

Pollen morphology of some species of *Vernonanthura* (Asteraceae, Vernonieae) from southern South America

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Pollen grains from 16 species of *Vernonanthura* H. Rob. were studied. All the species exhibit the type 'A' pollen characteristic of the genus. These grains are spheroidal to prolate-spheroidal, subechinolophate, tricolporate, with a continuous tectum which is densely microporate, exhibiting lophae surrounding irregular depressions and having prominent spines. Despite most of the species having a similar pollen type, some taxa can be recognised by the morphology of the spines. According to the spine index (length/width), the species analysed can be divided into three groups having respectively short, medium and long spines. In addition to the size of the spines, some taxa can be distinguished by spine shape. *Vernonanthura pinguis* (Griseb.) H. Rob. has spines which are constricted at the base, while *V. oligactoides* (Less.) H. Rob. exhibits small conical spines. *Vernonanthura nudiflora* (Less.) H. Rob. and *V. schulziana* (Cabrera) H. Rob. have spines with rounded apices. This study confirms that *Vernonanthura* is a well-defined group based on pollen characteristics and that pollen morphology is a significant feature in the characterisation of species and genera of Vernonieae.

Keywords: pollen; evolution; taxonomy; *Vernonia*

1. Introduction

The Vernonieae Cass. (Asteraceae) are a pantropical tribe of 89 genera which are concentrated around two major centres of diversification, the central region of Africa and southern Brazil. The members of the tribe are grouped into six different subtribes based on inflorescence patterns, persistence of phyllaries, pollen morphology, chemical composition and chromosome numbers (Bremer 1994). The subtribe Vernoniinae Less, once constituted the largest group within the Vernonieae, including approximately 1100 species. The group comprised most of the species previously placed in the genus *Vernonia* Schreb. The majority of the American species of the latter broadly interpreted genus have been segregated into other genera by Robinson (1987, 1988, 1989, 1990, 1992a, 1993). *Vernonia* is a mostly North American genus, and is closely related to *Vernonanthura* with which it shares the distinctive parallel ducts in the corolla lobes (Robinson 1999).

Vernonanthura H. Rob. was established to separate taxa earlier assigned to *Vernonia* sect. *Lepidaploa paniculatae* Benth. & Hook., which consists of about 70 species with a distribution from southern Mexico to central Argentina, but mostly concentrated in south-east Brazil (Dematteis 2006). This genus is closely

related to *Vernonia sensu stricto*, but differs from it by the type of inflorescence, erect habit, often xylopodial bases and sometimes by the presence of tailed anther bases (Robinson 1992a). The species are shrubs or small trees having thyrsoid to pyramidal inflorescences, with individual branches cymose to corymbose (Robinson 1992a). In southern South America, the species are mainly concentrated in the mountains of northwest Argentina and the fields and forests of Paraguay and eastern Argentina (Cristóbal and Dematteis 2003; Vega and Dematteis 2008).

Pollen characters such as style bases and anther appendages are observable with the compound light microscope, and are useful in delimiting natural groups in the Vernonieae (Robinson 1992b). Pollen types of the tribe are particularly interesting, because the tectum consists of a pattern of lophae (crests or ridges of tectum) and lacunae or deep depressions on the tectum continuous with the lophae (Wodehouse 1928; Skvarla et al. 2005). Among the species, the pollen is also variable in aperture form, with both tricolporate and triporate forms (Stix 1960; Kingham 1976; Keeley and Jones 1979; Blackmore 1986). Pollen grains of *Vernonanthura* are tricolporate, subechinolophate, having a continuous microporate tectum, with depressions delimited by irregular ridges (Dematteis and Pire 2008).

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Pollen morphology in the Vernoniae is one of the most useful characters for taxonomic studies of the tribe. Based on the variation of pollen surface morphology, Jones (1979) proposed a new infrageneric classification for the American species of *Vernonia*. The segregation of different sections and subsections of *Vernonia* to new genera proposed by Robinson (1988, 1989) was based in several cases on the pollen type. A correlation between pollen data and the classification of the West Indian species of *Vernonia* has been demonstrated by Keeley and Jones (1979).

For the tribe Vernoniae, general contributions on the pollen morphology have been published (Jones 1979; Keeley and Jones 1979; Robinson 1999), which included some species of *Vernonanthura* within the old concept of *Vernonia* (see Dematteis and Pire 2008). However, few specific studies on the pollen morphology of *Vernonanthura* have been undertaken. The single available analysis included several species of *Vernonanthura* distributed exclusively in southern Brazil (Mendonça et al. 2009). Due to the relevance of pollen morphology in taxonomic treatments, the main purpose of this paper is to examine the pollen morphology of some species of *Vernonanthura* from southern South America.

2. Material and methods

The pollen samples were obtained by removing one or two florets of each species from herbarium specimens. All voucher specimens are deposited at the herbarium of the Instituto de Botánica del Nordeste (CTES), Corrientes, Argentina. The pollen grains were acetolysed using the procedure of Erdtman (1966). For light microscopy the pollen samples were mounted in glycerine 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), Corrientes, Argentina. For scanning electron microscopy, the acetolysed pollen grains were washed in 96° alcohol and absolute alcohol, then sputtered with gold-palladium and studied using a JEOL 5800 LV scanning electron microscope. Selected specimens are illustrated in Plates 1 and 2.

The terminology for pollen grain description in general follows Keeley and Jones (1979) and Punt et al. (1994). The spines were classified according to the terminology suggested by Fernandes Pinto da Luz et al. (2003). The spine index is the proportion between the length and width of the spines measured from the base. Spines having an average index lower than 2.0 are termed short spines, while the spines with a value between 2.0 and 2.5 are classified medium and those above 2.5 are considered to be long spines. Pollen measurements such as diameter, exine thickness and

spine size have been based on 30 grains (Table 1). The exine thickness was estimated in polar view.

2.1. Specimens examined

Vernonanthura amplexicaulis (R.E.Fr.) H. Rob.: ARGENTINA. Jujuy, Dept. Ledesma, Parque Nacional Calilegua, *A. Castellón 360* (CTES). PARAGUAY. Dept. Amambay, Cerro Corá, *A. Schinini & E. Bordas 20251* (CTES). BOLIVIA. Dept. Santa Cruz, Prov. Andrés Ibáñez, Santa Cruz de La Sierra, Municipal Zoo, *A. Jiménez 069* (CTES).

V. brasiliensis (L.) H. Rob.: BOLIVIA. Dept. Beni, Prov. Yacuma, Estancia Porvenir, Biological Station of Beni, *S. G. Beck 24171*. (CTES). BRAZIL. Minas Gerais, Mun. Tacarambi, Porto da Balsa, Rio São Francisco, *G. Hatschbach et al. 78011* (CTES). PARAGUAY. Dept. Cordillera, San Bernardino, Ciervocuá, *F. Mereles 1291* (CTES).

V. chamaedrys (Less.) H. Rob.: ARGENTINA. Formosa, Dept. Laishi, Ecological Reserve El Bagual, San Francisco de Laishi, *A. Digiacoimo 302* (CTES); Misiones, Dept. Concepción, on the road to Puerto Azara, 6 km E of Azara, *M. Dematteis et al. 3114*. (CTES). PARAGUAY. Dept. Concepción, 6 km west of Puentesíño, on the road to San Carlos del Apa, *M. Dematteis et al. 3316* (CTES).

V. chaquensis (Cabrera) H. Rob.: PARAGUAY. Dept. Caazapá, Santa Ursula, 55 km NE of Yuty, *A. Schinini et al. 27818* (CTES); Dept. Alto Paraná, Pirá Pytá, 12 km NE of Hernandarias, Estancia Santa Elena, *A. Schinini 28183* (CTES).

V. cupularis (Chodat.) H. Rob.: ARGENTINA. Corrientes, Dep. Mburucuyá, National Park Mburucuyá, *M. Dematteis & M. S. Ferrucci 1904* (CTES); Misiones, Dept. San Pedro, Monte Carlos, E. Schwindt 1071. (CTES.); Misiones, Santa Ana, *F. M. Rodríguez 57* (CTES).

V. lipoensis (Cabrera) H. Rob.: ARGENTINA. Salta, Dept. Santa Victoria, Baritú, *J. L. Novara et al. 11307* (CTES). BOLIVIA. Dept. Santa Cruz, Manuel María Caballero, *J. R. Abbott & A. Jardim 17191* (CTES).

V. lorentensis (Hieron.) H. Rob.: ARGENTINA. Misiones, Dept. San Ignacio, Teyú Cuaré, *M. Dematteis 474* (CTES); Misiones, Dep. San Ignacio, Casa de Horacio Quiroga. *M. Dematteis 511* (CTES). PARAGUAY. Dept. Paraguairí, Piraretá, *A. Schinini 4267* (CTES).

V. lucida (Less.) H. Rob.: ARGENTINA. Corrientes, Dept. Santo Tomé, Estancia Timbó, *A. Schinini et al. 23805* (CTES); Misiones, Dept. San Pedro, Parque Provincial Moconá, Embarcadero, *M. Dematteis et al. 3095* (CTES). PARAGUAY. Dept. Caaguazú, 5 km S of Yhú, *A. Schinini 36137* (CTES).

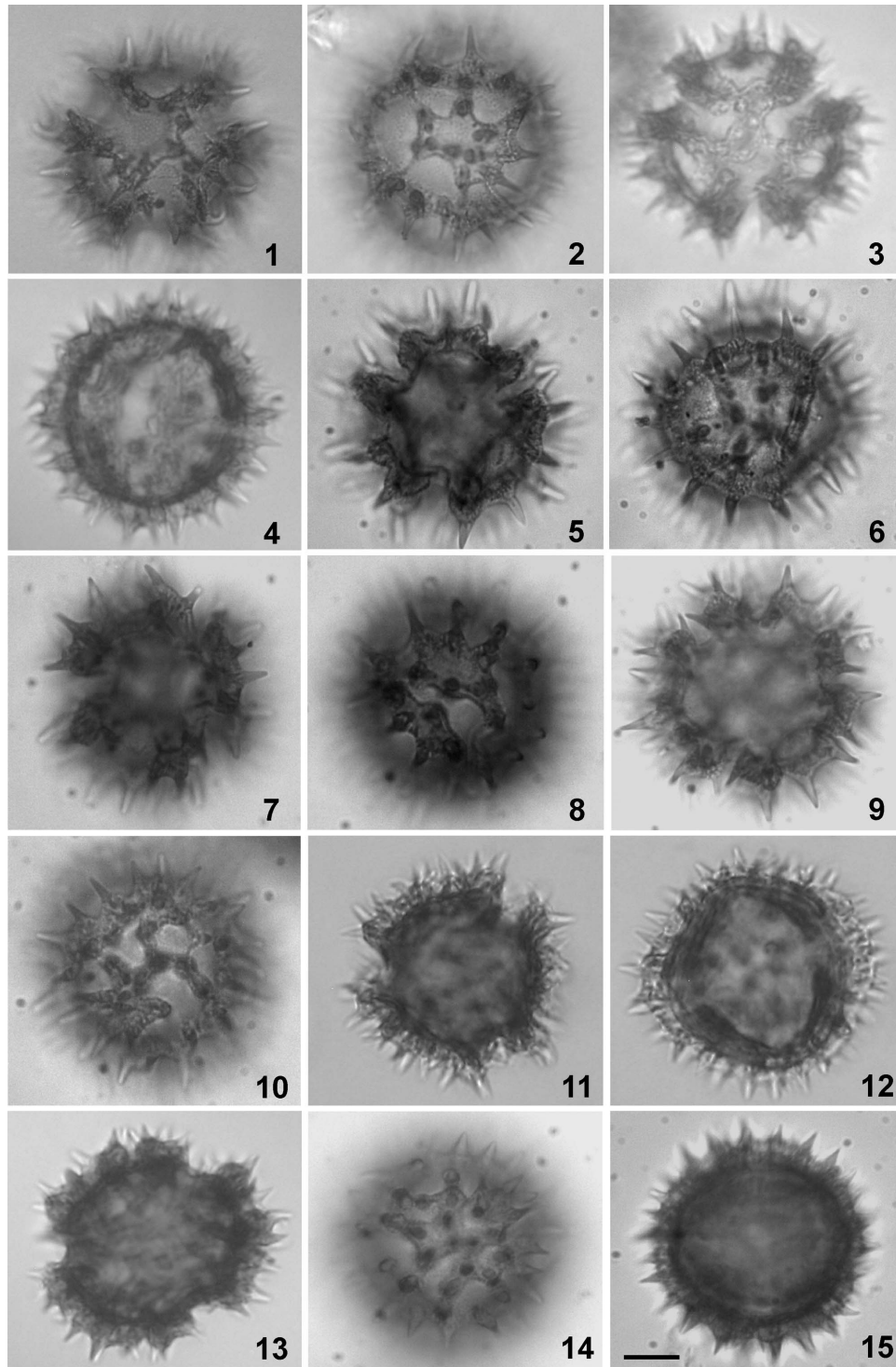


Plate 1. Pollen grains of *Vernanthura* taken using transmitted light microscopy. Figures 1–2. *V. amplexicaulis*, polar (1) and equatorial view, high focus (2). Figures 3–4. *V. chamaedryis*, polar (3) and equatorial view (4), mid focus. Figures 5–6. *V. pinguis*, polar (5) and equatorial view (6), middle and high foci. Figures 7–8. *V. montevidensis*, polar (7) and equatorial view (8), high focus. Figures 9–10. *V. nudiflora*, polar (9) and equatorial view (10), middle and high foci. Figures 11–12. *V. lipoensis*, polar (11) and equatorial view (12), mid focus. Figures 13–15. *V. oligactoides*, polar (13) and equatorial view (14–15), middle and low foci. Scale bar = 10 μm .

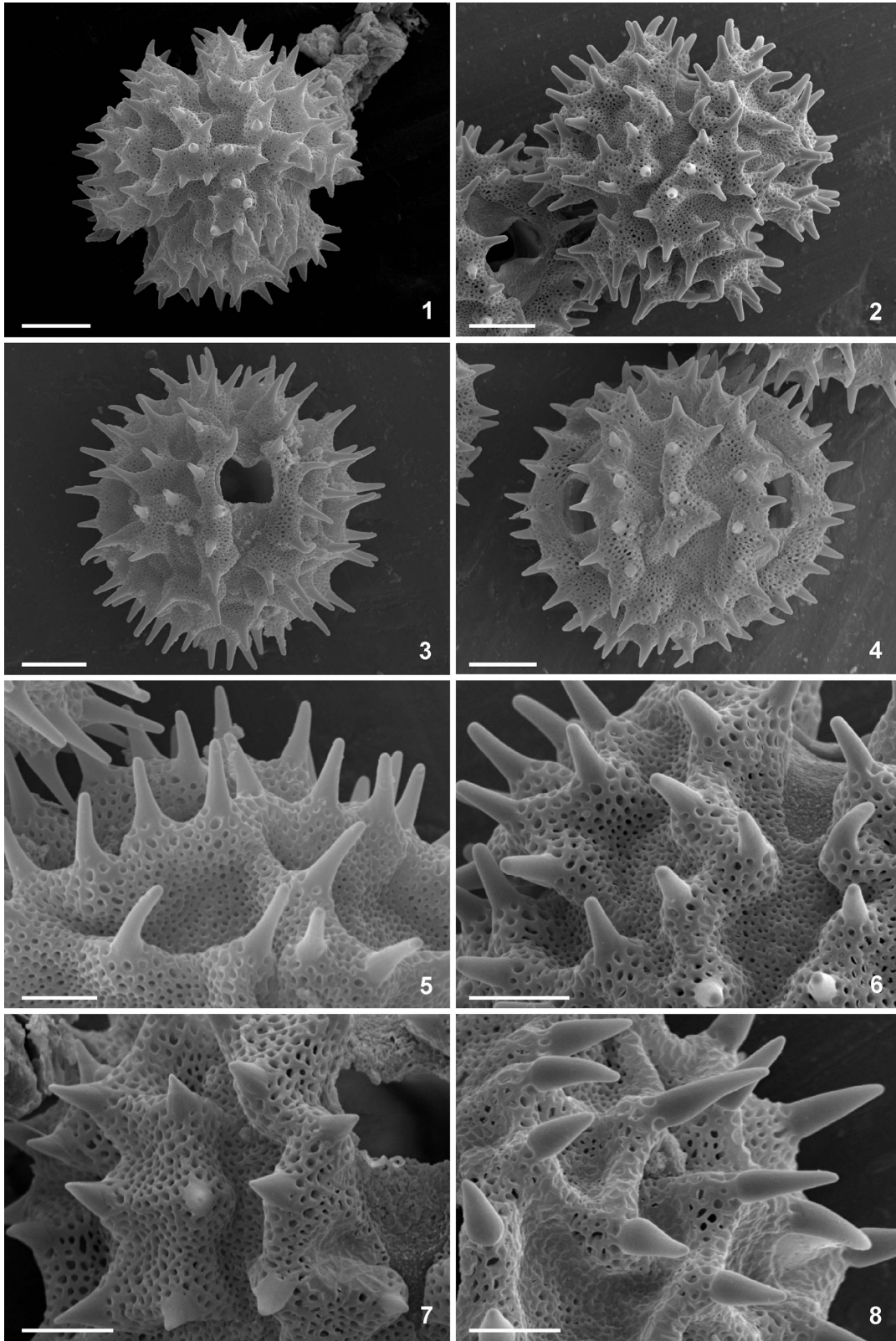


Plate 2. Pollen of *Vernonanthurina* taken with the scanning electron microscope. Figure 1. *V. lucida*, polar view. Figure 2. *V. nudiflora*, polar view. Figure 3. *V. loretensis*, equatorial, view. Figure 4. *V. squamulosa*, equatorial view. Figure 5. *V. loretensis*, detail of spines. Figure 6. *V. nudiflora*, spines. Figure 7. *V. oligactoides*, spines detail. Figure 8. *V. pinguis*, spines. Scale bar = 10 μm (1–4) or 5 μm (5–8).

Table 1. Species of *Vernonanthura* which were examined.

Species	<i>P</i>	<i>E</i>	<i>P/E</i>	Shape	Exine
<i>V. amplexicaulis</i>					
Jiménez 069	47.60(52.46)57.12	47.60(50.93)55.76	1.03	prolate-spheroidal	3.1(4.1)4.7
Castellón 360	36.72(39.03)40.80	36.72(38.26)40.80	1.02	prolate-spheroidal	2.7(3.3)4.0
Schinini and Bordas 20251	39.44(41.38)44.88	39.44(41.11)43.52	1.01	prolate-spheroidal	2.7(3.2)3.4
<i>V. brasiliiana</i>					
Hatschbach et al. 78011	31.96(33.45)35.36	31.28(33.34)35.36	1.00	spheroidal	1.6(2.0)2.4
Beck 24171	34.00(34.68)35.36	32.64(33.50)35.36	1.03	prolate-spheroidal	2.4(2.7)2.9
Mereles 1291	47.60(52.13)54.40	48.96(51.63)54.40	1.01	prolate-spheroidal	2.7(3.8)4.0
<i>V. chamaedrys</i>					
Digiacoimo 302	48.96(49.79)54.40	44.88(48.78)53.04	1.02	prolate-spheroidal	3.4(3.7)4.7
Dematteis et al. 3114	39.44(41.43)42.16	39.44(41.61)43.52	0.99	oblate-spheroidal	2.7(3.6)4.0
Dematteis et al. 3316	34.00(34.49)36.72	32.64(34.04)35.36	1.01	prolate-spheroidal	2.0(2.5)2.7
<i>V. chaquensis</i>					
Schinini 28183	36.72(37.71)38.08	35.36(36.85)38.08	1.02	prolate-spheroidal	2.7(2.7)3.4
Schinini et al. 27818	32.64(34.99)36.72	32.64(34.18)35.36	1.02	prolate-spheroidal	2.0(2.5)2.7
<i>V. cupularis</i>					
Dematteis and Ferrucci 1904	38.08(40.01)42.16	37.40(39.14)48.08	1.02	prolate-spheroidal	2.0(2.5)3.4
Schwindt 1071	36.72(39.86)40.08	38.08(39.90)40.80	0.99	oblate-spheroidal	2.7(2.8)3.4
Rodriguez 57	47.60(52.13)54.40	47.60(51.63)54.40	1.01	prolate-spheroidal	2.7(3.8)4.0
<i>V. lipoensis</i>					
Novara et al. 11307	31.28(33.78)36.72	29.92(32.41)34.00	1.04	prolate-spheroidal	1.3(2.2)2.7
Abbott and Jardim 17191	34.00(34.68)35.36	34.00(34.22)35.36	1.01	prolate-spheroidal	2.7(3.0)3.4
<i>V. loretensis</i>					
Dematteis 474	44.88(45.83)48.96	46.24(44.74)43.52	1.02	prolate-spheroidal	2.0(2.6)2.9
Dematteis 511	43.52(45.56)47.60	43.52(45.51)46.24	1.00	spheroidal	2.7(3.6)4.0
Schinini 4267	42.16(44.83)47.60	42.16(44.01)46.24	1.01	prolate-spheroidal	3.4(3.6)4.0
<i>V. lucida</i>					
Schinini 36137	35.36(37.37)40.81	35.30(36.38)38.08	1.02	prolate-spheroidal	2.0(2.6)3.4
Schinini et al. 23805	34.00(37.98)39.44	35.36(37.08)38.08	1.02	prolate-spheroidal	2.0(2.8)3.4
Dematteis et al. 3095	35.36(36.72)38.08	34.00(35.31)38.08	1.04	prolate-spheroidal	2.0(2.7)3.4
<i>V. montevidensis</i>					
Krapovickas and Cristobal 47509	36.72(38.44)39.44	35.36(38.35)42.16	1.00	spheroidal	1.3(2.7)4.0
Solis Neffa and Seijo 2092	36.72(38.57)40.80	36.72(38.08)40.80	1.01	prolate-spheroidal	2.7(3.5)4.0
Costa and Cordeiro 66	35.36(37.30)39.44	35.36(36.67)38.08	1.01	prolate-spheroidal	2.0(2.5)2.7
<i>V. nudiflora</i>					
Martinez Crovetto s. n.	39.44(41.67)43.52	39.44(41.10)43.52	1.01	prolate-spheroidal	3.4(3.7)4.0
Dematteis and Schinini 1766	39.44(41.29)42.16	39.44(40.52)42.16	1.01	prolate-spheroidal	2.7(3.21)4.0
Bueno 2184	42.16(44.47)46.24	42.16(43.61)46.24	1.02	prolate-spheroidal	3.4(3.8)4.0
<i>V. oligactoides</i>					
Schinini et al. 36022	39.44(41.02)42.16	38.08(41.02)42.16	1.00	spheroidal	2.0(3.2)4.0
Dematteis et al. 3383	40.80(41.61)42.16	39.44(41.29)42.16	1.00	spheroidal	2.7(2.9)4.0
<i>V. petiolaris</i>					
Hatschbach 57974	32.64(32.82)34.00	31.28(32.73)34.00	1.00	spheroidal	1.3(1.9)2.7
Silva and Barbosa 5026	47.60(52.13)54.40	47.6(51.63)54.40	1.01	prolate-spheroidal	2.7(3.8)4.0
Keller 3637	31.28(32.41)34.00	29.92(32.09)34.00	1.01	prolate-spheroidal	1.3(2.1)2.7
<i>V. pinguis</i>					
Saravia Toledo 14370	38.08(40.66)43.52	38.08(40.44)42.16	1.00	spheroidal	2.0(2.7)4.0
Dematteis et al. 985	38.08(39.89)40.80	36.72(37.98)40.80	1.05	prolate-spheroidal	2.7(2.9)3.4
Gualionone et al. 2556	39.44(42.97)46.24	39.44(43.02)46.24	1.00	spheroidal	2.7(3.6)4.0
<i>V. schulziana</i>					
Schulz 3757	35.10(39.1)44.20	36.40(39.80)44.20	1.07	prolate-spheroidal	2.6(4.0)5.2
<i>V. squamulosa</i>					
Novara et al. 11332	38.08(40.93)43.52	38.08(39.92)43.52	1.02	prolate-spheroidal	2.7(2.7)2.7
Silva and Hatschbach 5019	39.44(39.89)40.8	36.72(39.12)42.16	1.02	prolate-spheroidal	2.7(2.7)2.7
Dematteis et al. 852	36.72(38.30)39.44	35.36(37.30)39.44	1.02	prolate-spheroidal	2.0(2.6)2.7
<i>V. tweediana</i>					
Schinini and Cuadrado 30452	42.16(45.37)47.60	40.0(42.29)46.24	1.07	prolate-spheroidal	2.4(2.8)4.0
Fortunato 8541	39.44(41.07)42.16	38.08(40.07)42.16	1.02	prolate-spheroidal	2.0(2.7)3.4
Ribas et al. 6254	35.36(36.40)38.02	34.00(35.54)36.72	1.02	prolate-spheroidal	2.0(2.5)4.0

P = polar axis, *E* = equatorial diameter, *P/E* ratio = pollen shape and exine thickness (μm), respectively.

V. montevidensis (Spreng.) H. Rob.: ARGENTINA. Santa Fe, Dept. Capital, 3 km W of Manucho, *A. Krapovickas & C. L. Cristobal 47509* (CTES). BRASIL, Paraná, Mun Piên, *Boa Vista, Pedreira, E. F. Costa & J. Cordeiro 66* (CTES). URUGUAY. Dept. Colonia, from Cufre to Ismael Cortinas, Arroyo Rosario Chico, *V. Solís Neffa & G. Seijo 2092* (CTES).

V. nudiflora (Less.) H. Rob.: ARGENTINA. Corrientes, Paso de los Libres, *R. Martinez Crovetto s. n.* (CTES). BRASIL, Porto Alegre, *O. Bueno 2184* (CTES). URUGUAY. Dept. Tacuarembó, Arroyo Tacuarembó Chico, *M. Dematteis & A. Schinini 1766* (CTES).

V. oligactoides (Less.) H. Rob.: PARAGUAY. Dept. Amambay, around P. J. Caballero, on the road to Cerro Corá, *A. Schinini et al. 36022* (CTES); Dept. Amambay, Chirigüelo, 2 km W of P. J. Caballero, *M. Dematteis et al. 3383* (CTES).

V. petiolaris (DC.) H. Rob.: BRAZIL. Espírito Santo, Mun. Domingos Martins, next to Rio Araguaia, Route BR-262, *G. Hatschbach 57974* (CTES); Paraná, Mun. Rio Branco do sul, Serra do Bromado, *J. M. Silva & E. Barbosa 5026* (CTES). ARGENTINA. Misiones, Dept. Gral. Manuel Belgrano, *H. E. Keller 3637* (CTES).

V. pinguis (Griseb.) H. Rob.: ARGENTINA. Salta. Dept. Orán, San Andrés, La Maroma, *Saravia Toledo 14370* (CTES); Jujuy, Dept. Ledesma, Parque Nacional Calilegua, *E. R. Gualionone et al. 2556* (CTES). BOLIVIA. Dept. Santa Cruz, Prov. O'Connor, 69 km E of Tarija, on the road to Narvaez, *M. Dematteis et al. 985* (CTES).

V. squamulosa (Hook & Arn.) H. Rob.: ARGENTINA. Salta. Dept. Santa Victoria, Lipeo, *L. Novara et al. 11332* (CTES). BRASIL. Paraná, Antonina, Usina Hidrelétrica Parigot de Souza, *J. L. Silva &*

G. Hatschbach 5019 (CTES). BOLIVIA. Dept. Cochabamba, Campero, *M. Dematteis et al. 852* (CTES).

V. schulziana (Cabrera) H. Rob.: ARGENTINA. Chaco, Dept. 1° de Mayo, Colonia Benítez, *A. G. Schulz 3757* (CTES).

V. tweediana (Baker) H. Rob.: ARGENTINA. Formosa, Dept. Pilcomayo, Laguna Naick Neck, *A. Schinini & G. Cuadrado 30452* (CTES). BRASIL. Paraná, Mun. Capitão Leônidas Marques, Rio Iguaçu. *O. S. Ribas et al. 6254* (CTES). PARAGUAY. Dept. Caaguazú, ±2 km E of Caaguazú on national route 7, Barrio Tururú, Arroyo Tucurú, *R. H. Fortunato 8541* (CTES).

3. Results

The species examined yielded pollen grains which are radially symmetrical, isopolar and medium in size. The polar axis (*P*) ranged between 31.28 and 57.12 μm , while the equatorial diameter (*E*) varied from 29.92 to 55.76 μm (Table 1). The pollen grains were oblate-spheroidal, spheroidal or prolate-spheroidal (*P/E*: 0.99–1.07) in shape, subechinolphate and tricolporate (Plate 1). Colpus length ranged between 15 to 20 μm . The pori are elongate, and often slightly constricted in the central region (Plate 2, figure 3). The exine thickness, excluding spines, varied between 2.0 and 4.1 μm , with the sexine notably wider than the nexine. The tectum is continuous, comprising lophae surrounding irregular depressions (Plate 2, figures 1–4). The tectum surface is densely microperforate with prominent spines on the ridges, the spine length is 2.71–5.21 μm (Plate 2, figures 5–8).

The majority of the species have pollen grains which are prolate-spheroidal in shape, excluding *V. brasiliiana*, *V. lorentensis*, *V. montevidensis*,

Table 2. The shape and size of spines in species of *Vernonanthura*.

Taxa	Spine length	Spine base	Spine index	Size
<i>V. amplexicaulis</i>	3.46(3.85)4.45	1.31(1.43)1.54	2.69	long
<i>V. brasiliiana</i>	2.93(3.26)3.91	1.11(1.37)1.67	2.37	medium
<i>V. chamaedrys</i>	2.99(3.40)3.46	1.25(1.45)1.65	2.34	medium
<i>V. chaquensis</i>	3.42(3.61)3.77	1.11(1.32)1.62	2.73	long
<i>V. cupularis</i>	2.71(3.40)3.92	1.20(1.32)1.50	2.57	long
<i>V. lipeoensis</i>	3.42(3.86)4.10	1.20(1.33)1.54	2.90	long
<i>V. lorentensis</i>	4.11(4.40)5.09	1.37(1.57)1.71	2.80	long
<i>V. lucida</i>	3.71(3.20)3.77	1.11(1.31)1.53	2.44	medium
<i>V. montevidensis</i>	3.21(3.47)3.63	1.11(1.22)1.39	2.84	long
<i>V. nudiflora</i>	3.10(3.67)4.10	1.25(1.35)1.47	2.71	long
<i>V. oligactoides</i>	2.26(2.71)3.25	1.35(1.49)1.65	1.81	short
<i>V. petiolaris</i>	3.35(3.78)4.05	1.11(1.37)1.53	2.75	long
<i>V. pinguis</i>	4.26(5.04)5.57	1.58(1.75)1.96	2.88	long
<i>V. schulziana</i>	2.64(2.86)3.42	1.20(1.31)1.37	2.18	medium
<i>V. squamulosa</i>	2.26(3.07)3.63	0.91(1.15)1.39	2.66	long
<i>V. tweediana</i>	4.71(5.21)5.84	1.88(1.95)2.26	2.67	long

V. oligactoides, *V. petiolaris* and *V. pinguis* that occasionally exhibit spheroidal grains. All the taxa analysed exhibit the same basic pollen type. However, some differences in the shape and size of the spines were observed. Most species have spines which are relatively long, broad at base and apically acute, but some variations were observed (Table 2). *Vernonanthura pinguis* always has spines which are constricted at the base (Plate 2, figure 8), while *V. nudiflora* and *V. schulziana* have rounded spine apices (Plate 2, figure 6). *Vernonanthura oligactoides* is the single species with conical spines (Plate 2, figure 7). In this taxon, the spines are relatively short and widened at the base, which produces a low spine index of 1.81. In relation to size, the taxa studied are subdivided into three groups according to the spine index (Table 2). *V. tweediana* has the largest spines, with an average length of 5.1 μm , while *V. oligactoides* has the shortest spines, with an average length of 2.71 μm , which ranges from 2.26 to 3.25 μm .

4. Discussion

All the species analysed have pollen grains which are subechinolphate, tricolporate, with depressions delimited by irregular ridges and a continuous tectum, which is microporate over all the non-colpar areas. These features are similar to the descriptions of the type 'A' pollen of Keeley and Jones (1979), and is consistent with the pollen type of *Vernonanthura* (Robinson 1992a). There are many other genera with type 'A' pollen that occur in both the New and Old Worlds (Jones 1979, 1981; Robinson 1995). In the New World, one of them is *Vernonia sensu stricto*, which is closely related to *Vernonanthura*, but differs by its inflorescence type, erect stem base, habitat and sometimes by presence of tailed anther bases (Robinson 1999).

Mendonça et al. (2009) analysed 22 species of *Vernonanthura*, six of which were analysed in this study (*V. brasiliiana*, *V. chamaedrys*, *V. lucida*, *V. montevidensis* and *V. petiolaris*). In these species, the authors described oblate–spheroidal to suboblate pollen grains, while in the present study the shape of the grains was mostly prolate–spheroidal to spheroidal. Another study that included some species of *Vernonanthura* is Dematteis and Pire (2008). These authors analysed the pollen morphology of species of *Vernonia sensu lato* from Argentina and Paraguay, four of which (*V. chaquensis*, *V. cupularis*, *V. lipeoensis*, *V. schulziana*) belong to the genus analysed here. The results obtained by Dematteis and Pire (2008) are similar to our results, but they described oblate–spheroidal pollen grains for *V. lipeoensis* ($P/E : 0.99$), while in this paper we observed prolate–spheroidal grains ($P/E : 1.04$).

Despite most of the species having similar pollen types, some taxa can be recognised by the morphology of the spines. *Vernonanthura pinguis* exhibits spines which are constricted at the base, while *V. oligactoides* has small conical spines and is the single species with a spine index lower than 2.00. However, *V. nudiflora* and *V. schulziana* have spines with rounded apices, but differ from each other by the spine indices, which are 2.70 and 2.18, respectively. The spine index is an important feature that distinguishes the two species with rounded apices, but is also very important to separate *V. oligactoides* from other species of *Vernonanthura*. According to the spine index, the species analysed can be divided in three groups having short, medium and long spines, respectively. *Vernonanthura oligactoides* is the only species with short spines, while *V. brasiliiana*, *V. chamaedrys*, *V. lucida* and *V. schulziana* have medium-sized spines. The remaining eleven taxa have long spines, which seems to be prevalent in the pollen grains of *Vernonanthura*.

In other genera of the Vernoniaceae a positive correlation has been observed between the size of the pollen grains and the chromosome number. In *Lessingianthus* H. Rob., the species with higher ploidy levels always has larger pollen grains (Dematteis and Pire 2008; Angulo and Dematteis 2010). All the species of *Vernonanthura* have a basic chromosome number of $x = 17$ and the ploidy level can be diploid ($2n = 34$) or tetraploid ($2n = 68$) among different species (Dematteis 2002). Nevertheless, the pollen size of the diploid taxa seems to be similar to the tetraploid species. *Vernonanthura pinguis* is the single species analysed with $2n = 68$, while the remaining ones are diploids with $2n = 34$ (Angulo and Dematteis 2009). However, the pollen size of *V. pinguis* is similar or less than the diploid species and consequently a correlation between these two features cannot be established.

Further palynological studies are necessary to fully understand the systematics of *Vernonanthura*. However, the results here show that although the species have similar pollen type, several taxa can be recognised by the morphology or the length of the spines.

5. Conclusions

All the species of *Vernonanthura* studied exhibit the type 'A' pollen characteristic of this genus. However, some taxa can be recognised by the morphology of the spines. According to the spine index, the species analysed can be separated into three groups having short, medium and long spines. In addition to the size of the spines, some taxa can be distinguished by spine shape. The spines can be constricted at the base, with a conical shape or have rounded apices. The analysis

confirms that the genus constitutes a well-defined group based on their pollen features.

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