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Pollen morphology of *Senecio bergii* (Asteraceae), with special attention to the mesoaperture

Morfología polínica de *Senecio bergii* (Asteraceae), con especial referencia a la mesoapertura

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Abstract. Palynological studies contribute to understanding the taxonomy, phylogeny and ecology of the Asteraceae and other families. In this study, pollen morphology and ultrastructure of the exine of *Senecio bergii* Hieron. were studied using light, scanning and transmission electron microscopy. The pollen of this species is prolate-spheroidal, it has a *Senecioid pattern* on the exine and an apertural system composed of three apertures (ecto-, meso- and endoapertures). This pollen type is defined as tricolpororate due to the triple apertural system. This is the first description of the ultrastructure of the apertural system of the pollen of Argentine species of *Senecio*. The presence of mesoapertures and the description of the ultrastructure of the pollen of *Senecio bergii* contribute to the general knowledge of the *Senecio pollen* type, as well as to the taxonomic delimitation of species in this genus.

Keywords: *Senecio*; Pollen; Exine; Mesoaperture; Ultrastructure.

Resumen. Los estudios palinológicos contribuyen al entendimiento de la taxonomía, la filogenia y ecología de las Asteraceae y otras familias. En este trabajo, se estudió la morfología polínica y ultraestructura de la exina de *Senecio bergii* Hieron., utilizando microscopía óptica, electrónica de barrido y de transmisión. El polen de esta especie es prolado-esferoidal, presenta un patrón Seneciodeo de la exina y un sistema apertural compuesto por tres aperturas (ecto-, meso- y endoapertura). Este sistema apertural triple permite definir a este tipo polínico como 3-colporado. Este trabajo constituye la primera descripción de la ultraestructura del sistema apertural del polen en especies argentinas de *Senecio*. La presencia de mesoapertura en el polen de *Senecio bergii* contribuye al conocimiento general del tipo polínico *Senecio* así como también a la delimitación taxonómica de especies del género.

Palabras clave: *Senecio*; Polen; Exina; Mesoapertura; Ultraestructura.

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INTRODUCTION

The Asteraceae family is the most numerous of the Angiosperms, with approximately 23600 species. This family constitutes 8% of the flowering plants, and it is found in all continents except for Antarctica (Bremer, 1994; Panero & Funk, 2008).

According to the observations of numerous authors, palynological studies provide an excellent set of characters that complement traditional morphological studies, and contribute to the understanding of the taxonomy, phylogeny and ecology of the Asteraceae (Skvarla & Larson, 1965; Skvarla & Turner, 1966; Skvarla et al., 1977; Bolick, 1978; Tellería & Katinas, 2005; Wortley et al., 2007; Pereira Coutinho & Dinis, 2007; Pereira Coutinho et al., 2011; Tellería, 2012; Via do Pico & Dematteis, 2013).

The main palynological variables that have been studied are characteristics of the surface of the wall of the pollen grains. Skvarla et al. (1977) recognised three types of pollen in this family, psilate, echinate and lophate. Moreover, Skvarla & Turner (1966) studied the ultrastructure of the exine with transmission electron microscopy and they defined four main groups: Helianthoid, Senecioid, Arctotoid and Anthemoid. In particular, for the tribe Senecioneae they recognized the Helianthoid and Senecioid ultrastructural patterns, and a similar one found in the Anthemideae.

The complexity of the Asteraceae pollen often includes the characteristics of the apertural system, an issue widely discussed by several authors because of the different techniques of observation used and the heterogeneity of this taxonomic group (Tormo Molina & Ubera Jiménez, 1995).

Erdtman (1966) defined the Asteraceae pollen as tricolporate, with more or less lalongate ora. Dimon (1971) described an apertural system composed of an ectoaperture that includes a tectum, a mesoaperture at the level of the foot layer, and an endoaperture limited to the endexine.

In particular, the existence and origin of the mesoaperture (or middle aperture) has lead to doubts and discrepancies between different authors. Vasanthy (1978) suggested the use of the prefixes ecto-, meso-, and endo- to indicate the relative position of each of the apertures without taking into account which exine layers they were composed of. Tormo Molina & Ubera Jiménez (1990) defined the mesoaperture as an aperture situated between the ecto and the endoaperture, and they considered that it includes the foot layer and the outer layer of the endexine in the tribe Cardueae.

Different tribes of the Asteraceae have been studied in order to illustrate the apertural system in this family. In Lactuceae three aperture systems were described: (1) an external aperture that affected a very thin part of the foot layer, (2) a middle aperture composed of the external surface of the endexine, and (3) an internal aperture composed of the internal part of the endexine. The term colporate was used in this paper due to the existence of a triple aperture (El-Ghazaly, 1980). In later studies on the same tribe it was shown that the mesoaperture is located in the foot layer and has the form of a short lolongate colpus or pore (Blackmore, 1982). The mesoaperture may also be lalongate, as in the tribe Dicomeae (Pereira Coutinho et al., 2012). In some species in the tribes Gnaphalieae, Cardueae and Inuleae the apertural system is composed of (1) an ectoaperture that includes the tectal complex, (2) a mesoaperture that disrupts the foot layer and the external part of the endexine, and (3) an endoaperture that breaks up the internal layer of the endexine (Tormo Molina & Ubera Jiménez, 1990; Pereira Coutinho & Dinis, 2007; Pereira Coutinho & Dinis, 2009).

Osman (2011) defined the *Senecio* pollen type for the tribe Senecioneae as tricolpororate without mentioning the presence of the mesoaperture.

In the *Senecio* genus the mesoaperture has been observed in some species from the Iberian Peninsula (Blanca et al., 1991; Pérez Romero et al., 2003), but in spite of this some authors define this pollen type as tricolporate.

In Argentina, this genus has been studied by Markgraf & D'Antoni (1978) and Naab (2004) without any mention of the presence of a mesoaperture.

The aim of this study was to study the morphology and ultrastructure of the pollen grains of *Senecio bergii* Hieron. with special reference to the apertural system and the exine layers that are involved in its formation.

MATERIALS AND METHODS

Senecio bergii, an endemic species from the Atlantic coast of Argentina, was used to describe the ultrastructure of the apertural system of the pollen of this species.

Light microscopy (LM). The pollen was obtained from specimens deposited in the herbarium of the Departamento de Biología, Bioquímica y Farmacia in the Universidad Nacional del Sur (BBB). Closed flowers from different capitula were selected and conserved in 7% glacial acetic acid. The pollen grains were then acetolyzed according to Erdtman's technique (1960), mounted in gelatin-glycerin and observed using a Carl Zeiss Primo Star iLED optical microscope. Two specimens from different populations were studied, and measurements were taken from 30 grains per specimen using the Axio Vision Rel. 4.8. programme. The following characteristics were measured: polar axis, equatorial diameter, maximum width and length of the colpus, dimensions of the spines, distance between spines, and thickness of the exine and the cavea (the latter in transverse section). Whereas the polar diameter was measured in a meridian optical section, the equatorial diameter was measured in an equatorial optical section and in both cases the spines were excluded (Tormo et al., 1986). The measurements were taken with an X100 oil immersion objective. The results are shown as ranges, means and standard deviations.

Scanning electron microscopy (SEM). The pollen grains, acetolyzed and conserved in distilled water, were sonicated for 90 minutes in an ultrasonic bath at low frequency to eliminate the remaining impurities. They were then washed several times in an increasing series of alcohols (50%, 70%, 96% and 100%), mounted on a cover slip fixed to the support of the SEM and air dried. They were metalized in gold and observed under a microscope LEO model EVO XVP.

Transmission electron microscopy (TEM). Samples that had been acetolyzed, sonicated and conserved in distilled water were used for observations under TEM. Following the technique of Hayat (2000), 2% OsO4 was used and dehydration was carried out with a gradient of ethyl alcohol/ distilled water up to 96% alcohol. Thereafter, the dehydration was completed with acetone/ethyl alcohol (50 % v/v) until 100% acetone was reached. The sections obtained with an ultramicrotome (LKB, 2088) were contrasted with uranyl acetate and lead citrate. The images were obtained using a TEM (JEOL 100CXII) with a voltage of 80 kV.

The layers of the exine proposed by Faegri and Iversen (1964) and the terminology of Punt et al. (2007) were used.

Specimens examined

Long 485. *Senecio bergii* Hieron. Argentina. Prov. Buenos Aires. Pdo de Necochea. Quequén. Leg. Long. 25/11/1994.

Montes 82. *Senecio bergii* Hieron. Argentina. Buenos Aires. Pdo de Coronel Rosales. Pehuen Co. Leg. Montes. 17/11/2012.

RESULTS

Size and shape. The *Senecio bergii* pollen grain was monad, isopolar and radiosymmetric. It has a prolate-spheroidal shape or more rarely suboblate. The studied material has a P/E of 1.01 ± 0.10. It was circular in the meridional transverse section (Fig. 1A), and trilobed in the equatorial transverse section (Fig. 1B).

Characteristics of the exine. The exine was tectate and echinate. The spines were conical, with a solid upper part with a canal or subapical cavity, and perforations in the lower part (Fig. 2). They were 3.24 µm long, the width of the base was 3.97 µm and they were less than 13 µm apart (Table 1). The spines were of the structural type as the tectal columellae were closely related (Fig. 3). The tectum had ovate or elliptical, rounded perforations (Fig. 2). The exine was thick and had a wide cavea (Fig. 1B, Fig. 3). The tectal columellae were simple or branched (Fig. 3). They might either have lateral expansions in the distal and basal part, united to the lateral expansions of the adjacent columellae be free (Fig. 3). The foot layer was 0.73 µm thick and smooth. The endexine was a little thicker than the foot layer, measuring 1.00 µm. These pollen grains showed a Senecioid type structural wall pattern (Figs. 3 and 4).

Apertural system. The grain was tricolporate, with an apertural system that included a colpus type of ectoaperture with tapered extremities; a lolongate pore type of mesoaperture and a lalongate endoaperture, tapered at the extremes, and a constriction in the centre (Fig. 5), or none. The colpi were not attached at the poles and had two apocolpate and three mesocolpate zones. The ectoaperture included the ectexine (Figs. 6 and 7) and had a granulose colpus membrane (Fig. 6). The mesoaperture was between the foot layer and the distal part of the endexine (Fig. 7), and its limits were partly covered by the edges of the ectoaperture (Fig. 6). The endoaperture was found at the level of the proximal part of the endexine (Fig. 7).

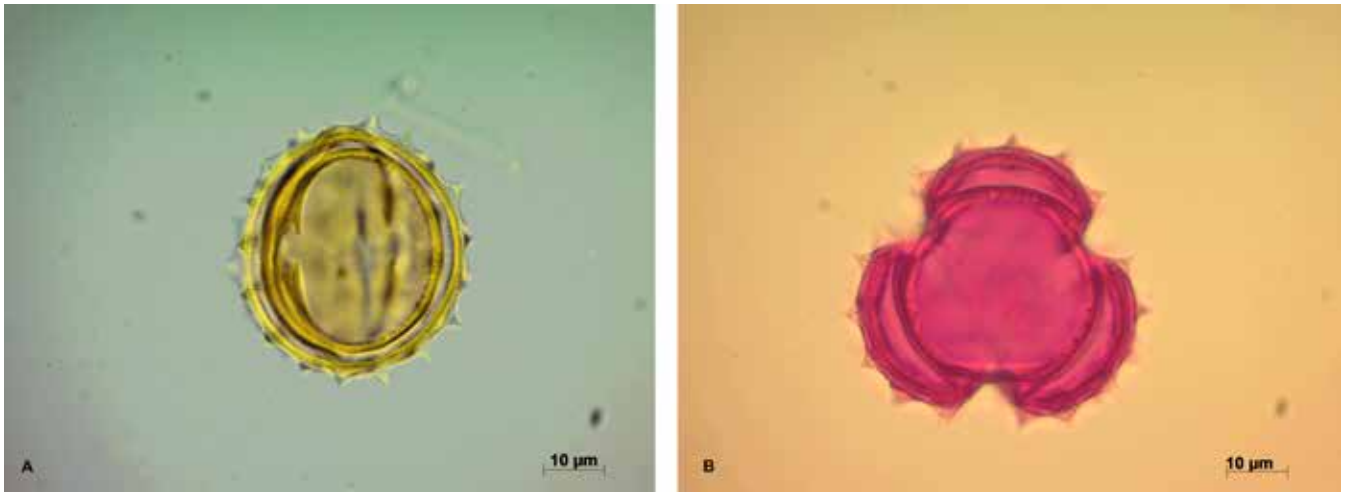

Fig. 1. (A) LM. *Senecio bergii* pollen grain, equatorial view. (B) *Senecio bergii* pollen grain, polar view.
Fig. 1. (A) Microscopía óptica. Grano de polen de *Senecio bergii*, vista ecuatorial. (B) vista polar.

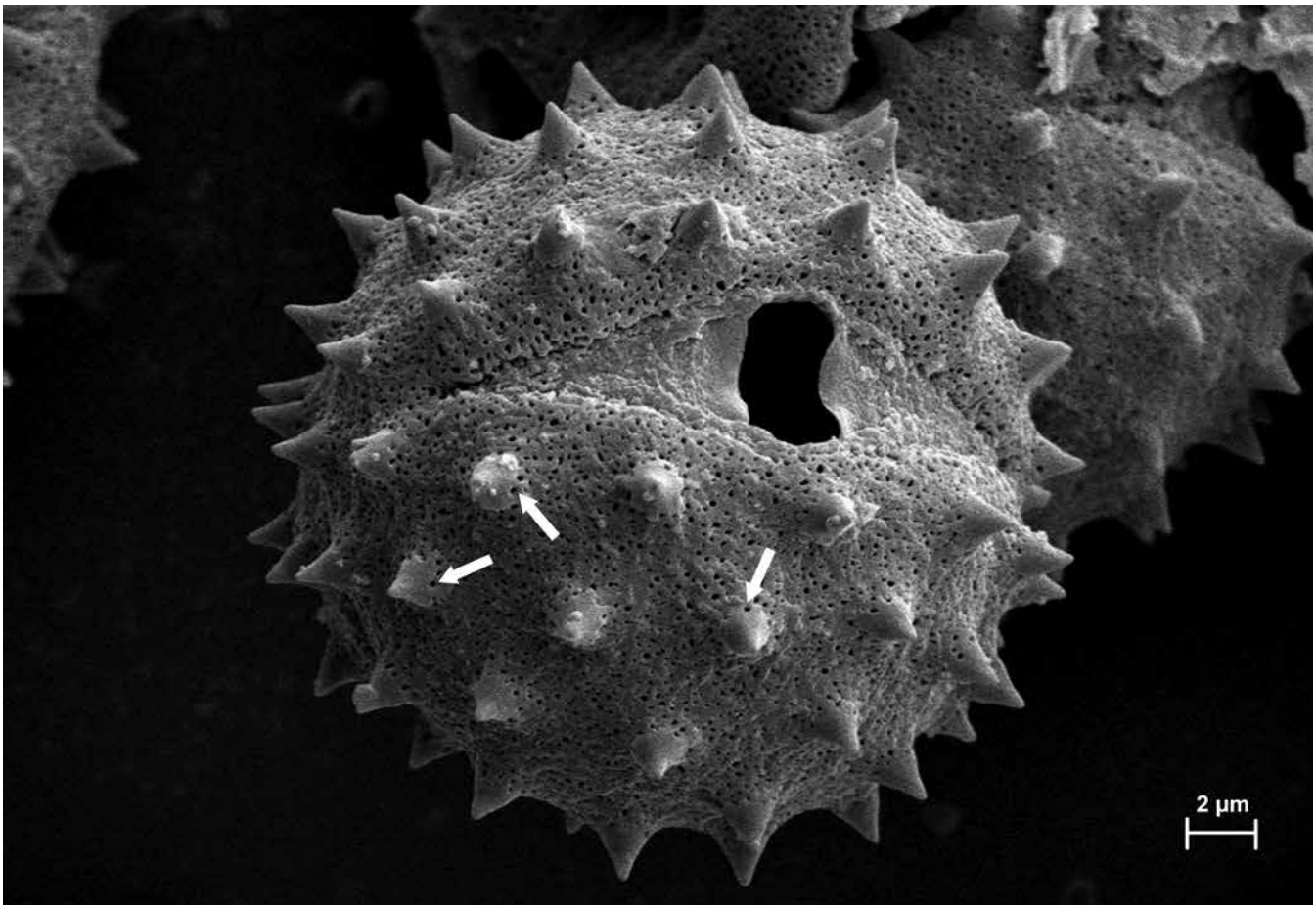

Fig. 2. SEM. Micrograph of exine sculpture. The arrow indicates the perforations in the base of the spine.
Fig. 2. Microscopía electrónica de barrido. Micrografía de la escultura de la exina. Las flechas indican las perforaciones en la base de la espina.

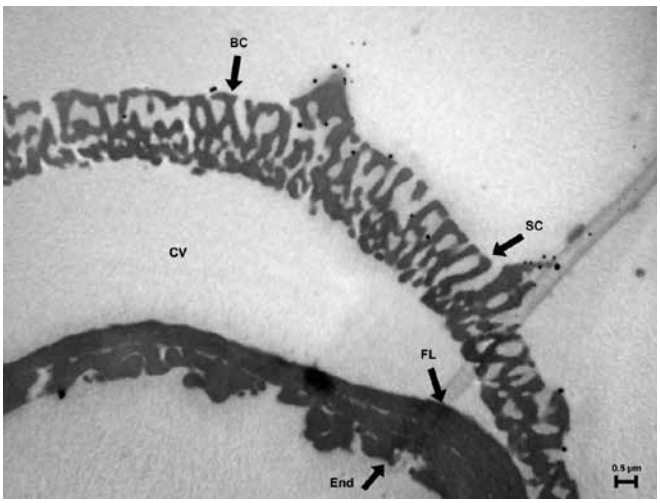

Fig. 3. TEM. Micrograph showing the exine structure. CV: cavea. BC: branched columellae. SC: simple columellae. FL: foot layer. End: endexina.
Fig. 3. Microscopía electrónica de transmisión. Micrografía de la estructura de la exina. CV: cávea. BC: columela ramificada. SC: columela simple. FL: base. End: endexina.

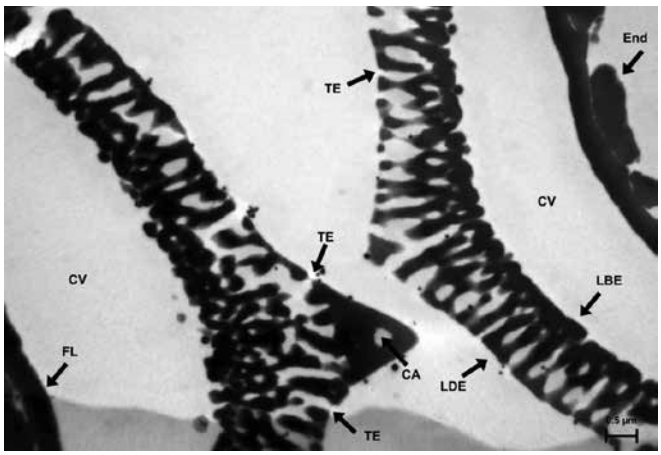

Fig. 4. TEM. Micrograph of a section of the exine. CA: subapical canal of the spine. CV: cavea. LBE: lateral basal expansions of the columella. LDE: lateral distal expansions of the columella. End: endexine. FL: foot layer. TE: tectum.
Fig. 4. Microscopía electrónica de transmisión. Micrografía de una sección de la exina. CA: canal subapical de la espina. CV: cávea. LBE: expansiones laterales basales de la columela. LDE: expansiones laterales distales de la columela. End: endexina. FL: base. TE: téctum.

Table 1. Range of values, means and standard deviations of the studied characters.
Tabla 1. Rango de valores, promedios y desvíos estándar de los caracteres estudiados.

Characters	Range (µm)	X ± DS
Polar axis	36.3 - 50.22	42.14 ± 2.50
Equatorial diameter	36.06 - 52.43	41.83 ± 3.07
Thickness of the exine	4.20 - 7.86	5.49 ± 1.09
Thickness of the cavea	1.51 - 5.62	3.12 ± 0.71
Length of the spine	1.92 - 4.44	3.24 ± 0.54
Base of the spine	2.31 - 5.33	3.97 ± 0.66
Distance between spines	6.17 - 12.89	9.02 ± 1.32
Length of the colpus	27 - 38.13	30.55 ± 2.88
Width of the colpus	2.01 - 6.39	3.59 ± 0.96

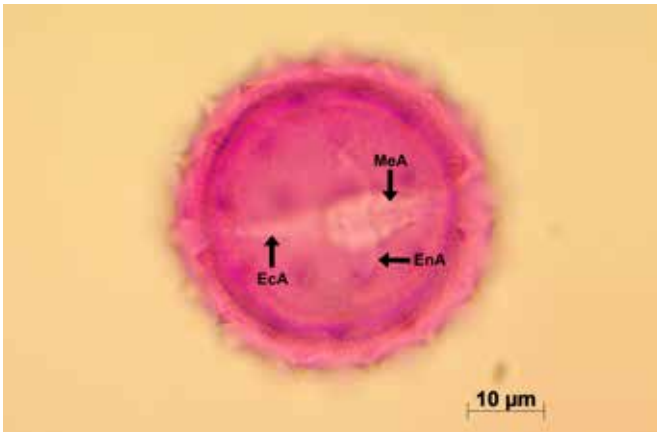

Fig. 5. LM. Apertural area. EcA: ectoaperture. MeA: mesoaperture. EnA: endoaperture.
Fig. 5. Microscopía óptica. Área apertural. EcA: ectoapertura. MeA: mesoapertura. EnA: endoapertura.

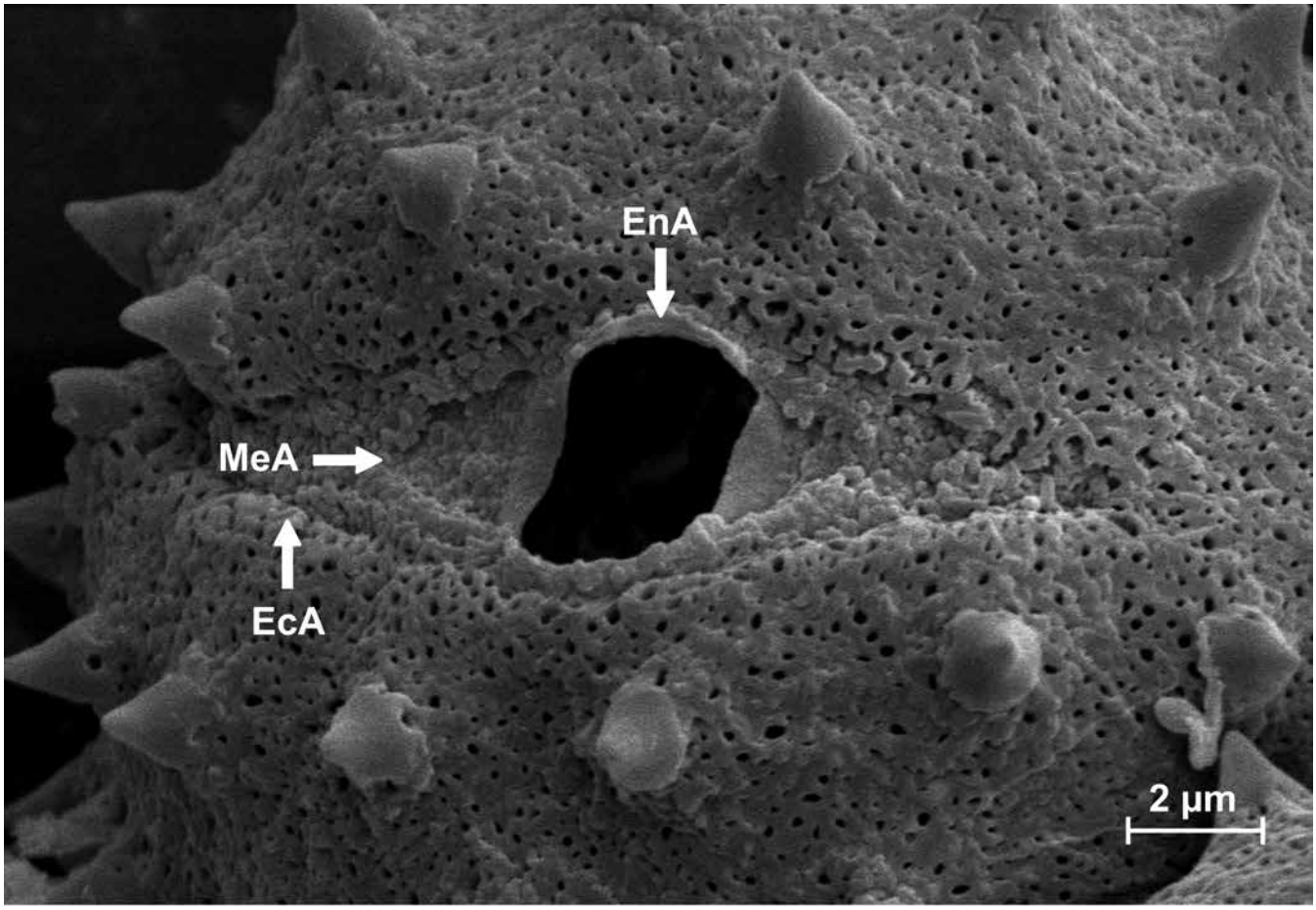

Fig. 6. SEM. Apertural area. EcA: ectoaperture. MeA: mesoaperture. EnA: endoaperture.
Fig. 6. Microscopía electrónica de barrido. Área apertural. EcA: ectoapertura. MeA: mesoapertura. EnA: endoapertura.

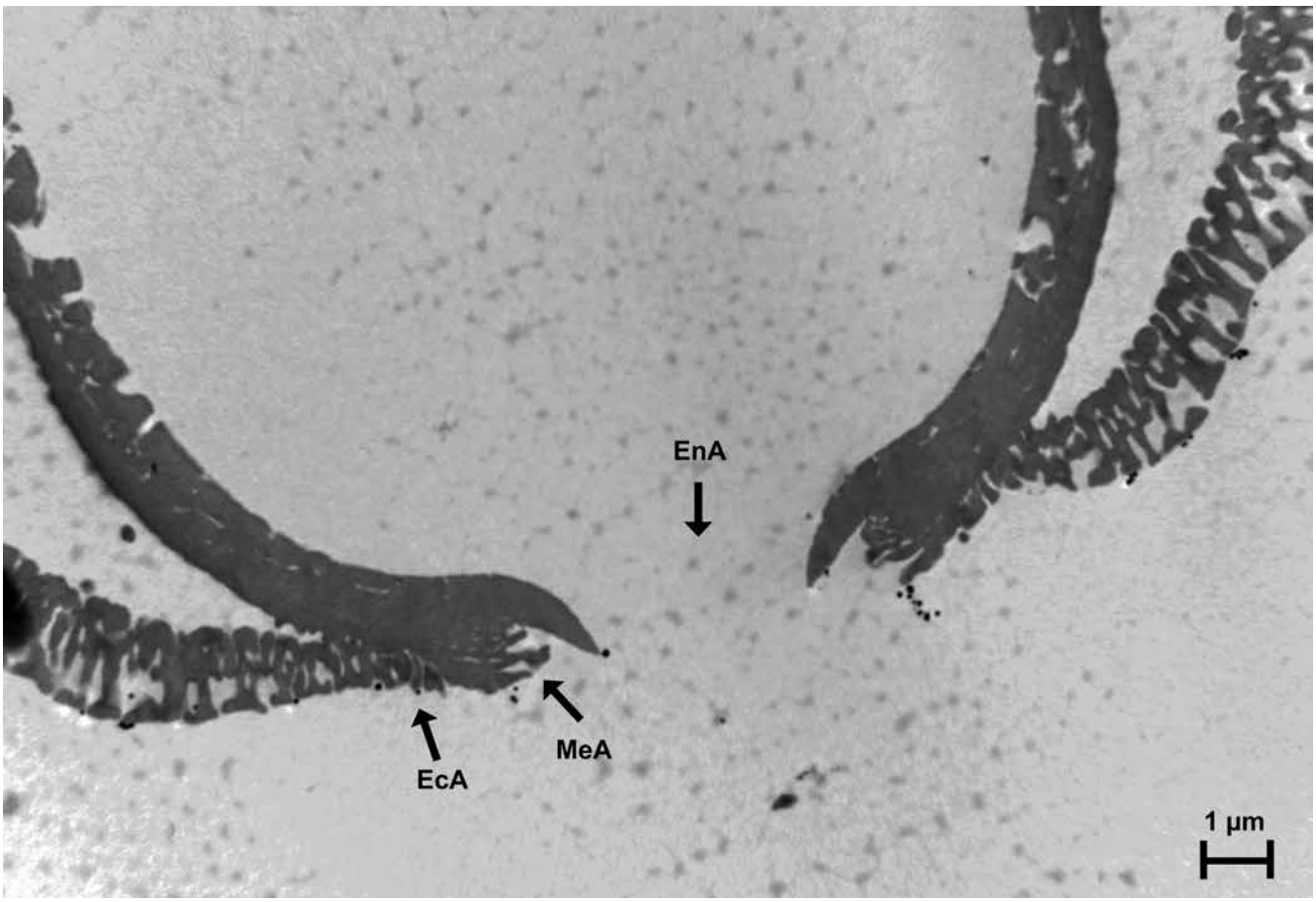

Fig. 7. MET. Apertural area. EcA: ectoaperture. MeA: mesoaperture. EnA: endoaperture.
Fig. 7. Microscopía electrónica de transmisión. Área apertural. EcA: ectoapertura. MeA: mesoapertura. EnA: endoapertura.

DISCUSSION

The *Senecio* pollen type has been described by several authors (Tormo Molina, 1985; Blanca et al., 1991; Osman, 2011). The *Senecio bergii* pollen conforms to that observed by these authors in general terms, but it differs in the size of the grain and in the characteristics of the apertural system, the number of apertures and their ultrastructure. The pollen of this species is mainly prolate-spheroidal as proposed by Osman (2011) for other species of *Senecio*.

Erdtman (1966) classified the pollen grains in six classes according to the largest dimension of one of their axes; following this criterion, the pollen grains of *Senecio bergii* fall within the medium and large sizes. These results are in partial agreement with those obtained by Tormo et al. (1985) for the *Senecio* genus who described this type of pollen as medium sized.

The exine of the grain is defined as the Senecioid type on account of the ultrastructure which shows cavea, a single layer of tectal columellae, a thin foot layer and the absence of internal foramina (Skvarla & Turner, 1966; Bain & Walker, 1995; Pereira Coutinho et al., 2011).

The spines are of the structural type, like those observed by Pérez Romero et al. (2003) in *Senecio pyrenaicus* L. from the Iberian Peninsula.

The issue concerning the pollen apertures of the Asteraceae has been treated at length. Although the mesoaperture was described by Dimon (1971) based on observations under light microscopy in a large group of Asteraceae, it is not an easy structure to see using this technique (Tormo Molina & Ubera Jiménez, 1995) and, on the other hand, it might be confused with structures such as the vestibulum and the fastigium (Thanikaimoni, 1978). Also, this structure can only be seen with difficulty unless there is good contrast in the image. Sometimes the fresh pollen in this family has a high oil content and, in this species in particular, numerous inorganic particles from its natural habitat are stuck to the surface of the pollen grain. Even if acetolysis is carried out for a long time, it is difficult to obtain samples without residues. Regarding this, sonification of the pollen helps to clean it and improve the subsequent observations.

The presence of the mesoaperture in *Senecio bergii* was confirmed in all grains observed. Moreover, the shape of the lolongate pore was confirmed using different microscopic

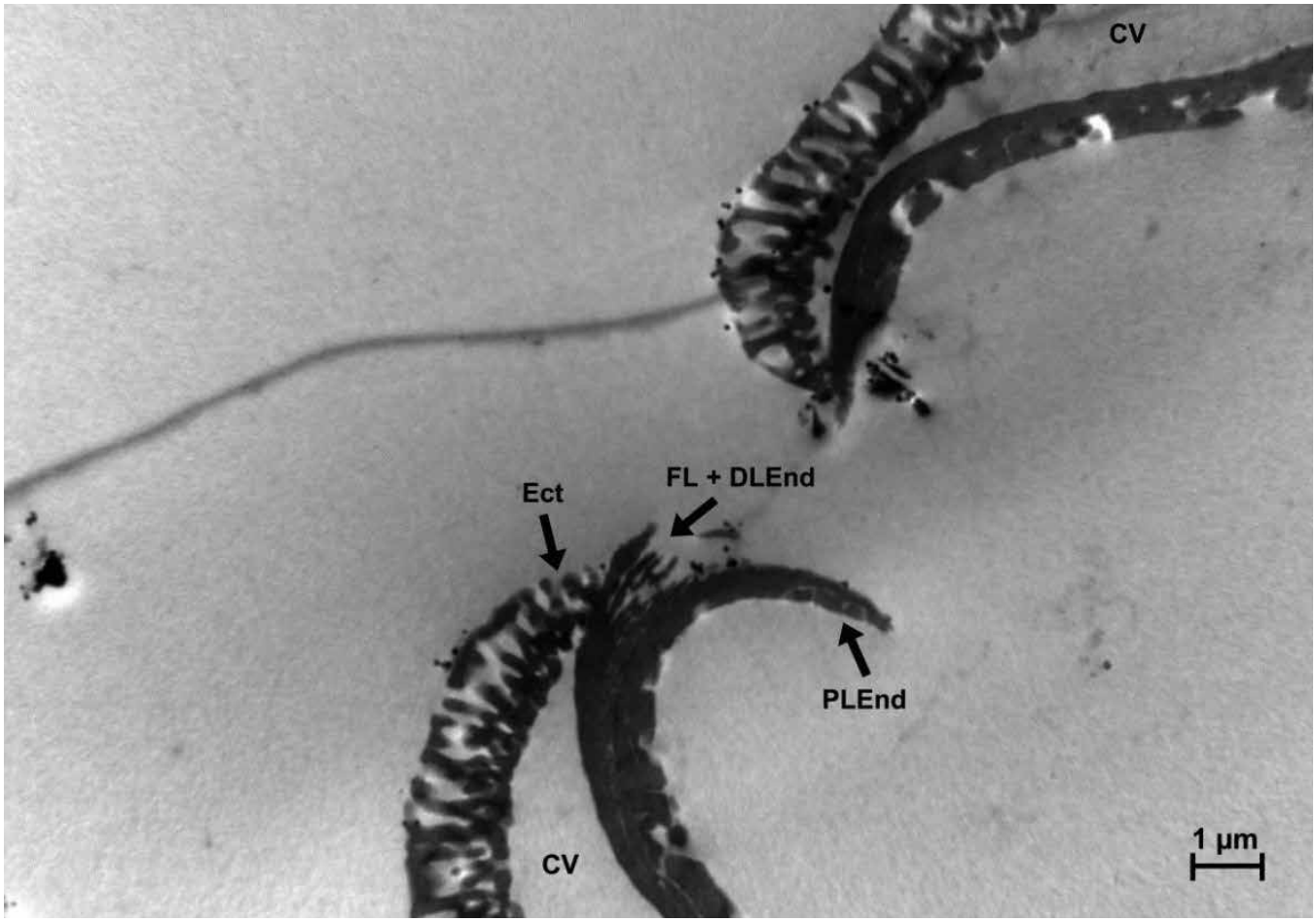

Fig. 8. MET. Apertural area. CV: cavea. Ect: ectexine. FL + DLEnd: foot layer + distal layer of the endexine. PLEnd: proximal layer of the endexine.
Fig. 8. Microscopía electrónica de transmisión. Área apertural. CV: cávea. Ect: ectexina. FL + DLEnd: base + capa distal de la endexina. PLEnd: capa proximal de la endexina.

techniques (light, and both scanning and transmission electron microscopy) in agreement with that observed by Blanca et al. (1991) for European species of *Senecio*.

The three apertures were identified using LM: an elongated aperture in the longitudinal direction, an apparent aperture of the lolongate pore type and a more internal one, elongated with tapered ends and lalongate. The relative location of the internal apertures (lolongate and lalongate) was not clearly observed and only the colpus type of ectoaperture could be confirmed. The presence of the mesoaperture and the relative position of the apertures were confirmed by using SEM. However, as in the case of LM, the layers of the exine involved in the formation of apertures could not be identified. In order to resolve this dilemma, TEM was used. Therefore the confirmation and accurate delimitation of the mesoaperture arose from utilization of the three techniques, coinciding with that performed by various authors for different tribes of the Asteraceae (Tormo & Ubera Jimenez, 1990; Pereira Coutinho & Dinis, 2007; Pereira Coutinho & Dinis, 2009; Pereira Coutinho et al., 2011; Pereira Coutinho et al., 2012 and Wang et al., 2013).

In regard to the apertural system of *Senecio bergii*, it is appropriate to define this pollen type as tricolpororate. The apertures are composite, integrated by (1) an ectoaperture in the form of a colpus that affects the ectexine (except in the foot layer); (2) a lolongate mesoaperture that includes the foot layer and the external or distal layer of the endexine, and (3) a lalongate endoaperture that affects the internal or proximal layer. This is in contrast to studies on *Senecio* species undertaken by other authors, who considered that the formation of the mesoaperture only includes the foot layer (Blanca et al., 1991).

In this study the middle aperture and the layers involved in its formation are recorded and described for the first time in an Argentine species of *Senecio*. The pollen morphology and details of the ultrastructure of the exine are described.

The presence of the mesoaperture in the *Senecio bergii* pollen contributes to the general knowledge of the *Senecio* pollen type. Moreover, it will be of great importance in the taxo-

nomic delimitation of species in this genus, and in the phylogenetic studies of the Xerosenecio series which are currently being studied in our research group.

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