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Pollen types in Southern New World Convolvulaceae and their taxonomic significance

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Abstract. Pollen morphology from 143 collections representing 11 genera and 75 species of native South American Convolvulaceae was analyzed with LM and SEM. Exine structure and sculpture allow to distinguish three main types, in two of these types some subtypes were recognized. 1) Tectate, microechinate-perforate exine, with ramified columellae. On the basis of apertures three subtypes were distinguished: tricolpate in *Aniseia*, *Bonamia*, *Convolvulus*, *Cressa*, *Dichondra*, *Merremia* and *Jacquemontia blanchetii*; penta-hexacolpate in *Merremia umbellata*; and pantoporate with elliptic and circular pores, in *Calystegia*. 2) Tectate, microechinate-perforate exine with microspines and single columellae in concordant pattern, relates pantocolpate pollen of *Jacquemontia* and *Evolvulus*. From pollen data generic status of *J. blanchetii* should be considered. 3) Semitectate, echinate or gemmate, microechinate-microreticulate exine with single columellae is exclusive of pantoporate pollen of *Ipomoea*. Four subtypes were recognized in this genera, which are discussed in relation to Austin's infrageneric classification.

Key words: Convolvulaceae, South America, pollen types, infrageneric classification, taxonomy.

The family Convolvulaceae Juss. comprises about 50 genera and more than 2000 species of vines, herbs and shrubs, which inhabit tropical and subtropical regions of the world (Austin 1975). The pollen morphology of Convolvulaceae is known to be highly diverse and has taxonomic importance. The earliest palynological observations were made at the end of the 19th century by Hallier (in Sengupta 1972), who recognized two groups, "Echinoconieae" with echinate pollen and "Psiloconiae" with psilate or granulate pollen. In line with this classification Erdtman (1952) morphologically grouped the pollen of this family in "*Ipomoea* type" and "other types". Later, Lewis and Oliver (1965) delimited *Calystegia* and *Convolvulus* on the basis of both pollen and style morphology. In 1966, Sengupta investigated the pollen morphology of nine Indian species of *Ipomoea*, and later in 1972 the same author proposed an evolutionary sequence in the Convolvulaceae based on pollen morphology of 170 species belonging to 30 genera.

Van Campo (1976) included Convolvulaceae in the broad group of Angiosperm families with successiform pollen evolutionary pattern from tricolpate to pantoporate pollen.

Ferguson et al. (1977) examined the taxonomic significance of pollen in *Merremia* and *Operculina*, concluding that there is no correlation between pollen types and subgen-

Table 1. List of species which present polar pollen ranging by genera (in bracket: numbers of species present in the region followed by the number of species examined) with collecting data, size of polar diameter (Dp) and equatorial diameter (De), shape index P/E, and exine thickness. *endemic species

Types and taxa	Collection	Dp (µm)	De (µm)	P/E	Exine thickness (µm)
Type 1, A (Tricolpate)					
Aniseia Choisy (2) 2					
A. argentina (N.E.Br.) O'Donell	Berro 4274 (MVM), Berro 8416 (MVFA), Del Puerto s.n. (MVFA), Pedersen 4557 LP)	52–70	49–66	Suboblate-spheroidal	4–5
A. martinicensis (Jack.) Choisy	Cabrera 10473 (LP)	41–66	45–60	Spheroidal-oblate	4,5–5
Bonamia Thouars (1) 1					
Bonamia sericea (Griseb.) Hallier*	17928 (LP)	26–36	31–39	Suboblate-spheroidal	ca.3
Convolvulus L.(9) 6					
C. bonariensis Cav.	Ruiz Huidobro s.n. (LIL), Hayward s.n. (LIL)	41–55	43–53	Spheroidal	4–5
C. chilensis Pers.	Marticorena et al. 1444 (LP), coll. unknown 9950 (CONC)	47–52	44–61,5	Oblate-spheroidal	4–5
C. crenatifolius Ruiz &Pav.	Lombardo s.n. (HAL), Birabén 5267 (LP), Bruch s.n. (LP)	45–55	47–51	Oblate-spheroidal	4–5
C. demissus Choisy	Garaventa 5673 (CONC)	51–62	50–61	Suboblate-subprolate	4–6
C. hermanniae L' Hér.	Hurrell et al. 1273 (LP)	46–50	48–52	Oblate-spheroidal	4–5
C. laciniatus Desr.	Lombardo s.n. (HAL)	36–54	44–67	Oblate-spheroidal	4–5
C. lilloi O'Donell	Meyer 5938 (LIL)	41–55	43–53	Spheroidal	4–5
Cressa L. (2) 2					
C. nudicaulis Griseb. *	O'Donell 17951 (LP)	24–30	23–28	Prolate-spheroidal	ca. 2
C. truxillensis Kunth.	Tur 1706 (LP), Alboff s.n. (LP), Forcone 382 (CORD)	26–30	24–28	Prolate-spheroidal	ca. 3
Dichondra J.R. Forst. & G. Forst.(4) 3					
D. argentea Humb. & Bonpl.	Cabrera et al. 13298, 179447 (LP)	27–31	29–32	Prolate-spheroidal	ca. 3,5
D. microcalyx (Hallier.f) Fabris	Izaguirre et al. s.n. (MVFA), Lombardo s.n. (HAL), Tellería s.n. (LP)	23–33	25–34	Suboblate-spheroidal	1,5–3

Table 1 (continued)

D. sericea Sw.	Izaguirre et al. s.n. (MVFA), Del Puerto s.n. (MVFA), Lombardo s.n. (HAL)	24–30	24–32	Suboblate-spheroidal	2–3
Iseia luxurians (Moric.) O'Donell	Tressens et al. 759, 1295 (CTES), Schultz 8354 (CTES)	56–65	53–65	Spheroidal	4
Jacquemontia (9) 9					
J. blanchetii Moric.	Coll. unknown18142 (LP)	41–48	50–58	Suboblate-spheroidal	4–5
Merremia (6) 6					
M. aegyptia (L.) Urb.		45–60	55–70	Suboblate	ca. 5
M. cissoides (Lam.) Hallier f.		40–65	44–70	Suboblate	4,4
M. dissecta (Jacq.) Hallier	Del Puerto & Marchesi 5910 (MVFA)	51–67	74–86	Oblate	5,6
M. hassleriana (Chodat. & Hassl.) Hassl.	O'Donell s.n. (LIL)	46–74	44–74	Spheroidal	3–5
M. macrocalyx (Ruiz et Pav.) O'Donell		64–82	51–71	Subprolate	4,8
Type 1, B (Hexacolpate)					
M. umbellata (L.) Hallier	Cuezzo & de la Sota 1508 (LIL), 18009 (LP)	55–76	62–79	Suboblate	5–6

Table 2. List of species which present apolar pollen ranging by genera (in brackets: numbers of species present in the region followed by the number of species examined), with collecting data, size of pollen, exine thickness and length of spines or gemmae.[1] subgen. *Ipomoea*,[2] subgen. *Eriospermum* and[3] subgen. *Quamoclit*. *endemic species. + sterile specimen

Types and taxa	Collection	Diameter (μm)	Exine thickness (μm)	Spine/gemma (μm)
Type 2 (Pantocolpate)				
Evolvulus L. (7) 4				
E. arizonicus A.Gray	Coll. unknown 17921, 026362 (LP)	29–35	2–3	
E. glomeratus Ness & Mat.	Berro 2948 (MVFA), Marchesi & Ferrés s.n. (MVFA), Krapovickas & Cristóbal 20821 (CTES); Ibarrola 3055 (LIL)	33–55	2–4	
E. nummularius (L.) L.	Saravia Toledo 1233 (LP)	31–40	2–2, 5	
E. sericeus Sw.	Aguilar 418 (LIL), Meyer 4687 (LIL), Quarín et al. 2581 (LP), Irigoyen & Schinini 187 (LIL), Berro 2156 (MVFA), Lombardo 238 (HAL), Bayce & Darries 18817 (MVFA)	36–40	2–3	
Jacquemontia Choisy (9) 9				
J. agrestis (Choisy) Meisn.	Nícora 17586 (SI)	55–63	4–5	
J. decumbens O'Donell	Birabén 5371 (LP), Krapovickas et al. 18031 (LP)	ca. 48–55	ca. 3	
J. heterotricha O'Donell	Coll. unknown 18067 (LP)	ca.48	ca.4, 5	
J. laxiflora O'Donell*	Bertoni s.n. (LIL)	52–64	ca. 4, 5	
J. lorentzii (Kuntze) Peter ex O'Donell	Abiatti & Claps 223 (LP), coll. unknown 17900 (LP)	46–52	ca. 3	
J. rusbyana Standl.	Cabrera et al. 22359 (LP)	50–57	4–5	
J. selloi (Meisn.) Hallier f.	Schwarz 180 (LIL), Birabén 5462 (LP), Brisarolli 2586 (LP)	47–52	4–5	
J. tamnifolia (L.) Griseb.	Coll. unknown 18085 (LP)	41–52	4	
Type 1, C (Pantoporate with circular and elliptic pores)				
Calystegia R. Br. (3) 3				
C. sepium (L.) R. Br.	Fabris & Cullen 2538 (LP), Tellería s.n. (LP), coll. unknown 18209 (LP), Lombardo s.n. (HAL), Gibert s.n. (MVFQ)	58–72	4–5	
C. soldanella (L.) Roem. & Schult.	Lombardo s.n. (HAL)	75–86	4, 5–6	

Table 2 (continued)

C. tuguriorum (G. Forst) R. Br.	Villagrán & Leiva 7387 (CONC), Mason 10695 (LP)	57–81	4–7	
Type 3 (Pantoporate with circular pores)				
Ipomoea L. (52) 42				
Subtype 3 A.				
I. amnicola Morong[2]	Coll. unknown 18184 (LP), Cabrera 14573 (LP)	64–72	ca. 11	6–8
I. aristolochiifolia G. Don[3]	Venturi 4359 (LP)	72–90	13, 5–16	6–9
I. cordatotriloba Dennst.[3]	Ahumada & Castellón 4617 (SI)	80–100	13, 5–20	5, 5–12
I. chiliantha Hallier f.[2]	Morel 2459, 9413 (LIL)	72–80	11–18	5–12
I. dumetorum (Kunth) Roem & Schult.[3]	Cabrera 12177 (LP), Cabrera et al. 23570 (LP)	84–110	12–13	ca. 6
I. indica (Burm. f.) Merr.[1]	Tellería s.n. (LP), Lombardo s.n. (HAL)	80–112	17–21	9–12
I. indivisa (Vell.) Hallier f.[3]	Tellería s.n. (LP), coll. unknown 001502 (LP), Lombardo s.n. (HAL)	83–114	19	7–9
I. jujuyensis O'Donell *[2]	Meyer 21007 (LIL)	48–49	12	8
I. lanuginosa O'Donell[2]	Schwarz 5447, 5646 (LI)	86–96	14–16	8–9
I. lilloana O'Donell *[2]	Peirano s.n. (LIL)	70–82	14–16	10–12
I. marginisepala O'Donell *[3]	Lillo 2524 (LIL)	90–112	15–18	8–10
I. nil (L.) Roth[1]	Salgado C5 (CTES), Rotman 167 (KP), Muñoz 861 (SI), Schultz 4255 (LP)	102–114	18–22	6–12
I. padillae O'Donell *[2]	Alboff s.n. (LP),	74–80	15–18	8–10
I. pubescens Lam.[1]	Petersen & Hyerling 218 (LIL)	86–100	14–15	9–10
I. purpurea (L.) Roth.[1]	Cabrera et al 26019 (LP), Boffa 1100 (LP), Berro 6109 (MVFA)	90–112	16–18	6–8
I. stuckertii O'Donell *[2]	Meyer 13546 (LIL),	74–82	16–21	9–16
I. rubriflora O'Donell[3]	Krapovickas et al. 28414 (LIL)	90–110	14–15	7–9
Subtype 3 B				
I. alba L.[3]	Salgado 332 (CTES), Arechavaleta s.n. (MVFQ)	140–162	18–21	8
I. turbinata Lag.[3]	Cabezas 51 (SI)	100–134	13–15	5–6
Subtype 3 C				
I. acutisepala O'Donell *[2]	Coll. unknown 18129 (LP)	66–94	14–18	8–11
I. argentinica Peter[2]	Cabrera et al. s.n. (LP)	85–92	12–19	8–11, 5
I. asarifolia (Desr.) Roem. & Schult.[2]	Hicken 17298 (SI)	74–80	16–17, 5	12–13
I. bonariensis Hook.[2]	Lombardo s.n. (HAL), Krapovickas et al. 21387 (LP), Job 130 (LP)+	74–86	14–16	8–10

Table 2 (continued)

Types and taxa	Collection	Diameter (μm)	Exine thickness (μm)	Spine/gemma (μm)
I. cairica (L.) Sweet[3]	Bridarolli 2206 (LP), Tellería s.n. (LP), Delucchi 65 (LP), Lombardo s.n. (HAL)	60–72	12–15	10–13
I. carnea Jacq. subsp. *fistulosa* (Choisy) D. F. Austin[2]	Gamerro 1208 (LP), coll. unknown 18181 (LP), Salgado 334 (CTES), Schwarz 10144 (LIL), Schinini et al. 9660 (LIL)	63–67, 5	14–16	7–8
I. cheirophylla O'Donell[2]	O'Donell 18123 (LP)	61–70	15–16	9–11
I. descolei O'Donell[2]	Cristobal at al. 163 (LIL), Schwarz 3543 (LIL)	ca. 80	ca. 16	ca. 12
I. fimbriosepala Choisy[1]	Schmidt 1307 (LIL), Bertoni 4127 (LIL)	70–82	13–14	8
I. hieronymi (O.K.) O'Donell[2]	Ramos s.n. (LP)	74–82	16–22	12–16
I. kunthiana Meisn.[3]	Meyer 11699 (LIL), Schwarz 1382 (LIL), Rossengurtt B-4995 (MVFA)	83–114	19	5–10
I. malpighipila O'Donell *[2]	Montes 9608, 9594 (LIL)	76–82	14–18	9–12
I. malveoides Meisn.*[2]	Schinini 10255 (LIL), Arbo et al. 7089 (LIL)	72–84	17–21	10–14
I. nitida Griseb.[2]	Martínez Crovetto & Piccinini 4884 (LIL), coll. unknown 18174 (LP) +	72–86	18–21	10–14
I. paludosa O'Donell[2]	Bridarolli 3690 (LP)	66–76	13–18	8–11
I. platensis Ker Gawl.[2]	Nuñez & Rivas 90 (LP), Birabén 5073 (LP), Rosengurtt B-2850 (MVFA), del Puerto & Berreta 14915 (MVFA)	68–72	15–22	8–14
I. ramosissima (Poir.) Choisy[2]	Irwin et al. 15321 (SI)	76–80	13–15	7–8
I. schultziana O'Donell *[2]	Willink 269 (LIL)	66–86	15–16	8–10
I. setifera Poir.[1]	Coll. unknown 18138 (LP), Bertoni 5173 (LP), Krapovickas et al. 23878 (LIL)	72–100	19–23	12–15
I. setosa Ker Gawl.[2]	Meyer 8393 (LIL)	86–90	15–17	7–10
I. volcanensis O'Donell *[2]	Meyer 16958 (LIL)	72–82	15–17	9–9, 5
Subtype 3 D				
I. syringifolia Meins.[2]	Zuloaga et al. 6699 (SI)	79–93	8–14	5–6, 5
I. wrightii A. Gray[2]	Stolz 320 (SI)	80–93	9–16	6, 5–8

eric categories. Hsiao and Kuoh (1995) examined the pollen morphology of 18 *Ipomoea* species from Taiwan by LM and SEM.

Recently, some cladistic treatments of *Ipomoea* and related genera have included pollen characters (Wilkin 1999, Manos et al. 2001).

Investigations of pollen morphology of Southern New World Convolvulaceae are scarce and restricted to the description of only few species belonging to regional floras (Laguardia 1961, Heusser 1971, Markgraf and D' Antoni 1978). No surveys have considered a high number of genera and species from South America.

The main goals of this study are: 1) to describe the pollen morphology of the native South American Convolvulaceae that grow in Argentina, Chile and Uruguay, through LM and SEM; 2) to define pollen types in these species; and 3) to contribute to the understanding of relationships within the family based on pollen types.

In Argentina, Convolvulaceae is represented by 11 genera and 95 species, 15 of which are endemic (O'Donell 1959a, Krapovickas 1999). In Chile there are 15 species belonging to 6 genera (O'Donell 1957, Marticorena pers. comm.) and in Uruguay 21 species belonging to 7 genera (O'Donell 1959b, Krapovickas 1999, Marchesi pers. comm.). The genera treated here are: *Aniseia*, *Bonamia*, *Calystegia*, *Convolvulus*, *Cressa*, *Dichondra*, *Evolvulus*, *Ipomoea*, *Jacquemontia*, *Merremia* and the monotypic *Iseia luxurians*.

Materials and methods

Pollen grains were obtained from herbarium specimens deposited at CONC, CORD, CTES, LP, LIL, SI, HAL, MVFA, MVFQ and MVM (Holmgren et al. 1990) (Table 1 and Table 2).

Pollen was acetolyzed following standard protocols (Erdtman 1960). For light microscopy (LM), slides were prepared by mounting the pollen in glycerol jelly and sealing them with paraffin. Pollen grain diameter measurements are based on at least 25 grains, and P/E ratio, when applicable, was calculated for each specimen; other character measurements are based on at least 15 grains. In *Ipomoea* pollen the diameter excludes the supratectal elements. The exine thickness was measured, when possible, by using broken pollen grains due to the difficulty of finding clear optical sections in complete grains. Data of *Merremia aegyptia*, *M. cissoides*, *M. dissecta*, *M. macrocalyx* and *M. umbellata* were taken from Ferguson et al. (1977). Measurements in Table 1 and Table 2 represent the range for all samples examined in each taxon. For scanning electron microscopy (SEM), fresh and acetolyzed pollen grains were suspended in 90 % ethanol and mounted on stubs. The samples were sputter-coated with gold palladium and examined in JEOL JSM T-100 and JEOL 6300.

General pollen terminology follows Punt et al. (1994). The term metareticulate was taken from Borsch and Barthlott (1998). Pollen types were circumscribed following the criteria of Borsch (1998).

The nomenclature of the Convolvulaceae genera follows Krapovickas (1999). The infrageneric classification of Austin and Huáman (1996) was considered for *Ipomoea*.

Results

General description of pollen morphology Isopolar or apolar grains; oblate to subprolate; tri-, penta-, hexa-pantocolpate or pantoporate with circular pores or with circular and elliptic pores in a single grain, with sculpturate apertural membrane. Exine tectate, punctate-microechinate with a layer of stout columellae distally ramified (e.g. Fig. 1c) or stout single columellae in concordant pattern with the microspines (e.g. Fig. 3d); or exine semitectate, echinate or gemmate-microreticulate-microechinate-microgranulate (Fig. 4a, 4g) in both cases with a layer of single and thin columellae (Fig. 6d, e). Nexine of uniform thickness.

Three pollen types were recognized on the basis of exine sculpture and structure: (1) exine tectate, punctate-microechinate-microgranulate, with a layer of stout columellae distally ramified; the type and number of aperture allows to distinguish three subtypes (1A, 1B and 1C); (2) exine tectate, punctate-microechinate-microgranulate, with a layer of stout single columellae in concordant pattern with the microspines; (3) exine semitectate, gemmate or echinate-microreticulate-microechinate-microgranulate, with a layer of single columellae; the presence of metareticulum with gemmae or spines, and the pore arrangement, allows to recognize four subtypes (3A, 3B, 3C and 3D).

Table 1 and Table 2 show measurements of polar (subtypes 1A and 1B) and apolar (types and subtypes 1C, 2, 3A, 3B, 3C and 3D) pollen grains respectively.

Morphological description of pollen types

Type 1. (Figs. 1–2–3, a, g–j).

Pollen grain colpate or porate, isopolar. Exine: tectate, punctate, microechinate. Sexine consisting of a single layer of stout and ramified columellae and tectum punctate with microspines. On the basis of aperture type and number, three subtypes were recognized.

Subtype 1A (Figs. 1, 2). Isopolar spheroidal pollen grains to elliptic in equatorial view, and circular in polar view. Tricolpate, long colpus, with tectate microgranulate membrane. SEM: apertural membrane granules often closely adjoined and provided with distinct surface microspines (Fig. 1 h). Ratio sexine/nexine: 1:1 to 2:1 in *Aniseia*, *Bonamia*, *Convolvulus*, *Cressa*, *Dichondra*, *Iseia* and *Jacquemontia blanchetii*; and 2:1 to 3:1 in *Aniseia*, *Convolvulus chilensis* and *C. demissus*. The columellae in pollen grain exine of *Dichondra microcalyx* appear to have a non ramified broad top (Fig. 2 b). SEM: the tectum sculpture exhibits distinct microgranules with surface microspines; these supratectal processes are conspicuous in *Dichondra microcalyx* (Fig. 2 c) and *Iseia luxurians* (Fig. 2 g).

Tetra- and pantocolpate pollen grains were commonly found in *Convolvulus demissus* specimens. Present in: *Aniseia* (*A. argentina* and *A. martinicensis*), *Bonamia sericea*, *Convolvulus* (*C. bonariensis*, *C. chilensis*, *C. crenatifolius*, *C. demissus*, *C. hermanniae*, *C. laciniatus* and *C. lilloi*), *Cressa* (*C. nudicaulis* and *C. truxillensis*), *Dichondra* (*D. argentea*, *D. microcalyx* and *D. sericea*), *Iseia luxurians*, *Jacquemontia blanchetii* and *Merremia* (*M. aegyptia*, *M. cissoides*, *M. dissecta*, *M. hassleriana* and *M. macrocalyx*).

Subtype 1B (Fig. 3 a).

Isopolar spheroidal pollen grains, hexacolpate. Long colpi with granulate membrane. Present in *Merremia umbellata*.

Subtype 1C (Fig. 3 h–j).

Apolar, pantoporate pollen grains with circular and elliptic pores. Pores diameter of c. 8-10 μm, and provided with microgranulate membrane. Ratio sexine/nexine: 2:1 to 3:1. Note: it must be stressed that the length/breadth ratio in some of the elliptic pores of *Calystegia* is in the limit of the pore/colpus definition as stated by Punt et al. (1994) (see discussion). Present in *Calystegia* (*C. sepium*, *C. soldanella* and *C. tuguriorum*).

Type 2. (Fig. 3 b, c–f).

Pollen grain pantocolpate, apolar. Colpi c. 10 μm long, with a thin margin and microgranulate membrane; aperture number ranging from 15 to 21 delimiting tetra-, penta- or hexagonal areas. Exine tectate, punctate, microechinate. Sexine consisting of a single layer of stout columellae and tectum punctate with microspines; columellae and microspines in concordant pattern. Ratio sexine/nexine: 1,5:1; 2:1 or 3:1 in *Evolvulus* and 2:1 in *Jacquemontia*. *SEM*: the tectum of *J. rusbyana* pollen grains shows tendency to a microreticulate pattern (Fig. 3 e).

Present in: *Evolvulus* (*E. arizonicus*, *E. glomeratus*, *E. nummularius* and *E. sericeus*)

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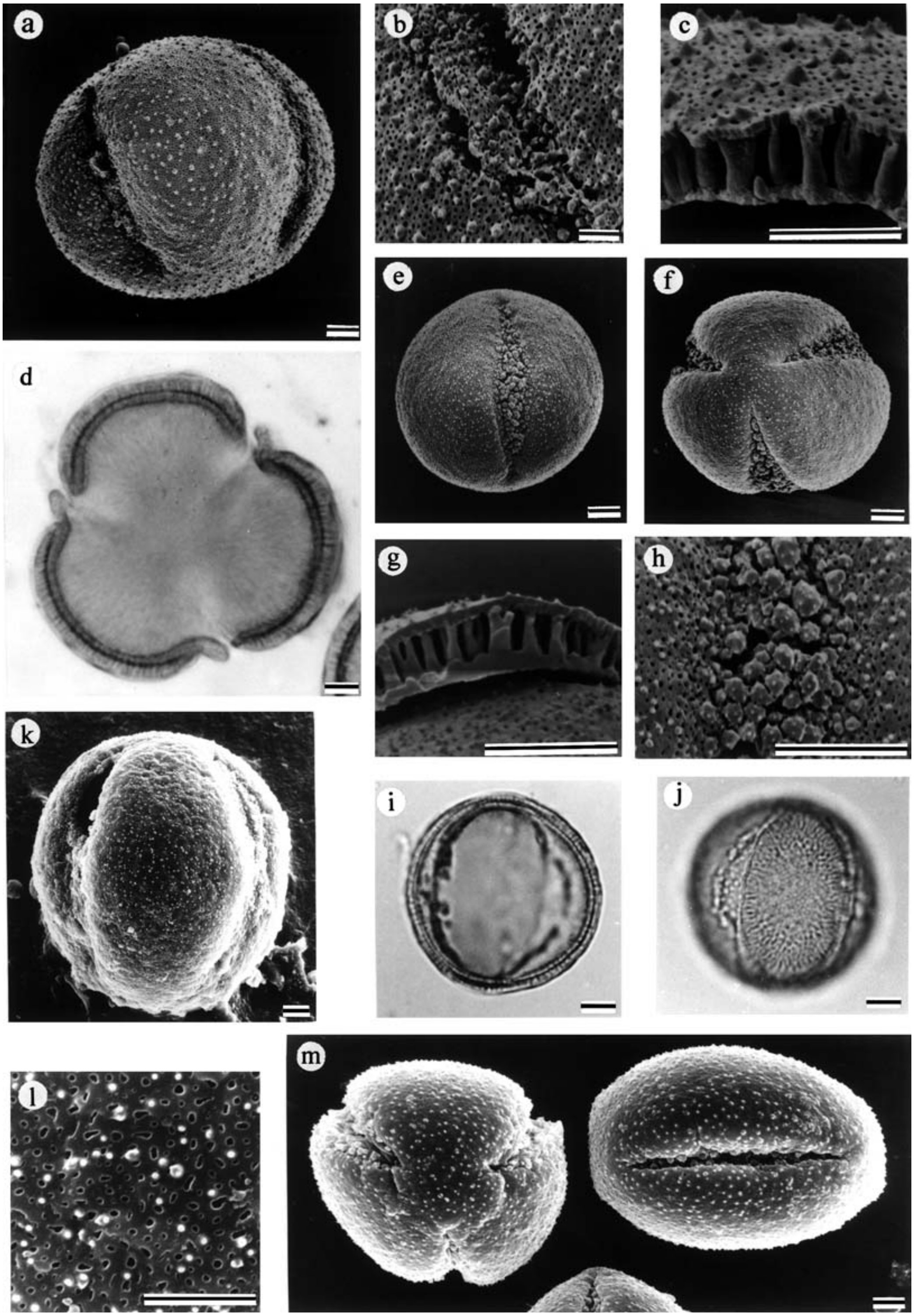
Fig. 1. SEM and LM micrographs of the tricolpate pollen type. **a–d** *Aniseia argentina*. **a** Equatorial view. **b** Detail of tectate apertural membrane. **c** Exine section, note ramified columellae. **d** Polar view, optical section. **e–j** *Bonamia sericea*. **e** Equatorial view. **f** Polar view. **g** Exine section, note ramified columellae. **h** Detail of sculpture membrane showing microgranules with microspines on their surface. **i** Equatorial view, optical section. **j** Equatorial view, high focus. **k, l** *Convolvulus chilensis*. **k** Equatorial view. **l** Detail of exine surface showing puncta and microspines. **m** *Cressa truxillensis*, polar and equatorial view. Bars: 5 μm.



and *Jacquemontia* (*J. agrestis*, *J. decumbens*, *J. heterotricha*, *J. laxiflora*, *J. lorentzii*, *J. rusbyana, J. selloi* and *J. tamnifolia*).

Type 3. (Figs. 4, 5 and 6)

Pollen grain pantoporate, apolar. Pores with microechinate-microgranulate membrane, arranged equidistantly or irregularly over the surface.

Exine semitectate, microreticulate-microechinate-microgranulate, metareticulate with a conspicuous spine, gemma or group of few gemmae at each conjunction point of mesoporia, or echinate with microreticulate mesoporia. Sexine consisting of a layer of single columellae, which form a basal rootlet at the spine (Fig. 5e), and tectum microreticulate with microspines and spines. Nexine thick in most of the species.

Present in *Ipomoea*.

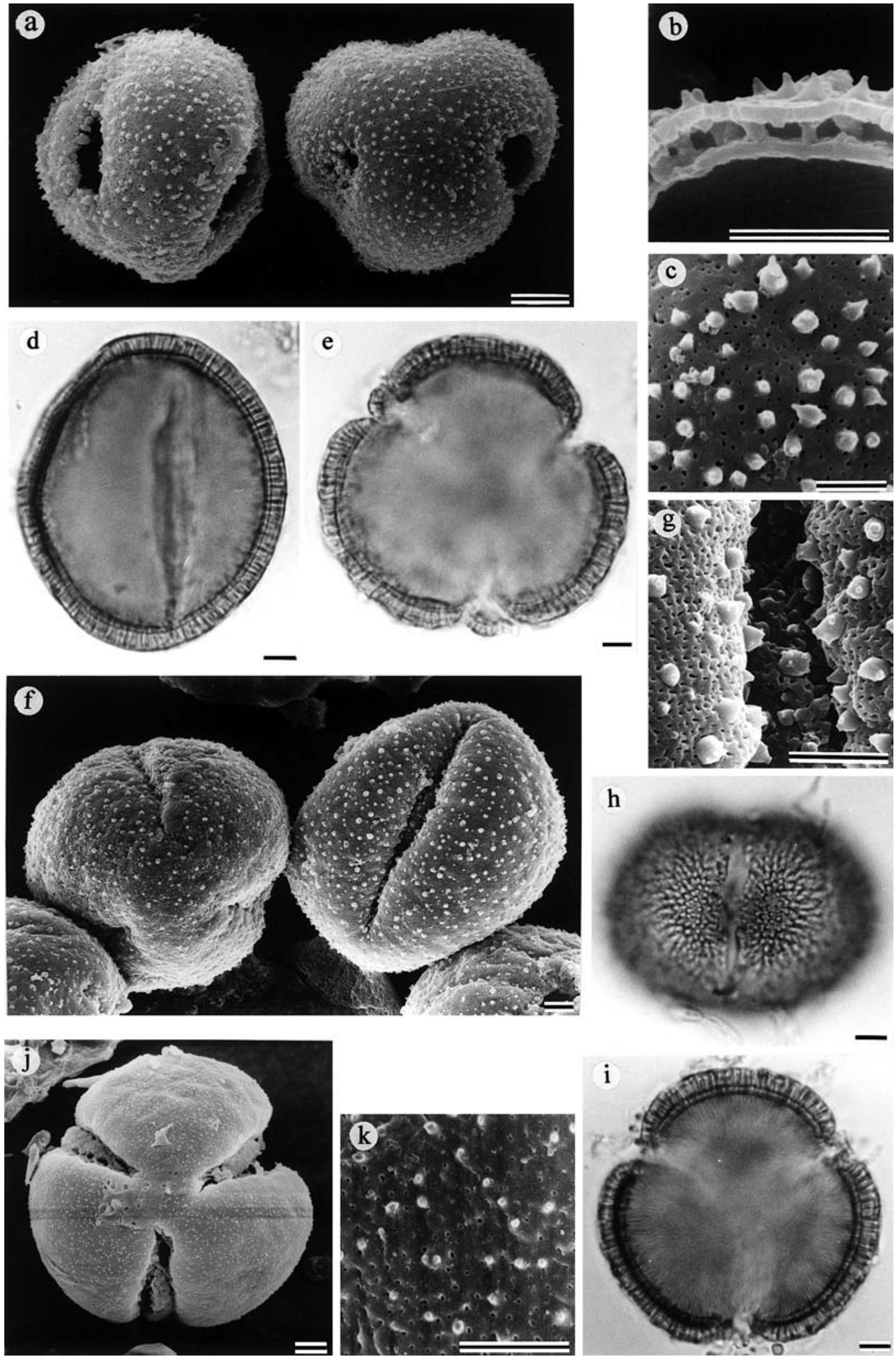
Four subtypes were recognized; two of them are defined by sculpture features and the other two subtypes by the pore arrangement:

– **Subtype 3A**: (Fig. 4a–d; Fig. 5): metareticulate-echinate, mesoporia vaulted with a high spine with basal cushion reduced at each conjunction point of mesoporia; present in: *I. indica*, *I. nil*, *I. pubescens*, *I. purpurea*, and *I. rubriflora*. In this subtype, we observed that some species show metareticulate pollen along with a transitional pattern between metareticulate and non-metareticulate (Fig. 5). The morphological features shown by the transitional pattern were already observed by Borsch and Barthlott (1998). At least two types of transitional patterns are present in a single specimen: grains with generally flat mesoporia and spines with basal cushion, (Fig. 5a, c), and grains with slightly vaulted mesoporia and spines with poorly developed basal cushion (Fig. 5b); nevertheless in both cases the spines are arranged more or less following a geometrical pattern around the pores; present in: *I. amnicola*, *I. aristolochiifolia*, *I. cordatotriloba*, *I. chiliantha*, *I. dumetorum*, *I. indica*, *I. indivisa*, *I. jujuyensis*, *I. lanuginosa*, *I. lilloana*, *I. marginisepala*, *I. nil*, *I. padillae*, *I. pubescens, I. purpurea*, *I. rubriflora* and *I. stuckertii.*
– **Subtype 3B** (Fig. 4e–g): metareticulate-gemmate, mesoporia vaulted with a gemma at each conjunction point of mesoporia, found in *I. alba*; or with a group of gemmae, found in: *I. turbinata*.
– **Subtype 3C** (Fig. 6a–f): echinate, pores distributed regular and equidistantly over the surface, mesoporia no wider than two times the pore diameter; present in: *I. acutisepala*, *I. argentinica*, *I. asarifolia*, *I. bonariensis*, *I. cairica*, *I. carnea*, *I. cheirophylla*, *I. descolei*, *I. fimbriosepala*, *I. hieronymi, I. kunthiana*, *I. malpighipila*, *I. malveoides*, *I. nitida*, *I. paludosa*, *I. platensis*, *I. ramosissima*, *I. schultziana*, *I. setifera*, *I. setosa*, and *I. volcanensis*;
– **Subtype 3D** (Fig. 6g–i): echinate, pores distributed irregularly over the surface, mesoporia usually wider than two times the pore diameter; present in: *I. syringifolia* and *I. wrightii*.

Discussion

Morphology of the pollen types. In Convolvulaceae palynological diversity is evident in exine sculpture and structure and type and number of apertures (Table 3). Exine structure and sculpture appear to be more relevant from a taxonomical point of view than aperture number, and three pollen types can be recognized on the basis of these characters. Within the first type, with punctate-microechinate tectum and with ramified columellae, we distinguished three subtypes that although sharing the exine features, differ in type and

Fig. 2. SEM and LM micrographs of the tricolpate pollen type. **a–c** *Dichondra microcalyx*. **a** Equatorial and polar view. **b** Exine section. **c** Detail of exine surface showing microspines and microgranules with microspines on their surface. **d–g** *Iseia luxurians*. **d** Equatorial view, optical section. **e** Polar view, note the tectate apertural membrane, optical section. **f** Polar and equatorial view of whole grain. **g** Detail of exine and apertures surface, note the microgranules with microspines on the surface. **h–i** *Jacquemontia blanchetii*. **h** Equatorial view showing colpus and columellae, high focus. **i** Polar view, optical section. **j–k** *Merremia hassleriana*. **j** Polar view. **k** Detail of exine surface with puncta and microspines. Bars: 5 μm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number of apertures. The tricolpate subtype is present in a higher number of genera: *Aniseia*; *Bonamia*; *Convolvulus*; *Cressa*; *Dichondra*; *Iseia*; *Jaquemontia* and *Merremia*. Pollen from these genera also share the strongly sculpturate apertural membrane (Figs. 1, 2).

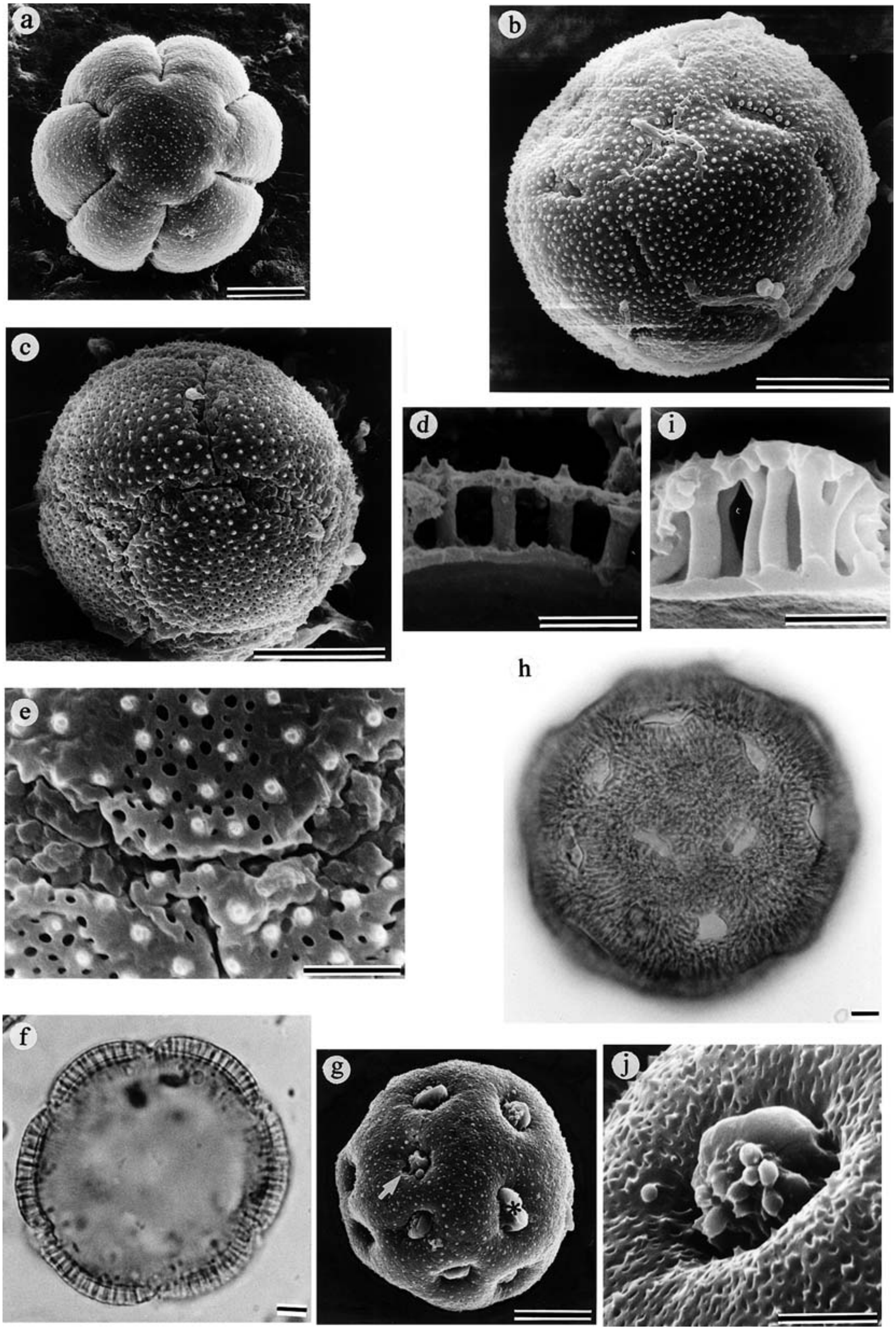
The penta-hexacolpate type occurs only in *Merremia umbellata*, as it was already noticed by Ferguson et al. (1977).

The pantoporate type, with both circular and elliptic pores in a single grain, occurs only in *Calystegia* (*C. sepium*, *C. soldanella* and *C. tuguriorum*). The elliptic pores in *Calystegia* were also observed by other authors (Erdtman 1966, Sengupta 1972). From this peculiar pore shape, *Calystegia* pollen grains appear as an intermediate type between pantocolpate and pantoporate pollen into the successiform pattern from tricolpate through pantocolpate to periporate proposed by Van Campo (1976). However this presumption must be justified by a phylogenetic analysis. A microreticulate-echinate exine with single stout columellae and microspines in concordant pattern is exclusive of the pantocolpate pollen type and as far as we know this pattern has not been reported for Convolvulaceae; it is present in *Evolvulus* (*E. arizonicus*, *E. glomeratus* and *E. sericeus*) and *Jacquemontia* (*J. heterotricha*, *J. lorentzii*, *J. rusbyana*, *J. selloi* and *J. tamnifolia*). The four microreticulate-gemmate and microreticulate-echinate subtypes are included in the pantoporate type with circular pores. These subtypes characterize *Ipomoea* and include the biggest pollen grains in the family (Table 2). The structure comprises a layer of thin and single columellae which support a tectum with an intrincate sculpture characterized by a microreticulum with microspines, microgranules, and spines or gemmae. *Ipomoea* pollen has been defined by the presence of a metareticulate pattern (Borsch and Barthlott 1998), a particular shape of spines or pore number by earlier authors (Sengupta 1966, 1972; Hsiao and Kuoh 1995). However, the pollen diversity in *Ipomoea* species presented in this paper appears to be not well reflected by such classifications. In the commonly applied classifications of the pollen type with a geometrically arrangement pattern, the metareticulate one, a transitional pattern has not been considered. In addition, spine shape is difficult to describe because intraspecific variations were detected in many species, and pore number is extremely difficult to establish due to the density of spines and thick exine in this pollen type. Four subtypes were recognized in the present study among *Ipomoea* species pollen grains. The morphological features that allow to characterize the subtypes defined here, also occur in *Ipomoea* species from other geographical regions according to data provided by Sengupta (1966, 1972), Hsiao and Kuoh (1995), and Melhem and Silva Corrêa (1987).

Taxonomic significance. The morphology of pollen types of Convolvulaceae has shown different relevance when intrafamiliar taxa have been characterized at different taxonomic levels. Tricolpate and pantocolpate subtypes are shared by two or more genera, whereas the two pantoporate types and subtypes characterize one genus each and penta-hexacolpate subtype characterizes a single species.

The tricolpate subtype supports the affinity between *Iseia luxurians* and *Aniseia*, but not with *Jacquemontia* (O'Donell 1953) where only one of the nine species treated, *J. blanchetii*, has tricolpate grains. Pollen of *J. blanchetii* also differs from the other species of *Jacque-*

Fig. 3. SEM and LM micrographs of hexacolpate, pantocolpate and pantoporate pollen grains with elliptic and circular pores types. **a** *Merremia umbellata*, polar view. **b** *Evolvulus glomeratus*, general view. **c–f** *Jacquemontia rusbyana*. **c** General view. **d** Exine section showing concordant pattern between columellae and microspines. **e** Detail of exine surface with perforations and microspines and densely sculpturate apertural membrane. **f** General view, optical section. **g–j** *Calystegia sepium*. **g** General view of grain with elliptic pore (*asterisk*) and circular pore (*arrow*). **h** General view showing apertures. **i** Exine section, note ramified columellae. **j** Detail of microgranulate apertural membrane. Bars: *a, b, c, g*: 20 μm, *d, e, f, h, i, j*: 5 μm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montia by possessing ramified columellae, while most other species in the genus have single columellae in concordant pattern with the microspines. From palynological characters, the generic status of *J. blanchetii* should be reconsidered.

Dichondra, although macromorphologically strongly different from the rest of Convolvulaceae by having a gamosepalous calyx, bilobulate ovary and fruit, indehiscent fruit and reniform leaves (O'Donell 1959a), shares most of the pollen features with diverse taxa of the tricolpate subtype. *Evolvulus* and most of the species of *Jacquemontia* share the pantocolpate type and an exclusive concordant pattern between columellae and supratectal processes.

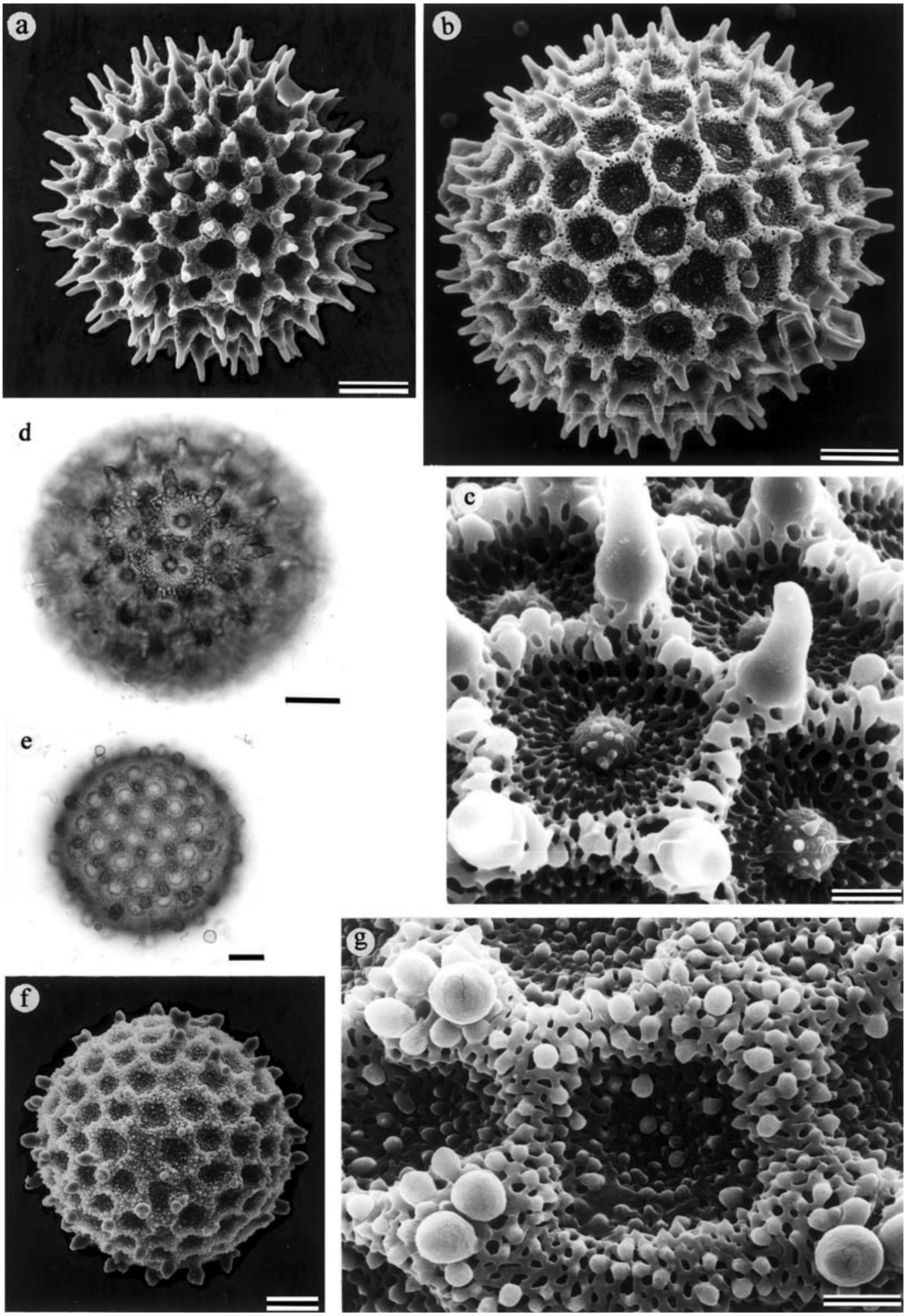
Calystegia is characterized by the unique type that includes the presence of both elliptic and circular pores.

According to pollen features *Ipomoea* has an isolated position, and with the exception of the identification of a transitional pattern between echinate and metareticulate, pollen morphology is similar to that described for *Ipomoea* species belonging to other regions.

Some conclusions can be drawn taking into account the evolutive conception of metareticulate pollen (Borsch 1998). According to this paper a metareticulum results from a specialization of a pantoporate grain with flat mesoporia to a reticulum like structure of mesoporia and pores, this pollen type occurs in families with a sucessiform pollen evolutionary pattern as Convolvulaceae (Van Campo 1976). From this point of view, most species of *Ipomoea* studied here show a primitive pollen type characterized by echinate sculpture with flat mesoporia, followed by specialized pollen which have a metareticulate pattern or a pattern which is transitional to a metareticulate. The echinate non-metareticulate subtype is dominant in the subgenus *Eriospermum* (Austin and Huáman 1996), the more widely represented in the considered area (Table 2), supporting the primitive character of this subgenus (Mc Donald and Mabry 1992). The species belonging to subgenus *Quamoclit* and section *Pharbitis* of subgenus *Ipomoea* (*I. fimbriosepala* and *I. setifera*) share pollen subtypes, the metareticulate type being predominant. Molecular data (waxy gene and ITS) indicate that both sections are closely related (Miller et al. 1999). In the section *Pharbitis* of subgenus *Ipomoea*, *I. purpurea* and *I. nil* have similar sporophytic characters (Austin and Huáman 1996) and chromosome morphology (Chiarini 2001), also sharing a metareticulate-echinate pollen.

Pollen features are consistent in section *Calonyction* of subgenus *Quamoclit*, where the two species studied of this section, *I. alba* and *I. turbinata*, share the metareticulate-gemmate pattern. However they can be distinguished by the number of gemmae at each conjunction point of the mesoporia, being one in *I. alba* and more than one in *I. turbinata*. Because of its chromosome characters and the sphingophile pollination syndrome, *I. alba* is considered evolutionaryly advanced (Chiarini 2001), which is reinforced by the metareticulate pattern of its pollen. In subgenus *Quamoclit*, *I. cairica* and *I. alba* have different pollen types and also differ in chromosome morphology (Chiarini 2001). On the contrary, pollen sculpture does not support the affinity between *I. rubriflora* and *I. hederifolia* (Chiarini 2000) because *I. rubriflora* has metareticulate pollen and *I. hederifolia* has echinate pollen (Machado and Melhem 1987).

Fig. 4. SEM micrographs of pantoporate pollen (with circular pores) type. *Ipomoea*. Subtype 3 A: **a** *I. indica*, general view. **b–c** *I. nil*. *b* General view. **c** Detail of metareticulate exine, showing microreticulum with microspines, granules and spines at each point of conjunction of mesoporia; apertural membrane with microspines. **d** *I. purpurea*, general view, high focus. Subtype 3 B: **e** *I. alba* showing metareticulum with gemae. **f–g** *I. turbinata*. **f** General view. **g** Detail of metareticulate exine, showing microreticulum densely microgranulate and a variable number of gemmae at each point of conjunction of mesoporia. Bars: *a, b, d, e, f*: 20 μm, *c, g*: 5 μm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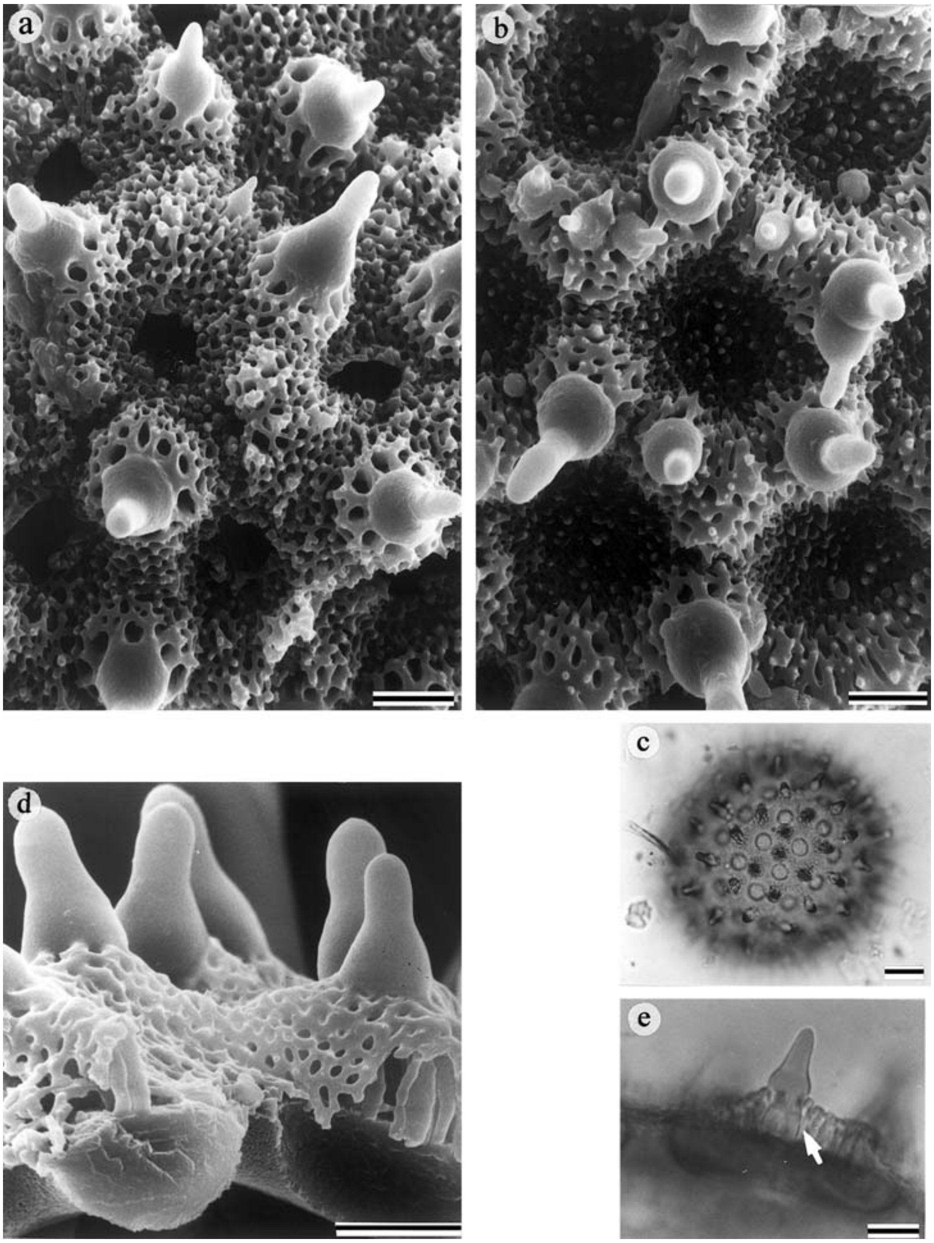

Fig. 5. SEM micrographs of a transitional pattern between metareticulate and non-metareticulate pollen. *Ipomoea*. **a–b** *I.cordatotriloba*. **a** Exine surface with mesoporia more or less flat, and spines with developed basal cushion. **b** Exine surface showing a more defined metareticulum, the basal cushion of spines is slightly developed. **c** *I. indivisa* general view showing spines and pores distributed in a regular pattern, high focus. SEM and LM micrographs of exine structure: **d** *I. marginisepala*, exine partially sectioned showing single columellae and thick nexine. **e** *I. padillae*, optical section showing basal rootlet structure beneath spine. Bars: *a, b, c, e*: 5 µm, *d*: 20 µm

Fig. 6. SEM and LM micrographs of pollen Subtype 3 C and 3 D. *Ipomoea*. **a–c** *Ipomoea kunthiana*. **a** General view. **b** Detail of exine surface, showing microreticulum between spines and on the basal cushion. **c** General view, note the pores equidistantly distributed. **d** *I. malveoides*. **e** *I. cheirophylla*. **f** *I. bonariensis*. **g–i** *I. syringifolia*. **g** General view, note that the pores are not equidistantly distributed over the surface. **i** Detail of exine surface showing microreticulum and spines with basal cushion, note a bifurcate spine tip. Bars: *a–h*: 20 µm, *b, i*: 5 µm

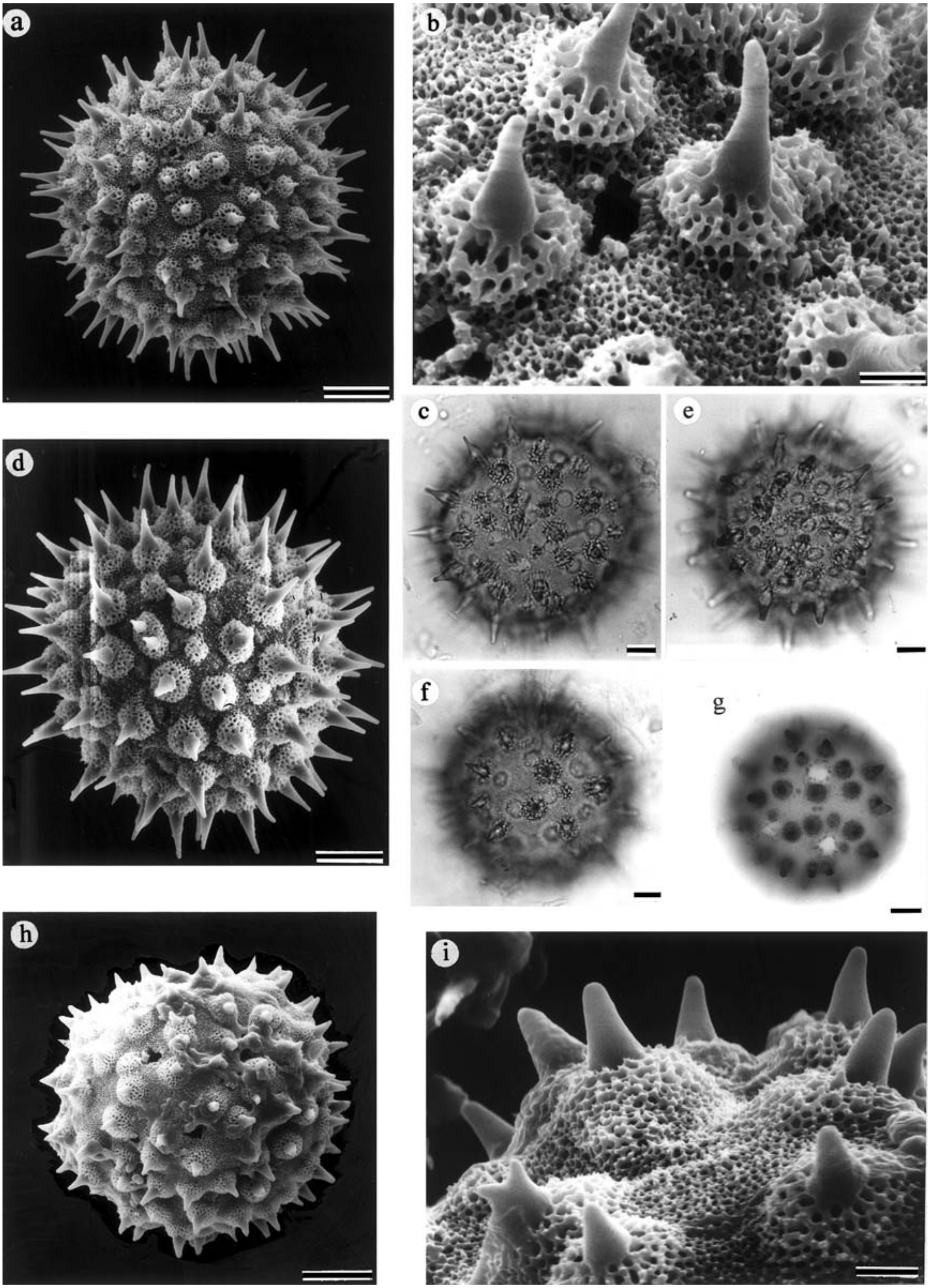
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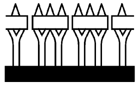
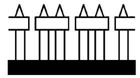
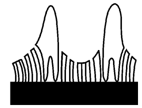
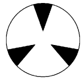
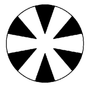
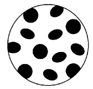
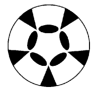
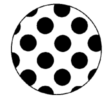
Table 3. Schematic representation of the distribution of the main pollen features in Convolvulaceae

Sculpture and structure						
Aperture (type and number)						
Taxa	*Aniseia* *Bonamia* *Convolvulus* *Cressa* *Dichondra* *Iseia* *Jacquemontia blanchetii* *Merremia* (except *M. umbellata*)	*Merremia umbellata*	*Calystegia*	*Evolvulus* *Jacquemontia* (except *J. blanchetii*)	*I. alba* *I. turbinata*	*I. acutisepala*, *I. amnicola, I. argentinensis*, *I. aristolochiifolia*, *I. asarifolia*, *I. bonariensis*, *I. cairica*, *I. carnea*, *I. cheirophylla*, *I. cordatotriloba,* *I. chiliantha*, *I. descolei*, *I. dumetorum*, *I. fimbriosepala*, *I. hieronymi*, *I. indica*, *I. indivisa*, *I. jujuyensis*, *I. kunthiana*, *I. lanuginosa*, *I. lilloana*, *I. malpighipila*, *I. malveoides*, *I. marginisepala*, *I. nil*, *I. nitida*, *I. padillae*, *I. paludosa*, *I. platensis*, *I. pubescens*, *I. purpurea*, *I. ramosissima*, *I. rubriflora*, *I. schultziana*, *I. setifera*, *I. setosa*, *I. stuckertii* *I. syringifolia*, *I. volcanensis*, *I. wrightii.*

General conclusions Pollen morphology of Convolvulaceae genera including both South American and Old World species is consistent within each genus. The difficulties reported by many authors to delimite some genera are reflected in pollen characters, e.g. the tricolpate subtype (*Aniseia*, *Bonamia sericea*, *Cressa*, *Dichondra*, *Jacquemontia blanchetii* and *Merremia* except *M. umbellata*), and the pantocolpate subtype (*Evolvulus* and *Jacquemontia*). Within the diversity of pollen types, the exine structure relates tricolpate and penta-hexacolpate pollen subtypes, along with the pantoporate subtype of *Calystegia*, whose apertures seem to be in a middle stage between pore and colpus. According to pollen features *Ipomoea* is clearly isolated, the metareticulate state appears to be derived in Convolvulaceae, based on phylogenetic data. The dominance of pollen with non-metareticulate exine in most species and the presence of a transitional pattern to metareticulate, enclose a phylogenetic significance that should be included in forthcoming phylogenetic treatments of this genus.

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References

Austin D. F. (1975) Convolvulaceae. Flora of Panama. Ann. Missouri Bot. Gard. 62: 157–224.

Austin D. F., Huáman Z. (1996) A synopsis of *Ipomoea* (Convolvulaceae) in the Americas. Taxon 45: 3–38.

Borsch T. (1998) Pollen types in the Amaranthaceae. Morphology and evolutionary significance. Grana 37: 129–142.

Borsch T., Barthlott W. (1998) Structure and evolution of metareticulate pollen. Grana 37: 68–78.

Chiarini F. E. (2000) Números cromosómicos en dos especies de *Ipomoea* (Convolvulaceae) argentinas. Kurtziana 28 (2): 309–311.

Chiarini F. E. (2001) Estudios cromosómicos en algunas especies de *Ipomoea* (Convolvulaceae). Bol. Soc. Argent. Bot. 36 (3–4): 289–296.

Erdtman G. (1952) Pollen morphology and plant taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

Erdtman G. (1960) The acetolysis method, a revised description. Svensk. Bot. Tidskr. 54, 561–564.

Ferguson I. K., Verdcourt B., Poole M. M. (1977) Pollen morphology in the genera *Merremia* and *Operculina* and its taxonomic significance. Kew Bulletin 31 (4): 763–773.

Heusser C. J. (1971) Pollen and Spores of Chile: Modern Types of the Pteridophyta, Gymnospermae and Angiospermae. The University of Arizona Press, Tucson Arizona.

Holmgren P. K., Keuken W., Schofield E. K. (1990) Index Herbariorum, Part 1. The Herbaria of the World. 8th ed. New York Botanical Garden, Bronx, New York.

Hsiao L.C., Kuoh C.S. (1995) Pollen morphology of the *Ipomoea* (Convolvulaceae) in Taiwan. Taiwania 40 (3): 299–316.

Krapovickas A. (1999) Convolvulaceae. In: Zuloaga F.O., Morrone O.E. (eds.) Catálogo de las plantas vasculares de la República Argentina II. Acanthaceae - Euphorbiaceae (Dicotyledonae). Monographs of Systematics Botany from the2-Museum Botanical Garden, No 74, pp. 547–565.

Laguardia A. M. (1961) Morfología del grano de polen de algunas Convolvuláceas uruguayas. Bol. Soc. Argent. Bot. IX: 187–192.

Lewis W. H., Oliver R. L. (1965) Realignment of *Calystegia* and *Convolvulus* (Convolvulaceae). Ann. Missouri Bot. Gard. 52 (2): 217–222.

Machado I. C. S., Melhem T. S. A. (1987) Morfología polínica de *Ipomoea hederifolia* L. e *I. quamoclit* L. (Convolvulaceae). Hoehnea 14: 31–52.

Manos P.S., Miller R.E., Wilkin P. (2001) Phylogenetic analysis of *Ipomoea*, *Argyreia*, *Stictocardia* and *Turbina* suggests a generalized model of morphological evolution in morning glories. Syst. Bot. 26 (3): 585–602.

Markgraf V., D'Antoni H.L. (1978) Pollen Flora of Argentina. Tucson, Arizona Press.

McDonald J.A., Mabry T.J. (1992) Phylogenetic systematics of New World *Ipomoea* (Convolvulaceae) based on chloroplast DNA restriction site variation. Plant Syst. Evol. 180: 243–259.

Melhem T.S.A., Silva Corrêa A.M. (1987) Flora polínica da reserva do parque estadual Das Fontes do Ipiranga (São Paulo, Brasil). Hoehnea 14: 15–24.

Miller R.E., Rausher M.D., Manos P.S. (1999) Phylogenetic systematics of *Ipomoea* based on ITS and *waxy* sequences. Syst. Bot. 24 (2): 209–227.

O'Donell C.A. (1953) Un nuevo género de Convolvuláceas: *Iseia* O'Donell. Bol. Soc. Argent. Bot. V (1–2): 75–80.

O'Donell C.A. (1957) Convolvuloideas chilenas. Bol. Soc. Argent. Bot. 6: 143–184.

O'Donell C.A. (1959a) Las Convolvuláceas argentinas. Lilloa XXIX: 87–348.

O'Donell C.A. (1959b) Las Convolvuloideas de Uruguay. Lilloa XXIX: 349–376.

Punt W., Blackmore S., Nilsson S., Le Thomas A. (1994) Glossary of pollen and spores terminology. LPP Foundation, Utrecht.

Sengupta S. (1966) A contribution to the pollen morphology of *Ipomoea* with special reference to exine stratification. Trans. Bose Res. Inst., 29: 123–129.

Sengupta S. (1972) On the pollen morphology of Convolvulaceae with special reference to taxonomy. Rev. Palaeobot. Palynol. 13: 157–212.

Van Campo M. (1976) Patterns of pollen morphological variation within taxa. In: Ferguson I.K., Muller J. (eds.) The evolutionary significance of the exine. Linn. Soc. Symp. Ser. 1. Academic Press, London pp. 125–137.

Wilkin P. (1999) A morphological cladistic analysis of the Ipomoeae (Convolvulaceae). Kew Bulletin 54: 853–876.

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