Phytotaxa 244 (1): 001–025
http://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.244.1.1

Floral Microcharacters in South American species of *Senecio* s.str. (Asteraceae) with considerations on the circumscription of this genus

LUCIANA SALOMÓN[1, 2], MARCELO P. HERNÁNDEZ[3], DANIEL A. GIULIANO[3] & SUSANA E. FREIRE[1]
[1]*Instituto de Botánica Darwinion, Casilla de Correo 22, Labardén 200, San Isidro (B1642HYD), Buenos Aires, Argentina.*
[2]*Author for correspondence (lsalomon@darwin.edu.ar).*
[3]*Área de Botánica, Departamento de Ciencias Biológicas, Facultad de Ciencias Agrarias y Forestales, Universidad Nacional de La Plata, Avda. 60 entre 116 y 118, 1900 La Plata, Argentina.*

Abstract

Senecio L. s.str. is the largest genus in the tribe Senecioneae (Asteraceae) and it has been commonly characterized by its truncate, penicillate stylar tips, separated stigmatic lines, and stamens usually with ecaudate anther bases and balusterform filament collar. A micromorphological study was carried out to determine if South American species of *Senecio* s.str. present these diagnostic micromorphological characters, as a contribution towards a circumscription of this genus supported by morphology. The study included 72 South American *Senecio* species from eight sections and 16 series, as well as species from six other genera of subtribe Senecioninae (*Delairea, Dendrophorbium*, *Dendrosenecio*, *Graphistylis*, *Lomanthus*, *Pentacalia*), three genera of subtribe Tussilagininae (*Aequatorium*, *Nordenstamia*, *Roldana*), and one of subtribe Brachyglottidinae (*Acrisione*). The studied characters include: style branches (stigmatic surface, and apices), anthers (filament collar, bases, and appendages), as well as pollen features (shape, size, and sculpture). Analyses of these characters suggested that *Senecio* s.str. can be defined only by the presence of balusterform filament collars, which are present in 61 out of the 72 studied *Senecio* s.str. species (vs. cylindrical collar in remaining species). The genera *Graphistylis* and *Delairea* also show this trait, however, *Graphistylis* presents some microcharacters (e.g. "banded" stigmatic surface) that are rather infrequently found in *Senecio* s.str. *Senecio grandis* showed cylindrical collars and sagittate anther bases and should be excluded from the genus. The other microcharacters analyzed appeared to be taxonomically uninformative, since their predominant states were found in *Senecio* s.str. as well as in other genera of Senecioneae.

Key Words: *Acrisione, Aequatorium,* anthers, *Delairea, Dendrophorbium, Dendrosenecio, Graphistylis, Lomanthus, Nordenstamia, Pentacalia,* pollen, *Roldana, Senecio*, stigma, taxonomy

Introduction

The variable generic and sectional concepts applied by different authors to *Senecio* Linnaeus (Asteraceae, Senecioneae) have long been recognized as a major taxonomic problem in the genus. According to Cabrera (1949, 1957, 1985) and Jeffrey *et al.* (1977), *Senecio* s.l. comprises ca. 3000 species of cosmopolitan distribution, with a high diversity in mountainous areas and deserts of America, Africa, and Asia, being scarcely represented in the wet tropics. On the contrary, several authors have removed numerous species from *Senecio* s.l. and placed them in new genera, or raised to the genus rank previously recognized sections within *Senecio* s.l., e.g. *Aequatorium*, *Aetheolaena*, and *Dendrosenecio* (Robinson & Brettell 1973a, 1973b, 1973c, Robinson 1974, Nordenstam 1978, Cuatrecasas 1981, Jeffrey & Chen 1984, Jeffrey 1986, 1992, Nordenstam *et al.* 2009). Most of the new taxa were established on the basis of micromorphological characters, such as the configuration of the endothecial cells in the filament collar of anthers, the distribution of the stigmatic area on the style branches, the presence of calcium oxalate crystals in the ovary, and the structure of the carpopodium cells (Wetter 1983, Vincent 1996). As circumscribed by Nordenstam (2007), the genus *Senecio* s.str. includes at present about 1250 species of cosmopolitan distribution, distinguished by its style branches truncate with short sweeping hairs, separated stigmatic lines, and stamens with ecaudate anther bases and a balusterform filament collar (Nordenstam 2007). On the basis of molecular studies, Pelser *et al.* (2007) proposed a new delimitation of *Senecio* containing ca. 1000 species distinguished mainly by style tips truncate with short sweeping-hairs, sometimes with a median hair pencil. In this new circumscription, species of six genera i.e. *Aetheolaena* Cassini, *Culcitium*

Accepted by Alexander Sennikov: 17 Dec. 2015; published: 15 Jan. 2016

Humboldt & Bonpland, *Hasteola* Rafinesque, *Iocenes* B. Nordenstam, *Lasiocephalus* Willdenow ex Schlechtendal, and *Robinsonia* Candolle, were transferred to *Senecio*, whereas eight species or species assemblages (four of them from South America, i.e. *Senecio arnaldii* Cabrera, *S. otites* Kunze ex Candolle, *S. ayopayensis* Cuatrecasas-*S. subnemoralis* Dusén group and *S. adamantinus* Bongard-*S. hemmendorffii* Malme-*S. stigophlebius* Baker group) formerly placed in *Senecio* s.l. were removed from this genus.

South America is the most diverse area of *Senecio* with about 500 species, followed by Africa with approximately 350 species (Bremer 1994). South American species have played an important role in the early taxonomic history of *Senecio*, with several relevant taxonomic and floristic contributions made by Cabrera (1949, 1954, 1957, 1985), Cuatrecasas (1950, 1951), Vision & Dillon (1996), Cabrera *et al.* (1999), Beltrán *et al.* (2007), Cabrera & Freire (2009), and Freire *et al.* (2014).

The objective of this study was to determine if *Senecio* s.str. presents micromorphological characters that could be considered diagnostic, as a contribution to define morphologically the circumscription of *Senecio* s.str. suggested by Pelser *et al.* (2007) based upon molecular analyses. To accomplish this, we examined several microcharacters, such as style branches (stigmatic surface, style-branch apices), anthers (filament collar, anther bases, anther appendages), and pollen (shape, size and sculpture) in 72 South American species of *Senecio* (including *S. adamantinus, S. hemmendorffii*, *S. otites*), which were chosen because of the high number of species they represent within *Senecio*, and ten genera previously included in *Senecio.*

Materials & Methods

Studied Material

Microcharacters of styles, anthers, and pollen were analyzed for a total of 72 South American *Senecio* species from eight sections and 16 series, representing seven of 16 of the Andean sections according to Cuatrecasas (1951), 29 of 36 southern South American sections according to Cabrera (1939, 1949, 1957, 1985) and Cabrera *et al.* (1999) (*S.* sect. *Delairea* as *Delairea*; *S.* sect. *Dichroa* as *Graphistylis*; *S.* sect. *Myriocephalus* as *Dendrophorbium*) and 17 of 18 series according to Cabrera (1985) and Cabrera *et al.* (1999) (*S.* ser. *Myriocephali* as *Dendrophorbium*); 26 of these species were included in molecular studies (Pelser *et al.* 2007). The type species of each infrageneric taxon (except for *S.* sect. *Cacaliastrum*, *S.* sect. *Latiflori* and *S.* sect. *Paranenses*) was included in the study; additional species were analyzed for the most species-rich taxa (i.e. *S.* sect. *Senecio*). In order to examine the taxonomic value of the characters, ten species, six of them belonging to other genera of subtribe Senecioninae (*Delairea, Dendrophorbium*, *Dendrosenecio*, *Graphistylis*, *Lomanthus*, *Pentacalia*), three belonging to genera of subtribe Tussilagininae (*Aequatorium*, *Nordenstamia*, *Roldana*), and one of subtribe Brachyglottidinae (*Acrisione*), were also sampled. The study was based on herbarium material from CTES, CORD, LP, MO, NY, SI (abbreviations according to Thiers 2016). A list of studied genera, infrageneric taxa, species with their respective authors, and examined specimens is provided in Table 1.

Styles & Anthers

Mature, fully developed disc florets (5–10 florets per specimen) were selected for the analysis. Herbarium samples were rehydrated in warm soapy water and fixed in FAA. Anthers and styles were dissected, clarified with diluted chlorine 5% and stained with Safranin 80%, and samples were mounted in glycerin 60%. Observations were done with LM (Light Microscope) Nikon Microphot-FXA, equipped with a photographic camera, and Gemalux equipped with a photographic camera PAL CCD with Hyper Media Center software.

Scanning Electron Microscopy observations with SEM (scanning electron microscopy) were done on selected styles from the material. For SEM observations, samples were rehydrated with warm soapy water and fixed with FAA. Disc florets were dehydrated in a graded series of ethanol and criticalpoint-dried with Electron Microscopy Sciences-EMS 850. Dried samples were partially dissected, mounted on stubs, sputter-coated with gold/palladium (Mini Sputter SC 7620) and observed with SEM (PHILIPS XL30).

Pollen

Immature disc florets (5–20 florets per specimen) were selected for acetolysis. The acetolysis was performed following the protocol presented by Erdtman (1960) with some modifications. The samples were mounted in semi-permanent medium (distilled water, gelatin, glycerin, and phenol). Observations were done with LM (Light Microscope) Nikon Microphot-FXA, equipped with a photographic camera.

TABLE 1. Studied genera, infrageneric taxa, species, and examined specimens.

Genus	*Section*	*Series*	*Species*	*Specimen [Collector & Site (herbarium)]*
Acrisione			*A. denticulata* (Hook. & Arn.) B. Nordenstam	Gentili in 1973. Neuquén, Argentina (SI)
Aequatorium			*A. polygonoides* (Cuatrec.) B. Nordenstam	Cuatrecasas 27678. Tolima, Colombia (US)
Delairea			*D. odorata* Lemaire (= *S. scandens* DC., non D. Don)	Cabrera 329. Buenos Aires, Argentina (LP)
Dendrophorbium			*D. catharinense* (Dusén ex Cabrera) C. Jeffrey	Pérez Moreau in 1937. Misiones, Argentina (LP)
Dendrosenecio			*D. johnstonii* (Oliver) B. Nordenstam subsp. *cottonii* (Hutchinson & Taylor) B. Nordenstam	Greenway 3772. Kilimanjaro, Tanzania (US)
Graphistylis			*G. organensis* (Casaretto) B. Nordenstam	Cabrera 12223. Río de Janeiro, Brazil (LP)
Lomanthus			*L. bangii* (Rusby) B. Nordenstam & Pelser	Beck 26229. La Paz, Bolivia (SI)
Nordenstamia			*N. fabrisii* (Cabrera) B. Nordenstam	Sleumer 3848. Salta, Argentina (SI)
Pentacalia			*P. epiphytica* (Kuntze) Cuatrecasas	Cabrera 26439. Jujuy, Argentina (SI)
Roldana			*R. petasitis* (Sims) H. Robinson & Brettell	Molina 18373. Honduras (US)
Senecio	*Acanthifolii* Cabrera		*S. acanthifolius* Hombron & Jacquinot	Biganzoli 769. Tierra del Fuego, Argentina (SI)
	Adamantini Cabrera		*S. adamantinus* Bongard	Occhioni in 1940. Minas Gerais, Brazil (LP)
	Aetheolaena (Cassini) O.Hoffmann		*S. imbaburensis* Sklenář & Marhold	Cazalet 5775. Imbabura, Ecuador (NY)
			S. involucratus (Kunth) Candolle	Rimbach 78. Riobamba, Ecuador (MO)
			S. lingulatus (Schlechtendal) Cuatrecasas	Balslev 69122. Cotopaxi, Ecuador (MO)
			S. puracensis (Cuatrecasas) Cuatrecasas	Sneidern 1943. Cauca, Colombia (NY)
			S. quitensis Cuatrecasas	Mena C 47. Pichincha, Ecuador (MO)

...Continued on next page

TABLE 1. (Continued)

Genus	*Section*	*Series*	*Species*	*Specimen [Collector & Site (herbarium)]*
	Cacaliastrum Cabrera		*S. grandis* Gardner	Dusén 12197. Paraná, Brazil (SI)
	Latiflori Cuatrecasas		*S. niveo-aureus* Cuatrecasas	Harriet 7351. Boyacá, Colombia (SI)
	Paranenses Cabrera		*S. hemmendorffii* Malme	Pott 6016. Bocaiuva S, Brazil (SI)
	Reflexi Cuatrecasas		*S. superandinus* (Schlechtendal) Cuatrecasas	Van der Merff 12224. Pichincha, Ecuador (MO)
	Senecio	*Andina* (Cabrera) Cabrera & S.E. Freire	*S. eriophyton* J.Rémy	Kiesling 4663. San Juan, Argentina (SI)
		Chilenses Candolle ex M.G. López, A.F. Wulff & Xifreda	*S. achalensis* Cabrera	Hunziker 8558. Córdoba, Argentina (CORD)
			S. aspericaulis J.Rémy	Ricardi 962. Talca, Chile (LP)
			S. carnosus Philippi	Cabrera 19676. Bío Bío, Chile (LP)
			S. chilensis Lessing	Zavala 131. Río Negro, Argentina (SI)
			S. eightsii Hooker & Arnott	Rodriguez 11952. Tierra del Fuego, Argentina (LP)
			S. famatinensis Cabrera	Hieronymus 684. La Rioja, Argentina (LP)
			S. farinifer Hooker & Arnott	Zöellner 6501. Maitenes, Chile (CTES)
			S. humillimus Schultz Bipontinus ex Weddell	Hunziker 10488. Jujuy, Argentina (SI)
			S. krapovickasii Cabrera	Flossdorf 82. La Rioja, Argentina (LP)
			S. leucomallus A.Gray	Rafael 33. Punta Arenas, Chile (SI)
			S. madariagae Philippi	Ricardi 349-A. Antofagasta, Chile (LP)
			S. pflanzii (Perkins) Cuatrecasas	Ceballos 560. Bolivia (SI)
			S. poeppigii Hooker & Arnott	Werdermann 1265. Volcán Llaima, Chile (SI)
			S. polyphyllus Kunze ex Candolle	Marticorena 840. Curicó, Chile (CONC)

...Continued on next page

TABLE 1. (Continued)

Genus	*Section*	*Series*	*Species*	*Specimen [Collector & Site (herbarium)]*
			S. portulacoides J.Rémy	Jiles 2122. Coquimbo, Chile (LP)
			S. potosianus Klatt	Cabrera 25268. La Paz, Bolivia (LP)
			S. pseudalmeidae Cabrera	Barros 618. Antofagasta, Chile (LP)
			S. pseudoaspericaulis Cabrera	Ezcurra 158. Neuquén, Argentina (SI)
			S. punae Cabrera	Cabrera 8842. Salta, Argentina (LP)
			S. retanensis Cabrera	Hunziker 9641. Córdoba, Argentina (CORD)
			S. segethii Philippi	Kiesling 7470. San Juan, Argentina (NY)
			S. subpubescens Cabrera	Eskuche 1599. Río Negro, Argentina (SI)
			S. triodon Philippi	Marticorena 844. Curicó, Chile (CTES)
			S. volkmannii Philippi	Kiesling 7957. San Juan, Argentina (SI)
		Columbaria (Cabrera) Cabrera & S.E. Freire	*S. calocephalus* Poeppig & Endlicher	SI 10005. Malleco, Chile (SI)
		Corymbosi (Cabrera) Cabrera	*S. brasiliensis* (Sprengel) Lessing	Burkart 28114. Entre Ríos, Argentina (SI)
			S. cuneatus Hooker f.	Inter Patagonicus 914. Santa Cruz, Argentina (SI)
			S. grisebachii Baker	J. Hunziker 11746. Entre Ríos, Argentina (SI)
			S. hieracium J.Rémy	Rentzell 14686. Río Negro, Argentina (SI)
			S. oreophyton J.Rémy	Kiesling 9501. San Juan, Argentina (SI)
		Crassicephali (Cabrera) Cabrera	*S. burkartii* Cabrera	Rodriguez 1359. Salta, Argentina (SI)
			S. hypsobates Weddell	Harriet 9380. Carchi, Ecuador (COL)
		Culcitium (Humboldt & Bonpland) Cabrera	*S. aspleniifolius* Grisebach	Salomón 203. Catamarca, Argentina (SI)

...Continued on next page

TABLE 1. (Continued)

Genus	*Section*	*Series*	*Species*	*Specimen [Collector & Site (herbarium)]*
			S. candidans Candolle	Biganzoli 458. Tierra del Fuego, Argentina (SI)
			S. candollei Weddell	Zuloaga 13162. Salta, Argentina (SI)
			S. canescens (Humboldt & Bonpland) Cuatrecasas	Ranch Hinch 1823. Peru (NY)
			S. cocuyanus (Cuatrecasas) Cuatrecasas	Cleef 5630. Boyacá, Colombia (US)
			S. comosus Schultz Bipontinus	Smith 3014. Tarma, Peru (MO)
			S. expansus Weddell	Zuloaga 14291. Salta, Argentina (SI)
			S. gilliesii Hooker & Arnott	Boelcke 15591. Mendoza, Argentina (SI)
			S. haenkeanus Cuatrecasas	Haenke 1776. Peru (NY)
			S. jarae Philippi	Kiesling 3851. Tarija, Bolivia (SI)
			S. keshua Cabrera	Zuloaga 14342. Jujuy, Argentina (SI)
			S. magellanicus Hooker & Arnott	Isern 8518. Magallanes, Chile (SI)
			S. martinensis Dusén	Tesslef 6053. Patagonia, Argentina (BAB)
			S. modestus Weddell	Solomon 12293. La Paz, Bolivia (NY)
			S. neeanus Cuatrecasas	Loza de la Cruz 305. Sajama, Bolivia (S)
			S. pavonii (Weddell) Cuatrecasas	Cerrate 2344. Bolognesi, Peru (LP)
			S. santanderensis (Cuatrecasas) Cuatrecasas	Killip 17517. Santander, Colombia (NY)
			S. serratifolius (Meyen & Walpers) Cuatrecasas	Zamalloa 1005. Peru (LP)

...Continued on next page

TABLE 1. (Continued)

Genus	*Section*	*Series*	*Species*	*Specimen [Collector & Site (herbarium)]*
		Graveolentes (Cabrera) Cabrera	*S. nutans* Schultz Bipontinus	Vuilleumier 308. La Paz, Bolivia (SI)
		Haplostichi (Philippi) Cabrera & S.E. Freire	*S. zosterifolius* Hooker & Arnott	Hollermeyer 387. Valdivia, Chile (LP)
		Hualtatini Candolle	*S. fistulosus* Poeppig ex Lessing	Cabrera 32970. Neuquén, Argentina (SI)
		Leucanthemifolii (Cabrera) Cabrera & S.E. Freire	*S. monttianus* J.Rémy	Philippi in 1875. Colchagua, Chile (SI)
		Madagascarienses Candolle	*S. madagascariensis* Poiret	Cabrera 34086. Buenos Aires, Argentina (SI)
		Metazanthi (Meyen) Cabrera & S.E. Freire	*S. subdiscoideus* Schultz Bipontinus ex Weddell	Zavala 49. Mendoza, Argentina (SI)
		Otopteri (Cabrera) Cabrera	*S. otites* Kunze ex Candolle	Gentili 435. Neuquén, Argentina (SI)
		Senecio	*S. vulgaris* Linnaeus	Hicken 236. Montevideo, Uruguay (SI)
		Websteria (Cabrera) Cabrera & S.E. Freire	*S. websteri* Hooker f.	Dudley 1121. Tierra del Fuego, Argentina (SI)
		Xerosenecio (Cabrera) Cabrera & S.E. Freire	*S. filaginoides* Candolle	Múlgura 4220. Jujuy, Argentina (SI)

Scanning Electron Microscopy observations with SEM (scanning electron microscopy) were done on selected pollen samples. Acetolyzed samples were treated with Hexamethyldisilazane (HMDS) according to the protocol presented by Brown (1993), and mounted on double-sided tape, sputter-coated with gold/palladium (Mini Sputter SC 7620) and observed with SEM (PHILIPS XL30).

Results and Discussion

Style-Branches of Disc Florets

In all species examined the style-branches are minutely papillate to papillate in the distal half (Fig. 1A) and apically truncate to subconvex. *Senecio vulgaris*, the type species of *Senecio*, has truncate stylar tips dorsally glabrous (Riva *et al.* 2009).

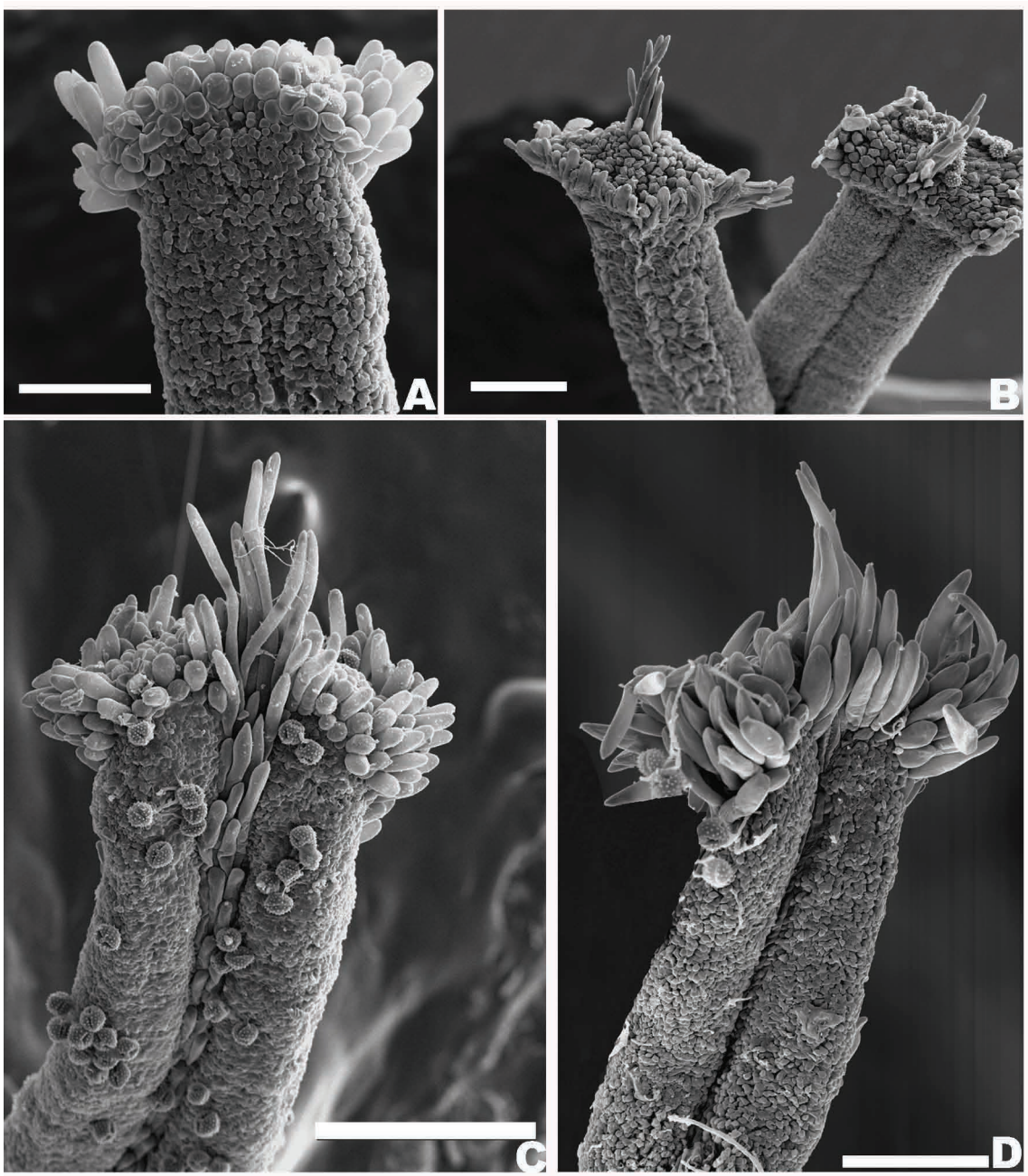


FIGURE 1. Style branches (SEM): **A, B, D.** Cleft stigmatic configuration; **C.** Banded stigmatic configuration. **A.** Style-branch showing subconvex apex surrounded by a crown of short and few hairs; **B–D.** Style-branch apex subconvex surrounded by a crown of many and differently long hairs and with apical tuft with many longer hairs. **A.** *Senecio eightsii;* **B.** *S. acanthifolius;* **C.** *S. imbaburensis;* **D.** *S. superandinus.* Scale bars = 100 μm.

Stigmatic surface of the style branches. Some authors (e.g. Robinson & Brettell 1973c, Nordenstam 1977, Jeffrey *et al.* 1977) consider the extension of the stigmatic area on the style branch to be a useful diagnostic character, e.g. the bands are fused in "cacalioid" Senecioneae and discrete or separate in non-"cacalioid" Senecioneae. According to Wetter (1983), two configurations were found in the taxa examined in the present study. The first one was referred to as a "cleft" by Wetter (1983). In a 'cleft' the stigmatic surface has a narrow, longitudinal, medial cleft along the style branches without any apparent morphological distinction between the cells of the ridges and those in the cleft (Fig. 1A, B, D). The cleft stigmatic surface is present in most of the analyzed species (Table 2). In the second configuration, referred to as "banded" by Wetter (1983), there is a conspicuous morphological distinction between the cells of the groove and the cells of the bands (Fig. 1C). This configuration is present in e.g. *Graphistylis organensis*; *Senecio* sect. *Aetheolaena*: *S. imbaburensis, S. lingulatus*; *Senecio* sect. *Reflexi*: *S. superandinus*; *Senecio* sect. *Senecio*: *S. canescens, S. comosus, S. oreophyton, S. pflanzii, S. serratifolius, S. zosterifolius*. The typical "banded" form of *S. vulgaris* (Wetter 1983) was suggested by Riva *et al.* (2009) as a distinguishing character for the genus. However, the "cleft" configuration was found in most of the species of South American *Senecio* here analyzed.

TABLE 2. Morphological features of style and anthers in *Senecio* s.str. and other genera of subtribes Brachyglottidinae, Senecioninae and Tussilagininae.

Species	Stigmatic Surface	Style-branch apices	Filament collar	Anther Bases	Anther Appendages l:w
Acrisione					
denticulata	cleft	crown of hairs	cylindrical	auriculate	2:1
Aequatorium					
polygonoides	cleft	crown of hairs	cylindrical	sagittate	2:1
Delairea					
odorata	cleft	crown of hairs	balusterform	auriculate	2:1
Dendrophorbium					
catharinense	cleft	crown of hairs	cylindrical	sagittate	2:1
Dendrosenecio					
johnstonii subsp. *cottonii*	cleft	crown of hairs	cylindrical	auriculate	2:1
Graphistylis					
organensis	banded	tuft of longer hairs	balusterform	auriculate	2:1
Lomanthus					2:1
bangii	cleft	crown of hairs	cylindrical	auriculate	
Nordenstamia					
fabrisii	cleft	tuft of longer hairs	cylindrical	auriculate	2:1
Pentacalia					
epiphytica	cleft	crown of hairs	cylindrical	sagittate	2:1
Roldana					
petasitis	cleft	crown of hairs	cylindrical	auriculate	2:1
Senecio					
Sect. *Acanthifolii*					
acanthifolius	cleft	tuft of longer hairs	balusterform	auriculate	2:1
Sect. *Adamantini*					
adamantinus	cleft	crown of hairs	balusterform	auriculate	2:1
Sect. *Aetheolaena*					
imbaburensis	banded	tuft of longer hairs	balusterform	auriculate	2:1
involucratus	cleft	tuft of longer hairs	balusterform	auriculate	2:1
lingulatus	banded	tuft of longer hairs	balusterform	auriculate	2:1
puracensis	cleft	tuft of longer hairs	balusterform	auriculate	2:1
quitensis	cleft	tuft of longer hairs	balusterform	auriculate	1:1
Sect. *Cacaliastrum*					
grandis	cleft	crown of hairs	cylindrical	sagittate	2:1
Sect. *Latiflori*					
niveo-aureus	cleft	crown of hairs	balusterform	auriculate	2:1

...Continued on next page

TABLE 2. (Continued)

Species	Stigmatic Surface	Style-branch apices	Filament collar	Anther Bases	Anther Appendages l:w
Sect. *Paranenses*					
hemmendorffii	cleft	crown of hairs	balusterform	auriculate	2:1
Sect. *Reflexi*					
superandinus	banded	tuft of longer hairs	balusterform	auriculate	2:1
Sect. *Senecio*					
achalensis	cleft	crown of hairs	balusterform	auriculate	1:1
aspericaulis	cleft	crown of hairs	cylindrical	auriculate	2:1
aspleniifolius	cleft	crown of hairs	balusterform	auriculate	2:1
brasiliensis	cleft	crown of hairs	balusterform	auriculate	2:1
burkartii	cleft	crown of hairs	cylindrical	auriculate	2:1
calocephalus	cleft	crown of hairs	cylindrical	auriculate	2:1
candidans	cleft	crown of hairs	balusterform	auriculate	1:1
candollei	cleft	crown of hairs	balusterform	auriculate	2:1
canescens	banded	crown of hairs	balusterform	auriculate	2:1
carnosus	cleft	crown of hairs	balusterform	auriculate	2:1
chilensis	cleft	crown of hairs	balusterform	auriculate	2:1
cocuyanus	cleft	tuft of longer hairs	balusterform	auriculate	2:1
comosus	banded	crown of hairs	cylindrical	rounded	1:1
cuneatus	cleft	crown of hairs	balusterform	auriculate	2:1
eightsii	cleft	crown of hairs	balusterform	auriculate	1:1
eriophyton	cleft	crown of hairs	balusterform	auriculate	2:1
expansus	cleft	crown of hairs	balusterform	auriculate	2:1
famatinensis	cleft	crown of hairs	balusterform	auriculate	2:1
farinifer	cleft	crown of hairs	balusterform	auriculate	1:1
filaginoides	cleft	crown of hairs	balusterform	auriculate	2:1
fistulosus	cleft	crown of hairs	balusterform	rounded	1:1
gilliesii	cleft	crown of hairs	balusterform	auriculate	2:1
grisebachii	cleft	crown of hairs	balusterform	auriculate	1:1
haenkeanus	cleft	crown of hairs	balusterform	auriculate	2:1
hieracium	cleft	crown of hairs	cylindrical	auriculate	2:1
humillimus	cleft	crown of hairs	balusterform	auriculate	2:1
hypsobates	cleft	crown of hairs	balusterform	auriculate	1:1
jarae	cleft	crown of hairs	balusterform	auriculate	2:1
keshua	cleft	crown of hairs	balusterform	auriculate	2:1
krapovickasii	cleft	crown of hairs	balusterform	auriculate	2:1
leucomallus	cleft	crown of hairs	balusterform	auriculate	2:1
madagascariensis	cleft	crown of hairs	balusterform	auriculate	1:1
madariagae	cleft	crown of hairs	balusterform	auriculate	1:1
magellanicus	cleft	crown of hairs	balusterform	auriculate	2:1
martinensis	cleft	crown of hairs	balusterform	auriculate	1:1
modestus	cleft	crown of hairs	balusterform	auriculate	2:1
monttianus	cleft	crown of hairs	balusterform	auriculate	1:1

...Continued on next page

TABLE 2. (Continued)

Species	Stigmatic Surface	Style-branch apices	Filament collar	Anther Bases	Anther Appendages l:w
neeanus	cleft	crown of hairs	balusterform	auriculate	2:1
nutans	cleft	crown of hairs	balusterform	auriculate	2:1
oreophyton	banded	crown of hairs	cylindrical	auriculate	2:1
otites	cleft	crown of hairs	balusterform	auriculate	2:1
pavonii	cleft	crown of hairs	balusterform	auriculate	1:1
pflanzii	banded	crown of hairs	balusterform	auriculate	2:1
poeppigii	cleft	crown of hairs	balusterform	auriculate	2:1
polyphyllus	cleft	crown of hairs	balusterform	auriculate	1:1
portulacoides	cleft	crown of hairs	balusterform	auriculate	1:1
potosianus	cleft	crown of hairs	balusterform	auriculate	2:1
pseudalmeidae	cleft	crown of hairs	balusterform	auriculate	2:1
pseudoaspericaulis	cleft	crown of hairs	cylindrical	auriculate	2:1
punae	cleft	crown of hairs	balusterform	auriculate	1:1
retanensis	cleft	crown of hairs	balusterform	auriculate	2:1
santanderensis	cleft	tuft of longer hairs	balusterform	auriculate	2:1
segethii	cleft	crown of hairs	balusterform	auriculate	2:1
serratifolius	banded	crown of hairs	balusterform	auriculate	2:1
subdiscoideus	cleft	crown of hairs	cylindrical	auriculate	2:1
subpubescens	cleft	crown of hairs	cylindrical	auriculate	1:1
triodon	cleft	crown of hairs	balusterform	auriculate	1:1
volckmannii	cleft	crown of hairs	balusterform	auriculate	2:1
vulgaris	banded	crown of hairs	balusterform	rounded	2:1
websteri	cleft	crown of hairs	cylindrical	rounded	2:1
zosterifolius	banded	crown of hairs	balusterform	rounded	1:1

Style-Branch Apices. In nearly all taxa examined in the present study, the style branches are apically papillate, and surrounded by a crown of hairs of different lengths (Fig. 1A; Table 2). However, *Graphistylis organensis, Nordenstamia fabrisii, Senecio* sect. *Acanthifolii*, *Senecio* sect. *Aetheolaena*, *Senecio* sect. *Reflexi*, *Senecio* sect. *Senecio* (*S. cocuyanus*, *S. santanderensis*), have apically a tuft with scanty or many longer hairs (Figs. 2B–D). The style branches apically truncate and penicillate have often been considered a diagnostic character in the taxonomy of *Senecio*. Consequently, many species with stylar branches convex or conical to truncate, apically with an elongated central tuft, were removed from *Senecio* into e.g. *Pseudogynoxys* (Greenman) Cabrera (Cabrera 1950), *Paragynoxys* (Cuatrecasas) Cuatrecasas (Cuatrecasas 1955), *Aequatorium* (Nordenstam 1978), *Aetheolaena* (Nordenstam 1978), *Iocenes* (Nordenstam 1978), *Graphistylis* (Nordenstam 1978), *Lasiocephalus* (Cuatrecasas 1978). However, the value of this character is controversial since the molecular studies of Pelser *et al.* (2007, Fig. 1) indicate that *Aetheolaena* (= *Senecio* sect. *Aetheolaena*) and *Iocenes* (= *S. acanthifolius*), both without typical style tips, are sunk in *Senecio*. Our observations support this inclusion since we found transitional states in hairs that conform the tuft, ranging from a few short hairs, poorly differentiated into a crown of hairs, to numerous long hairs (Fig. 1), thus this character does not provide reliable taxonomic information.

Filament Collar

The filament collars (Koyama 1967, Drury 1973, Nordenstam 1978) or anther collars (Robinson & Brettell 1973d, Jeffrey *et al.* 1977) have been used to separate 'Cacalioid' Senecioneae (with 'cylindrical' collar) from 'non Cacalioid' Senecioneae (with 'balusterform' collar). The so called 'balusterform' collar by Drury (1973) is an elongated filament collar, strongly or somewhat dilated towards the base, broader than the filament (Fig. 2A, C). In the present study, this type was found in two species included in *Senecio* s.l., i.e. *Delairea odorata* and *Graphistylis organensis,* and in most

of the species of *Senecio* s.str. (Table 2). On the other hand, the 'cylindrical' filament collar type is very elongated and uniformly thick or slightly thicker than the filament (Fig. 2B). In the present study, this type was found in 11 species included in *Senecio* s.str. (see Table 2).

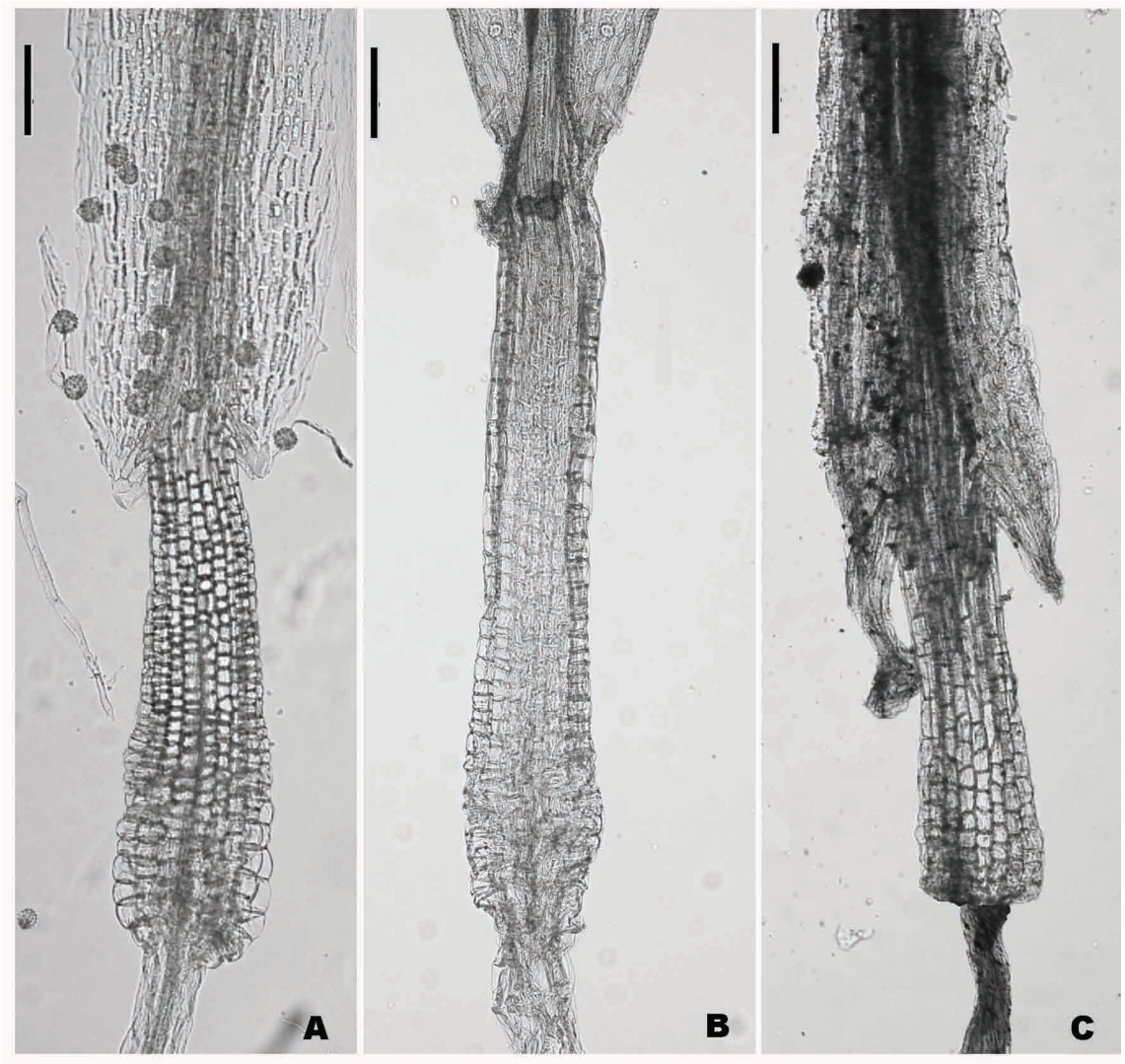


FIGURE 2. Anther collars and anther bases (LM): **A.** *Senecio brasiliensis:* balusterform collar, auriculate base; **B**. *S. comosus:* cylindrical collar, rounded base; **C**. *S. grandis:* balusterform collar, sagittate base. Scale bars = 100 µm.

Anther Bases

Anther bases have been considered important diagnostic features of Senecioneae (Jeffrey 1987). Traditionally, obtuse to slightly acute anther bases were considered as diagnostic for *Senecio* (e.g. Cabrera 1949, 1957). In fact, our analysis revealed that 64 species of *Senecio* s.str. (Table 2) have auriculate anthers, i. e. slightly acute (Fig. 2A). In addition, our study shows that only 2 sections include species with rounded anther base, i. e. obtuse (Fig. 2B): *Senecio* sect. *Adamantini* and *S.* sect. *Senecio* (*S.* ser. *Acanthifolii*; *S.* ser. *Culcitium*; *S.* ser. *Haplostichi*; *S.* ser. *Hualtatini*; *S.* ser. *Senecio*; *S.* ser. *Websteria*). As well as most of the species of *Senecio* s.str., many of the species previously included in *Senecio* s.l., i.e. *Acrisione denticulata, Delairea odorata, Dendrosenecio johnstonii* subsp. *cottonii*, *Graphistylis organensis, Lomanthus bangii, Nordenstamia fabrisii,* and *Roldana petasitis*, have auriculate anther bases. Sagittate anthers bases (Fig. 2C) distinguish *Senecio grandis* (*S.* sect. *Cacaliastrum*) from the remaining species of *Senecio* s.str. and are also present in *Aequatorium polygonoides*, *Dendrophorbium catharinense,* and *Pentacalia epiphytica*.

Anther Appendages

Jeffrey (1980) mentioned the taxonomic value of the shape of the apical anther appendages, a character not emphasized by other authors. In almost all studied taxa the apex of anther appendages is acute or obtuse (Fig. 3A, B). However, *Senecio comosus* and *S. pavonii*, *S. otites*, and *S. vulgaris* have rounded anther appendages (Fig. 3C). The anther

appendages about twice as long as broad (Fig. 3A) were found in all species included in *Senecio* s.l. (2:1, Table 2). Anther appendages about as long as broad (Fig. 3B) are present in 20 species of *Senecio* s.str. (1:1, Table 2).

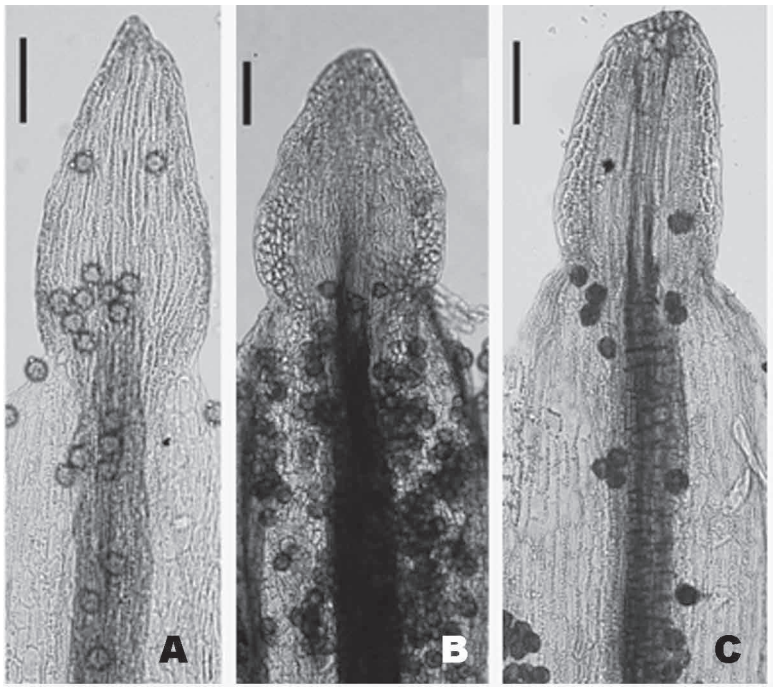


FIGURE 3. Anther appendages (LM): **A.** *Senecio brasiliensis:* twice as long as broad, acute; **B.** *S. candidans:* as long as broad, obtuse; **C.** *S. comosus:* rounded. Scale bars = 100 μm.

Pollen

Apertures. As generally found within the family Asteraceae (Erdtman 1966, Mesfin 1984), the pollen grains of the species examined in the present study were tricolporate.

Shape, size, and symmetry. Pollen grains in all investigated taxa were oblate spheroidal to prolate spheroidal in the equatorial view (Erdtman 1969). The size of the pollen grains ranged from 25–30 μm (polar axis with spines included), as in *Acrisione denticulata, Delairea odorata, Nordenstamia fabrisii,* and *Senecio* sect. *Senecio* (*S. vulgaris*, *S. zosterifolius*), to 54–57 μm (polar axis with spines included) in *Senecio* sect. *Crassicephali* (*S. burkartii*). In all studied taxa the pollen grains were radially symmetrical and isopolar.

Spines. In all studied taxa, the sculpture of the grains was either echinate (spines 3.5–6 μm long) or microechinate (spinules 1–3 μm long). Except for *Dendrosenecio johnstonii* subsp. *cottonii* and *Delairea odorata*, the species previously segregated from *Senecio* and here studied have echinate grains. Within *Senecio* s.str., *S.* sect. *Aetheolaena* was the only section in the present study where all the sampled species had microechinate grains (Fig. 4A). In *S.* sect. *Senecio* we found microechinate and echinate grains in same proportion.

The length vs. basal width ratio of the spines ranged from 0.6 in *Senecio neeanus* to 3 in *S. candollei*, with the majority of the species having ratio range between 0.8 and 1.5. In all taxa analyzed the shape of the spines is conical as was previously mentioned by Vincent & Getliffe Norris (1989) for African species of *Senecio*. However, in some taxa we found an interesting variation of this conical shape when length, width, and apex are considered: typically conical (in most of the taxa analyzed), and three additional types here called conical linear, present in *S. eightsii* (Fig. 4B); conical mamelliform, present in *Graphistylis organensis* (Fig. 4C)*, Pentacalia ephiphytica* and *Senecio* ser. *Chilenses* (*S. chilensis*, *S. polyphyllus*); this type was also observed in some taxa of tribe Liabeae by Dillon *et al.* (2009); and conical curved, present in *Senecio* sect. *Acanthifolii* (*S. acanthifolius,* Fig. 4D). Under the Light Microscope (LM) we found that the spine bases were perforated, but this character was verified with SEM only for *S. candidans* (Fig. 4E, F), *S. aspericaulis* and *S. niveo-aureus*. Details of pollen morphological features studied in *Senecio* s.str. and the additional genera are showed in Table 3.

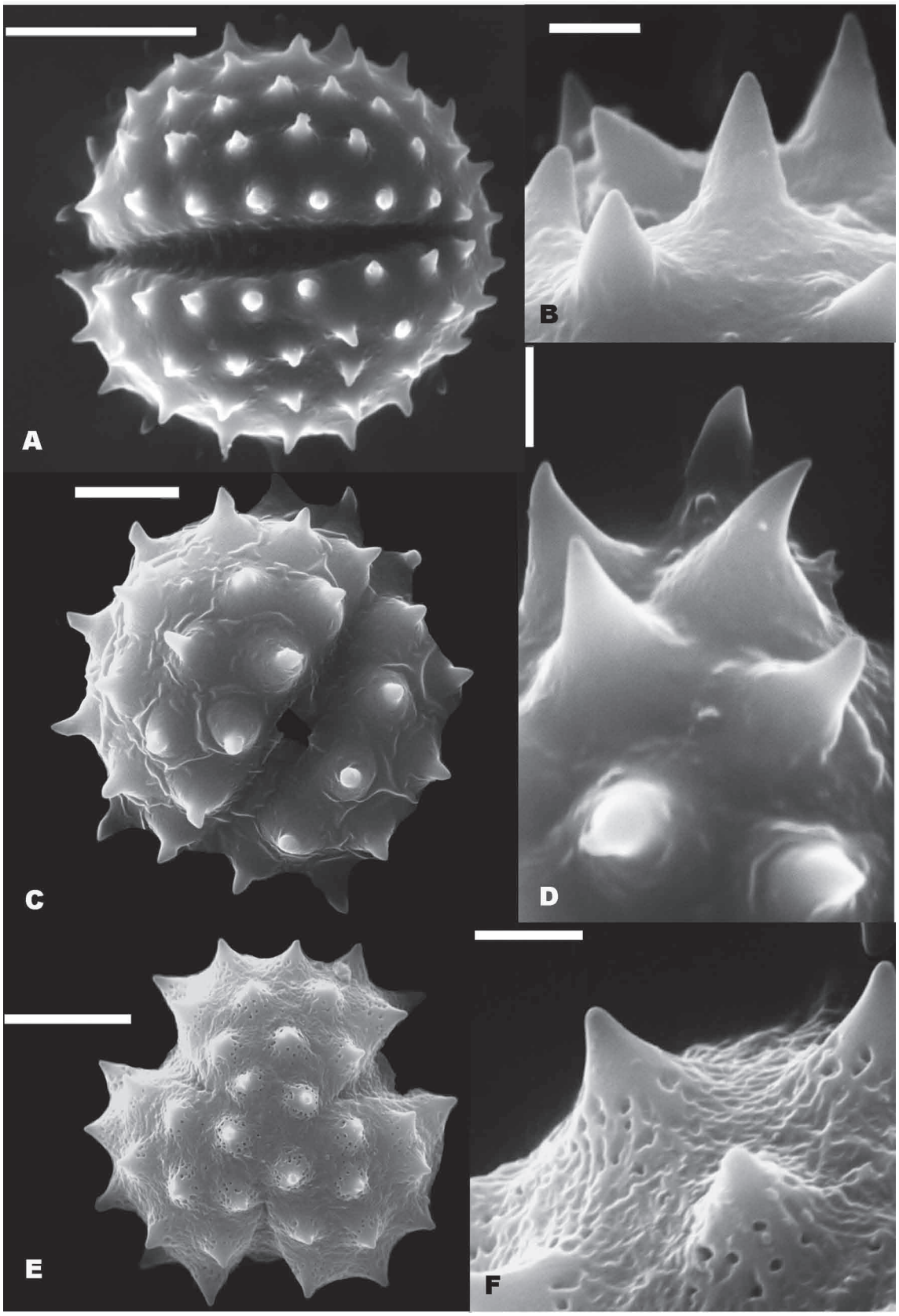


FIGURE 4. Pollen grains (SEM). **A.** *Senecio involucratus:* microechinate grain; **B.** *S. eightsii:* conical linear spine; **C.** *Graphistylis organensis:* conical mamelliform spine; **D.** *S. acanthifolius:* conical curved spine; **E.** *S. candidans:* echinate grain; **F.** *S. candidans:* conical spine. Scale bars: A, E = 10 μm; C = 8 μm; B, D, F = 2 μm.

TABLE 3. Pollen morphological features in *Senecio* s.str. and other genera of subtribes Brachyglottidinae, Senecioninae and Tussilagininae.

Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
Acrisione denticulata	25–28	25	1.06	echinate	3.5	2–3	1.2	conical
Aequatorium polygonoides	38–43	37–39	1.07	echinate	3.5–4	4	0.87	conical curved
Delairea odorata	30	27–30	1.05	microechinate	2	2–3	0.8	conical
Dendrophorbium catharinense	30–32	30	1.03	echinate	3.5–4	4	0.88	conical
Dendrosenecio johnstonii subsp. *cottonii*	41–45	43–45	0.98	microechinate	1 –2	1–2	1	conical
Graphistylis organensis	45–49	43–45	1.07	echinate	3.5–5	3–6	0.89	conical mamelliform
Lomanthus bangii	36–38	42	0.88	echinate	3.5–5	3–4	1.14	conical
Nordenstamia fabrisii	30	30–33	0.95	echinate	4	3–4	1.14	conical
Pentacalia epiphytica	38–42	36–38	1.08	echinate	3.5–4	4–5	0.78	conical mamelliform

...Continued on next page

TABLE 3. (Continued)

Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
Roldana petasitis	30–33	30	1.05	echinate	3.5–4	2	1.075	conical
Senecio								
Sect. *Acanthifolii*								
acanthifolius	39–43	40–45	0.96	echinate	3.5–5	4–5	0.89	conical curved
Sect. *Adamantini*								
adamantinus	40–41	37–42	1.03	echinate	3.5–5	4–5	0.89	conical
Sect. *Aetheolaena*								
imbaburensis	40	35–40	1.07	microechinate	2–3	2–3	1	conical
involucratus	36	33–35	1.06	microechinate	1.5–2	1–1.5	1.4	conical
lingulatus	35	33–35	1.03	microechinate	1–2	1–2	1	conical
puracensis	35	35–40	0.93	microechinate	1–1.5	1–1.5	1	conical
quitensis	36–40	35–37	1.06	microechinate	2–3	2–3	1	conical
Sect. *Cacaliastrum*								
grandis	38–40	39–40	0.99	echinate	3.5–4	3–4	1	conical
Sect. *Latiflori*								
niveo-aureus	46	46	1	echinate	4–5	4	1.13	conical
Sect. *Paranenses*								
hemmendorffii	37–41	38–42	0.97	echinate	3.5–5	3–5	1	conical

...Continued on next page

TABLE 3. (Continued)

Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
Sect. *Reflexi*								
superandinus	35–40	37–39	0.99	microechinate	1–2	1–2	1	conical
Sect. *Senecio*								
achalensis	42–43	40–42	1.04	echinate	4	4	1	conical
aspericaulis	34–36	34–36	1	microechinate	2.5	3	0.83	conical
aspleniifolius	35–39	41	0.9	echinate	4–5	3	1.5	conical
brasiliensis	33–36	36–39	0.92	echinate	4–5	4–5	1	conical
burkartii	54–57	52–57	1.02	echinate	4–6	4–5	1.11	conical
calocephalus	42–45	40–45	1.02	echinate	3.5–4	4–5	0.78	conical
candidans	40–41	40–41	1	echinate	4–5	5	0.9	conical
candollei	38–39	40–41	0.95	microechinate	3	1	3	conical
canescens	40	40–41	0.99	microechinate	2–3	1	2.5	conical
carnosus	40	37	1.08	microechinate	3	3	1	conical
chilensis	39–41	37–41	1.03	echinate	4–5	4–6	0.9	conical mamelliform
cocuyanus	36–38	35–38	1.01	microechinate	1–2	1–2	1	conical
comosus	35	35	1	echinate	4–5	4–5	0.87	conical
cuneatus	36–39	35–39	1.01	echinate	3.5–4	4	0.9	conical
eightsii	39–40	40–42	0.96	echinate	4–5	2–3	1	conical lineal

...Continued on next page

TABLE 3. (Continued)

Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
eriophyton	38–40	35–45	0.97	microechinate	3	3–4	0.86	conical
expansus	33–35	30–35	1.05	echinate	3.5–4	3–4	1	conical
famatinensis	38–40	38–40	1	microechinate	2.5–3	2.5–3	1	conical
farinifer	40–44	36–38	1.13	echinate	4–5	4–5	1	conical
filaginoides	30–35	33–35	0.96	microechinate	2	2	1	conical
fistulosus	35–40	37–40	0.97	echinate	3.5–4	3.5–4	0.93	conical
gilliesii	36–40	38–41	0.96	echinate	3.5–4	3	1.17	conical
grisebachii	35–37	35–36	1.01	echinate	4–5	5	0.9	conical
haenkeanus	32–35	31–36	1	echinate	3.5–4	3–4	1	conical
hieracium	43–47	43	1.05	echinate	3.5–5	4–5	0.89	conical
humillimus	35–37	34–37	0.99	echinate	3.5–4	2–4	1.5	conical
hypsobates	30–32	30	1.03	microechinate	1–2	1	1.5	conical
jarae	40–45	42–46	0.97	echinate	3.5–4	4–5	0.78	conical
keshua	38–39	33–35	1.13	microechinate	1–2	1	1.5	conical
krapovickasii	33–35	33–35	1	microechinate	2–3	2–3	1	conical
leucomallus	38–43	37–42	1.03	echinate	3.5–4	3–4	1	conical
madagascariensis	27–30	26–30	1.02	microechinate	2–3	2–3	1	conical
madariagae	32–33	32–33	1	microechinate	3	3	1	conical

...Continued on next page

TABLE 3. (Continued)

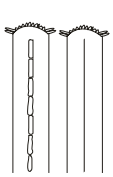
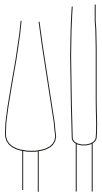
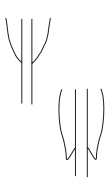
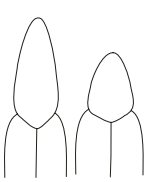
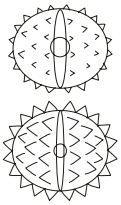
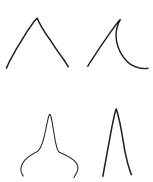
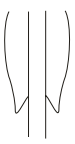
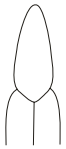
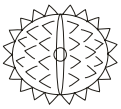
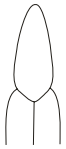
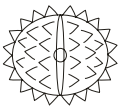
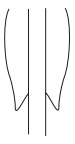
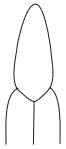
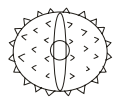
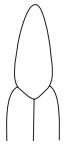
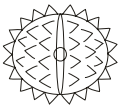
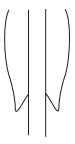
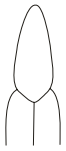
Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
magellanicus	35	38–42	0.87	echinate	3.5–4	3–5	0.87	conical
martinensis	40–45	40–41	1.05	microechinate	2–3	3–4	0.86	conical
modestus	40–45	40–43	1.02	microechinate	1–2	1–2	1	conical
monttianus	35	40–41	0.86	echinate	3.5–5	3–5	1	conical
neeanus	40	36–43	1.01	microechinate	1–2	2–3	0.6	conical
nutans	35–37	35–38	0.99	microechinate	1–2.5	1–2	1.17	conical
oreophyton	40–42	38–41	1.04	microechinate	2–3	3–4	0.71	conical
otites	36–40	38–41	0.96	echinate	4–5	4–5	1	conical
pavonii	41–43	40	1.05	echinate	3.5–5	4–5	0.89	conical
pflanzii	35–41	33–40	1.04	microechinate	2	1–1.5	1.6	conical
poeppigii	36–38	38	0.97	echinate	3.5–4	3–4	1	conical
polyphyllus	43	43	1	echinate	5	5	1	conical mamelliform
portulacoides	32–34	32–35	0.98	microechinate	2–2.5	2–2.5	1	conical
potosianus	36	38	0.95	echinate	4	4	1	conical
pseudalmeidae	41–42	40–42	1.02	echinate	5–6	5–6	1	conical
pseudoaspericaulis	33–35	33–35	1	microechinate	2	2–2.5	0.89	conical

...Continued on next page

TABLE 3. (Continued)

Species	Polar axis (µm)	Equatorial axis (µm)	P/E	Exine ornamentation	Spines/spinules length (µm)	Spines/spinules basal width (µm)	l/w	Spines/spinules form
punae	38–45	38–45	1	echinate	5	5	1	conical
retanensis	36–37	36	1.01	echinate	5	5	1	conical
santanderensis	38–40	35–38	1.07	microechinate	1.5–2	1–2	1.17	conical
segethii	44–53	44–54	0.99	echinate	4	4	1	conical
serratifolius	40–42	40	1.02	microechinate	2–3	2–3.5	1	conical
subdiscoideus	41–47	40–45	1.02	microechinate	2–3	3–4	0.71	conical
subpubescens	45–46	46–47	0.98	echinate	4	4	1	conical
triodon	44	46	0.96	microechinate	3	3	1	conical
volckmannii	45	40–41	1.11	echinate	3.5–5	3–5	1	conical
vulgaris	25–30	27–30	0.96	microechinate	3	2–3	1.2	conical
websteri	36–40	35–40	1.01	echinate	3.5–4	3–4	1	conical
zosterifolius	25–30	36	0.76	echinate	3.5–4	3–4	1	conical

TABLE 4. Morphological comparison between *Senecio* s.str and other genera of subtribes Brachyglottidinae, Senecioninae and Tussilagininae.

Genera	Style branch apices	Stigmatic surfaces	Filament collar	Anther bases	Anther appendages	Exina ornam.	Spines/ spinules shape
Senecio (Senecioninae)							
Acrisione (Brachyglottidinae)							
Aequatorium (Tussilagininae)							
Delairea (Senecioninae)							
Dendrophorbium (Senecioninae)							
Dendrosenecio (Senecioninae)							
Graphistylis (Senecioninae)							
Lomanthus (Senecioninae)							
Nordenstamia (Tussilagininae)							
Pentacalia (Senecioninae)							
Roldana (Tussilagininae)							

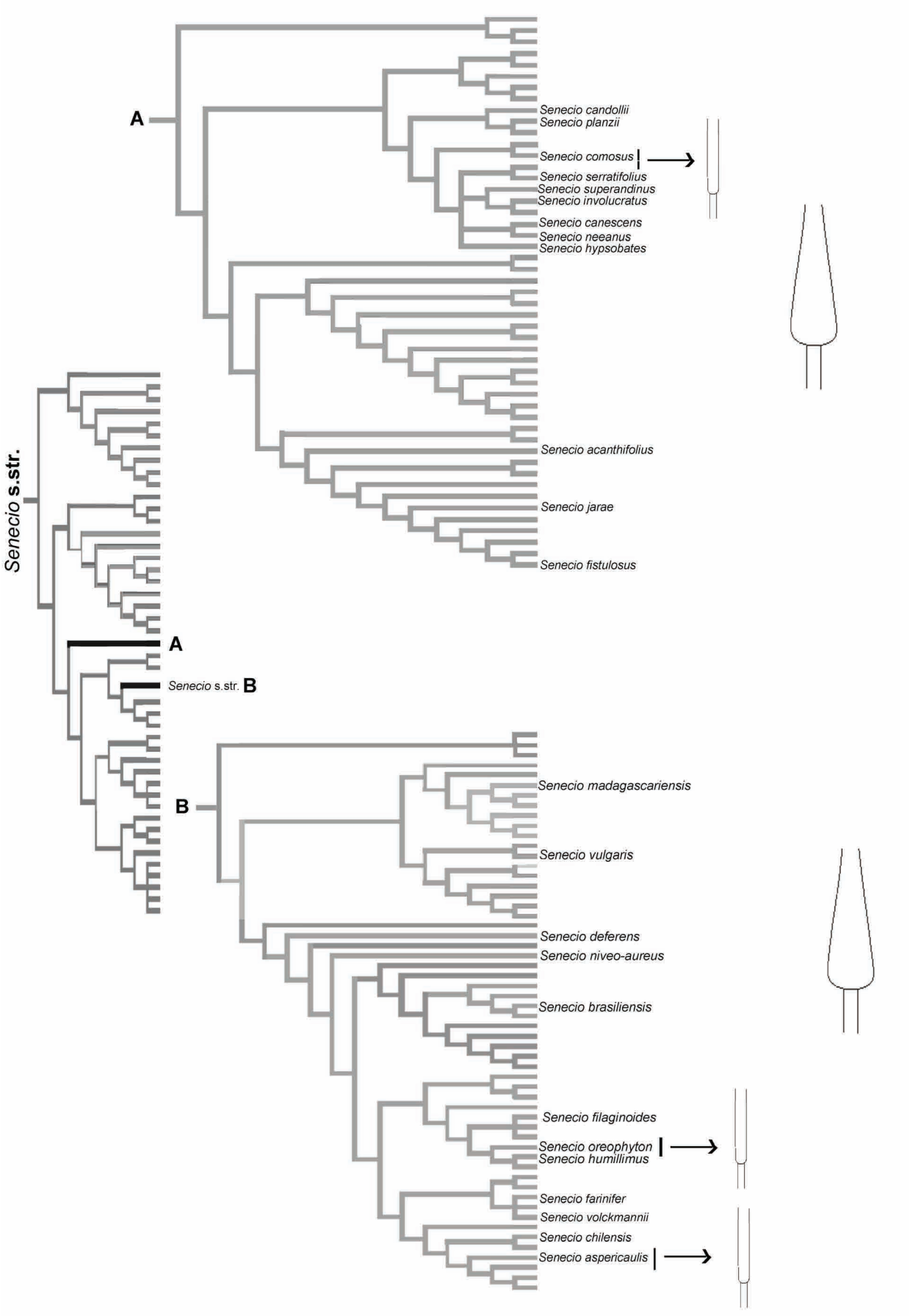


FIGURE 5. Phylogeny of *Senecio* s.str. (modified from Pelser *et al.* 2007) showing configuration of filament collars for 23 of 72 species sampled in the present study.

Taxonomic Considerations and Conclusions

Considering the micromorphological characters analyzed in our study, only the shape of the anther filament collars showed systematic value. In fact, 61 out of the 72 studied species of *Senecio* s.str. (including *S. vulgaris*, the type species of the genus) present balusterform filament collars; this trait was not found in eight out of the ten analyzed genera of Senecioneae (i.e. *Acrisione, Aequatorium, Dendrophorbium, Dendrosenecio, Lomanthus, Nordenstamia, Pentacalia,* and *Roldana*), so it would allow to circumscribe *Senecio* s.str., at least from the perspective of the South American species sampled; furthermore, balusterform collars are also predominantly found in European, African and Assian species of *Senecio* s.str. (Nordenstam 1978, Pelser *et al.* 2007). Balusterform collars are also present in the genera *Graphistylis* and *Delairea*; however, the former shows features that are rather infrequently found in *Senecio* s.str., e.g. banded stigmatic surfaces, and conical mamelliform pollen spines; furthermore, the segregation of *Graphistylis* from *Senecio* s.str. is also supported by molecular studies (Pelser *et al.* 2007). Even if *Delairea* shares all the studied micromorphological characters with *Senecio* s.str., molecular analyses (Knox & Palmer 1995) showed that this genus is nested in a clade with genera distantly related from *Senecio* s.str., which in some cases present typical anthers of *Senecio* s.str., e.g *Jacobaea* (incl. *Senecio jacobaea* L. with balusterform collar), and *Gynura* (subcylindric collar present in *G. aurantica* (Blume) DC.). Some of the species of *Senecio* s.str. that have cylindrical filament collars, i.e. *S. aspericaulis*, *S. comosus*, and *S. oreophyton*, lie within the clade of *Senecio* s.str. in previous molecular studies (Pelser *et al.* 2007); this fact could be considered a reversal to the plesiomorphic condition. *Senecio grandis* should be excluded from the genus considering the concurrence of cylindrical collars and sagittate anther bases. However, further phylogenetic analyses are required to confirm the position of *Senecio grandis* as well as the remaining species with cylindrical collars (*S. burkartii*, *S. calocephalus*, *S. hieracium, S. pseudaspericaulis*, *S. subdiscoideus*, *S. subpubescens*, and *S. websteri*), which so far have not been included in molecular studies. Other analyzed micromorphological features previously considered valuable in terms of circumscribing *Senecio* s.str. (cfr. Robinson & Brettell 1973c, Nordenstam 1977, Jeffrey *et al.* 1977, Jeffrey 1980, Nordenstam 2007) appeared to be taxonomically uninformative as their predominant states are shared by *Senecio* s.str. and all the other genera studied. In fact, our study shows that the style-branch apices are mainly papillate and surrounded by a crown of hairs of different lengths (the style-branch apices with apical central hair tuft having been found in *Senecio* s.str. as well as in some of the segregated genera), whereas the stigmatic surfaces are mostly cleft; the anther bases are predominantly auriculate, and the anther appendages are mostly twice as long as broad. The pollen characters here examined in search of additional diagnostic traits also did not provide valuable taxonomic information.

Table 4 shows a morphological comparison between *Senecio* s.str. and other genera studied for all analyzed features, and Figure 5 shows the species of *Senecio* s.str. analyzed in the present study that were included in the molecular phylogenetic analysis of Pelser *et al.* (2007).

Acknowledgments

We give special thanks to Fernando O. Zuloaga and Lone Aagesen for their valuable comments and critical reading of the manuscript. We are very grateful to Celina Fernández from Palynology and Paleobotany Laboratory FCEyN (UBA) for training at acetolysis protocol and useful comments. Special thanks to Gustavo Daujotas from FFyL (UBA) and Raúl Pozner (SI) for their help with the terminology in Latin. Thanks to the curators of CTES, CORD, LP, MO, NY, and SI herbaria for providing the specimens that made this study possible. Support for this work by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, is gratefully acknowledged.

References

Beltrán, H., Granda, A., León, B., Sagástegui, A., Sánchez, I. & Zapata, M. (2007) Asteráceas endémicas del Perú. *In*: León, B., Roque, J., Ulloa, C., Pitman, N., Jörgensen, P.M. & Cano, A. (Eds.) El Libro Rojo de las Plantas endémicas del Perú. *Revista Peruana de Biología* Número Especial 13 (2): 64–164.

Bremer, K. (1994) *Asteraceae: Cladistics and classification*. Timber Press, Portland, 752 pp.

Brown, B.V. (1993) A further chemical alternative to critical point drying for preparing small (or large) files. *Fly Times* 11: 10.

Cabrera, A.L. (1939) Las especies tucumanas del género *Senecio* (Compositae). *Lilloa* 5: 65–120.
Cabrera, A.L. (1949) El género *Senecio* en Chile. *Lilloa* 15: 27–501.
Cabrera, A.L. (1950) Notes on the Brazilian Senecioneae. *Brittonia* 7 (2): 53–74. http://dx.doi.org/10.2307/2804930
Cabrera, A.L. (1954) Senecios Sudamericanos nuevos o críticos. *Darwiniana* 10: 547–605.
Cabrera, A.L. (1957) El género *Senecio* (Compositae) en Brasil, Paraguay y Uruguay. *Archivos do Jardim Botânico do Rio de Janeiro* 15: 161–269.
Cabrera, A.L. (1985) El género *Senecio* (Compositae) en Bolivia. *Darwiniana* 26: 79–217.
Cabrera, A.L. & Freire, S.E. (2009) Tribu Senecioneae (Compositae). *In*: Spichiger, R. & Ramella, L. (Eds.) *Flora del Paraguay* 39. Editions des Conservatoire et Jardin botaniques de la Ville de Genève & Missouri Botanical Garden, pp. 9–64.
Cabrera, A.L., Freire, S.E. & Ariza Espinar, L. (1999) Género *Senecio*. *In*: Hunziker, A.T. (Ed.) *Flora Fanerogámica Argentina Fascículo* 62. Proflora (Conicet), Córdoba, pp. 12–158.
Cuatrecasas, J. (1950) Contributions to the flora of South America. Studies on Andean Compositae I. *Fieldiana Botany* 27 (1): 1–53.
Cuatrecasas, J. (1951) Contributions to the flora of South America. Studies on Andean Compositae II. *Fieldiana Botany* 27 (2): 1–74.
Cuatrecasas, J. (1955) A new genus and other novelties in Compositae. *Brittonia* 8 (2): 151–163. http://dx.doi.org/10.2307/2804857
Cuatrecasas, J. (1978) Studies in Neotropical Senecioneae, Compositae. I. Reinstatement of genus *Lasiocephalus*. *Phytologia* 40: 307–312.
Cuatrecasas, J. (1981) Studies in neotropical Senecioneae II. Transfers to genus *Pentacalia* of north Andean species. *Phytologia* 49: 241–260.
Dillon, M.O., Funk, V.A., Robinson, H. & Chan, R. (2009) Liabeae. *In*: Funk, V.A., Susanna, A., Stuessy, T.F. & Bayer, R.J. (Eds.) *Systematics, Evolution and Biogeography of the Compositae*. IAPT, Vienna, pp. 417–437.
Drury, D.G. (1973) Annotated key to the New Zealand shrubby Senecioneae-Compositae and their wild and garden hybrids. *New Zealand Journal of Botany* 11: 731–784. http://dx.doi.org/10.1080/0028825X.1973.10430309
Erdtman, G. (1960) The acetolysis method, a revised description. *Svensk Botanisk Tidskrift* 54: 561–564.
Erdtman, G. (1966) *Pollen morphology and plant taxonomy*. Hafner, New York & London, 553 pp.
Erdtman, G. (1969) *Handbook of Palynology*. Munksgaard, Copenhagen, 580 pp.
Freire, S.E., Ariza Espinar, L., Salomón, L. & Hernández, M.P. (2014) *Senecio*. *In*: Zuloaga, F.O., Belgrano, M.J. & Anton, A.M. (Eds.) *Fl. Vasc. Argent*, vol. 7 (3). Estudio Sigma S.RL., Buenos Aires, pp. 27–220.
Jeffrey, C. (1980) Generic and sectional limits in *Senecio* (Compositae): II. Evaluation of some recent studies. *Kew Bulletin* 34: 49–58. http://dx.doi.org/10.2307/4117970
Jeffrey, C. (1986) Notes on Compositae, IV: The Senecioneae in East Tropical Africa. *Kew Bulletin* 41: 873–943. http://dx.doi.org/10.2307/4102988
Jeffrey, C. (1987) Developing descriptors for systematic analyses of Senecioneae (Compositae). *Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie* 108: 201–211.
Jeffrey, C. (1992) Notes on Compositae, VI: The tribe Senecioneae (Compositae) in the Mascarene Islands with an annotated world check-list of the genera of the tribe. *Kew Bulletin* 47: 49–109. http://dx.doi.org/10.2307/4110768
Jeffrey, C. & Chen, Y.L. (1984) Taxonomic studies on the tribe Senecioneae (Compositae) of Eastern Asia. *Kew Bulletin* 39: 205–446. http://dx.doi.org/10.2307/4110124
Jeffrey, C., Halliday, P., Wilmot-Dear, M. & Jones, S.W. (1977) Generic and sectional limits in *Senecio* (Compositae): I. Progress report. *Kew Bulletin* 32: 47–67. http://dx.doi.org/10.2307/4117259
Knox, E.B. & Palmer, J.D. (1995) The Origin of *Dendrosenecio* within the Senecioneae (Asteraceae) Based on Chloroplast DNA Evidence. *American Journal of Botany* 82 (12): 1567–1573. http://dx.doi.org/10.2307/2446185
Koyama, H. (1967) Taxonomic studies on the tribe Senecioneae of Eastern Asia. I. General part. *Memoirs of the Faculty of Science, Kyoto University, Series of Biology* 33: 181–209.
Mesfin, T. (1984) The genus *Bidens* (Compositae) in Tropical Africa. *Symbolae Botanicae Upsalienses* 24 (1): I–VIII + 1–138.
Nordenstam, B. (1978) Taxonomic studies in the tribe Senecioneae (Compositae). *Opera Botanica* 44: 1–84.
Nordenstam, B. (2007) Tribe Senecioneae. *In*: Kadereit, J.W. & Jeffrey, C. (Eds.) *Kubitzki's The families and Genera of Vascular Plants*, vol. 8. Springer, Berlin, pp. 208–241.
Nordenstam, B., Pelser, P.B. & Watson, L.E. (2009) *Lomanthus*, a new genus of the Compositae-Senecioneae from Ecuador, Peru, Bolivia

and Argentina. *Compositae Newsletter* 47: 33–40.

Pelser, P.B., Nordenstam, B., Kadereit, J.W. & Watson, L.E. (2007) An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
http://dx.doi.org/10.2307/25065905

Riva, A., Pozner, R. & Freire, S.E. (2009) Micromorphological characters supporting the removal of *Senecio* series *Otopteri* from *Senecio* (Aseraceae, Senecioneae). *Darwiniana* 47: 327–334.

Robinson, H. (1974) Studies in the Senecioneae (Asteraceae). VI. The genus *Arnoglossum*. *Phytologia* 28: 294–295.

Robinson, H. & Brettell, R.D. (1973a) Studies in the Senecioneae (Asteraceae). I. A new genus, *Pittocaulon*. *Phytologia* 26: 451–453.

Robinson, H. & Brettell, R.D. (1973b) Studies in the Senecioneae (Asteraceae). II. A new genus, *Nelsonianthus*. *Phytologia* 27: 53–54.

Robinson, H. & Brettell, R.D. (1973c) Studies in the Senecioneae (Asteraceae). III. The genus *Psacalium*. *Phytologia* 27: 254–264.

Thiers, B. (2016) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden´s Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (accessed 10 January 2016)

Vincent, P.L.D. (1996) Progress on clarifying the generic concept of *Senecio* based on an extensive world-wide sample of taxa. *In*: Hind, D.J.N. & Beentje, H.J. (Eds.) *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1. Royal Botanic Gardens, Kew, pp. 597–611.

Vincent, P.L.D. & Getliffe Norris, F.M. (1989) An SEM study of the external pollen morphology in *Senecio* and some related genera in the subtribe Senecioninae (Asteraceae: Senecioneae). *South African Journal of Botany* 55 (3): 304–309.

Vision, T.J. & Dillon, M.O. (1996) Sinopsis de *Senecio* L. (Senecioneae, Asteraceae) para el Perú. *Arnaldoa* 4 (1): 23–46.

Wetter, M.A. (1983) Micromorphological characters and generic delimitation of some New World Senecioneae (Asteraceae). *Brittonia* 35: 1–22.
http://dx.doi.org/10.2307/2806039