

## *Acanthostyles* (Asteraceae, Eupatorieae): a revision with a multivariate analysis

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**Abstract.** The Neotropical genus *Acanthostyles* R.M.King & H.Rob. (Asteraceae, Eupatorieae) occurs from northern Argentina up to northern Patagonia, southern Brazil, central and southern Bolivia, and Uruguay. Different taxonomic treatments have suggested that *Acanthostyles* might include two species (*A. buniifolius* (Hook. & Arn.) R.M.King & H.Rob. and *A. saucechicoensis* (Hieron.) R.M.King & H.Rob.), or even only a single, highly variable, species. Therefore, a detailed morphological study and a taxonomic revision of *Acanthostyles* were carried out. A principal component analysis of 73 specimens, representing the morphological variability and geographic distribution of *Acanthostyles*, was conducted to test the validity of these taxa. Results showed that the morphological variation of *A. saucechicoensis* is included within the infraspecific variation of *A. buniifolius*. No clearly separated groups were revealed by the principal component analysis. We, therefore, propose that *A. saucechicoensis* is treated as a synonym of *A. buniifolius*, and thus *Acanthostyles* becomes a single, highly variable species throughout its range.

**Additional keywords:** Compositae, Disynaphiinae, morphological variability, Neotropics.

### Introduction

*Acanthostyles* R.M.King & H.Rob. (Asteraceae) is a southern Neotropical genus belonging to the tribe Eupatorieae. Depending on the authors, it has one or two species both formerly placed in *Eupatorium* L., ranging from northern Argentina up to northern Patagonia, southern Brazil, central and southern Bolivia, and Uruguay, from ~20°S to 41°S. *Acanthostyles* was named for its most distinctive feature, the flagelliform style apical appendage with laxly distributed, large, acicular papillae, which is unique in the tribe (King and Robinson 1971, 1987). This genus includes resinous shrubs with highly variable leaves (i.e. linear and entire to pinnatifid or bipinnatifid), paniculiform capitulescences with tendency to be pendulous, typically five florets per capitulum, nectaries lacking, glabrous style bases and cypselae exclusively with twin hairs. Some of these reproductive characters such as pendent capitulescences, flagelliform style apical appendages with laxly distributed large, acicular papillae, and short-spined pollen grains are probably associated with an anemophilous pollination (King and Robinson 1987; Grossi *et al.* 2009), which occurs in some North American eupatorian genera and a few Helianthean species (Payne 1963; Grashoff and Beaman 1970; Sullivan 1975; Lane 1996).

*Acanthostyles* was placed by King and Robinson (1987) in the South American subtribe Disynaphiinae, together with the genera *Campovassouria* R.M.King & H.Rob. (one species),

*Disynaphia* DC. (16 species), *Grazielia* R.M.King & H.Rob. (11 species), *Raulinoreitzia* R.M.King & H.Rob. (three species), and *Symphypappus* Turcz. (12 species) (Hind and Robinson 2007). Originally, King and Robinson (1987) noted that the most diagnostic subtribal feature was the presence of five florets per capitulum. Recently, other features (e.g. woody plants, glabrous style shaft) were pointed out to distinguish Disynaphiinae from the other eupatorian subtribes (Hind and Robinson 2007; Robinson *et al.* 2009). *Acanthostyles* was considered closely related to *Raulinoreitzia* because they share pyramidal paniculate cymes with a grass-like aspect (King and Robinson 1971, 1987). Both can be easily distinguished by the type of style appendage (flagelliform, with laxly distributed large papillae in *Acanthostyles* v. not flagelliform, with densely distributed short papillae in *Raulinoreitzia*), the type of leaf margin (entire to dissected v. serrulate), type of leaf venation (pinnately nerved v. three-veined) and pappus setae apex (not enlarged v. enlarged).

Some authors include two species in *Acanthostyles* (e.g. King and Robinson 1987; Bremer *et al.* 1994): namely *A. buniifolius* (Hook. & Arn.) R.M.King & H.Rob. and *A. saucechicoensis* (Hieron.) R.M.King & H.Rob. *A. buniifolius*, commonly called ‘romerillo’ or ‘chilca’, a widely distributed and dominant species in the ecosystems where it occurs (e.g. Funes and Cabido 1995). In contrast, *A. saucechicoensis* is restricted to the southern-most

portion of the range of the genus. Other authors, however, regard *Acanthostyles* to be monospecific (e.g. Hind and Robinson 2007). Moreover, these taxa are also treated as varieties (e.g. Ariza Espinar 1994; Cabrera *et al.* 1997; Freire 2008). *A. buniifolius* and *A. saucechicoensis* can be distinguished with difficulty by the leaf length (3–6 cm *v.* 2–2.5 cm, respectively) and the width of the leaf segments (1–3 mm *v.* 0.5 mm, respectively) (Cabrera *et al.* 1997, sub-*Eupatorium*). However, we have found intermediate measurements for these traits.

Multivariate analysis of variance and principal component analysis have proven to be useful in recognition of morphologically close infraspecific taxa or species (e.g., Martínez-Azorín *et al.* 2007; Robyn *et al.* 2008; Sun *et al.* 2008). Thus, to resolve the taxonomy of *Acanthostyles*, the objectives of the present study were (1) to conduct a revision of *Acanthostyles*, with a detailed analysis of its morphology, and (2) to test the validity of its two species, through statistical analyses, on the basis of morphometric variation in vegetative and reproductive traits.

#### Brief history of *Acanthostyles*

The genus *Acanthostyles* was established by King and Robinson in 1987. Despite the fact that this genus was recently described, its taxonomic history began many years ago with the description of two species by Hooker and Arnott (1835), namely *Eupatorium buniifolium* and *E. virgatum*. *E. buniifolium* was described on the basis of specimens from north-western Argentina, and *E. virgatum* on specimens from several places from Argentina and Uruguay. Thus, from the beginning, these species were recognised as widely distributed in southern South America.

De Candolle (1836) described *E. pinnatifidum* from South America, and Grisebach (1874) described *E. crithmifolium* from central Argentina. Baker (1876) cited *E. pinnatifidum* from Brazil and recognised *E. virgatum* as a variety of that species.

Hieronymus (1897) included all the previously mentioned names under *E. buniifolium*, recognising the great morphological diversity, mainly regarding leaf traits. He noted the following five forms, although they were not validly published: Form 1 from northern Argentina (Salta and Tucuman Provinces) characterised by its pinnatifid or bi-pinnatifid leaves (up to 3 mm wide); Form 2 from north-western Argentina (Catamarca and La Rioja Provinces), with pinnatifid leaves (up to 3 mm wide); Form 3 from western and central Argentina (Córdoba, Mendoza and San Luis Provinces), with leaves similar to those of Forms 1 and 2, but with narrower divisions (up to 1.5 mm wide); Form 4 from Uruguay and the Brazilian State Rio Grande do Sul, with leaves similar to those of Form 1; and Form 5 from Sierras Pampeanas and Sierras de Ventania in Argentina, with leaves similar to those of Form 3, but with narrower divisions (0.5–0.75 mm wide). In addition, Hieronymus (1897) cited other traits to distinguish his forms, i.e. capitulescence (pendent or erect) and types of trichomes on the cypselae. In his work, Hieronymus (1897) described *E. saucechicoense* on the basis of some specimens from northern Patagonia. At that time, he did not find any specimens with leaf morphology intermediate between *E. buniifolium* and *E. saucechicoense*. However, he pointed out that *E. saucechicoense* could be

included into *E. buniifolium* if intermediate specimens were found.

In 1898, Kuntze described the following two varieties on the basis of Hieronymus' work: *Eupatorium buniifolium* var. *bakeri* and *E. buniifolium* var. *hieronymii*, based on the first and third Hieronymus' forms, respectively. Later, these varieties were recognised as synonyms of *E. buniifolium* (e.g. Ariza Espinar 1994; Cabrera *et al.* 1997). Almost a century after, the species *E. saucechicoense* was regarded as a variety of *E. buniifolium* (Ariza Espinar 1993, 1994).

Currently, according to different botanists, *Acanthostyles* includes two species (King and Robinson 1987; Bremer *et al.* 1994), one species with two varieties (Cabrera *et al.* 1997; Cabrera and Freire 1999; Freire 2008, sub-*Eupatorium*) or even just a single species (Hind and Robinson 2007).

#### Materials and methods

Studies were based on dried specimens from BA, BAA, BAB, CORD, CTES, E, G, K, NY, LP and SI (abbreviations as in Holmgren *et al.* 1990) and fresh material collected during field trips in Argentina; the data were supplemented with data from the literature. For microscopic examination, vegetative and reproductive parts were rehydrated when dry, treated with a clearing process, stained with 2% safranin and mounted on microscope slides. Plant organs were isolated and transverse cross-sections were cut by free hand. Drawings were made by using a SMZ 1000 stereomicroscope (Nikon, Tokyo) with a camera-lucida attachment (Nikon). Light microscope (Nikon Eclipse E200) photographs were taken with a Nikon Coolpix S10. For scanning electron microscopy (SEM) studies, dehydrated material was applied critical-point technique or dry material was placed directly on the stubs and coated with gold. The samples were scanned and photographed in a JSM-T 100 SEM (Jeol, Tokyo). We followed Ramayya (1962a, 1962b) for hair types and its terminology.

#### Statistical analysis

To analyse the morphometric variation of *Acanthostyles*, we measured the following vegetative and reproductive characters in 73 mature specimens: (1) leaf length, (2) leaf width, (3) length of the first leaf lobe, (4) width of the first leaf lobe, (5) length of the terminal leaf lobe, (6) width of the terminal leaf lobe, (7) involucre length, (8) involucre diameter, (9) cypselae length, (10) cypselae diameter, (11) pappus length, (12) corolla length, (13) width of the corolla limbs, (14) style branch length and (15) style appendage length (Table 1). We used univariate and multivariate analyses to assess the geographic variation, so as to differentiate morphological and taxonomical groups.

*Leaf (1–6).* Leaf length was measured from the base of the petiole to the apex of the last lobe in lobed, pinnatifid or bi-pinnatifid leaves, or up to the apex of the leaf blade when the leaf had an entire margin. Leaf width was measured in the middle of the total length of the leaf for leaves with entire margins. When the leaves were lobed, pinnatifid or bi-pinnatifid, we measured the rachis width but not the total width. Length and width of the terminal lobe were measured when present.

*Involucre (7, 8).* Involucre length was measured from the base of the outer phyllary up to the apex of the inner phyllary.

**Table 1. Morphological characters and their statistics (mean, and  $\pm$ s.d. and range in parentheses) for *Acanthostyles buniifolius* and *A. saucechicoensis***

Character no.	Character	<i>A. buniifolius</i>	<i>A. saucechicoensis</i>
1	Leaf length (cm)	4.52 ( $\pm$ 1.08) (2.3–7.53)	2.93 ( $\pm$ 0.98) (1.83–4.3)
2	Leaf width (cm)	0.64 ( $\pm$ 0.46) (0.1–1.9)	0.08 ( $\pm$ 0.05) (0.1–1.7)
3	Length of the first leaf lobe (cm)	1.31 ( $\pm$ 0.73) (0.17–2.67)	1.23 ( $\pm$ 0.66) (0.47–2.3)
4	Width of the first leaf lobe (cm)	0.12 ( $\pm$ 0.17) (0.02–1.2)	0.06 ( $\pm$ 0.02) (0.03–0.1)
5	Length of the terminal leaf lobe (cm)	0.17 ( $\pm$ 0.9) (0.07–4.5)	0.97 ( $\pm$ 0.4) (0.43–1.73)
6	Width of the terminal leaf lobe (cm)	0.17 ( $\pm$ 0.25) (0.02–1.8)	0.06 ( $\pm$ 0.02) (0.03–0.1)
7	Involucre length (cm)	0.55 ( $\pm$ 0.07) (0.37–0.76)	0.63 ( $\pm$ 0.03) (0.57–0.67)
8	Involucre diameter (cm)	0.29 ( $\pm$ 0.07) (0.18–0.6)	0.29 ( $\pm$ 0.05) (0.25–0.38)
9	Cypsela length (mm)	0.21 ( $\pm$ 0.04) (0.12–0.31)	0.22 ( $\pm$ 0.08) (0.15–0.39)
10	Cypsela diameter (mm)	0.06 ( $\pm$ 0.01) (0.04–0.1)	0.05 ( $\pm$ 0.008) (0.04–0.06)
11	Pappus length (mm)	0.38 ( $\pm$ 0.05) (0.28–0.52)	0.44 ( $\pm$ 0.06) (0.36–0.5)
12	Corolla length (mm)	0.43 ( $\pm$ 0.04) (0.3–0.53)	0.48 ( $\pm$ 0.06) (0.4–0.56)
13	Width of the corolla limb (mm)	0.09 ( $\pm$ 0.1) (0.049–0.85)	0.07 ( $\pm$ 0.01) (0.06–0.09)
14	Style branch length (mm)	0.24 ( $\pm$ 0.06) (0.14–0.45)	0.26 ( $\pm$ 0.03) (0.21–0.3)
15	Style appendage length (mm)	0.26 ( $\pm$ 0.04) (0.1–0.35)	0.28 ( $\pm$ 0.05) (0.23–0.36)

Width of the involucre was measured in the middle of the total length.

*Corolla (12, 13).* Corolla length was measured from the apex of the lobes up to the insertion of the corolla tube with the cypsela. Width of the corolla was measured in the middle of the total limb length.

*Style and style appendages (14, 15).* Style branch lengths were measured from the point of division of the branches up to the insertion with the style appendage, whereas style appendage lengths were measured from insertions with the style branches up to their apices.

*Cypselae and pappus (9–11).* Length and diameter of the cypsela were measured. Diameter of the cypsela was measured in the middle of the total cypsela length. Pappus length was measured from the basal ring up to its apex.

We assessed the correlation among measurements by using Pearson correlation test. We performed a principal component analysis (PCA) on the correlation matrix to characterise the morphological variation among the specimens analysed. Later,

we calculated the pairwise Euclidean distance between specimens to perform a Mantel test to assess their correlation with geographical distance. We conducted this analysis with 10 000 permutations. Finally, to find patterns of geographical variation, we performed linear regression analyses, with the morphological measurements as dependent variables, and latitudinal and altitudinal data as independent variables. Latitude data were from 20°S to 41°S and altitude data were from 0 to 2800 m. Normal distribution of residuals was tested with Shapiro–Wilks test. Homogeneity of variance was checked by visually plotting the residual of each variable and the predicted residual under the model tested. Statistical analyses were performed with InfoStat (2008) and PAST (Hammer *et al.* 2001).

## Results

### Morphometric variation

The analysis of correlation among the measurements is shown in Table 2. The only highly correlated (i.e.  $r > 0.75$ ) characters

**Table 2. Pearson correlation test for the measurements of morphological characters used for quantitative analyses**

The values of Pearson correlation are below and the *P*-values for the pairwise correlations above the principal diagonal. The morphological characters relating to each character number are as given in Table 1. \*\*, values of correlation that are equal or higher than 0.75

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	<b>1.00</b>	0.00	0.00	0.12	0.05	0.04	0.62	0.90	0.37	0.20	0.50	0.49	0.26	0.68	0.74
2	0.49	<b>1.00</b>	0.00	0.96	0.00	0.01	0.18	0.41	0.27	0.02	0.86	0.58	0.08	0.76	0.77
3	0.59	0.61	<b>1.00</b>	0.03	0.01	0.10	0.71	0.97	0.73	0.47	0.50	0.48	0.03	0.40	0.84
4	0.23	0.01	0.32	<b>1.00</b>	0.53	0.49	0.32	0.10	0.41	0.38	0.52	0.12	0.02	0.48	0.22
5	0.29	0.42	0.40	0.09	<b>1.00</b>	0.40	0.78	0.98	0.70	0.91	0.07	0.63	0.53	0.66	0.69
6	0.30	0.37	0.24	0.10	0.13	<b>1.00</b>	0.43	0.46	0.11	0.06	0.54	0.32	0.76	0.29	0.44
7	0.07	0.20	0.06	0.15	0.04	0.12	<b>1.00</b>	0.25	0.81	0.36	0.02	0.03	0.33	0.76	0.18
8	0.02	0.12	0.00	0.24	0.00	0.11	0.17	<b>1.00</b>	0.04	0.77	0.65	0.79	0.98	0.50	0.50
9	0.13	0.16	0.05	0.12	0.06	0.24	0.04	0.29	<b>1.00</b>	0.00	0.00	0.00	0.57	0.09	0.18
10	0.19	0.34	0.11	0.13	0.02	0.28	0.14	0.04	0.47	<b>1.00</b>	0.02	0.01	0.10	0.75	0.36
11	0.10	0.03	0.10	0.10	0.27	0.09	0.34	0.07	0.45	0.34	<b>1.00</b>	0.00	0.45	0.31	0.01
12	0.10	0.08	0.10	0.23	0.07	0.15	0.32	0.04	0.54	0.36	0.77**	<b>1.00</b>	0.31	0.01	0.01
13	0.17	0.26	0.32	0.33	0.09	0.04	0.14	0.00	0.08	0.24	0.11	0.15	<b>1.00</b>	0.79	0.15
14	0.06	0.05	0.13	0.11	0.07	0.16	0.04	0.10	0.25	0.05	0.15	0.36	0.04	<b>1.00</b>	0.40
15	0.05	0.04	0.03	0.18	0.06	0.11	0.20	0.10	0.20	0.14	0.37	0.39	0.21	0.12	<b>1.00</b>

were corolla and pappus lengths ( $r=0.77$ ,  $P=2 \times 10^{-10}$ ). The PCA revealed that the first three principal components account for 48.51% of the total variation. Table 3 summarises the information of these first three principal components and the loadings of each variable measured. The plots of the principal components show that the variation of *Acanthostyles saucechicoensis* is included in the intraspecific variation of *A. buniifolius* (Fig. 1).

The Mantel test revealed a positive correlation between morphometric distance and geographical distance ( $r=0.2355$ ,  $P<0.001$ ), indicating some isolation-by-distance pattern in the morphological variation. In addition, the summary of linear regression analyses of morphometric variables and latitudinal and altitudinal factors as explicatory variables is shown in Table 4. We found that the leaf length is negatively related with latitude ( $R^2=0.21$ ,  $P<0.0001$ ), but positively related with altitude ( $R^2=0.22$ ,  $P<0.0001$ ). The cypsela length is also positively related with altitude ( $R^2=0.23$ ,  $P<0.0001$ ) (Fig. 2).

## Discussion

The PCA showed that the morphological variation (i.e. leaf length and leaf width) of *Acanthostyles saucechicoensis*, used to distinguish it from *A. buniifolius*, is included within the intraspecific variation of *A. buniifolius*. On the basis of these results, we include *A. saucechicoensis* in the synonymy of *A. buniifolius*, and thus the genus *Acanthostyles* is composed of one single, but highly variable, species throughout its range. The observed correlation between the corolla length and pappus length could be due to developmental aspects of these

structures. Mainly, the pappus within the Asteraceae acts as a structure of the cypsela dispersion (Jeffrey 2009), and some authors (Bremer *et al.* 1994) have proposed that the pappus is a modification of the calyx, structure associated with the corolla.

The Mantel test indicated a pattern of isolation by distance in the morphometric variation, with the nearest populations being more similar to each other than to the more distant ones. This result could indicate that there is intraspecific variation within the species, which, after sufficient time, could give rise to new species.

Developmental responses to small-scale environmental heterogeneity can be important for plant adaptation (Novoplansky 1996). Leaves are the plant organs most exposed to aerial conditions and changes in leaf characters have been interpreted as adaptations to specific environments (Fahn and Cutler 1992). The relationships found between leaf length and latitude and elevation suggest that environmental variables exert some influence on the morphological characteristics of the species, and the relationship found between the cypsela length and elevation reinforces the idea that environmental variables can have a marked influence on some morphological traits in plants. The identification of these relationships is crucial for distinguishing plant species and for recognising intraspecific variation that is providing phylogenetic information. It is important to complement future work with genetic characters, which would permit us to determine whether the isolation-by-distance pattern found with morphological characters is determined by both particular population histories (genetic drift) or by local adaptations to climatic variables.

**Table 3.** Factor loadings on the first three principal components for the quantitative characters used in principal component analysis  
The variance explained is shown for each principal component

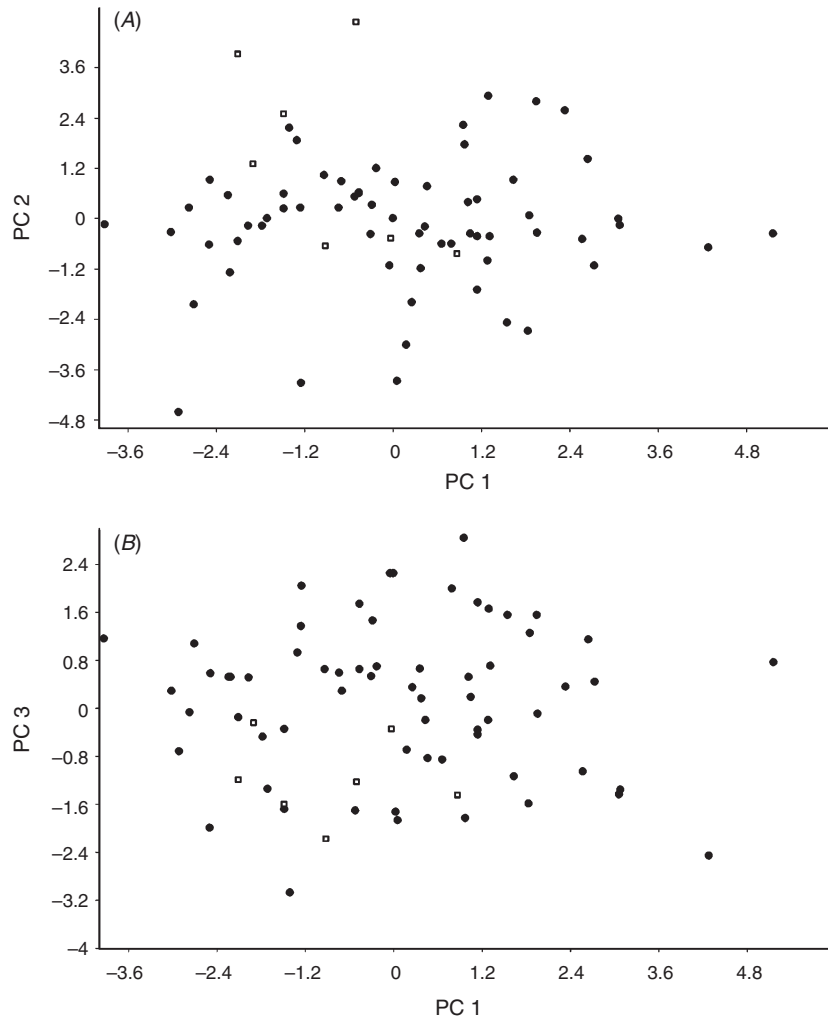
Measurement	Eigenvector		
	PC1	PC2	PC3
Leaf length (cm)	0.3261	-0.3127	0.07096
Leaf width (cm)	0.3297	-0.2682	-0.2375
Length of the first leaf lobe (cm)	0.2491	-0.3674	-0.2929
Width of the first leaf lobe (cm)	-0.05765	-0.1009	0.1083
Length of the terminal leaf lobe (cm)	0.1621	-0.3103	-0.191
Width of the terminal leaf lobe (cm)	0.2576	-0.06948	0.1042
Involucre length (cm)	0.05178	0.2455	-0.3922
Involucre diameter (cm)	-0.08187	0.005455	-0.2536
Cypsela length (mm)	0.367	0.1817	0.3145
Cypsela diameter (mm)	0.329	0.07048	-0.03103
Pappus length (mm)	0.1747	0.448	-0.1702
Corolla length (mm)	0.2617	0.4503	-0.05651
Width of the corolla limb (mm)	0.2177	0.01048	-0.3321
Style branch length (mm)	0.1948	0.1543	0.3441
Style appendage length (mm)	0.1769	0.2317	-0.3099
Presence/absence of the corolla constriction.	0.3987	0.06856	-0.3447
Eigenvalue	3.3573	2.7316	1.6726
Variance (%)	20.983	17.072	10.454

## Taxonomy

*Acanthostyles* R.M.King & H.Rob., *Phytologia* 22: 111. 1971

*Type:* *Eupatorium buniifolium* Hook. & Arn.

Shrubs resinous. Stems striate, glabrous. Leaves resinous, mainly opposite, rarely alternate in some terminal branches, usually petiolate, blades entire, narrowly lobed to pinnatifid or bipinnatifid, surface glandular, punctate. Inflorescences pendent or suberect, long, paniculate cym. Capitula discoid, homogamous. Involucres cylindrical, rarely campanulate; phyllaries subimbricate, 3–5 seriate, outer surface usually glandular; receptacles convex, epaleate, glabrous, with irregular surface. Florets usually 5 per capitulum; corolla tubular funnelform, purplish or whitish; lobes ovate–triangular, outer surface glandular; anther collar elongate, cylindrical; anther appendages ovate to triangular; anther bases rounded; style bases not enlarged, glabrous, nectary lacking; style branches long-linear, with stigmatic papillae elongated in two lines, flagelliform apical sterile appendages with large non-septate sweeping hairs scattered along the entire surface. Cypselae prismatic, 4- or 5-costate, with short twin hairs, carpopodium inconspicuous or minutely annuliform; pappus of ~30–40 bristles, persistent, uniseriate, basally fused in a ring, barbellate, not enlarged at apex, yellowish or whitish. Pollen grains with very short spines.



**Fig. 1.** Principal component analyses (PCA) from a correlation matrix of quantitative characters for *Acanthostyles buniifolius* (dots) and *A. saucechicoensis* (empty squares). (A) Plot of Principal component 1 v. Principal component 2. (B) Plot of Principal component 1 v. Principal component 3.

### Distribution

*Acanthostyles* occurs in southern South America, from central Bolivia and southern Brazil and Uruguay, to central Argentina (northern Patagonia). This genus is one of the most southern South American genera of the tribe Eupatorieae.

### Etymology

From the Greek *acanthos* or *akanthos*, thorny; and *styles*, in reference to the appendages of the style branches with elongated papillae.

***Acanthostyles buniifolius*** (Hook. & Arn.) R.M.King & H.Rob., *Phytologia* 22: 111, 1971

(Figs 3–6)

*Eupatorium buniifolium* Hook. & Arn., *Companion Bot. Mag.* 1: 240, 1835.

*Type:* Argentina. Tucumán: woods of Tucumán, *Tweedie* 1128 (holotype: K488850, digital image seen, photo LP!) (Fig. 3). *Protologue:* ‘Woods of Tucumán, rare, *Tweedie* (n. 1128)’.

*Eupatorium virgatum* D.Don ex Hook. & Arn., *Companion Bot. Mag.* 1: 241, 1835.

*Type:* Argentina. Mendoza: Villavicencio (as Villavicencio), Andes of Mendoza, *Gillies* 183 (lectotype here designated: K488854, digital image seen; isolectotype: E249959, digital image seen); Mendoza, *Gillies* 184 (syntypes: K488849, digital image seen, photo LP!; E249958, digital image seen); San Luis: Aguadita, *Gillies* 184 (La Plata) (syntypes: K488853, digital image seen; E249957, digital image seen); Uruguay. Locality not indicated: Uruguay, *Tweedie* (syntype: K488852, digital image seen; syntype: E249963 [*Tweedie*], digital image seen). *Eupatorium pinnatifidum* DC. var. *virgata* (Hook. & Arn.) Baker, in Martius, *Fl. Bras.* 6(2): 321, 1876. *Protologue:* Mendoza, valleys near Villa Vicenzia (sic), Aguadita, province of St Luis, *Dr Gillies*; called Chilca by the natives. Uruguay (sic), *Tweedie*.

*Eupatorium pinnatifidum* DC, *Prodr.* 5: 149, 1836.

**Table 4. Linear regressions of quantitative characters onto the latitude and altitude variables**  
Regression coefficients, s.e., *t*-test of significance of predictors and *R*<sup>2</sup> are given

Variable	Latitude					Altitude				
	Coefficient	s.e.	<i>t</i> -value	<i>P</i> -value	<i>R</i> <sup>2</sup>	Coefficient	s.e.	<i>t</i> -value	<i>P</i> -value	<i>R</i> <sup>2</sup>
Leaf length (cm)	-0.12	0.03	-4.49	<0.0001	0.21	6.40E-04	1.40E-04	4.55	<0.0001	0.22
Leaf width (cm)	-0.02	0.01	-1.33	0.1876	0.01	1.20E-04	6.30E-05	1.97	0.0534	0.04
Length of the first leaf lobe (cm)	-0.03	0.02	-1.55	0.1248	0.02	1.40E-04	9.40E-05	1.49	0.1399	0.02
Width of the first leaf lobe (cm)	-0.01	4.00E-03	-2.46	0.0163	0.07	2.10E-05	2.30E-05	0.93	0.3563	0
Length of the terminal leaf lobe (cm)	-0.06	0.02	-2.86	0.0057	0.09	2.20E-04	1.20E-04	1.92	0.059	0.04
Width of the terminal leaf lobe (cm)	-0.01	0.01	-2.03	0.0465	0.04	5.60E-05	3.20E-05	1.77	0.0813	0.03
Involucre length (cm)	0.01	1.70E-03	3.21	0.002	0.12	-1.00E-05	9.70E-06	-1.06	0.295	1.60E-03
Involucre diameter (cm)	1.20E-03	1.70E-03	0.67	0.5028	0	-1.10E-05	9.30E-06	-1.15	0.2524	4.70E-03
Cypsel length (mm)	-0.03	0.01	-3.71	0.0004	0.15	2.10E-04	4.40E-05	4.72	<0.0001	0.23
Cypsel diameter (mm)	-2.00E-03	2.50E-03	-0.78	0.4352	0	2.10E-05	1.40E-05	1.55	0.126	0.02
Pappus length (mm)	0.04	0.01	3.44	0.001	0.13	2.00E-05	7.00E-05	0.28	0.7774	0
Corolla length (mm)	0.01	0.01	0.65	0.5148	0	1.60E-04	6.20E-05	2.56	0.0127	0.07
Width of the corolla limb (mm)	-8.30E-04	2.70E-03	-0.31	0.7607	0	3.10E-05	1.30E-05	2.32	0.0234	0.06
Style branch length (mm)	-0.02	0.02	-1.46	0.1495	0.02	1.90E-04	7.30E-05	2.62	0.0107	0.08
Style appendage length (mm)	0.01	0.01	0.93	0.3569	0	8.30E-05	5.50E-05	1.5	0.1375	0.02

*Type*: unknown country. Locality not indicated, *Née s.n.* (herb. Thieb.), 1813 (holotype: G210192, digital image seen). *Protologue*: 'America austr. legit. cl. Née, sed locus propr. mihi ignotus'.

*Eupatorium crithmifolium* Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 19: 169. 1874.

*Type*: Argentina. Córdoba, Calera de D. Martín Ferreyra (Malagueña), *P.G.Lorentz* 428, 24.viii.1871 (lectotype here designated: CORD!). *Protologue*: 'Cordoba, in collibus apricis'. P. G. Lorentz.

*Eupatorium sauechicoënsis* Hieron., *Bot. Jahrb. Syst.* 22: 775, 1897.

*Type*: Argentina. Buenos Aires: Río Sauce Chico, *Lorentz and Niederlein s.n.* (syntype: B, destroyed, photo FM 16357: LP!; lectotype here designated: CORD! [Pampa aberhalb Río Sauce Chico, *Lorentz and Niederlein s.n.*, 6.v.1879]; isolectotype: (fragment) BA4953!); Sauce Chico, Sierras Pampeanas, *Lorentz* 54, 5.iii.1881 (probable syntype: B, destroyed; isosyntypes: CORD! [sheets A and B]), K488848, digital image screen. Buenos Aires–La Pampa: Indianerpampa (sic) nördl vom Río Colorado, *Lorentz and Niederlein s.n.*, 20–26.iv.1879 (probable syntype: B, destroyed; isosyntype: CORD!). *Acanthostyles sauechicoënsis* (Hieron.) R.M.King & H.Rob., *Phytologia* 22: 112, 1971. *Eupatorium buniifolium* Hook. & Arn. var. *sauechicoënsis* (Hieron.) Ariza, *Kurtziana* 22: 155, 1993. *Protologue*: Argentina. 'Buenos Aires: am Arroyo Sauce Chico in der Pampa im Süden der Provinz nordöstlich von Bahia Blanca nördlich des Ortes Sauce Chico (*Lorentz and Niederlein*, 6 Mai 1879; *Lorentz* 54, 15 März 1881); in der Pampa nördlich vom Río Colorado (*Lorentz and Niederlein* 20–26 April 1879); an nicht angegebenen Orte (*Lorentz* 423, 1881)'.

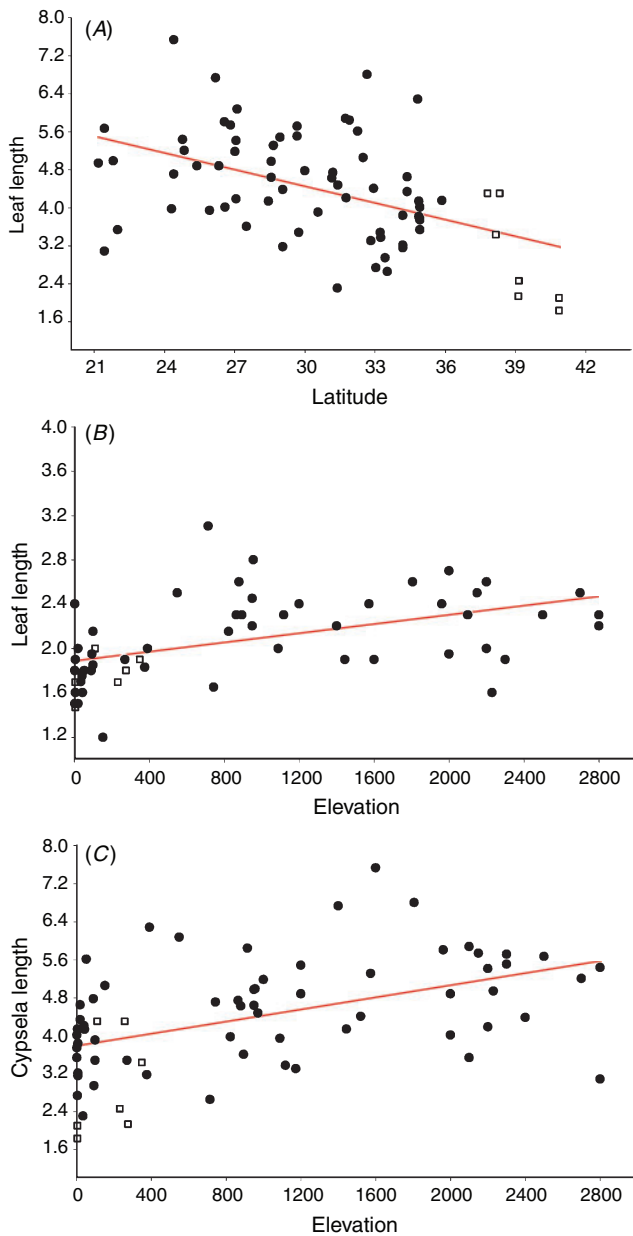
*Eupatorium buniifolium* var. *bakeri* Kuntze, *Revis. Gen. Pl.* 3(3): 146, 1898.

*Type*: Bolivia. Santa Cruz: Sierra de Santa Cruz, 1000 m, *Kuntze s.n.*, v.1892 (lectotype here designated: NY622137, digital image seen). Argentina. Salta: entre Clavisan y La Oyada, *Lorentz and Hieronymus*

1201, 5.ii.1873 (syntype probably: B, destroyed; syntypes: CORD!); Tucumán: 'in der Sierra de Tucuman bei Tafi, *Lorentz* 317, iii.1872' (probable syntypes: B, destroyed; CORD, not found). *Protologue*: 'Bolivia: 1000 m Sierra de Santa Cruz'. Argentina: 'Tucuman, in der Sierra de Tucuman bei Tafi etc. (*Lor.*, März 1872, n. 317); Salta, zwischen Clavisan und La Oyada im Gebiet del Rio del tala im Süden der Provinz (*Lor. u. Hieron.*, 5 Febr. 1873, n. 1201)'.

*Eupatorium buniifolium* var. *hieronymii* Kuntze, *Revis. Gen. Pl.* 3(3): 146, 1898.

*Type*: Argentina. Córdoba: al sud de la Cuesta de Copina, Sierra Achala, *Galander s.n.*, 29.iii.1881 (lectotype here designated: CORD!, syntype: NY1104914, digital image seen); Cuesta de San Ignacio, Sierra Chica de Córdoba, *Galander s.n.*, 23.iii.1881 (syntypes: CORD!, G! [overwritten collection date with black ink as in 1884], NY1104915, digital image seen); San Bartolo, *Lorentz* 248, ii.1872 [1871 in another label on the same sheet] (syntype: CORD!); Cerro Negro cerca de San Bartolo, *Lorentz* 248, ii.1872 (syntype: CORD!); in montanis pr. S. Bartolo, *Lorentz s.n.*, 1872 (syntype: BA24761!); en el valle entre la Sierra Grande y la Sierra Chica de Córdoba, *Hieronymus* 239, 27.iii.1875 (syntype: CORD!). San Luis: Sierra de la Estanzuela, *Galander s.n.*, 3.iii.1882 (syntype: CORD!). *Protologue*: 'Argentina: Sierra chica de Cordoba–Sierra Achala (*Galander*)'. Argentina: 'Mendoza: in der Sierra Lucas und im Norden des Cerro Payen bis in die Gegend um die Stadt Mendoza (*Niederl.*, Juli 1879); San Luis: in der Sierra de la Estanzuela (*Galander*, 3 März 1882); Córdoba: im Gebirgszug des Cerro negro bei San Bartolo im Süden der prozinz (sic) (*Lor.*, Febr. 1871, n. 248 und 661); auf sonnigen Hügeln bei der Calera von D. Martin Ferreyra in Malagueña (*Lor.*, 24 Aug. 1871, n. 428) [type of *Eupatorium crithmifolium* Griseb.]; auf Cuesta de San Ignacio (*Galander*, 23 März 1881) und sonst in der Sierra Chica sehr häufig auf trockenen Bergen; südlich vos der Cuesta de Copina (*Galander*, 29 März 1881) im Thal zwischen der Sierra Chica und Sierra Achala häufig (*Hieron.*, 27 März 1875)'.



**Fig. 2.** Plots of linear regression analyses for *Acanthostyles buniifolius* (dots) and *A. saucechicoensis* (empty squares). (A) Latitude v. leaf length. (B) Elevation v. leaf length. (C) Elevation v. cypsel length.

Shrubs 0.5–3 m tall, resinous, laxly branched. Stems hexagonal or terete, striate, glabrous. Leaves resinous, mainly opposite, rarely alternate in terminal branches, petiolate, petiole rarely inconspicuous in entire leaves; blades narrowly oblong or linear, entire, or lobed to pinnatisect, sometimes bi-pinnatisect, 2–8 cm long in total length, up to 0.1–2 cm broad in the middle of rachis, lobes (if present) becoming linear, 1–7, 0.15–2.6 cm long, up to 0.02–1.2 cm broad, terminal lobe (if present) (0.07–) 0.18–4.5 cm long, up to 0.02–0.65(–1.8) cm broad, surface with punctuations of glandular hairs. Inflorescences long pendent or suberect, paniculate cym, capitula numerous;

pedunculates or subsessile, peduncles up to 0.5 cm long. Involucres usually cylindrical, rarely campanulate, 3.7–7.6 mm long, up to 1.8–4.3(–6) mm broad; phyllaries ~25, 2.5–4 mm long, up to 0.8–1.3 mm broad, subimbricate, 3–5 seriate, with glandular hairs on the outer surface, mainly on the margins and at the apex, otherwise glabrous; receptacles convex, glabrous, with irregular surface. Florets 5(–6) per capitulum; corollas funnellform, 3–5.6 mm long, limb 0.49–1 mm broad, purplish or whitish; lobes ovate–triangular, ~0.5 mm long, up to ~0.3 mm broad, with inner surface smooth, outer surface glanduliferous; cells of limb elongate, often with closely sinuous lateral walls; anthers ~1.6 mm long, up to 0.5 mm broad, anther appendages ~0.25 mm long, up to 0.2 mm broad, thecae ~1.4 mm long, up to 0.3 mm broad, anther collars elongate, cylindrical, ~0.1 mm long, up to 0.05 mm broad, with subquadrate cells below, cell walls with annular to intricately ornate thickenings; anther appendages oblong to triangular, longer than wide; style 6.5–12 mm long, style base not enlarged and glabrous, without nectary; style branches long-linear, 1.4–3.6(–4.5) mm long, with stigmatic papillae elongate in two lines and forming a brush, with flagelliform apical appendages, (1–)1.5–3.6 mm long, with many large non-septate sweeping hairs scattered along surface. Cypselae prismatic, 4- or 5-ribbed, 1.2–3.1(–3.9) mm long, up to 0.4–0.7(–1) mm broad, with few short twin hairs on ribs, clustered at the base, and scattered at the apex; carpodium inconspicuous or minutely annuliform, uniseriate with minute subquadrate cells; pappus of ~30–40 bristles, 2.9–5.2 mm long, persistent, uniseriate, basally fused in a ring, densely and divaricately barbellate, not enlarged at apex, yellowish or whitish. Pollen grains spheroidal, polar view (P) × equatorial view (E) 17 × 20 μm, tricolporate, echinate, with very short spines.

#### Chromosome number

$2n = 20 + 2B$  (Wulff *et al.* 1996).

#### Etymology

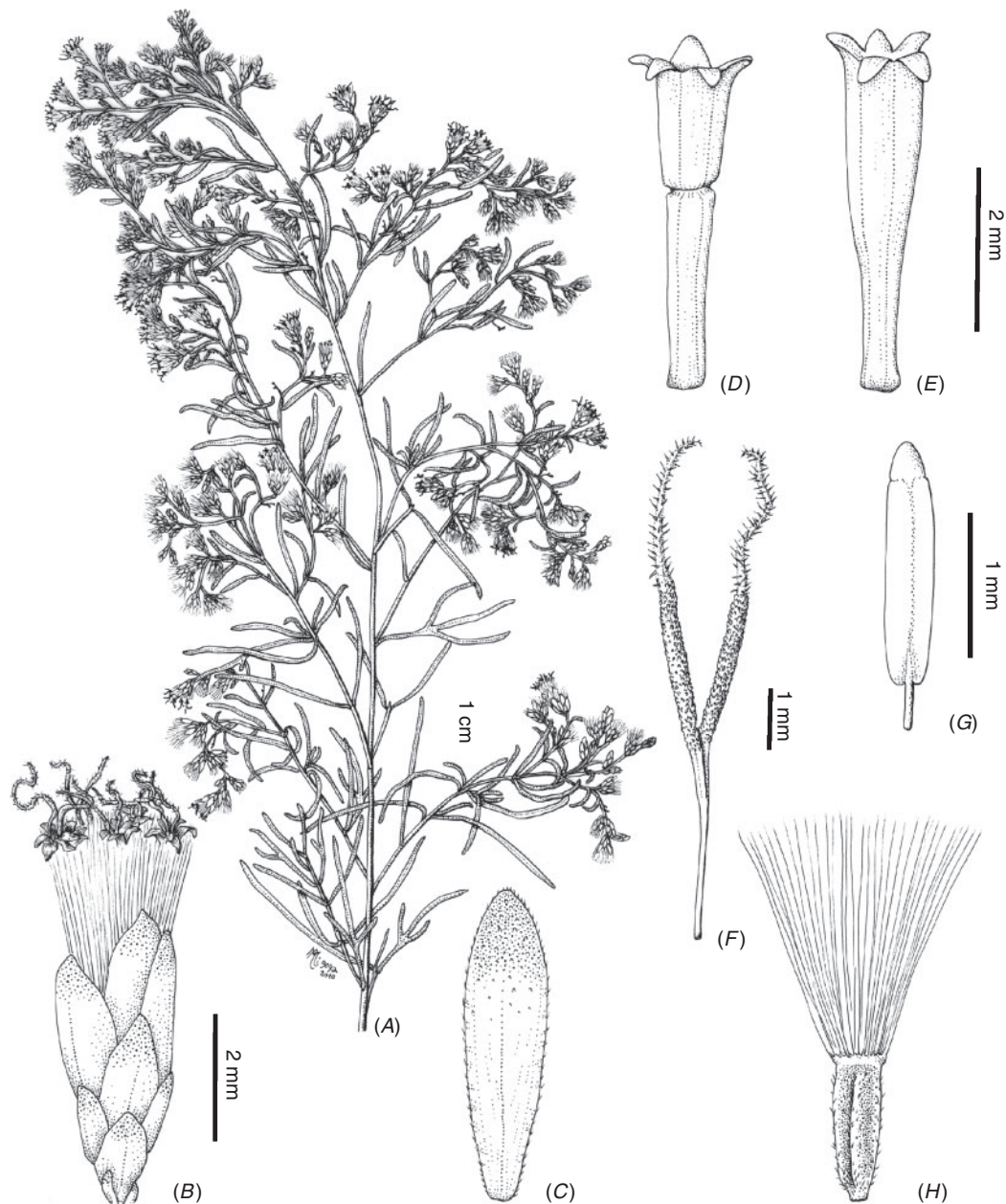
From Greek *bounion*, a classical name used by Dioscorides for a plant, *Bonium ferulaceum* Sm. (earth-nut), or Latin *bunio* or *bunii* for a kind of Swedish turnip (Plinius) (Quattrocchi 1999), and Latin *folium*, leaf. It probably refers to the pinnatifid leaves of *Bonium* L. (Apiaceae) that resemble those of this species.

#### Additional illustrations

Cabrera (1971), fig. 3 (sub-*Eupatorium saucechicoense*); Cabrera (1974), fig. 100 (sub-*E. buniifolium*); Cabrera (1978), fig. 47 (sub-*E. buniifolium*); King and Robinson (1987), plate 8.

#### Distribution and biogeographical considerations

*Acanthostyles buniifolius* is widely distributed in southern South America (Fig. 6), from sea level to 2985 m. It occurs in the west from central Bolivia (eastern Cochabamba and western Santa Cruz Departments) to central Argentina (San Luis Province). In the east, it occurs from southern Brazil (Rio Grande do Sul State), Uruguay and eastern Argentina, to the southern coast on Rio de la Plata estuary. It also appears on the hills of southern Buenos Aires Province (Sierra de la Ventana and surrounding



**Fig. 3.** *Acanthostyles buniifolius*. (A) Reproductive terminal branch; (B) capitulum; (C) phyllary; (D) corolla with a constriction or fold; (E) corolla without constriction; (F) style and style appendages; (G) stamen; (H) cypsela with pappus. (A–D, F–H) from Grossi *et al.* 2 (LP); and (E) from Venturi 1988b (LP). Scale bar for A=1 cm; B, C, D, E and H=2 mm; F and G=1 mm.

areas), and La Pampa Province (Sierras Mahuidas), reaching the Rio Negro river. It is important to mention that only one specimen kept at G was labelled as coming from Colombia ('San Francisco prope Bogotá, Nov 1909, *Apollinaire s.n.*, Herbarium Reineck'). However, *A. buniifolius* does not reach that latitude, and the location on the label is interpreted as an error. According to several studies (King and Robinson 1971, 1987; Ariza Espinar 1994; Hind and Robinson 2007), this species may, however, occur in Paraguay, although it has

not been cited from that country in floristic treatments or check-lists (Cabrera 1996; Cabrera *et al.* 1997, 1999; Freire 2008), and we have not been able to find specimens from there.

From a biogeographical point of view (Cabrera and Willink 1973), *A. buniifolius* is from the Neotropical region, in Pampean, Espinal, Monte, western and mountainous Chacoan, and Prepuna Biogeographical Provinces. This species is commonly found as introductions of the Espinal vegetation in the Pampa of





**Fig. 4.** *Acanthostyles buniifolius*. (A) Habitat and plant; (B) leaves in a terminal branch; (C) capitulescence; (D) capitula, showing the purple style appendages; (E) adaxial leaf surface, showing a densely pubescent area on the midvein; (F) leaf surface with glandular hairs in epidermal depressions. (A–D) from Gutiérrez *et al.* 464, 465 (LP); and (E, F) from Grossi *et al.* 2 (LP). Scale bar for E = 150  $\mu$ m; F = 100  $\mu$ m.

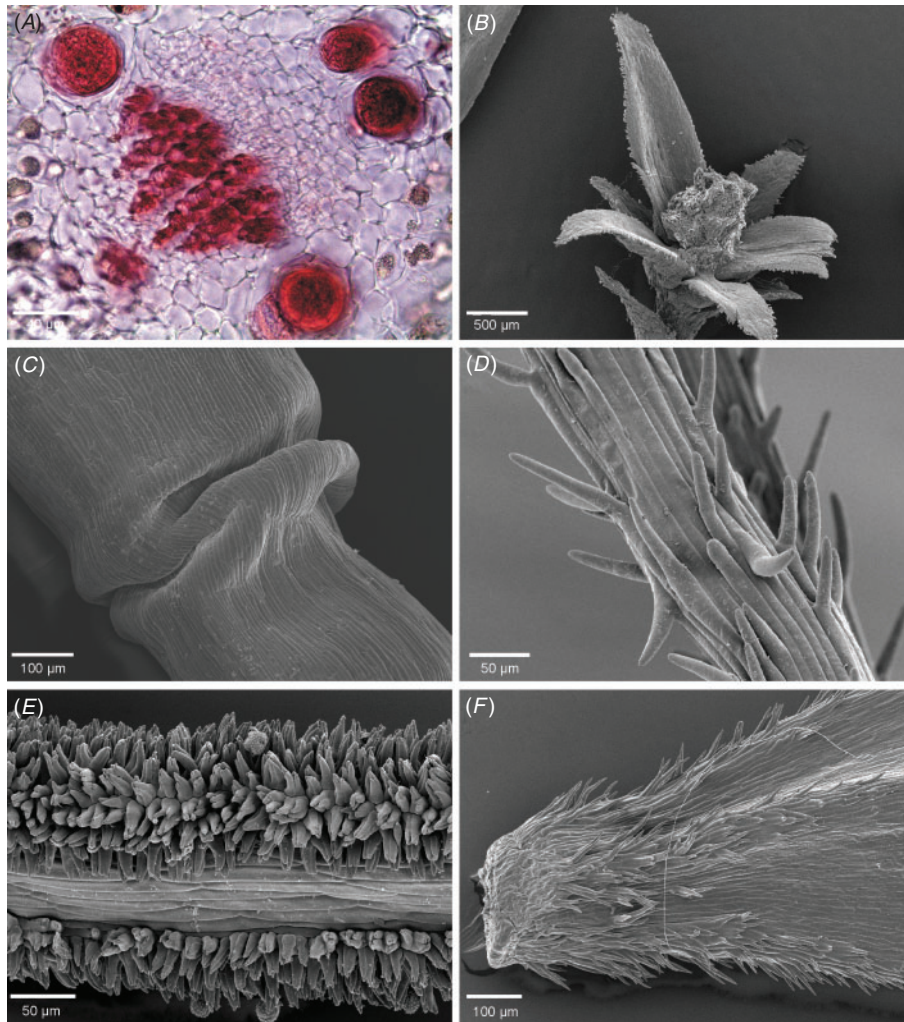
Argentinean Buenos Aires and La Pampa Provinces. A biotic migrational route from the Andes to Brazil, through Pampean ranges, Tandilia and Ventania ranges, Uruguayan ranges and the Brazilian Plateau and southern Brazilian ranges was postulated many years ago (i.e. Brade 1942). Frenguelli (1950) gave the name of peripampasic orogenic arc to the biotic corridor constituted by Sierras Pampeanas, and other mountainous areas near Ventania, Mahuidas and Tandilia ranges. According to Crisci *et al.* (2001), a main distributional pattern was found connecting the mountain ranges of southern Brazil, Uruguay, Tandilia, Ventania and Sierras Pampeanas. Particularly, the evolution of Asteraceae in Ventania and related areas was hypothesised to have been affected mainly by Tertiary and Quaternary geologic events, and some discontinuous patterns could be explained also by vicariance under dry conditions (Crisci *et al.* 2001).

#### Habitat

*Acanthostyles buniifolius* grows in sandy, rocky (Fig. 4A), silicon and loamy soils, on streams embankments, floodplains, hillsides, quebradas, foothills, slopes and roadsides. The species occurs in shrubby vegetation, forest and grassland. It is very common in the steppe climax of the province of Buenos Aires, especially in poor soils and rocky places (Cabrera 1963). Also, it was collected in natural fields loaded with cattle, where it is an invasive species (Cabrera 1974). *A. buniifolius* behaved as a sprouter in fire responses in temperate savannas (Galíndez *et al.* 2009).

#### Vernacular names and uses

‘Alecrim do campo’ (Brazil, Avila de Araujo 31); ‘chilca’ (Argentina, Gillies 182; Ariza Espinar 1994); ‘chilca’ or ‘chirca’



**Fig. 5.** *Acanthostyles buniifolius*. (A) Leaf transection, showing secretory cavities; (B) receptacle; (C) constriction and fold of the corolla; (D) sweeping hairs of the style appendage; (E) part of a style branch, showing the smooth sterile line and stigmatic papillae; (F) basal part of the cypsela, showing twin hairs at the base and ribs. (A–F) from Grossi *et al.* 2 (LP). Scale bar for A = 40 µm; B = 500 µm; C and F = 100 µm; D and E = 50 µm.

(Uruguay, *Osten 5510*; *Rosa-Mato 462*); ‘chilquilla’ (Ariza Espinar 1994); ‘mio-mio’ (Argentina, *López 6*); ‘pichanilla del cerro’ (Ariza Espinar 1994); ‘romerillo’ (Argentina, *Falcone and Castellanos 361519*; *López 8*; *Velázquez and Godoy 19*; Ariza Espinar 1994); ‘romerillo crespo’ (Argentina, *Hunziker 6660*; Ariza Espinar 1994); ‘romerito’ (Ariza Espinar 1994); ‘romero’ (Argentina, *Lorentz s.n., 1872*); ‘tolilla’ (Argentina, *Jørgensen 1379*). Leaves and stems are used as a bitter tonic. Fenilpropanoids, flavonoids, diterpens and triterpens have been found in aerial organs, and biological activities have been studied (antioxidant, antiviral, antihemolytic activities, inhibition of DNA polymerase, and cell inhibition–proliferation) (Ariza Espinar 2006, and references therein).

#### Conservation status

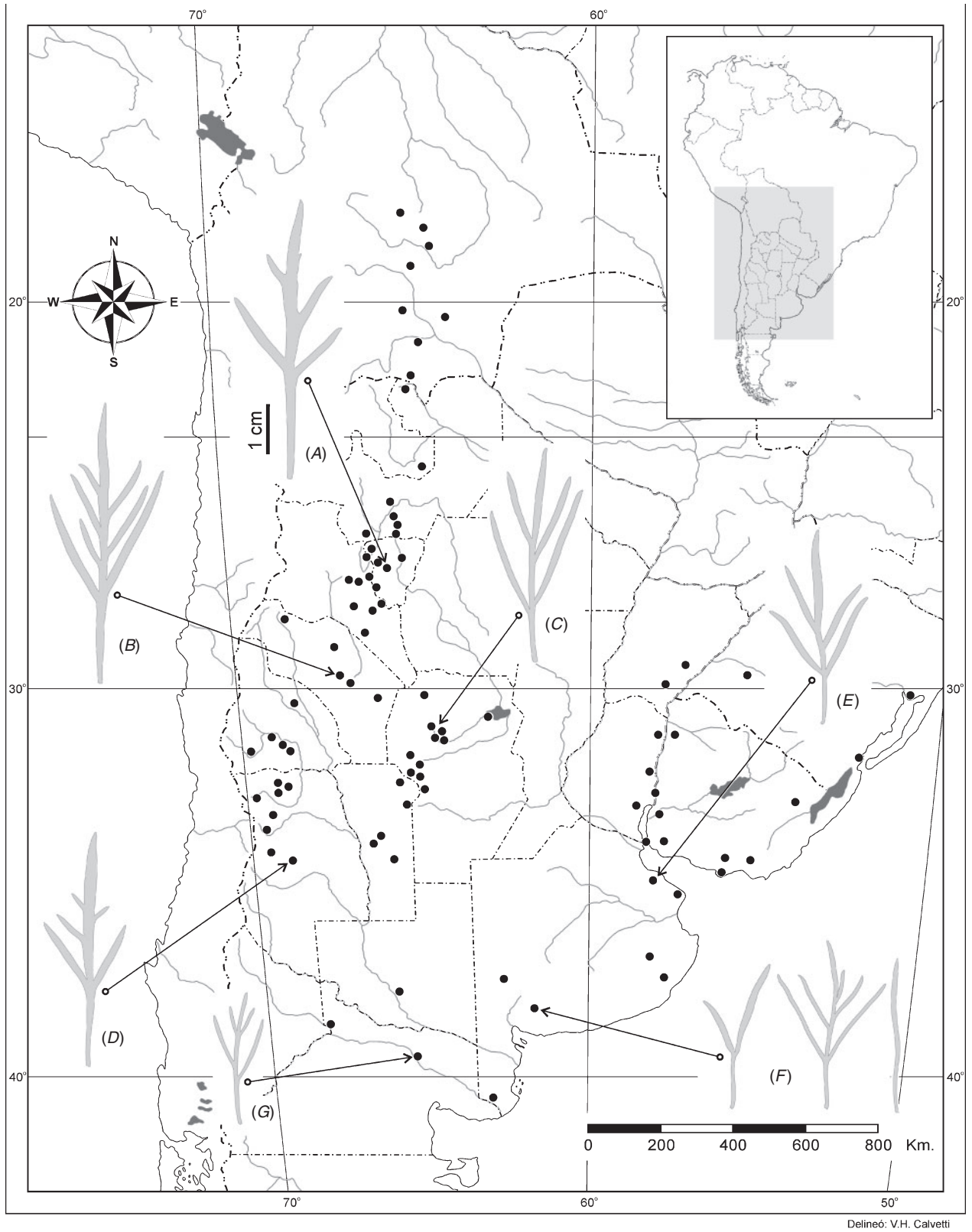
According to IUCN criteria (IUCN 2010), *A. buniifolius* is here proposed to be included in the Least Concern (LC) category,

because of its widespread distribution range and the presence of recent collections suggesting an increase in population size.

#### Taxonomic and nomenclatural observations

*Eupatorium buniifolium* Hook. & Arn.

Many specimens that Hooker and Arnott studied were either deposited in GL (currently on permanent loan to E) or transferred by Hooker to K. However, it is often assumed that when Hooker moved to Kew, the collections he brought with him were the holotypes of many Hooker and Arnott names. This is not always the case, and material kept at K (if it exists) has to be considered, along with that at E (N. Hind, pers. comm.). However, in this case, E does not have specimens of *Tweedie 1128* (H. Noltie, pers. comm.), so we recognised the unique specimen deposited in K as the holotype of this species,



Delineo: V.H. Calvetti

**Fig. 6.** Geographical distribution of *Acanthostyles buniifolius*, showing the morphological leaf variation. (A) Drawn from *Venturi 1988b* (LP); (B) from *Falcone and Castellanos 3615* (LP); (C) from *Bernardello and Ariza Espinar 407* (CORD); (D) from *Ruiz Leal and Roig 16107* (LP); (E) from *Grossi et al. 2* (LP); (F) from *Proyecto Ventania 9* (LP); and (G) from *Estrada s.n.* (BAB 80701). Scale is the same for all leaves. Scale bar (A–G) = 1 cm.

following Article 9.1 and Recommendation 9.A4 of the ICBN (McNeill *et al.* 2007).

*Eupatorium virgatum* D. Don ex Hook. & Arn.

There are many specimens labelled with original data housed at E and K, and several original localities and two collectors cited in the protologue. Thus, we selected *Gillies 183* collected in Villavicencio (Las Heras Department, Mendoza Province, Argentina) housed at K, as lectotype, following Articles 9.9, 9.10, and Recommendation 9.A of the ICBN (McNeill *et al.* 2007). This specimen fits appropriately with the original description and was collected from a more precise location than were the other specimens. *Gillies 182* from Quebrada de Canota in Argentina (mounted with *Gillies 184*, *Gillies 183*, and *Tweedie s.n.* on the same sheet at K, and with *Tweedie s.n.* at E) is not considered type material of *E. virgatum*, because the collection locality cited on the label was not mentioned in the protologue by Hooker and Arnott.

*Eupatorium crithmifolium* Griseb.

According to Stafleu and Cowan (1979), the main Grisebach herbarium is at GOET, containing most of his types, although no type material of *E. crithmifolium* was located at GOET (J. Heinrichs, pers. comm.). Thus, it is not clear which specimen was analysed by Grisebach for describing *E. crithmifolium*, but we assume that the specimen was once housed at GOET. More recently, Hunziker (1960) and Ariza Espinar (1994) recognised a specimen deposited at CORD as an isotype. Ariza Espinar (1994) noted that Grisebach used to cite in his protologues only the original province, sometimes with a short ecological sentence; however, he indicated neither dates nor collection numbers. In the case of *E. crithmifolium*, Grisebach (1874) cited only ‘Cordoba, in collibus apricis’, but additional data were found on the original label (Hunziker 1960; M. A. Grossi, D. G. Gutiérrez, P. C. Berrueta and J. J. Martínez, pers. obs.). It is important to mention that original labels handwritten by Lorentz and Hieronymus on the sheets of type specimens at CORD were once removed, and replaced by other typed labels, without the observations of the collectors. The original labels were found later and reattached to the corresponding sheets (Hunziker 1960). Another interesting point is that the specimen at CORD could never have been analysed by Grisebach because he never visited Argentina. According to Articles 9.2, 9.9, 9.10, and Recommendation 9.A of the ICBN (McNeill *et al.* 2007), the isotype kept at CORD is selected here as the lectotype of *E. crithmifolium*. Hieronymus (1897) included this specimen within his third form of *Eupatorium buniifolium*.

*Eupatorium saucechicoense* Hieron.

Hieronymus (1897) cited several original specimens with different localities, collectors, collector’s numbers and dates in the protologue of this species. According to Stafleu and Cowan (1979), Hieronymus’ collections were mainly housed at B, but with many specimens also at CORD. Because no Hieronymus type material is extant at B (R. Vogt, pers. comm.), we select a

syntype (*Lorentz and Niederlein s.n.*) at CORD as a lectotype of this species, following Articles 9.9, 9.10, and Recommendation 9.A of the ICBN (McNeill *et al.* 2007).

*Eupatorium buniifolium* var. *bakeri* Kuntze

According to Article 7.7 of the ICBN (McNeill *et al.* 2007), Kuntze (1898) validly published this variety using the description of ‘Forma 1’ made by Hieronymus (1897). Typifications of Kuntze’s names are therefore brought about by following the same article, in that the types are elements selected from the context of the validating description, unless the validating author has definitely designated a different type. Although Kuntze (1898) mentioned a collection under his name, he did not exclude the specimens cited by Hieronymus (1897); thus, the material cited under the relevant forms by Hieronymus (1897) also have to be considered as original material, along with the collections specified by Kuntze (N. Hind, pers. comm.). In this case, var. *bakeri* has, as original material, the Kuntze collection from the Sierra de Santa Cruz as well as the Lorentz and Hieronymus collections cited by Hieronymus. Ariza Espinar (1994) previously took this point of view and recognised the specimen *Lorentz and Hieronymus 1201* at CORD as an isosyntype. Therefore, following Articles 9.9, 9.10, and Recommendation 9.A, we select as lectotype the specimen cited by Kuntze housed at NY (and collected by Kuntze) that fits appropriately with the diagnosis made by Hieronymus (1897).

*Eupatorium buniifolium* var. *hieronymii* Kuntze

In addition, Kuntze (1898) validly published *E. buniifolium* var. *hieronymii* using the description of ‘Forma 3’ made by Hieronymus (1897). However, in this case, Kuntze (1898) cited two specimens collected by Galander (without numbers) that were mentioned by Hieronymus, namely one from Sierras Chicas and another from Sierras de Achala (both from Córdoba, Argentina). Similarly, following the same ICBN article mentioned above, var. *hieronymii* has the Galander material (cited by Kuntze), as well as the Galander, Niederlein, Hieronymus and Lorentz materials (cited by Hieronymus). In neither instance, did Kuntze actually specify a type, or exclude any material. *Lorentz 428* must be excluded from consideration because it was previously selected by Grisebach as original material of *Eupatorium crithmifolium*. Thus, following Articles 9.9, 9.10 and Recommendation 9.A of the ICBN (McNeill *et al.* 2007), we designate the specimen collected by Galander on 29 March 1881 from Sierra de Achala (Cuesta de Copina), housed at NY, as lectotype. This specimen fits appropriately with the original description made by Hieronymus (1897) and was one of the specimens seen by Kuntze and cited in his work.

*Specimens examined* (\*specimens of *A. saucechicoense* used in multivariate analysis)

ARGENTINA. Buenos Aires: Isla Martín García, Hurrell *et al.* 3010, 3011, 20.iii.1996 (LP); Partido La Plata, Elizalde, alrededores de La Plata, Cabrera 781, 22.iv.1929 (LP);

Partido Patagones, Carmen de Patagones, Oficina–Pocho, *Spezzini s.n.* ii.1898 (LP, ex LPS 13045)\*; Partido Tornquist, Sierra de la Ventana, Sierra Central, *Alboff 92*, 23.xi.1895 (LP). Catamarca: Department (Dpto) Ambato, El Ocho, 1400 m, *Parodi 14096*, ii.1941 (LP). Córdoba: Dpto Calamuchita, Valle de Los Reartes, Sierra Chica, *Castellanos 215*, 24.iv.1917 (SI). Corrientes: Dpto Curuzú Cuatiá, 10 km N de Curuzú Cuatiá, por Ruta 14, *Schinini et al. 17613*, 23.ii.1979 (LP). Jujuy: Dpto Santa Bárbara, Abra de Los Morteros, 1600 m, *Cabrera et al. 21725*, 28.ii.1971 (LP). Río Negro: Dpto Avellaneda, Isla Choele-Choel, *Jørgensen and Girola s.n.*, 6.iii.1913 (BAB)\*. Salta: Dpto Candelaria: Río Unquillo, 1400 m, *Venturi 3825*, 7.iv.1925 (SI). BOLIVIA. Tarija: Tarija, 1900 m, *Fiebrig 2835*, iv.1904 (G). BRAZIL. Rio Grande do Sul: Tupacretá, *Avila de Araujo 31*, ii.1939 (LP); Viamão prope Porto Alegre, *Rambo 46709*, 10.iv.1950 (LP). URUGUAY. Canelones: Carrasco, *Felippone 4704*, without date (SI); Toledo, *Herter 924*, v.1927 (SI).

### Morphology and anatomy of selected structures

#### Vegetative traits

*Acanthostyles* has laxly grouped and highly variable leaves (Fig. 4A, B) that can be simple with entire margins, lobed, pinnatifid or even bi-pinnatifid (Fig. 6A–G). The epidermis is uniseriate with a somewhat thick cuticle. The leaf blade is amphistomatous with anomocytic stomata, at the same level as the other epidermal cells and each one shows a conspicuous substomatal chamber. The chlorophyllous mesophyll is anatomically isolateral, usually with two to four layers of palisade. There are several resin cavities into the mesophyll, which are associated with the phloem, in the middle of all the leaf transection (Fig. 5A). These resin cavities could be considered to have adaptive value in xerophytic conditions (Fahn and Cutler 1992).

Two types of glandular hairs were found on both leaf surfaces. The first type (a) are capitate hairs, with a simple foot, stalk uniseriate (one- or) two- to six-celled, cylindrical or slightly tapering below, with cells usually being longer than broad, and cross- and lateral walls thin; head is one-celled, spherical or ovoid, remaining intact or collapsing early, with thin lateral walls. When the head collapses early or during the first stages of its growth, it can be erroneously identified as a cylindrical hair. This type of hair can be found on the whole leaf surface, growing densely into low grooves of the main veins on the adaxial surface (Fig. 4E), or usually one or two hairs into low depressions associated with the biseriate vesicular glandular hair (Fig. 4F).

The other type of hairs (b) are biseriate vesicular glandular hairs, with a one- or two-celled foot, a biseriate, entire body, one or two cells in each row, isodiametric cells, thin cross- and lateral walls, cuticular vesicle enclosing terminal cells, restricted to the apex and persistent or collapsing early. This type of hair can be found on the whole leaf surface, usually associated with the capitate hair (Fig. 4F).

The association of different types of hairs into depressions on the leaf epidermis has already been mentioned in other tribes of

Asteraceae (e.g. *Baccharis* L.) as ‘tufted hairs’ or ‘hairs in tufts’ (e.g. Müller 2006).

#### Reproductive traits

The capitula are grouped into paniculate cymes (Fig. 4C). Hieronymus (1897) distinguished erect, suberect or subpendulous capitula that he associated with his five morphological forms. However, field observations showed a transitional variation of this trait. A tendency to a pendulous capitulescence was noted in several populations, even in the same plant.

The involucre of the capitulum is usually cylindrical (Figs 3B, 4D), although campanulate involucre may be found in some specimens. Phyllaries are shortly ovate to narrowly elliptical or obovate (Fig. 3C), and the outer ones are gradually smaller than the inner ones. They have biseriate vesicular glandular hairs on the outer surface, mainly in margins and at the apex. The lack of capitate hairs is notable. Receptacle is irregularly convex (Fig. 5B).

There are five or sometimes six florets with five-lobed tubular corolla per capitulum. Each lobe of the corolla has glandular trichomes on the outer surface, mainly at the apex. The biseriate vesicular glandular hairs have the same appearance as on leaves and phyllaries. Also, corollas lack capitate hairs.

An interesting morphological feature, not mentioned in any previous descriptions, is the presence of a constriction or fold of the corolla (Figs 3D, 5C) or lack thereof (Fig. 3E). This constriction marks the place of attachment of the stamen filaments in the area between the limb and the tube. This character was clearly illustrated in a previous drawing of *A. buniifolius* (Cabrera 1974, fig. 100, sub-*Eupatorium buniifolium*), but not in others (Cabrera 1971, fig. 3, sub-*E. saucechicoense*; Cabrera 1978, fig. 47, sub-*E. buniifolium*; King and Robinson 1987, plate 8).

As mentioned above, features of the style and its appendage are distinctive in *Acanthostyles* (Fig. 3F). Style base is not enlarged and it is glabrous, without nectary. Style branches are long-linear, with elongate stigmatic papillae in two densely marginal lines and forming a brush (Fig. 5E). Flagelliform appendages have many large non-septate sweeping hairs scattered along the whole surface (Fig. 5D). Cypselaes are prismatic and four- or five-costate (Fig. 3H). Typical asteracean twin hairs were found on ribs, and were clustered at the base (Fig. 5F) and scattered at the apex.

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**Appendix 1. Additional specimens examined (\*specimens of *Acanthostyles saucechicoensis* used in the multivariate analysis)**

ARGENTINA. Buenos Aires: Isla Martín García, *Delucchi 2380*, 16.iii.2000 (LP). Partido Bahía Blanca, Bahía Blanca, camino a Cueva de los Leones, *Hunziker 4406*, 2.iii.1942 (CORD)\*. Partido Balcarce, Balcarce, sierras, *Cabrera 19891*, iii.1969 (LP). Partido La Plata, La Plata, *Cabrera 874*, 30.iv.1929 (LP); Elizalde, cerca de La Plata, *Cabrera 1686*, 22.iii.1931 (LP); Elizalde, alrededores de La Plata, *Cabrera 2129*, 5.iv.1932 (LP); alrededores de La Plata, barrio Cementerio, *Grossi et al. 1*, 12.iii.2008 (LP); La Plata, Altos de San Lorenzo, calles 25 y 76, *Gutiérrez et al. s.n.*, 19.iii.2008 (LP). Partido Magdalena, cerca de Ruta 11 y camino a Atalaya, *Gutiérrez and Brianese s.n.*, 15.iii.2010 (LP). Partido Patagones, without locality, *Scala s.n.* (LP 1854); without locality, *Spagazzini s.n.* (LP, ex LPS 13044). Partido Tandil, Tandil, *Clos 10*, iii.1921 (LP); iii.1971, *Cabrera 21852* (LP). Partido Tornquist, Sierra de la Ventana, *Cabrera 4458*, 24.v.1938 (LP); Sierra de la Ventana, La Península, *Cabrera and Fabris 7*, 19.iii.1948 (LP); Sierra de la Ventana, Ruta 76 a 500 m del cruce a Sierra de la Ventana, 350 m, *Proyecto Ventania 9*, 29.iii.1978 (LP)\*; Sierra de la Ventana, quebrada del arroyo San Bernardo, 400–550 m, *Proyecto Ventania 673*, 14.iii.1979 (LP); Sierra de la Ventana, camino al Hueco de la Paloma, sitios 1 y 2, *Barrera 22*, 24, iii.1991 (LP); Sierra de la Ventana, Parque La Gruta, sitio 5, iii.1991, *Barrera 23* (LP); Sierra de la Ventana, acceso Cerro de la Ventana, sitio 4, iii.1991, *Barrera 25* (LP); Sierra de la Ventana, Hueco de la Paloma, sitio 3, *Barrera 26*, iii.1991 (LP). Catamarca: Dpto Ambato, Sierra de Ambato, camino antes de llegar a El Rodeo desde Catamarca, *Ulibarri 853*, 14.ii.1974 (CORD). Dpto Andalgalá, El Candado, 2700 m, *Jorgensen 38126*, ii.1915 (LP); El Candado, *Jörgensen 1379*, 10.iv.1916 (BA); Cuesta de la Chilca, 1600 m, *Parodi 14256*, ii.1941 (LP); Andalgalá a Capillita, *O'Donnell and Meyer 5243*, 21.iii.1947 (LP); Cuesta de Chilca, 27 2/3°S., 1900 m, *Böcher et al. 2320*, 15.i.1956 (LP); Cuesta de Mina Capillitas, lado S, 2500 m, *Cabrera et al. 14120*, 11.ii.1961 (LP); Cuesta de Minas Capillitas, 2500 m, *Cabrera et al. 24770*, 30.i.1974 (LP); Ruta Provincial 18, de Andalgalá a la provincia de Tucumán, 27.83549°S, 65.81038°W, 1401 m, *Gutiérrez et al. 517*, 12.iv.2008 (LP). Dpto Belén, Yacutula, *Lorentz 664*, 24.i.1872 (CORD); en el altivalle de Las Granadillas cerca de Yacutula, *Lorentz s.n.*, 1.i.1872 (CORD); Belén, *Cabrera 98*, 3.iii.1929 (LP); Corral de Ramas, Condor Huasi, 1950–2250 m, *D'Antoni 120*, 16.iii.1974 (LP). Dpto Capital, Cuesta El Portezuelo, *Bartlett 19621*, 5.ii.1943 (LP). Dpto Paclín: por el camino de La Merced a Balcozna, entre Balcozna y Villa Collantes, 1100–1280 m, *Hunziker 18792*, 8.iv.1966 (CORD). Dpto Santa María, La Cuesta, *Reales 1767*, 2.iii.1949 (LP). Dpto unknown, Region Andina, 189?, without collector (LP). Córdoba: Dpto Calamuchita, Valle de los Reartes, *Castellanos 4854*, ii.1922 (BA); Valle Los Reartes, without collector, 15.vi.1940 (LP 37811); Embalse del Río Tercero, *Hunziker 6498*, 24.ii.1944 (LP); Valle de los Reartes, 760 m, *Morello 5231*, 22.i.1950 (LP). Dpto Capital, inmediaciones de La Carolina, en los suburbios noroeste de la ciudad de Córdoba, *Hunziker 15396*, 23.iv.1960 (CORD). Dpto Colón, Unquillo, *Bruch s.n.*, 1926 (LP 1891, 1892); camino El Cuadrado, *Dawson 245*, iii.1938 (LP); Salsipuedes, *Lahitte 60451*, vi.1939 (LP); La Quebrada, cerca de Río Ceballos, *Cozzo 31*, iv.1946 (LP); Río Ceballos, sierras, *Lanfranchi 770*, 28.ii.1949 (LP); Sierra Chica, Quebrada de Río Ceballos, *Guzman 31*, 16.iii.1968 (CORD); Sierra Chica, poco antes de La Calera, *Bernardello and Ariza Epinar 407*, 22.iii.1983 (CORD); Cabana, *Chiarini 330*, 28.iii.2000 (CORD); Río Ceballos, Reserva Hídrica La Quebrada, camino a Pozo Verde, *Ariza Espinar 3657*, 14.iii.2005 (CORD). Dpto Ischilín, sierras al este de Deán Funes, *Sayago 702*, iv.1951 (LP). Dpto Punilla: Cuesta de San Ignacio, Sierra Chica de Córdoba, *Galander s.n.*, 23.iii.1884 (G); Huerta Grande, Sierra Chica de Córdoba, *Stuckert 1689*, 16.ii.1897 (G); Valle de Punilla, Capilla del Monte, en el cerro Uritorco, *Hosseus 426*, 10.iii.1917 (CORD); Capilla del Monte, *Lahitte 60448*, vi.1939 (LP); Los Cocos, Sierra Chica, *Cabrera 6384*, iii.1940 (LP); La Falda, 'Molino de Oro', *Rodrigo 2783*, ii.1941 (LP); San Esteban, *Soriano 1103*, 9.iii.1944 (LP); La Falda, Valle de Punilla, *Rossi 935*, 22.ii.1947 (LP); Valle Hermoso, 850 m, *Gutiérrez 157*, 19.iv.1947 (CORD); márgenes del Lago San Roque, *Lanfranchi 998*, 8.iii.1952 (LP); El Cuadrado, *Sayago 1315*, 15.vii.1952 (LP); Ruta Nacional 20, márgenes y alrededores del arroyo de La Suela, a 4 km al SE por la ruta de Copina, 1181 m, 31°34.59'S, 64°39.489'W, *Gutiérrez et al. 420*, 9.iv.2008 (LP). Dpto Río Cuarto: Alpa Corral, Río de las Barrancas o Alpa Corral, *Hosseus 726*, 19.iv.1946 (CORD). Dpto Río Primero, El Suncho, 1500 m, *Jörgensen 1379*, v.1915 [another label as Andalgalá, *Jörgensen*, 1915] (SI); Dpto San Javier, Quebrada del Tigre, *Ruiz Leal 12476*, 9.v.1949 (LP). Dpto Santa María, La Granja, Alta Gracia, *Birabén 25*, 53, ii.1937 (LP); alrededores de Malagueño, *Hunziker 6660*, 9.vii.1946 (LP). Dpto Calamuchita–Colón–Punilla–Santa María, Sierra Chica, *Lossen 265*, iii.1925 (SI). Dpto unknown, locality unknown, *Stuckert 6820*, 25.iv.1899 (LP); *López 6*, 8, without date (LP); locality and collector unknown, provincia de Córdoba (LP 1888). Corrientes: Dpto Paso de los Libres, 2 km NE del Río Miriñay, por Ruta 127, 16.ii.1979, *Schinini et al. 17293* (LP). Entre Ríos: Dpto Colón, arroyo El Pelado, 60 km al S de Ubajay, *Burkart et al. 23550*, 9.iii.1962 (LP, SI); Parque Nacional El Palmar, alrededores del camping, *Gutiérrez 672*, xi.2008 (LP). Dpto Concordia, Pederal, *Friedman 539*, i.1936 (LP); Colonia Yerúa, Estación Experimental del INTA, *Burkart and Gamero 21973*, 11.iv.1960 (LP). Dpto Gualaguaychú: Palavecino, *Myndel Pedersen 9801*, 4.iv.1971 (SI). Dpto Paraná, Paraná, *Báez 15*, ii.1922 (LP). Dpto Uruguay, Colonia Elía a [puerto] Campichuelo, *Burkart and Troncoso 24271*, 10.iv.1963 (LP). Jujuy: Dpto Santa Bárbara, *Cabrera et al. 22148*, 17.ii.1972 (LP); camino a Cachipunco, loma pelada del Fuerte, subida al abra, *Guaglianone et al. 1830*, 15.iii.1983 (SI); Sierra de Santa Bárbara, El Fuerte, 24°15'S 64°27'W, *Cocucci 1354*, 23.ii.2001 (CORD). La Pampa: Dpto Lihuel Calel: Lihuel Calel, *Monticelli s.n.*, iii.1932 (Herbarium Hicken C-78) (SI). La Rioja: Dpto Capital: Sierra de Velazco, cerca de la mina El Cantadero (= La Esperanza), 2300 m, *Hunziker 5281*, 5–6.iii.1944 (CORD, LP, SI). Dpto Chilecito: Cuesta de Miranda, Sierra Famatina, *Hieronymus and Niederlein 878*, iii.1879 (CORD, G); Las Higueras, *Falcone and Castellanos 3615*, 25.iii.1957 (LP); Los Talas, al W de Chilecito, *Cabrera et al. 16674*, 25.ii.1965 (LP); Los Manzanos, finca Los Bordos, 2400 m, *Okada 2705*, 12.ii.1967 (LP); Guanchín, Sierra de Famatina, 2300 m, *Okada 2820*, 15.ii.1967 (LP); Cuesta de Guanchín, *Cabrera et al. 25602*, 26.i.1974 (LP). Dpto Famatina: Trancas, Sierra de Famatina, 2200 m, *Hunziker 1995*, 13.i.1947 (BA, LP); Quebrada de la Aguadita, *Cabrera et al. 18076*, 2.iii.1967 (LP). Dpto General Belgrano, Cumbre de la Sierra de Olta, *Castellanos 34033*, 8.ii.1940 (BA). Dpto General Sarmiento, Cienaguita, quebrada río Bonete, 2200 m, *Hunziker 2231*, 9.ii.1947 (LP). Dpto General Sarmiento-Lavalle, Río Tambillos, *Del Vó 20*, 22.ix.1953 (LP). Dpto Gobernador Gordillo [=Chemical]: Sierra de los Llanos desde La Aguadita, frente a Chamental, quebrada del río Los Nacimientos, 800 m al N del Puesto El Durazno, ladera NO, 1100 m, *Velázquez and Godoy 19*, 7.iii.2001 (LP). Dpto Lavalle: Guandacol, 950 m, *Meyer 4207*, 3.ii.1942 (LP, SI). Mendoza: Dpto Capital: Mendoza, *Burkart 1896*, 5.iv.1928 (LP); Mendoza, *Carette s.n.*, 1916 (LP). Dpto Guaymallén: Guaymallén, avenida de acceso, *Seokiv 26069*, 12.i.1968 (LP). Dpto Las Heras: prope Papagayos, *Ruiz Leal 4495*, 4.iv.1907 (LP); Potrerillos, precordillera de Mendoza, 1200 m, *Hauman s.n.*, i.1910 (G); Villavicencio, *Sanzin 321*, 7.i.1914 (SI); Potrerillos, *Sanzin 904*, 21.i.1916 (BA); Quebrada San Isidro, 1500 m, *King 180*, 23.i.1927 (LP); Potrerillos, estancia El Salto, *Ragonese 24*, ii.1934 (BA, LP); arroyo Picheuta, *Pérez Moreau 12749*, 10.ii.1934 (BA, LP); Villavicencio, *Covas 430*, 27.ii.1942 (LP); Villavicencio, *Burkart et al. 1437*, 27.ii.1942 (LP); Villavicencio, *Ruiz Leal 8025*, 20.iv.1942 (BA); Uspallata, *Soriano 1070*, 12.iii.1944 (LP); Paramillo de Uspallata, *Cobas 1857*, 6.iv.1945 (SI); Cacheuta, *Cuezzo and Barkley 20Mz255*, 21.i.1950 (G); N of Uspallata, 32 1/2°S, 2050 m, *Böcher et al. 2213*, 8.i.1956 (LP). Dpto Luján de Cuyo: Ruta Nacional 7, entre Potrerillos y Cacheuta, 1300 m, *Hunziker 25629*, 12.ii.1997 (CORD). Dpto San Carlos: entre Eugenio Bustos y estancia El Cepillo, *Cobas 354*, 20.iii.1945 (SI). Dpto San Rafael: Cuesta de Los Terneros, *Dawson 1084*, 21.ii.1941 (LP); Cuesta del Agua de Los Terneros, *Ruiz Leal and Roig 16107*, 7.iii.1954 (LP); Rincón del Atuel, entrada cañón izquierdo, 800–1000 m, *Lagiglia 1072*, 31.iii.1972 (LP). Dpto Tunuyán, prope Los Arboles, *Ruiz Leal 3123*, 20.iii.1935 (LP); 10 km al E de Campo Los Andes, 1500 m, *Barkley 20Mz184*, 15.i.1950 (G). Dpto Tupungato, Arroyo Chupasangral, *Castellanos 36223*, 23.ii.1941 (BA). Río Negro: Dpto Avellaneda, Isla Choele-Choel, *Clos 3594*, 7.iv.1928 (BAB, LP)\*; Luis Beltrán, *Burkart 15898*, 15.ii.1948 (SI). Dpto General Roca, estación Cipolletti, *Jörgensen and Girola s.n.*, 3.iii.1913 (BAB); Dpto unknown, valle del Río Negro, *Estrada s.n.*, without date (BAB 80701)\*; Río Negro, *Scala 7*, i.1916 (LP, SI)\*. Salta: Dpto Cafayate: El Alisal, Sierra del Cajón, 2800 m, *Rodríguez 1426*, 22.iii.1914 (LP), idem, 2700 m (SI). Dpto Guachipas:



Cuesta del Cebilar, 1400–1600 m, *Novara and Neumann 3141*, 7.ii.1983 (CORD). Dpto La Viña: Potrero de Castilla, a 35 km al O de Apascachi, 2000–2100 m, *Novara 3473*, 21.vi.1983 (CORD). Dpto Santa Victoria, Los Toldos, entrada a la Quebrada Cotomayo, *Meyer et al. 21630*, 21.ii.1960 (LP). Dpto Rosario de la Frontera, Hoyada, *Lahitte 49906*, iv.1934, (LP). Dpto and locality unknown, *Gerling s.n.*, 1897 (LP). San Juan: Dpto Calingasta, Río del Palque, *Fabris and Marchionni 2378*, ii.1960 (LP). Dpto Jáchal, Huaco, *Burkart 12605*, 4.iii.1941 (LP). Dpto Sarmiento: Sierra de Ansilta, Quebrada Santa Clara, unos 30 km al SW de Pedernal, 1800 m, *Burrin et al. 5809bis*, 21.iii.1999 (SI). Dpto Ullún: desde Ullún hasta la Angostura, a casi 1800 m, *Hosseus 2515*, 28.ii.1921 (CORD). Dpto Zonda: Agua Pinta, Maradones, *Rodenbender 4926*, ii.1897 (BA); estancia Maradona, 1000–1500 m, *Kiesling et al. 5964*, 7.ii.1986 (SI). San Luis: Dpto Coronel Pringles, Ruta Provincial 17, 33.11028°S, 66.00229°W, 1034 m, Embalse La Florida, pasando La Florida desde Trapiche a 7.2 km al E del empalme Ruta Provincial 9, *Gutiérrez et al. 464, 465*, 10.iv.2008 (LP). Dpto General Pedernera: entre estancias San Marcelo y El Tala, 22 km sur de Nueva Escocia, 560 m, *Anderson and d'Hiriart 1716*, 14.iv.1970 (CORD); Cerro El Morro, estancia San Cayetano, *Anderson 204*, 30.i.1971 (CORD); estancia Don Enrique, al sur de Fraga, potrero 13, 715 m, *Anderson and Villar 3109*, 8.iv.1976 (CORD); estancia Don Manuel, a 25 km al sur de Fraga, 715 m, *Anderson et al. 4042*, 20.iii.1984 (CORD). Dpto Junín: entre Merlo y Rincón, *Yepes 20/107*, iii.1929 (LP); Pasos Malos, arroyo Piedras Blancas, 1100 m, *Anderson 2323*, 7.iii.1972 (CORD). Dpto La Capital, San Francisco, Quebrada del Palmar, *Castellanos 1029*, 12.ii.1925 (BA); El Volcán, *Lagiglia 6484*, 1.iv.1983 (SI). Sierras de San Luis, Cuesta de los Picazos, *Castellanos 1051*, 21.ii.1925 (BA). Tucumán: Dpto Faimallá, Villa Nougés, 1000 m, *Venturi 1745*, 8.iii.1922 (LP). Dpto Tafí del Valle, Tafí [del Valle], *Loretz 155*, 3.iv.1872 (CORD); Tafí del Valle, *Morello 1022*, 25.v.1949 (LP); Cuesta del Infiernillo, *Cabrera and Frangi 20764*, 25.ii.1970 (LP); 3 km N de Tafí del Valle, 2150–2300 m, *Maruñak et al. 362*, 17.iii.1972 (LP); Amaichá del Valle, *O'Donnell and Meyer 5310*, 22.iii.1947 (LP); Ruta 40, ~10 km NW de Tafí del Valle, 26.7048°S, 65.7989°W, 2985 m, *Paula-Souza et al. 7898*, without date (SI). Dpto Tafí Viejo, El Duraznito, 550 m, *Venturi 1988*, 27.iii.1924 (LP). Dpto unknown, La Criolla, 1200 m, *Rodríguez 513*, 17.iv.1912 (SI). Without province: Costas del Paraná, Las Delicias, *Baez 432*, v.1921 (BA).

BOLIVIA. Chuquisaca: Prov. Yamparaez, an der Straße, 15 km westlich Tarabuco, 3100 m, *Höhne and Feuerer 4560*, 26.xi.1980 (SI). Tarija: Prov. Cercado, 19 km hacia Camargo, 2230 m, without collector 799, 26.iii.1979 (SI); Prov. Arce, 23.8 km S of Padcaya on road to Bermejo, 2100 m, 21°59'S, 64°40'W, *Solomon 10185*, 27.ix.1983 (SI); Prov. Cercado, Abra del Cóndor, camino de Tarija a Entre Ríos, ~21°25'S, 64°30'W, 2800 m, *Krapovickas and Schinini 38668*, 28.iv.1983 (SI); Prov. Cercado, 40 km E of Tarija–Padcaya road, on road to Entre Ríos (near Abra Cóndor), 2500 m, 21°25'S, 64°26'W, *Solomon 10289*, 1.v.1983 (SI); Prov. Mendez, Tomatas Grande, campo experimental, ~1950 m, *Bastión 753*, 13.ii.1986 (SI); Prov. Cercado, cerca de Tucumilla, 2650 m, *Bastión 1182*, 22.iv.1986 (SI). Localities selected from TROPICOS. Cochabamba: 800 m, *Fosberg 28455*, 22.viii.1947 (US); Carrasco, 2950 m, 17°42'00"S, 64°52'00"W, *Solomon and Nee 17903*, 5.iii.1988 (MO). Santa Cruz: 2450 m, 18°06'30"S, 63°57'00"W, *Nee 34035a* (NY); Vallegrande, 2050 m, 18°31'05"S, 64°05'08"W, *Vargas C. and Vargas 1072*, 5.viii.1991 (USZ); idem, 18°31'05"S, 64°05'08"W, *Vargas C. 972*, 14.iv.1991 (USZ); idem, 2050 m, 18°31'00"S, 64°05'00"W, *Vargas C. 972*, 14.iv.1991 (USZ).

BRAZIL. Rio Grande do Sul: Alegrete a Capivari, *Palacios Cuezco 1917*, 16.iii.1948 (LP); Pelotas, campos da Estação Central do I.A.S., *Gomes 20*, 14.iii.1950 (SI); prope Viamão, *Rambo 46702*, 10.iv.1950 (SI); without locality, *Barroso 57646*, 1946 (LP); *Matzemocher s.n.*, 26.iii.1976 (G).

URUGUAY. Colonia: Colonia, *de la Rúa s.n.* (*Hicken 98*), ii.1910 (SI); Colonia, *Hauman 24948*, i.1917 (BA); Riachuelo, *Cabrera 3281*, iv.1935 (LP); *Cabrera 4023*, 22.iii.1937 (LP); Nueva Palmira, *Scolnik 31/2*, xii.1943–i.1944 (LP). Maldonado: Piriápolis, *Osten 5510*, 7.iv.1911 (SI); Montevideo: Colón, *Rosa-Mato 462, 463*, v.1934 (LP). Treinta y Tres: Serranías del Yerbál, *Legrand 732*, 8.iv.1936 (LP). Salto: Salto, *Berro (Herbarium Boissier) 3140*, 21.iv.1905 (G). Soriano: Vera, *Berro (Herbarium Boissier) 2109*, iii.1900 (GH).