

Oxalis section *Alpinae* (Oxalidaceae): orbicule diversity and pollen grain morphology

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Abstract: Orbicule characteristics and pollen morphology were studied using light microscopy and scanning electron microscopy with 13 species of *Oxalis* section *Alpinae*, endemic to South America. Orbicules are either homogeneous or heterogeneous in size; surface smooth or with punctuations; margin smooth, lobed, or wavy; rounded, oblong, or irregular shapes; variable clustering. According to orbicule characteristics, six groups are proposed. The *Oxalis* pollen grain is 3-colpate and the shape is prolate spheroidal, oblate spheroidal, or spheroidal; ambit rounded or triangular. Exine microreticulate, semitectate, brochate. Brochi circular, oval, triangular to polygonal. Lumen with or without content. Sporopollenin generally forming groups that may be in rows in the margins or in the center of colpus.

Key words: Andes, Argentina, Chile, South America, *Oxalis* pollen, Ubisch bodies

1. Introduction

Oxalis L. (Oxalidaceae) is a diverse genus comprising approximately 500 species. The genus is divided in four subgenera: *Oxalis* L., *Monoxalis* (Small) Lourteig (1980), *Trifidus* Lourteig (1995), and *Thamnoxyis* (Endl.) Reich. emend. Lourteig (2000) (Lourteig, 1994, 1995, 2000). Section *Alpinae* is included in subgenus *Oxalis*, originally published by Reiche in 1894. The species in this section can be described as follows: annuals or perennial herbs, cushion-like loose to very dense, 1–30 cm high. Roots long, deep, sometimes tubers. Acaulescent or subacaulescent, woody stems. Stipules welded, generally covering the stem, sometimes covering the branches. Leaves always trifoliolate, leaflets obcordate, cuneiform, apex retuse or emarginate, with variable incisions, unequal lobes, calli sometimes present, pubescent on one or both sides, hairs on the margin sometimes present. Flowers in few- to many-flowered cymes, umbeliform, cymes embedded into the cushions or exceeding the foliage. Corolla mostly yellow, in a few species purple. Capsule globose to cylindrical (López and Heibl, unpublished data).

Orbicules, also known as Ubisch bodies (Bhandari, 1984) can be defined as corpuscles of variable size (0.14–20 µm) that show the same electron density, autofluorescence, resistance to electrolysis, and reaction to dyes compared to pollen exine (Rosenfeldt and Galati, 2008). Orbicules are

species-specific structures as seen in *Oxalis*, *Fagopyrum*, *Lilium*, *Silene*, and *Gnetum*, among other species (Hesse, 1986), and they have been used to contribute to the taxonomy in *Oxalis* (Rosenfeldt and Galati, 2005, 2007, 2008; López and Rosenfeldt, 2015).

Descriptive works in palynology have gained new value. Knowledge of the pollen of extant species allows us to identify ancient pollen and to provide new material to use to date phylogenies and improve macroevolutionary studies. Pollen grain morphology was previously studied in *Oxalis* considering aspects such as morphology (Wan and Chen, 2001; Perveen and Qaiser, 2003; Rosenfeldt and Galati, 2007; López and Rosenfeldt, 2015), types of pollen grain (Ghosh and Verma, 1985), ontogeny (Herr, 1972; Guth and Weller, 1986; Rosenfeldt and Galati, 2005), formation of aberrant pollen (Erdtman, 1952; Huynh, 1969; Cerceau, 1995; Rosenfeldt and Galati, 2012), and categories of grain aberrations and succesiform series (Dreyer and Van Wyk, 1998).

In this treatment we included 13 out of 18 *Oxalis* species circumscribed to section *Alpinae*: *O. cinerea* Zuccarini, *O. compacta* Gillies, *O. erythrorhiza* Gillies, *O. famatinae* Knuth, *O. holosericea* Philippi, *O. hypsophila* Philippi, *O. micrantha* Bertero, *O. muscoides* Philippi, *O. nahuelhuapiensis* Spegazzini, *O. pycnophylla* Weddell, *O. squamata* Zuccarini, *O. subacaulis* Gillies, and *O. valdiviensis* Barnéoud.

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Considering the absence of such studies in the species of *Oxalis* section *Alpinae*, the aims of this study were to assess orbicule diversity in species of this endemic group and to provide detailed morphological pollen descriptions.

2. Material and methods

Thirteen species of *Oxalis* were analyzed; anthers were removed from herbarium specimens deposited at SI (Table 1).

For light microscopy, slides were prepared by mounting the pollen in glycerol jelly and were sealed with paraffin. For scanning electron microscopy (SEM), anthers were transferred to 100% alcohol and then air-dried. Sputtering treatment was done with gold-palladium for 3 min. Scanning microphotographs were taken with a Zeiss Supra 40 FESEM microscope. The terminology in general follows that of Punt et al. (1994).

3. Results and discussion

Here a general description is provided for the orbicules and pollen grains of species of *Oxalis* section *Alpinae* (Figures 1–4).

Orbicules: The orbicules are randomly dispersed on the inner surface of the anther locule. They are variable in size; with smooth surface or perforations that do not cross the entire structure of the orbicule; margin smooth, lobed, or wavy; rounded or oblong shapes, sometimes “doughnut-like” orbicules are present; aggregates of two or more orbicules can be observed forming units of variable shape.

Pollen grains: Pollen 3-colpate, prolate spheroidal, oblate spheroidal to spheroidal; ambit rounded or triangular. Exine microreticulate, semitectate, brochate. Brochi circular, oval, triangular to polygonal. Lumen with or without granular content. Granules of sporopollenin generally forming groups that may be in rows in the margins or in the center of colpus membrane.

Oxalis cinerea – Figures 1A–D. Orbicules: Homogeneous in size, rounded, margin and surface smooth; sometimes forming groups; “doughnut-like” orbicules present. Pollen grain: 20–22 μm in diameter; rounded, oblong to subtriangular brochi; no visible lumen content; granules in rows, at the edges and in the center of the colpus membrane.

Oxalis subacaulis – Figures 1E–H. Orbicules: Homogeneous in size; rounded shape; smooth margin and surface, sometimes forming aggregations displayed in both axes; “doughnut-like” orbicules present. Pollen grain: 22–25 μm in diameter; rounded or oblong brochi; no visible lumen content; granules forming rows at the edges and congregated on the center of the colpus membrane.

Oxalis micrantha – Figures 1I–1L. Orbicule: Heterogeneous in size; irregular shape; lobulated margins, smooth surface; aggregations sometimes forming irregular wheel-like, “L-like”, or fancy structures; “doughnut-like”

orbicules present. Pollen grain: 22–25 μm in diameter; irregular brochi, variable both in shape and sizes; visible lumen content; granules forming aggregates in rows, at the edges and the center of the colpus membrane.

Oxalis erythrorhiza – Figures 2A–2D. Orbicules: Heterogeneous in size, rounded, lobulated margins; perforations at the surface; sometimes forming aggregations in linear rows or branched. Pollen grain: 22–25 μm in diameter; rounded, oblong, or triangular brochi, visible lumen content, granules in rows, at the edges of the colpus membrane.

Oxalis famatinae – Figures 2E–H. Orbicules: Heterogeneous in size, rounded or with variable shapes, margin wavy, surface with perforations, sometimes forming aggregations. Pollen grain: 25–30 μm in diameter; irregular brochi, variable both in shape and size, visible lumen content, granules aggregated in rows, mainly at the edges of the colpus membrane.

Oxalis holosericea – Figures 2I–L. Orbicules: Heterogeneous in size, irregular shape, wavy margin; surface with perforations; sometimes forming aggregations in linear rows or “L-shaped”. Pollen grain: 20–22 μm in diameter; rounded, oblong, subtriangular, or polygonal brochi; visible lumen content, granules forming aggregates in rows at the center of the colpus membrane.

Oxalis hypsophila – Figures 3A–3D. Orbicules: Heterogeneous in size, rounded shape; smooth margins; surface with perforations; aggregations sometimes forming irregular wheel-like structures; “doughnut-like” orbicules present. Pollen grain: 25–30 μm in diameter; rounded, oblong, or triangular brochi; no visible lumen content; granules aggregated in rows, at the edges and the center of the colpus membrane.

Oxalis nahuelhuapiensis – Figures 3E–3H. Orbicules: Heterogeneous in size; rounded or oblong shape; smooth margin, surface with perforations; sometimes forming aggregates; “doughnut-like” orbicules present. Pollen grain: 22–25 μm in diameter; irregular or polygonal brochi; visible lumen content; granules forming irregular lumps on the colpus membrane.

Oxalis pycnophylla – Figures 3I–3L. Orbicules: Heterogeneous in size; rounded or oblong shape; smooth margin, surface with perforations; sometimes forming linear aggregates or branched in “Y-” to “L-shape”; “doughnut-like” orbicules present. Pollen grain: 18–24 μm in diameter; polygonal brochi; visible lumen content; granules distributed homogeneously on the colpus membrane.

Oxalis compacta – Figures 4A–4D. Orbicules: Heterogeneous in size, irregular shape with lobulated margins, surface with perforations; sometimes forming aggregations in linear rows or branched; “doughnut-like” orbicules present. Pollen grain: 23–27 μm in diameter;

Table 1. Material examined: species, collector, collection number, date, country, province/region, locality, and altitude (m a.s.l.).

Species	Collector	Number	Date	Country	Province/region	Locality	Altitude
<i>Oxalis cinerea</i> Zucc.	Behn, K.	(SI 19769)	23/11/1929	Chile	-	-	1100
	Grandjot, K.	3209	/11/1937	Chile	Región Metropolitana	Santiago	2000
	Morrison, J. L.	16772	08/12/1938	Chile	Región Metropolitana	Melipilla	1860
<i>O. compacta</i> Gill.	Kiesling, R.	1358	15/02/1977	Argentina	San Juan	Calingasta	3300
	Kiesling, R.	9037	19/03/1998	Argentina	San Juan	Iglesia	3820
	Zuloaga, F. O.	12338	22/11/2010	Argentina	Mendoza	Malargüe	1850
<i>O. erythrorhiza</i> Gill.	Zanotti, C. A.	270	27/01/2012	Argentina	Jujuy	Dr. Manuel Belgrano	4740
	Sede, S. M.	392	09/01/2012	Argentina	Mendoza	Malargüe	2985
	Prina, A.	2458	11/12/2003	Argentina	Mendoza	Malargüe	2600
<i>O. famatinae</i> Knuth	Zuloaga, F. O.	5943	16/02/1997	Argentina	Jujuy	Humahuaca	
	Morrone, O.	2497	12/02/1998	Argentina	Jujuy	Humahuaca	4500
	Kiesling, R.	6389	20/02/1986	Argentina	La Rioja	Famatina	
<i>O. holosericea</i> Phil.	Boelcke, O.	14283	01/02/1970	Argentina	Neuquén	Minas	2600–2750
	Boelcke, O.	14067	29/01/1970	Argentina	Neuquén	Minas	
	Kiesling, R.	8865	28/01/1997	Argentina	San Juan	Calingasta	3280
<i>O. hypsophila</i> Phil.	Morrison, J. L.	16989	21/12/1938	Chile	IV Región de Coquimbo	Elqui	
	Biurrun, F.	5278	25/03/1998	Argentina	La Rioja	-	3800
	Behn, K.	(SI 19767)	14/09/1930	Chile	V Región de Valparaíso	-	
<i>O. micrantha</i> Bert.	Zuloaga, F. O.	12555	28/11/2010	Argentina	Neuquén	Minas	1570
	Zuloaga, F. O.	12608	29/11/2010	Argentina	Neuquén	Ñorquín	1380
	Biurrun, F.	5856	31/03/1999	Argentina	San Juan	Sarmiento	2050
<i>O. muscoides</i> Phil.	Kiesling, R.	9135	17/01/1999	Argentina	San Juan	Calingasta	2200
	Tombesi, T. S.	90	17/02/2000	Argentina	San Juan	Sarmiento	1700
	Cabrera, A. L.	33092	12/12/1981	Argentina	Chubut	Futaleufú	
<i>O. nahuelhuapiensis</i> Speg.	Biganzoli, F.	2126	12/01/2009	Argentina	Neuquén	Minas	1790
	Biganzoli, F.	1213	17/01/2001	Argentina	Neuquén	Huiliches	1740
	Humziker, J. H.	10591	04/03/1983	Argentina	Jujuy	Humahuaca	4670–4730
<i>O. pycnophylla</i> Wedd.	Kiesling, R.	9075	03/11/1998	Argentina	San Juan	Ullum	3160
	Kiesling, R.	6874	05/02/1988	Argentina	San Juan	Calingasta	2950–3100
	Sede, S. M.	349	07/01/2012	Argentina	Neuquén	Minas	1678
<i>O. squamata</i> Zucc.	Zuloaga, F. O.	12520	26/11/2010	Argentina	Neuquén	Minas	1520
	Urtubey, E.	692	24/01/2012	Chile	Región Metropolitana	-	3025
	Kiesling, R.	4154	14/11/1982	Argentina	San Juan	Sarmiento	2000
<i>O. subacaulis</i> Gill.	Salomón, L.	245	03/02/2013	Argentina	Catamarca	Andalgá	3921
	Boelcke, O.	15904	22/01/1974	Argentina	Mendoza	San Rafael	2320–2400
	Sede, S. M.	351	07/01/2012	Argentina	Neuquén	Minas	1678
<i>O. valdiviense</i> Barn.	Zavala-Gallo, L.	81	04/01/2011	Argentina	Neuquén	Los Lagos	820
	Morrone, O.	5520	18/11/2006	Chile	X Región de Los Lagos	-	912

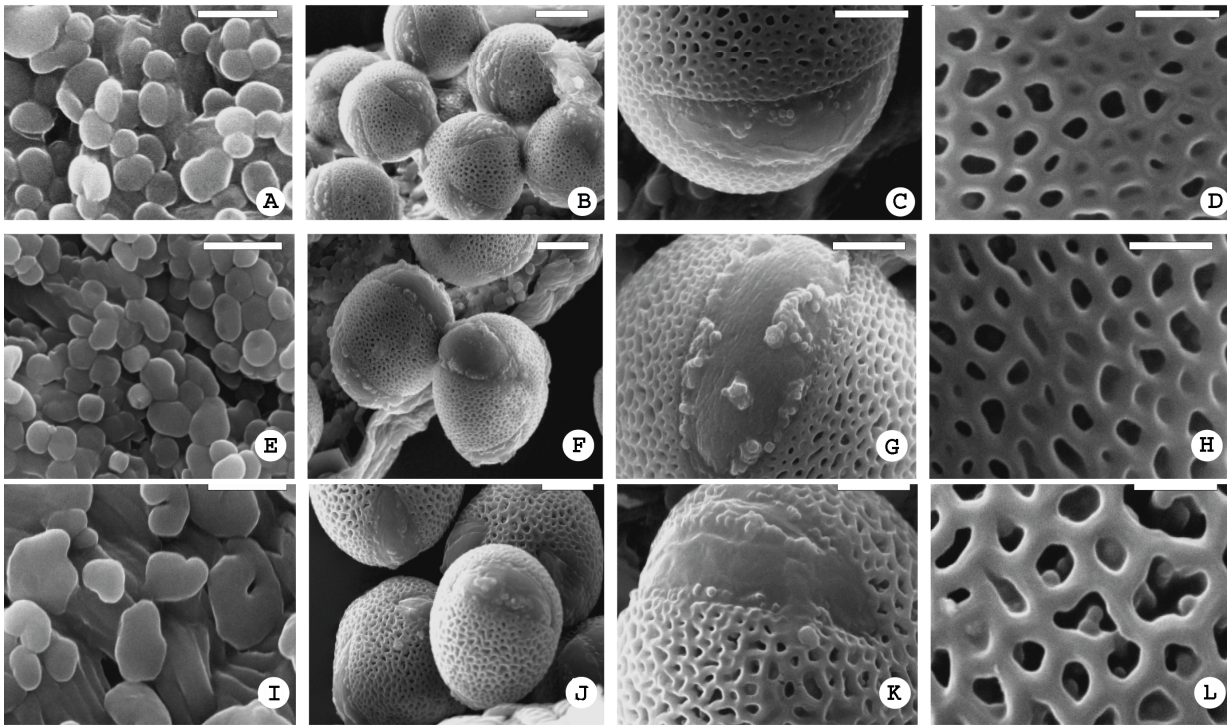


Figure 1. SEM photographs of orbicules and pollen grains of Group 1: *O. cinerea* (A–D), *O. subacaulis*, (E–H); and Group 2: *O. micrantha* (I–L). General view of the orbicules: A, E, I. Scale bar = 5 µm. General views of the pollen grains: B, F, J. Scale bar = 10 µm. Detail of the colpus: C, G, K. Scale bar = 5 µm. Detail of the reticule: D, H, L. Scale bar = 2 µm.

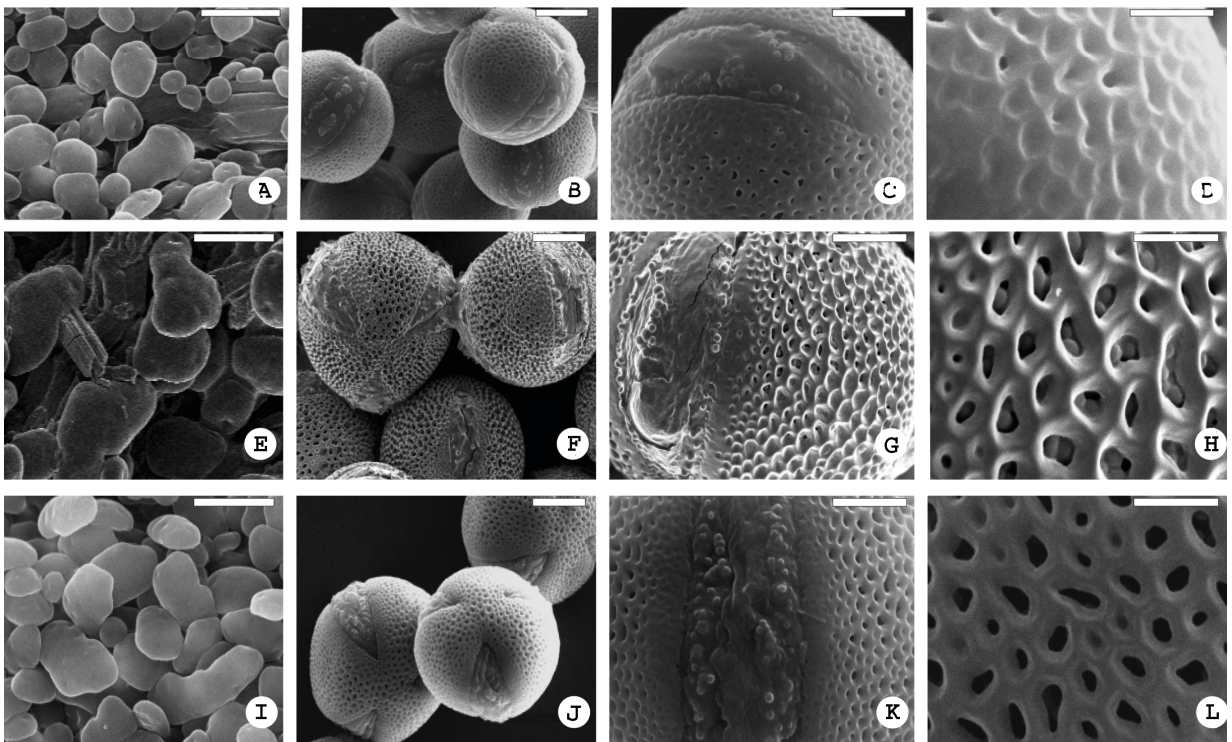


Figure 2. SEM photographs of orbicules and pollen grains of Group 3: *O. erythrorhiza* (A–D), *O. famatinae* (E–H), *O. holosericea* (I–L). General view of the orbicules: A, E, I. Scale bar = 5 µm. General views of the pollen grains: B, F, J. Scale bar = 10 µm. Detail of the colpus: C, G, K. Scale bar = 5 µm. Detail of the reticule: D, H, L. Scale bar = 2 µm.

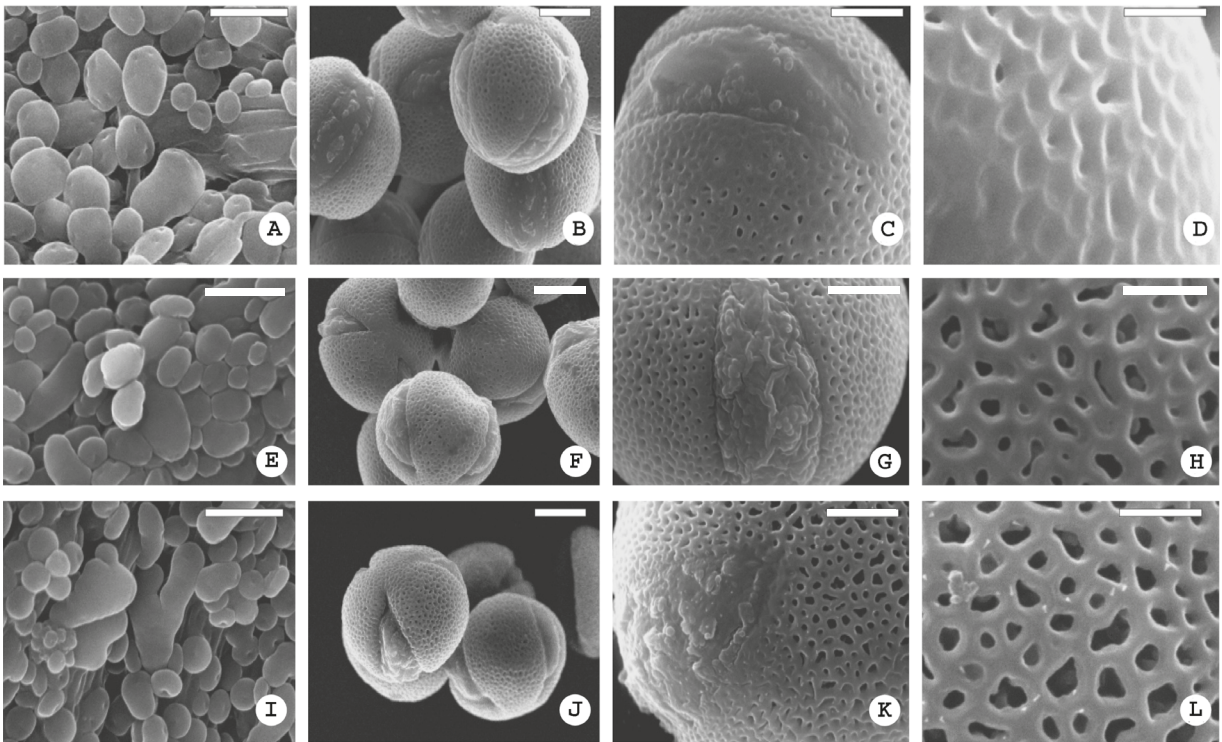


Figure 3. SEM photographs of orbicules and pollen grain of Group 4: *O. hypsophila* (A–D), *O. nahuelhuapiensis* (E–H), *O. pycnophylla* (I–L). General view of the orbicules: A, E, I. Scale bar = 5 μ m. General views of the pollen grain: B, F, J. Scale bar = 10 μ m. Detail of the colpus: C, G, K. Scale bar = 5 μ m. Detail of the reticulate: D, H, L. Scale bar = 2 μ m.

polygonal brochi, visible lumen content, granules in rows, at the center of the colpus membrane.

Oxalis muscoides – Figures 4E–4H. Orbicules: Heterogeneous in size; rounded or irregular shape; wavy margins; surface with perforations; sometimes forming aggregations in linear rows or branched. Pollen grain: 15–18 μ m in diameter; rounded, oblong or triangular brochi; no visible lumen content; granules in rows at the edges of the colpus membrane.

Oxalis squamata – Figures 4I–4L. Orbicules: Very heterogeneous in size; rounded, oblong, or irregular shape; smooth margin and surface, sometimes forming linear or branched aggregates. Pollen grain: 20–25 μ m in diameter; rounded to polygonal brochi, visible lumen content; granules congregated in rows, at the edges and the center of the colpus membrane.

Oxalis valdiviensis – Figures 4M–4P. Orbicules: Very heterogeneous in size; rounded, oblong or irregular shape; smooth margin and surface, linear or branched aggregates sometimes forming irregular wheel-like structures. Pollen grain: 28–30 μ m in diameter; rounded, oblong, or polygonal brochi; visible lumen content; granules forming isolated groups distributed irregularly on the colpus membrane.

Considering the orbicule characteristics, six groups can be proposed (Table 2). Group 1 (Figures 1A–1H) includes *O. cinerea* and *O. subacaulis*, which share a homogeneous size, smooth margin and surface, rounded shape, and the presence of “doughnut-like” orbicules. *Oxalis micrantha* is in a single-species group, Group 2 (Figures 1I–1L), given its heterogeneous size, smooth surface, and lobulated margin. Group 3 (Figures 2A–2L) includes *O. erythrorhiza*, *O. famatinae*, and *O. holosericea*, sharing the presence of punctuations in the surface and the absent of “doughnut-like” orbicules. Group 4 (Figures 3A–3L) presents a combination of heterogeneous size, surface with punctuations, smooth margin, and “doughnut-like” orbicules and includes *O. hypsophila*, *O. nahuelhuapiensis*, and *O. pycnophylla*. Group 5 (Figures 4A–4H) is formed by *O. compacta*, presenting a lobulated margin, and *O. muscoides*, presenting wavy margins; they share a combination of heterogeneous size, surface with punctuations, “doughnut-like” orbicules, and linear or anastomosed aggregations. The last is Group 6 (Figures 4I–4P), with conspicuous differences in size, smooth surface and margins, and the absence of “doughnut-like” orbicules, including *O. squamata* and *O. valdiviensis*.

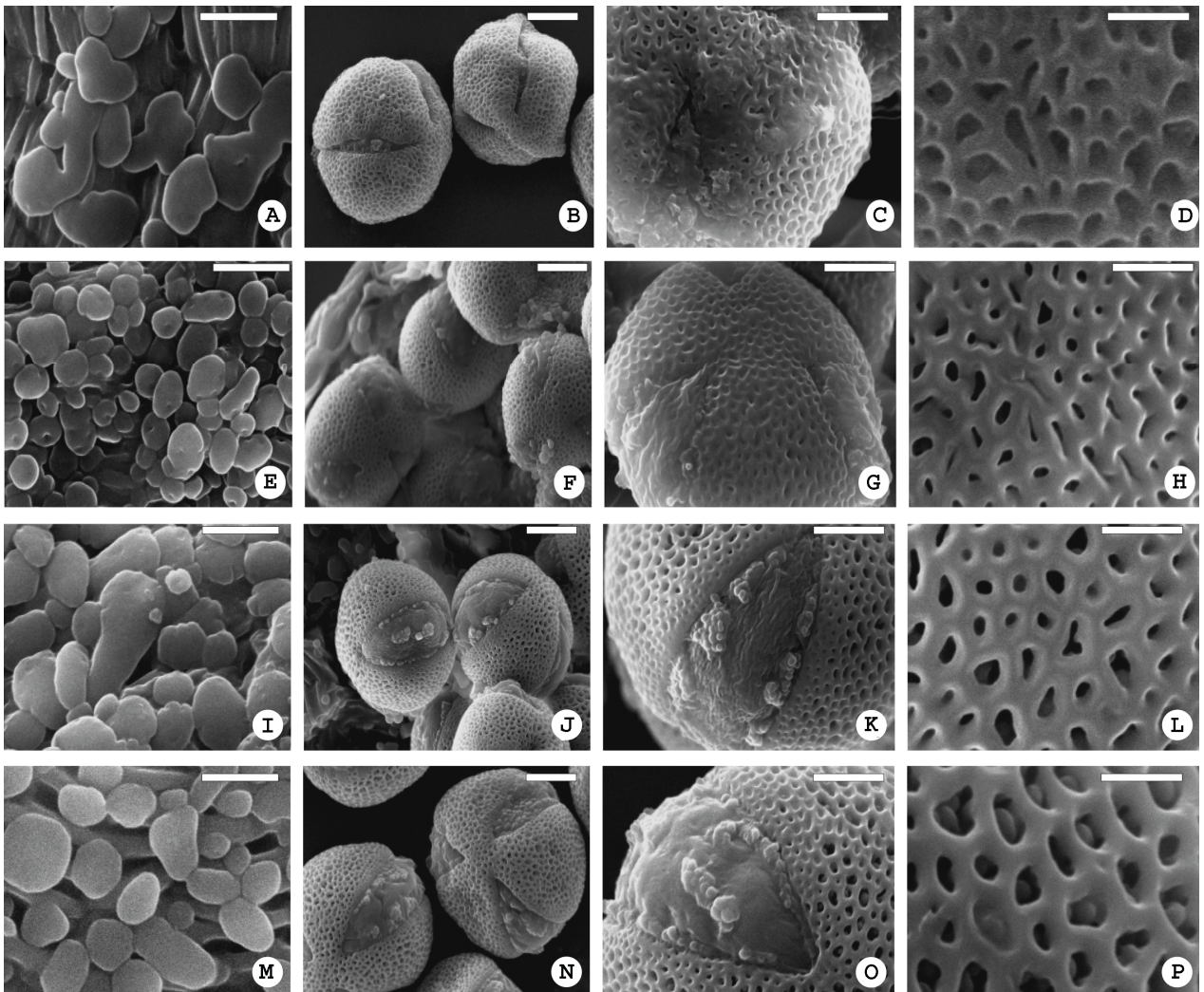


Figure 4. SEM photographs of orbicules and pollen grain of Group 5: *O. compacta* (A–D), *O. muscoides* (E–H); and Group 6: *O. squamata* (I–L), *O. valdiviensis* (M–P). General view of the orbicules: A, E, I, M. Scale bar = 5 μ m. General views of the pollen grain: B, F, J, N. Scale bar = 10 μ m. Detail of the colpus: C, G, K, O. Scale bar = 5 μ m. Detail of the reticulate: D, H, L, P. Scale bar = 2 μ m.

According to the present study, species of *Oxalis* section *Alpinae* have pollen grains 3-colpate, prolate spheroidal to oblate spheroidal. These characteristics coincide with those described for other *Oxalis* species of Argentina (Rosenfeldt and Galati, 2005, 2007, 2008; López and Rosenfeldt, 2015). The visible lumen content present in some of the pollen grains corresponds to the columellae, which may vary in height and may or may not have tectum, as was previously reported by Rosenfeldt and Galati (2007).

The results of this study allow us to contribute to the knowledge of this complex genus and to provide characters

for differentiation of species in this particular section, complementing the molecular and taxonomic studies.

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Table 2. Orbicule characteristics and proposed groups: species, size, surface, margin, shape, and aggregation.

	Size	Surface	Margin	Shape	Aggregations
<i>O. cinerea</i>	Homogeneous	Smooth	Smooth	Rounded - doughnut-like	Yes, but only a little
<i>O. subacaulis</i>	Homogeneous	Smooth	Smooth	Rounded - doughnut-like	Yes, in both axes
<i>O. micrantha</i>	Heterogeneous	Smooth	Lobulated	Flattened, fancy, irregular - doughnut-like	Yes, forming irregular wheels-like structures, "L" or other fancy shapes
<i>O. erythrorhiza</i>	Heterogeneous	With punctuations	Lobulated	Rounded	Yes, linear or anastomosed
<i>O. famatinae</i>	Heterogeneous	With punctuations	Smooth	Rounded, fancy	Yes, in both axes
<i>O. holosericea</i>	Heterogeneous	With punctuations	Wavy	Flattened, irregular	Yes, linear or in "L-shape"
<i>O. hypsophila</i>	Heterogeneous	With punctuations	Smooth	Rounded, oblong - doughnut-like	Yes
<i>O. nahuelhuapiensis</i>	Heterogeneous	With punctuations	Smooth	Rounded, oblong - doughnut-like	Yes, linear or anastomosed, "Y" or "L-shape"
<i>O. pycnophylla</i>	Heterogeneous	With punctuations	Smooth	Rounded - doughnut-like	Yes, forming irregular wheels-like structures
<i>O. compacta</i>	Heterogeneous	With punctuations	Lobulated	Fancy - doughnut-like	Yes, linear or anastomosed
<i>O. muscoides</i>	Heterogeneous	With punctuations	Wavy	Rounded, irregular - doughnut-like	Yes, linear or anastomosed
<i>O. squamata</i>	Heterogeneous, large difference in sizes	Smooth	Smooth	Rounded, oblong	Yes, linear or anastomosed
<i>O. valdiviensis</i>	Heterogeneous, large difference in sizes	Smooth	Smooth	Rounded, oblong, fancy	Yes, linear or anastomosed, forming irregular wheels-like structures, or other fancy shapes

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