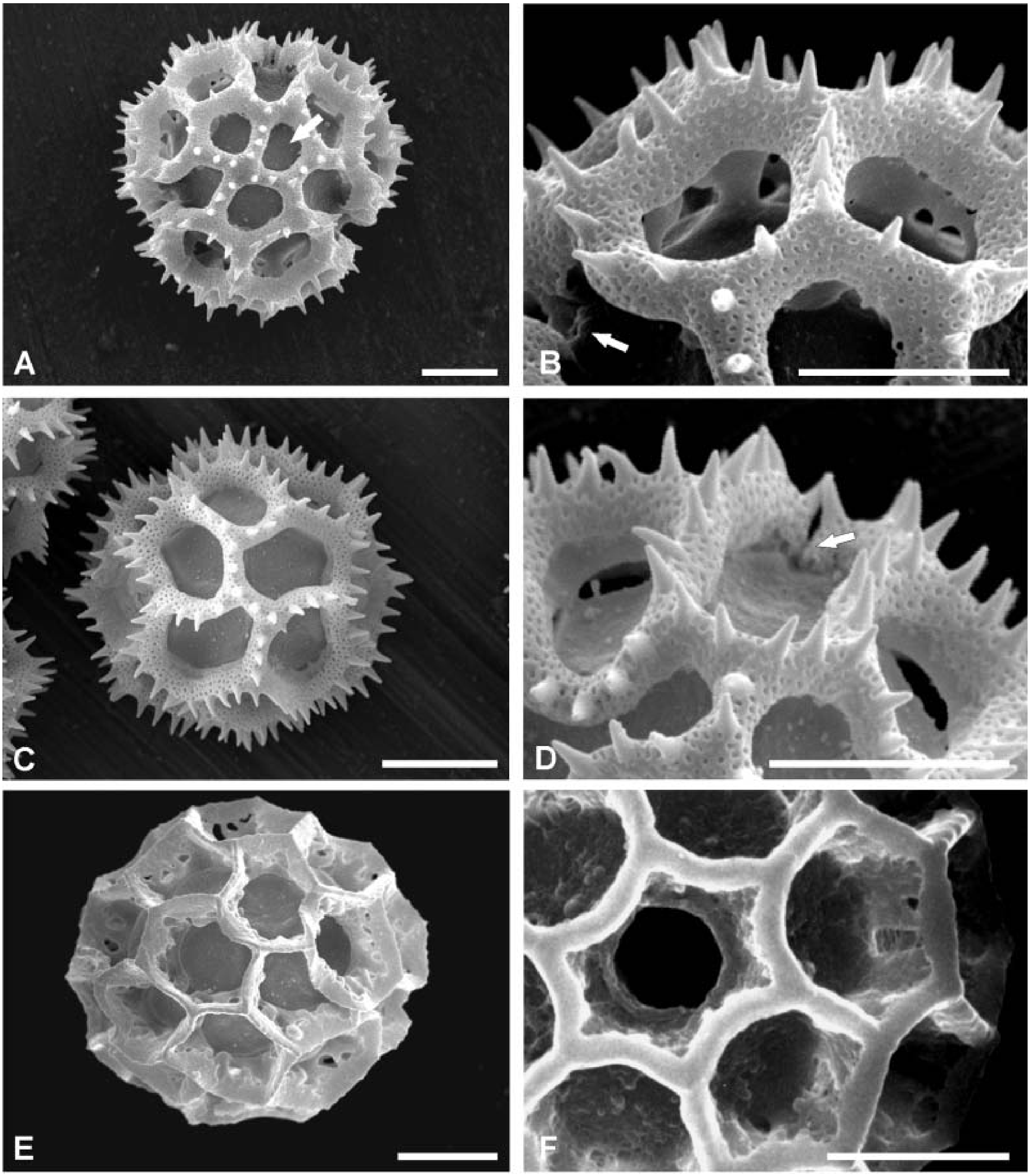

Figure 3. Pollen of *Vernonia*, Types C–E (SEM). **A, B**. Type C – *V. propinqua* var. *canescens*. Dematteis 888: **(A)** Polar view showing polar lacuna (*arrow*); **(B)** Detail of 'A' note colpate interruption to spinose lophate ridge (*arrow*); **C, D**. Pollen Type D – *V. amambaia*. Dematteis 867: **(C)** Equatorial view, mesocolpia, showing the 4 intercolpar lacunae, one interporal lacuna also visible (top centre); **(D)** Close up, perimeter of polar view note colpus interruption to lophate ridge (*arrow*). **E, F**. Type E – *V. brunneri*. Brunner 1720: **(E)** Mesocolpial view; **(F)** Close up of pore. Scale bars – 10 μm.

37.0–44.5 μm long, with apices visible in polar view; the colpi interrupt the lophae that separate the poral lacunae from the abporal lacunae (Figure 4Ciii); pori subcircular. Pollen size, P: 37.7 (41.0) 44.5 μm, E: 37.7 (40.0) 42.9 μm. Exine thickness, excluding spines, 2.6–6.5 μm. Tectum continuous, comprising

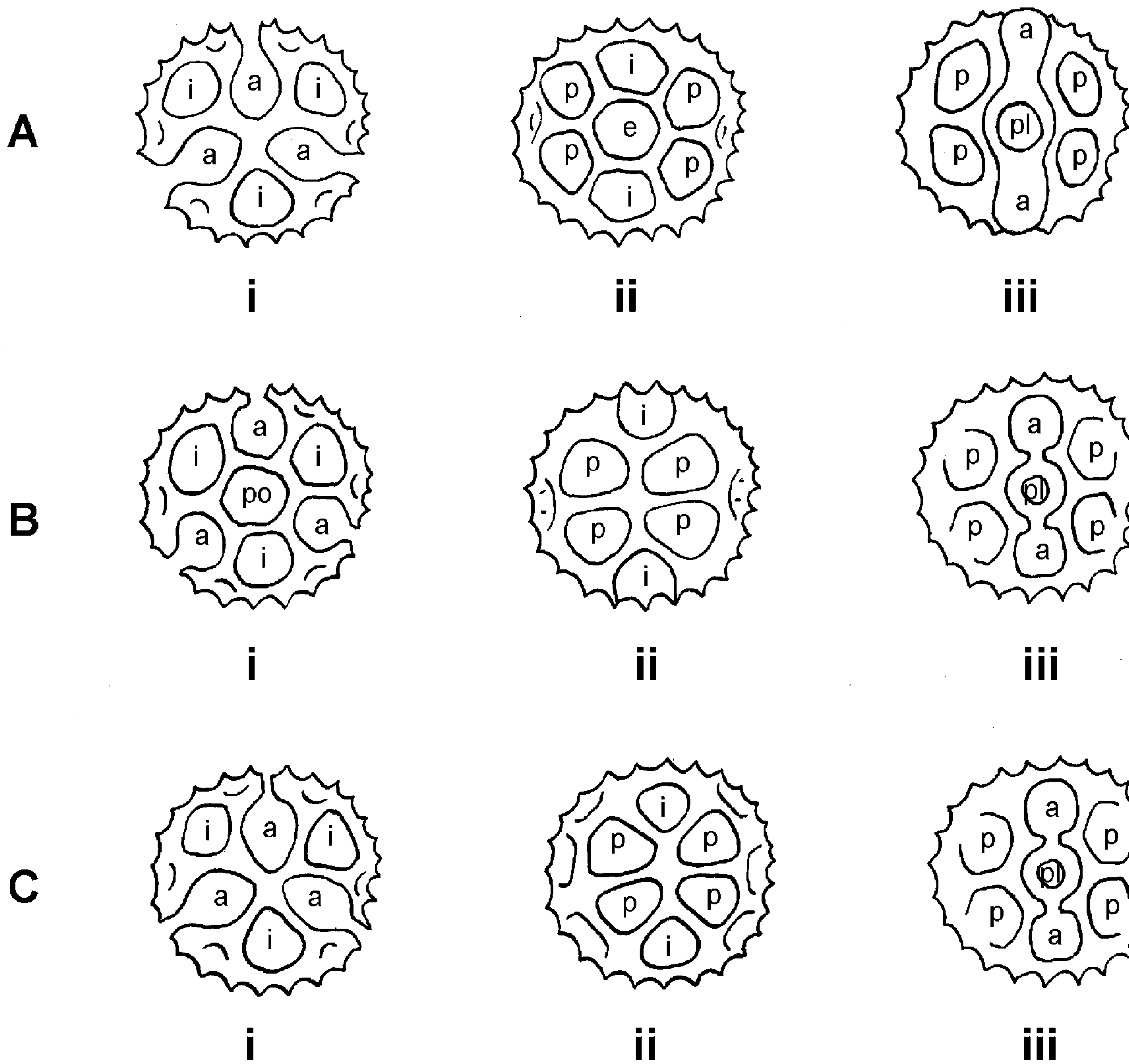

Figure 4. Diagrammatic representation of the variations to the arrangement of the lacunae in the 3 echinolophate pollen types (B–D) of *Vernonia*. **Ai–Aiii**. Pollen Type B: **(Ai)** Polar view, note absence of polar lacuna; **(Aii)** Equatorial view - mesocolpium, note presence of equatorial lacuna (*e*); **(Aiii)** Equatorial view - colporus, note slight lophate constriction between abporal (*a*) and poral (*pl*) lacunae. **Bi–Biii**. Pollen Type C: **(Bi)** Polar view, note presence of polar lacuna (*po*); **(Bii)** Equatorial view – mesocolpium, note absence of central mesocolpial lacuna; **(Biii)** Equatorial view – colporus, note lophate constrictions demarcating colpus between abporal (*a*) and poral (*pl*) lacunae. **Ci–Ciii**. Pollen Type D: **(Ci)** Polar view, note absence of polar lacuna; **(Cii)** Equatorial view – mesocolpium, note absence of equatorial lacuna; **(Ciii)** Equatorial view – colporus, note lophate constrictions demarcating colpus between abporal (*a*) and poral (*pl*) lacunae. Symbols on diagram: a – abporal lacuna; i – interpolar lacuna; e – equatorial lacuna; p – paraporal lacuna; po – polar lacuna; pl – poral lacuna.

lacunae surrounded by lophae (Figure 3C); outline and disposition of lacunae more or less regular (Figure 3D); total number of lacunae 27 (Figure 4Ci–iii): 3 poral, 6 abporal, 12 paraporal and 6 interporal lacunae, polar lacunae absent, equatorial lacunae absent. Tectum surface densely microperforate and spinose, spines with a linear distribution along the ridges of the lophae, spine length: 2.4–4.0 μm, apices acute.

Species included: *V. amambaia*

Type E (Figures 1N, O, 3E, F)

Pollen grains prolate spheroidal (P/E 1.02); 3-porate, psilolophate. Pori more or less circular, 6–8.5 μm in diameter (Figure 3F). Pollen size, P: 49.4 (51.9) 54.6 μm, E: 45.5 (50.8) 54.6 μm. Exine thickness 6.5–9.1 μm. Tectum discontinuous, comprising narrow thin-walled lophae surrounding lacunae (Figure 3E); outline and disposition of lacunae more or less regular and disposed in a geometric pattern; total number of lacunae

30–34, including 3 poral. Surface of lophae imperforate-psilate.

Species included: *V. brunneri*

Key to the pollen types

1a.	Pollen grains psilolophate.	2a
1b.	Pollen grains spinose & microperforate lophate	2b
2a.	3-porate	*Type E*
2b.	3-colporate	3
3a.	Irregular depressions or lacunae in tectum. .	4
3b.	More or less regular lacunae	5
4a.	Tectum continuous with depressions and lophate ridges	*Type A*
4b.	Tectum discontinuous with lacunae and lophate ridges	*Type Aa*
5a.	Pollen without equatorial lacunae	6
5b.	Pollen with equatorial lacunae	*Type B*
6a.	Pollen with polar lacunae.	*Type C*
6b.	Pollen without polar	*Type D*

Discussion

The pollen types for tribe Vernonieae were established initially by Keeley and Jones (1979). They described six pollen types for the genus *Vernonia s. l.* based mainly on variation in apertures and surface morphology. Robinson (1992) later made some modifications to the original six types and, currently, ten pollen types are recognised for the tribe. In the present study five of Keeley and Jones (1979) six pollen types have been found: A, B, C, D and E, as well as an additional discontinuous tectum variant of pollen Type A, which we have designated pollen Subtype Aa because we consider the exine to be similar to, but a modification of the continuous tectum of pollen Type A. Pollen Subtype Aa also has longer colpi than pollen Type A.

To date Keeley and Jones (1979) six pollen types have shown differing distributions between the Old and New Worlds. Pollen Type A (subechinolophate) as well as pollen Types B (echinolophate with central mesocolpial lacunae but no polar lacunae – Figure 4A) and C (echinolophate with central polar lacunae but no central mesocolpial lacunae – Figure 4B) occur in both the Old and the New World; while pollen Type D (echinolophate without central polar or central mesocolpial lacunae – Figure 4C) is restricted to Brazilian taxa. The two psilophate pollen types, E and F, are almost entirely restricted to Old World species. Type F is triporate and multilacunate as in Type E, but usually the tectum of the lophae is perforate with many short spinulae along the ridges of the lophae (Robinson, 1992).

Most of the species in our study have not been included previously in taxonomic treatments of tribe Vernonieae and, therefore, their taxonomic position within the tribe has not been considered yet.

The morphology of the pollen described for *V. amambaia* differs from a previous study that recorded Type G pollen in this species (Robinson, 1998). Type G pollen was defined by (Robinson, 1998) as encompassing characteristics which distinguish *V. amambaia*. Like Type D pollen it is tricolporate and echinolophate, but the abporal and poral lacunae are not separated completely by lophae. However, the two specimens of *V. amambaia* (one a paratype) that we have examined both have Type D pollen. In the light of this conflict of opinion, pollen of additional individuals should be examined to determine, more confidently, any possible disparity in pollen morphology between the pollen grains of a range of collections of *V. amambaia*.

Vernonia setososquamosa has sometimes been considered as a variety of the widespread *V. remotiflora* L.C. Rich. (Robinson, 1999), but was recently restored as a species on the basis of morphological features (Cristóbal & Dematteis, 2003). *Vernonia setososquamosa* is a perennial herb, and has a shorter growth habit than that of *V. remotiflora*, furthermore, the tip of the phyllaries are largely aristate and these characteristics suggest that *V. setososquamosa* is more closely related to *V. amambaia*, which is also a perennial and has aristate phyllaries. The most important difference between *V. setosoquamosa* and *V. amambaia* are the corolla lobes which, in *V. amambaia*, have small hairs. The difference in pollen type between *V. amambaia* (pollen Type D) and *V. setososquamosa* (pollen Type C) provides an additional feature to distinguish between the two species.

The pollen type observed in *V. novarae* is intermediate between pollen Type A and pollen Type B, although we consider it to be a modification of Type A. This modified form is uncommon in the tribe *Vernonieae* and has been previously found only in the Brazilian monotypic genus *Bishopalea* H. Rob. (Robinson, 1999) to which *Vernonia novarae* is not related.

The species with Type B pollen have, in general, larger pollen than the remaining species of the tribe. This is coincident with cytological information which indicates that these species include the greatest proportion of polyploid entities, and the highest ploidy levels in *Vernonia* (Dematteis, 2002). The greater number of chromosomes are likely to be responsible for the larger pollen size observed in these species, this is supported by the fact that, within Type B taxa, the larger grains tend to occur in the species with higher ploidy levels, such as *V. hystricosa* and *V. teyucuarensis*, which are octoploid and decaploid respectively.

Pollen Type C occurs mostly in the New World taxa of *Vernonia* Subsect. *Flexuosae* (=*Chrysolaena* H.Rob.) and *Vernonia* Sect. *Stenocephalum* (=*Stenocephalum* Sch. Bip.) two groups distributed in southern South America. However, they are not closely related and differ considerably in many morphological features, such as the inflorescence pattern, shape of the capitula, and chromosome number. Section *Stenocephalum* species have spicate inflorescences, cylindrical heads and a base chromosome number of x=17, while *Chrysolaena* has cymose inflorescences, campanulate heads and a base chromosome number of x=10 (Dematteis, 1997).

Pollen Type E occurs frequently in Old World species of Vernonieae, but in the New World, has been found only in four taxa from Paraguay: *Pacourina edulis* Aubl. (Robinson, 1999), *Vernonia echitifolia* Mart. ex DC. (Dematteis & Robinson, 1997), *V. rojasii* Cabrera (Dematteis & Salgado, 2001) and *V. brunneri* (Robinson, 1999); because of this it has been previously suggested (Robinson, 1999; Dematteis & Salgado, 2001), that the presence of Type E pollen in these New World species indicates that they are probably more closely related to Old World members of Vernonieae than to other New World taxa.

Conclusions

In our study we have found five of the six pollen types recognized for *Vernonia s.l.*, in South America, including pollen Type E which is only rarely recorded in New World Vernonieae. The pollen types recognised for Vernonieae tend to occur in different groups of the tribe and, consequently, often indicate the possible taxonomic position of a species. Multidisciplinary analyses of the species examined are still incomplete. Nevertheless, our pollen studies of recently described Argentinean and Paraguayan species of *Vernonia* again indicate how potentially useful pollen characters are in delimiting natural groups within the Vernonieae.

Acknowledgements

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Specimens investigated

Vernonia centauropsidea Hieron.
Argentina, Salta: Dept. Santa Victoria, National Park Baritú. Hilgert 2031 (MCNS).

V. chaquensis Cabrera
Argentina, Chaco: Estancia La Lonja. Schulz 13696 (CTES).
Paraguay, Alto Paraná: 12 km NE of Hernadarias. Schinini et al. 28183 (CTES).

V. correntina Cabrera & Cristóbal
Argentina, Corrientes: 8 km N of Curuzú Cuatía. Schinini & Ahumada 13895 (CTES).

V. cupularis Chodat
Argentina, Misiones: Dept. Santa Ana, Loreto. Montes s.n. (CTES).
Misiones: Dept. San Pedro, Montecarlo. Schwindt 1071 (CTES).

V. lipeoensis Cabrera
Argentina, Jujuy: Dept. Ledesma, on the road to Valle Grande, Abra de Cañas. Cabrera et al. 23971 (LIL isotype).

V. novarae Cabrera
Argentina, Salta: Dept. Santa Victoria, on road from Los Toldos to Lipeo, 13 km from Los Toldos. Vervoorst & Legname 4581(CTES).
Salta: Dept. Santa Victoria. On the road to San José river. O. Ahumada & J. Aguero 8177 (CTES).

V. schulziana Cabrera
Argentina, Chaco: Dept. 1° de Mayo, Colonia Benítez. Schulz 3757 (CTES isotype).
Chaco: Dept. 1° de Mayo, Colonia Benítez. Schulz 921 (CTES paratype).

V. setososquamosa Hieron.
Argentina, Salta: Dept. Rosario de Lerma, Dique Las Lomitas. Novara 10877 (CTES).
Salta: Dept. Orán, between Orán and Saucelito. Spegazzini & Girola s. n. (CTES).

V. spicata Cabrera
Argentina, Misiones: Dept. San Ignacio, Santo Pipó. Schulz 7185 (CTES).

V. teyucuarensis Cabrera
Argentina, Misiones: Dept. San Ignacio, Teyú Cuaré. Dematteis 476 (CTES).
Misiones: Dept. San Ignacio, Horacio Quiroga's house. Dematteis 515 (CTES).

V. amambaia (H.Rob.) Dematteis
Paraguay, Amambay: 25 km N of Pedro Juan Caballero, on the road to Colonia Estrella. Dematteis & Schinini 867 (CTES).

V. brunneri (H.Rob.) Cabrera
Paraguay, Concepción: Tagatiya-mi river. Brunner 1720 (G isotype).

V. bellula Dematteis
Paraguay, Canindeyú: between Ypé-Hú and Capitán Bado, 10 km from Itanará. Fernández Casas & Molero 5989 (CTES isotype).

V. cichoriiflora Chodat
Paraguay, San Pedro: 35 km N of San Estanislao. A. Krapovickas & C. L. Cristóbal 34263 (CTES).

V. hassleriana Chodat
Paraguay, Itapúa: Capitán Meza. Montes 7161 (CTES).

V. hystricosa Cabrera & Dematteis
Paraguay, Amambay: 30 km S of Bella Vista, on the road to the Aquidabán river. Dematteis et al. 905 (CTES).
Amambay: on the road to Colonia Estrella, 25 km N of Pedro Juan Caballero. Dematteis et al. 911 (CTES).

V. hystrix Chodat
Paraguay, Amambay: 25 km N of Igatimí. Dematteis & Schinini 852 (CTES).

Amambay: Colonia Marizcal López, near Capitán Bado. Schinini et al. 35505 (CTES).

V. lanata (Chodat) Cabrera
Paraguay, Cordillera: Eusebio Ayala. Schinini 2211 (CTES).
Cordillera: Itacurubí. Schinini 2633 (CTES).

V. parvifolia (Chodat) Cabrera
Paraguay, Cordillera: Emboscada. Bordas 1257 (CTES).
Cordillera: Tobatí, Huguaty Rozado - Itá Espejo. Bordas 4397 (CTES).
Paraguarí: Tuyá-Quindy Church. Schinini 2783 (CTES).

V. platyphylla Chodat
Paraguay, Amambay: 40 km N of Pedro Juan Caballero, on the road to Arroyo Estrella. Dematteis & Schinini 865 (CTES)

V. profusa Dematteis & Cabrera
Paraguay, Amambay: near Pedro Juan Caballero. Schinini et al. 30440 (CTES holotype).

V. propinqua var. *canescens* (Chodat) Dematteis
Paraguay, Amambay: Chiriguelo. Dematteis et al. 888 (CTES)
Amambay: Colonia Estrella. Schinini & Dematteis 33530 (CTES).

V. ramellae Cabrera
Paraguay, Paraguarí: in valle fluminis Y-acá. Hassler 6674 (G holotype).

V. valenzuelae Chodat
Paraguay, Cordillera: Piribebuy and Tobatí, Serranía Y-aguaí-guazú. Fiebrig 859 (G)
Amambay: Chiriguelo. Schinini & Dematteis 33467 (CTES).

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