



Systematics of *Podocoma* (Asteraceae: Astereae): a generic reassessment

GISELA SANCHO^{1*}, D. J. NICHOLAS HIND² and JOHN F. PRUSKI³

¹*División Plantas Vasculares, Museo de La Plata, Paseo del Bosque s.n., La Plata, 1900, Buenos Aires, Argentina*

²*The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK*

³*Missouri Botanical Garden, PO Box 299, Saint Louis, MI 63166-0299, USA*

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Podocoma is a southern South American genus of perennial herbs with short-radiate capitula with two- to four-seriate ray florets and a two- to three-seriate pappus of scabridulous setae. The ray florets have corollas with narrow limbs. The rostrate cypsela of *Podocoma* is one of the most distinct features of the genus. *Podocoma*, with many of the endemic southern South American genera of Astereae, is included in subtribe Podocominae. *Podocoma* traditionally contained seven mainly Brazilian species (*P. asperrima*, *P. bellidifolia*, *P. blanchetiana*, *P. hieracifolia*, *P. hirsuta*, *P. regnellii* and *P. spegazzinii*), and its expansion to include two species of *Conyza* (*C. notobellidiastrum* and *C. rivularis*) was, perhaps, the most significant recent change in the generic concept of *Podocoma*. However, recent molecular- and morphology-based phylogenetic analyses do not support the inclusion of these two species in *Podocoma*. Morphological and anatomical studies were carried out in order to clarify the taxonomy of *Podocoma* and to delimit the genus and its species. On the basis of the results of these morphological and anatomical studies, and those from molecular- and morphology-based phylogenetic analyses, *P. notobellidiastrum* and *P. rivularis* are excluded from *Podocoma* and transferred to a new genus that is currently under description. Moreover, *P. regnellii* and *P. asperrima* are placed in synonymy with *P. hirsuta* and *P. spegazzinii*, respectively. Three species, *P. bellidifolia*, *P. blanchetiana* and *P. hieracifolia*, are recognized here as a complex of closely related species from a morphological point of view; however, they are treated separately. © 2010 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2010, 163, 486–513.

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INTRODUCTION

Podocoma Cass. (Asteraceae) is a southern South American genus described by Cassini (1817). Cassini (1826: 60) indicated that the main characteristic of *Podocoma* is its rostrate cypsela, from which its name was derived. Species of *Podocoma* are perennial herbs with short-radiate capitula with two- to four-seriate ray florets and two- to three-seriate pappus of scabridulous setae. The ray florets have corollas with narrow limbs.

Bentham (1873) expanded the distributional range of *Podocoma*, resulting in the addition of two Australian species (Table 1). However, these are included

today in the separate genus *Ixyochlamys* F.Muell. & Sond. Other species previously included in *Podocoma* are currently placed in other South American genera, such as *Asteropsis* Less., *Blakiella* Cuatrec. and *Stenachaenium* Benth. Following these exclusions, seven mainly Brazilian species remain in *Podocoma* (hereon called *Podocoma* s.s.: *P. asperrima* Dusén ex Malme, *P. bellidifolia* Baker, *P. blanchetiana* Baker, *P. hieracifolia* (Poir.) Cass., *P. hirsuta* Baker, *P. regnellii* Baker and *P. spegazzinii* Cabrera). The recent addition of two species of *Conyza* Less., *C. notobellidiastrum* Griseb. and *C. rivularis* Gardner, by Nesom & Zanolak (1994) was, perhaps, the most significant recent change in the generic concept of *Podocoma*. However, a phylogenetic study by Sancho and Karaman-Castro (2008), which used molecular and morphological data,

*Corresponding author. E-mail: sancho@fcnym.unlp.edu.ar

Table 1. Taxonomic history of *Podocoma*

Author (year)	Taxonomic event
Cassini (1817)	Described <i>Podocoma</i> and placed it in tribe Astereae without indication of species
Cassini (1826)	Included <i>Podocoma hieracifolia</i> (Poir.) Cass. (= <i>Erigeron hieracifolium</i> Poir.) and <i>P. primulifolia</i> Cass. in <i>Podocoma</i>
de Candolle (1836)	Followed Cassini's definition of <i>Podocoma</i> , including <i>P. hieracifolia</i> and <i>P. primulifolia</i> in the genus
Hooker & Arnott (1836)	Described <i>Podopappus</i> , pointing out its resemblance to <i>Podocoma</i> . They described <i>Podopappus hirsutus</i> , <i>P. pubescens</i> and <i>P. tomentosus</i>
Bentham (1873)	Included <i>Podocoma</i> in subtribe Heterochromeae. As synonyms, he listed <i>Asteropsis</i> , <i>Podopappus</i> , <i>Moritzia</i> Sch. Bip. ex Benth. (nom. nud.) and <i>Ixiochlamys</i> (from Australia), expanding the distribution of <i>Podocoma</i> to the Australian continent
Baker (1882)	1. Included in <i>Podocoma</i> the species <i>P. hieracifolia</i> (with <i>P. primulifolia</i> as a synonym) and <i>P. hirsuta</i> (based on <i>Podopappus hirsutus</i>). 2. Described three new species: <i>P. blanchetiana</i> , <i>P. bellidifolia</i> and <i>P. regnellii</i> . 3. Regarded <i>Asteropsis</i> as separate genus. <i>Podopappus tomentosus</i> was included in <i>Asteropsis</i> . 4. Noted that two other species of <i>Podocoma</i> existed, one from Australia and one from Colombia based on the name <i>Moritzia glandulosa</i> of Schultz Bipontinus (albeit a nom. nud.)
Hochreutiner (1899)	Described <i>Podocoma reineckii</i> , later transferred to <i>Stenachaenium</i>
Ewart, White & Tovey (1908)	Described <i>Podocoma nana</i> from Australia, later transferred to <i>Ixiochlamys</i>
Blake (1917)	Described <i>Podocoma bartsiiifolia</i> and indicated that the name <i>Moritzia glandulosa</i> was presumably referable to his new species. <i>Podocoma bartsiiifolia</i> is basionym of the only species of <i>Blakiella</i> , a Colombian and Venezuelan genus of Astereae
Cabrera (1932)	Described <i>Podocoma spagazzinii</i> from northern Argentina
Malme (1933)	Described <i>Podocoma asperrima</i> and <i>P. foliosa</i> from Brazil
Grau (1977)	Redefined the concept of <i>Podocoma</i> by excluding <i>Ixiochlamys</i> and including <i>Asteropsis</i> and the Brazilian <i>Inulopsis</i> O.Hoffm. <i>Podocoma</i> was again restricted to South America
Bremer (1994)	1. Placed <i>Podocoma</i> in subtribe Asterinae (based on Zhang & Bremer, 1993), <i>Hinterhubera</i> group, together with <i>Blakiella</i> , <i>Flosmutisia</i> Cuatrec, <i>Hinterhubera</i> Sch. Bip. ex Wedd., <i>Microgyne</i> Less. and <i>Westoniella</i> Cuatrec. 2. Appeared to accept Grau's delimitation of <i>Podocoma</i>
Nesom (1994b)	Established the subtribe Podocominae including two geographically distant groups of genera from South America (<i>Asteropsis</i> , <i>Blakiella</i> , <i>Inulopsis</i> , <i>Laennecia</i> Cass., <i>Microgyne</i> , <i>Podocoma</i> and <i>Sommerfeltia</i> Less.) and Australasia (<i>Camptacra</i> N.T.Burb. and <i>Dichromochlamys</i> Dunlop, <i>Dimorphocoma</i> F.Muell. & Tate, <i>Elachanthus</i> F.Muell., <i>Iotasperma</i> G.L.Nesom, <i>Ixiochlamys</i> , <i>Kippistia</i> F.Muell., <i>Minuria</i> DC., <i>Peripleura</i> (N.T.Burb.) G.L.Nesom, <i>Tetramolopium</i> Nees and <i>Vittadinia</i> A.Rich.)
Nesom & Zanowiak (1994)	Published a taxonomic overview of <i>Podocoma</i> including <i>P. asperrima</i> , <i>P. bellidifolia</i> , <i>P. blanchetiana</i> , <i>P. hieracifolia</i> , <i>P. hirsuta</i> , <i>P. regnellii</i> and two species transferred by them from <i>Conyza</i> (<i>P. notobellidiastrum</i> and <i>P. rivularis</i>)
Nesom & Robinson ([2006] 2007)	Excluded <i>Blakiella</i> from Podocominae
Sancho & Karaman-Castro (2008)	Carried out phylogenetic analyses on Podocominae based on morphological and molecular data. Those analyses did not support: (1) the inclusion of <i>P. notobellidiastrum</i> and <i>P. rivularis</i> in <i>Podocoma</i> ; or (2) the circumscription of Podocominae as including Australasian and South American genera
Brouillet <i>et al.</i> (2009)	Carried out a phylogenetic analysis of tribe Astereae based on molecular data. The analysis showed: (1) <i>Podocoma</i> as defined with two independent lineages in the context of a large polytomy (including Australasian, North American and South American taxa of the whole tribe); (2) a paraphyletic Podocominae with the Australasian and South American taxa belonging to distantly related clades

did not support the inclusion of these two species in *Podocoma*.

Although the placement of *Podocoma* in tribe Astereae was never in doubt, its generic relationships were more debatable (Cassini, 1817; Bentham, 1873; Zhang & Bremer, 1993, Bremer, 1994; Nesom, 1994a, b; Nesom & Zanowiak, 1994). The creation of subtribe Podocominae (Nesom, 1994b, followed by Nesom & Robinson, [2006] 2007) seemed to define the generic relationships of *Podocoma*. However, molecular and morphological data do not support Nesom's circumscription of Podocominae including Australasian and South American genera (Sancho & Karaman-Castro, 2008; Brouillet *et al.*, 2009).

Furthermore, molecular and morphological phylogenetic analyses have provided new evidence that would modify the concept of *Podocoma* and its generic relationships (Sancho & Karaman-Castro, 2008; Brouillet *et al.*, 2009). This has prompted a taxonomic reassessment to define a monophyletic genus.

The goals of this study were: (1) to characterize *Podocoma* morphologically and anatomically; (2) to clarify the taxonomy of *Podocoma*; (3) to establish the limits of the genus on the basis of the morphological and anatomical studies carried out here and previous phylogenetic analyses; and (4) to delimit the species.

GENERIC RELATIONSHIPS

Since Bentham (1873), *Podocoma* has been considered to be closely related to the South American *Asteropsis* and the Australian *Ixiochlamys*. *Asteropsis* is restricted to Brazil and Uruguay and has a single species. It was described by Lessing as having a short rostrate cypselae and that, probably, is the main character used by authors to link it to *Podocoma*. *Asteropsis* and *Podocoma* also share compressed and marginally ribbed cypselae, but no other particular characters. *Asteropsis* differs from *Podocoma* in its densely leafy stems, usually solitary, strongly radiate capitula, short scaly receptacle, usually functionally male disc florets, subcampanulate disc corollas, glandular cypselae and a pappus with a short outer series (Bonifacino, Sancho & Marchesi, 2009). However, cypselae of *Asteropsis*, although attenuate at the apex, are not truly rostrate as in *Podocoma*. This morphological evidence is supported by recent molecular and morphological phylogenetic analyses that failed to demonstrate close phylogenetic relationships between these genera (Sancho & Karaman-Castro, 2008, Fig. 1; Brouillet *et al.*, 2009). In fact, *Podocoma* and other truly rostrate genera, for example *Blakiella* (once linked to *Podocoma*; Nesom, 1994b), are shown by these analyses to belong to distantly related clades. This would suggest that ros-

trate cypselae have evolved in parallel in different groups of Astereae (e.g. Sancho & Karaman-Castro, 2008).

Ixiochlamys shares with *Podocoma* capitula with two- to four-seriate ray florets (or even more seriate in *Ixiochlamys*), narrow ray corolla limbs that do not exceed the pappus and rostrate cypselae. However, *Ixiochlamys* differs from *Podocoma* in its basally branched habit, solitary capitula and uniseriate pappus or, if in three series, a short outermost series. Further, the rostrate cypselae of *Ixiochlamys* are different from those of *Podocoma* (Dunlop, 1980; G. Sancho, pers. observ.). The cypselae body of *Ixiochlamys* is neither conspicuously compressed nor marginally ribbed as in *Podocoma*, and, whereas the rostrum of *Podocoma* is scarcely delimited from the cypselae body, the distinction between body and rostrum in *Ixiochlamys* is abrupt and the rostrum is narrow and almost filiform. Grau (1975) also found differences in cypselae wall anatomy between *Ixiochlamys* and *Podocoma*. Close phylogenetic relationships were not demonstrated between *Ixiochlamys* and *Podocoma* (Brouillet *et al.*, 2009).

Two other genera with radiate capitula, *Inulopsis* O.Hoffm. and *Microgyne* Cass. (Grau, 1975; Bremer, 1994; Nesom, 1994a, b), have also been linked to *Podocoma*. However, the molecular analyses of Sancho & Karaman-Castro (2008) recovered a clade comprising *Asteropsis*, *Inulopsis*, *Microgyne* and *Sommerfeltia* Less. not closely related to *Podocoma* (Fig. 1). This suggests that, from the currently available data, the generic relationships of *Podocoma* remain unresolved.

PHYLOGENY

Phylogenetic analyses based on morphological and molecular data show an unresolved Podocominae. The Australasian taxa of Podocominae were analysed by Lowrey *et al.* (2001), who, however, did not include South American representatives of Podocominae in their analysis. According to molecular data obtained by Sancho & Karaman-Castro (2008) and Brouillet *et al.* (2009), close association between South American and Australasian genera of the Podocominae is not supported (Fig. 1). These latest molecular results also show that the morphological characters used to define Podocominae are homoplastic, probably as a result of convergence and parallelism. There are no morphological characters that support the delimitation of Podocominae as currently circumscribed, i.e. including American and Australasian genera. As noted by Sancho & Karaman-Castro (2008), a narrower concept of Podocominae, including *Podocoma* s.s., *Asteropsis*, *Inulopsis*, *Microgyne* and *Sommerfeltia*, and excluding the Australasian genera of

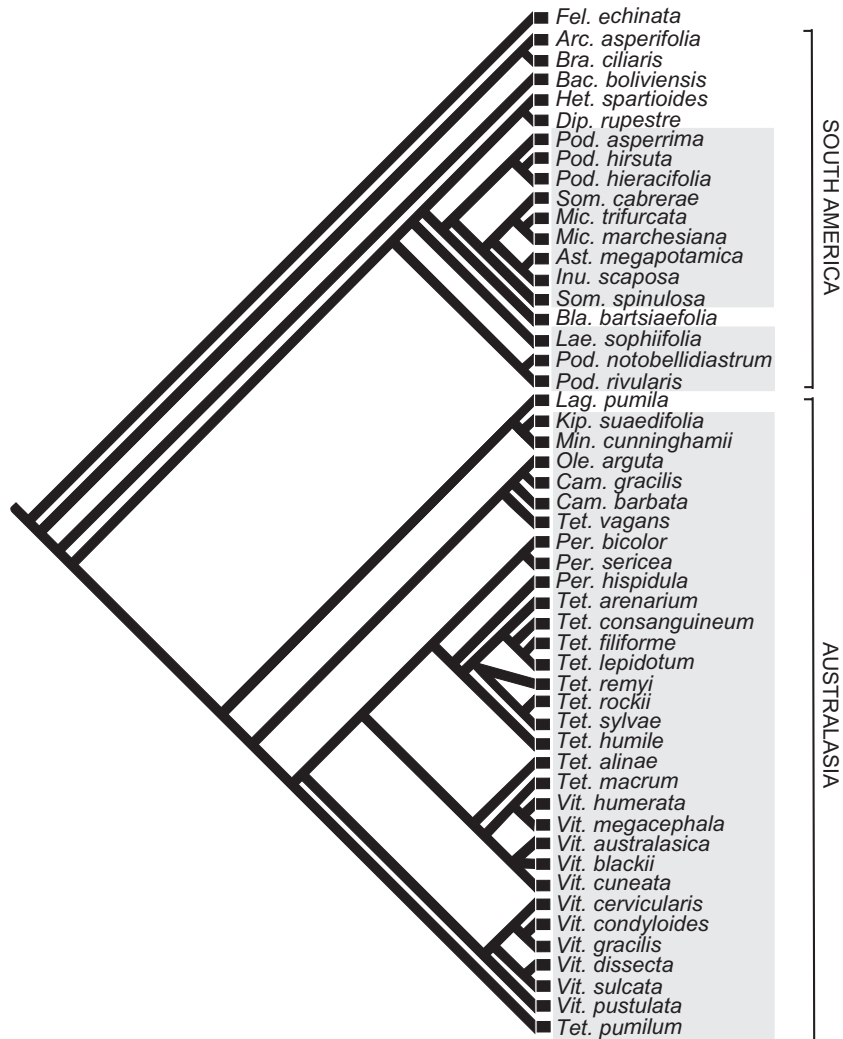


Figure 1. One of the 4722 most parsimonious trees based on the internal transcribed spacer (ITS) dataset of Podocominae. *Arc.*, *Archibaccharis*; *Ast.*, *Asteropsis*; *Bac.*, *Baccharis*; *Bla.*, *Blakiella*; *Cam.*, *Camptacra*; *Dip.*, *Diplostephium*; *Het.*, *Heterothalamus*; *Inu.*, *Inulopsis*; *Lae.*, *Laennecia*; *Lag.*, *Lagenophora*; *Mic.*, *Microgyne*; *Min.*, *Minuria*; *Per.*, *Peripleura*; *Pod.*, *Podocoma*; *Som.*, *Sommerfeltia*; *Tet.*, *Tetramolopium*; *Vit.*, *Vittadinia*. Grey surface includes subtribe Podocominae *sensu* Nesom (1994b). Modified from Sancho & Karaman-Castro (2008).

Podocominae, could be supported and characterized morphologically by pappus setae in two or three series. However, the association of these genera was not strongly supported in the latest molecular analyses (Brouillet *et al.*, 2009). The interpretation of molecular data suggests the exclusion from Podocominae of *Asteropsis*, *Inulopsis*, *Microgyne* and *Sommerfeltia*, which prompts a serious reassessment of the subtribe, as *Podocoma* would be its only remaining genus.

In the general context of Astereae, *Podocoma* (specifically *P. notobellidiastrum*) has been recovered as sister to the North American clade (Noyes & Rieseberg, 1999; Fiz *et al.*, 2002). However, in a more recent analysis of the tribe (Brouillet *et al.*, 2009) that

included two species of *Podocoma*, the genus is defined with two independent lineages in the context of a large polytomy. This polytomy includes Australasian, North American and South American taxa of the whole tribe. Therefore, *Podocoma* would not be sister to the North American clade of Astereae as suggested in other studies.

Although homoplastic at the tribal level, some morphological characters (e.g. presence of rostrum in *Podocoma*) could be regarded as diagnostic at the generic level. The results of Sancho & Karaman-Castro (2008) suggest that rostrate cypselae as in, for example, *Podocoma s.s.*, on the one hand, and eros-trate cypselae merely with attenuate apex as in, for example, *P. notobellidiastrum* and *P. rivularis*, on the

Figure 2. Morphology of *Podocoma*. Blade veins: A, blade with one medial and two lateral basal or suprabasal primary veins (*P. hieracifolia*); B, blade with a single, medial, primary vein (*P. hirsuta*). Leaf trichomes: C, conical with simple foot (*P. hieracifolia*); D, conical with compound foot (*P. hirsuta*); E, flagellate filiform (*P. hirsuta*); F, biseriate glandular (*P. asperrima*). Phyllary trichomes: G, trichome from phyllary margin (*P. asperrima*); H, conical (*P. hieracifolia*); I, flagellate filiform (*P. spegazzinii*); J, biseriate glandular (*P. hieracifolia*); K, whip (*P. rivularis*); L, M, twin hairs (*P. spegazzinii*). Ray corollas: N, with developed limb (*P. hirsuta*); O, with very short limb bifid at the apex (*P. notobellidiastrum*). Corolla trichomes: P, simple biseriate glandular (*P. asperrima*); Q, conical with thin-walled cells (*P. hirsuta*); R, twin hair (*P. asperrima*). Theca base of anthers: S, rounded (*P. asperrima*); T, auriculate (*P. hirsuta*). Style of disc floret: U, *P. hieracifolia*; V, *P. bellidifolia*; W, *P. hieracifolia*; X., *P. notobellidiastrum*. Pappus seta: Y, seta base (*P. blanchetiana*); Z, seta apex (*P. blanchetiana*). Scale bars: C–M, P–R, 100 µm; N, 2 mm; O, 3 mm; S, T, 0.6 mm; U, 1 mm; V–X, 3 mm; Y, Z, 100 µm. (*P. asperrima* from Sancho & Bonifacino 93, LP; *P. bellidifolia* from Hassler 9168, S; *P. blanchetiana* from Krapovickas et al. 26381, CTES; *P. hieracifolia* from Cabrera 10275, LP; *P. hirsuta* from Sancho & Bonifacino 73, LP; *P. notobellidiastrum* from Sancho & Bonifacino 89, LP; *P. rivularis* from Sancho 66, LP; *P. spegazzinii* from Spegazzini 101, LP.)

other, appear to have evolved independently, the last two species forming a clade distantly related to *Podocoma s.s.*

MATERIAL AND METHODS

All the species of *Podocoma s.l.* (*P. asperrima*, *P. bellidifolia*, *P. blanchetiana*, *P. hieracifolia*, *P. hirsuta*, *P. notobellidiastrum*, *P. regnellii*, *P. rivularis* and *P. spegazzinii*) were included in the morphological and anatomical analysis to confirm the results obtained in previous phylogenetic analyses with respect to the circumscription of *Podocoma*. Data were derived from the study of herbarium specimens from BM, CTES, GH, K, LP, MO, MVFA, NY, P, SI and US (Holmgren et al. <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>), and from field observations. For light microscopy examination, floral and vegetative parts were rehydrated and stained in 2% safranin. For anatomical observations, transverse sections were cut by free hand. Whenever possible, data from live specimens were added (involucre shape, corolla and pappus colour).

Drawings were made by the senior author (GS) using a Wild M3Z stereomicroscope and a Nikon Eclipse E200 light microscope with a camera lucida. The terminology follows Hickey (1974), Ramayya (1962), Stearn (1992), Harris & Harris (1994) and Freire et al. (2005).

RESULTS

MORPHOLOGY

Duration and habit

All species of *Podocoma* are perennial herbs. The species living in grasslands or rocky and open areas (*P. asperrima*, *P. bellidifolia*, *P. blanchetiana*, *P. hirsuta*, *P. hieracifolia*, *P. regnellii* and *P. spegazzinii*) have a thickened, horizontal, rhizomatous subterranean system from which the new shoots arise periodically

throughout its life cycle. This rhizomatous subterranean system bears fascicled roots that are usually somewhat thickened. *Podocoma notobellidiastrum* and *P. rivularis* inhabit the forest understorey and have a thinner, rhizomatous subterranean system.

Leaves

The leaves of *Podocoma* are alternate, sessile and simple. In some species, they are congested in the proximal third of the stem (*P. blanchetiana* and *P. hieracifolia*), whereas, in others (*P. hirsuta* and *P. spegazzinii*), they are more or less evenly arranged along the stem. When the leaves are congested at the base, proximal and distal leaves are distinct, in that the distal leaves differ in shape and are reduced in size towards the stem apex. Blades are oblanceolate, obovate or broadly obovate (*P. bellidifolia*, *P. blanchetiana* and *P. hieracifolia*), linear-elliptic (*P. asperrima* and *P. spegazzinii*) or elliptic (*P. hirsuta* and *P. regnellii*), bases are attenuate or long-attenuate, sometimes somewhat clasping, especially the distal leaves, and the apices are usually subacute. The leaf texture is usually chartaceous, although in *P. asperrima* leaves are thicker. Blade margins are denticulate (e.g. *P. blanchetiana*) to deeply dentate (e.g. *P. hirsuta*) and usually flat or slightly revolute (*P. asperrima*). Stereomicroscope examination led us to identify: (1) blades with a single primary midvein and two lateral primaries, somewhat thinner, basal or suprabasal veins (*P. bellidifolia*, *P. blanchetiana* and *P. hieracifolia*; Fig. 2A); and (2) blades with a single, medial, primary vein (*P. asperrima*, *P. hirsuta*, *P. notobellidiastrum*, *P. regnellii*, *P. rivularis* and *P. spegazzinii*; Fig. 2B).

Leaf anatomy

Most species have amphistomatic blades. Only abaxial stomata are present in *P. rivularis* and *P. notobellidiastrum*. The stomata are anomocytic. The cuticle is relatively thick in, for example, *P. blanchetiana* or relatively thin in, for example, *P. rivularis*.



The epidermis is a single layer of polygonal cells. The mesophyll is dorsiventral with two or three palisade layers. Medial vascular bundles are accompanied in most species by a few sclereids, whereas, in some species, the sclerenchyma cells are grouped in a weak adaxial and, less commonly, abaxial helmet (e.g. *P. bellidifolia* and *P. blanchetiana*). Secretory cavities are reported here for the first time in *Podocoma* and have been observed in most of its species. Secretory cavities are associated with the medial vascular bundle and, in some cases, with the secondary vascular bundles. Each secretory cavity (Fig. 3B, C) is an intercellular space surrounded by epithelial cells (G. Sancho *et al.*, unpubl. data.), as described in some Asteraceae (e.g. Curtis & Lersten, 1986; Simón, Katinas & Arambarri 2002, Andreucci *et al.*, 2008). Studies on secretory cavities are limited in the tribe Astereae, and the ecological or taxonomic value of these structures has not been explored in detail.

Leaf indumentum

The leaf indumentum is hirsute, pilose or pubescent. The pubescence ranges from dense in *P. blanchetiana* to glabrate in *P. rivularis* and *P. notobellidiastrum*. The leaf indumentum includes mostly simple conical hairs which may have a simple (Fig. 2C) or compound (Fig. 2D) foot. The compound feet of conical hairs in *P. asperrima* arise from the surface (Fig. 3A). The lateral walls of simple conical hairs are usually thick. Other less usual leaf trichomes are the small, flagellate filiform trichomes with thin lateral walls (e.g. *Podocoma hirsuta*; Fig. 2E) and biseriate glandular trichomes (e.g. *P. asperrima*; Fig. 2F), both found on the leaf abaxial surface. Features such as a thin cuticle and a glabrate indumentum in *P. notobellidiastrum* and *P. rivularis* might be associated with the forest understorey habitat in which they occur.

Capitula

The capitula in *Podocoma* are arranged in corymbiform arrays of usually two to nine heads. However, some individuals of some species (e.g. *P. hirsuta* and *P. notobellidiastrum*) have corymbiform arrays with relatively numerous capitula (20–30). Capitula are long-pedunculate (e.g. Figs 5, 11), although, in *P. notobellidiastrum* and *P. rivularis*, corymbiform arrays are mostly congested. Capitula are heterogamous with female ray florets and hermaphrodite disc florets (unusually functionally male). They have two to four series of ray florets with shortly radiating corolla limbs in, for example, *P. asperrima* and *P. hieracifolia* (Figs 11 and 8, respectively), although the limbs are more erect in, for example, *P. hirsuta* (Fig. 10). The ray corollas are not radiating in *P. notobellidiastrum* and *P. rivularis*.

Involucres

The involucres in live material can be cylindrical (e.g. *P. notobellidiastrum* and *P. rivularis*) or campanulate to broadly campanulate (e.g. *P. hieracifolia* and *P. hirsuta*; Figs 8 and 13B, respectively). The phyllaries are arranged in three to five gradate series. They are linear-lanceolate and foliaceous. Usually, they are purplish at the apex, becoming completely purple in mature involucres (*P. asperrima*; Fig. 13D). Phyllary margins and apices are usually ciliate, lacinate or fimbriate. In some cases (*P. asperrima* and *P. spegazzinii*), the walls of the cilia are thick, noticeably different from the other marginal cells (Fig. 2G), and may be regarded as true trichomes. On the abaxial surfaces, three different types of trichomes may be found: simple conical (Fig. 2H), flagellate filiform with thin lateral walls (Fig. 2I) and biseriate glandular (Fig. 2J), all similar to those of the leaves. Other trichomes found on phyllaries, although less common, are whip trichomes (*P. rivularis*; Fig. 2K) and twin hairs (Fig. 2L, M) (*P. spegazzinii*).

Receptacles

The receptacle in all species is slightly convex, naked and deeply alveolate.

Corollas

Ray corollas are white. They have well-developed limbs (Fig. 2N), or the limbs are short and bifid at the apex (Fig. 2O). Species of *Podocoma* s.s. have a well-developed limb, which is relatively short and narrow and does not exceed the pappus length by much. In the species with developed limbs, the limb apex usually has two minute lobes or is entire. The limb margins are usually slightly involute. Ray corollas in *P. notobellidiastrum* and *P. rivularis* are filiform and subrayed to dentate distally, or exceptionally they have entire limbs. The trichomes are usually found on the tube of ray corollas and on the limb only in *P. notobellidiastrum* and *P. rivularis*. Most trichomes are simple biseriate glandular (Fig. 2P), although twin hairs (Figs 2R, 3D) were also found in *P. asperrima*. The corollas of disc florets are yellow, funnel-form and shortly five-lobed. The tube is gradually ampliate apically. Corolla trichomes are found dorsally on lobes and in the tube and throat, depending on the species. As in ray corollas, most trichomes of disc corollas are simple biseriate glandular, although conical trichomes with thin-walled cells (Fig. 2Q) and twin hairs were also found in, for example, *P. blanchetiana*. Twin hairs are usually restricted to cypselae in Asteraceae (e.g. Hess, 1938; Freire & Katinas, 1995). However, their presence on other floral structures seems to be more common than expected, and has been documented previously (Sancho & Katinas, 2002). In *Podocoma*, twin hairs are found on the

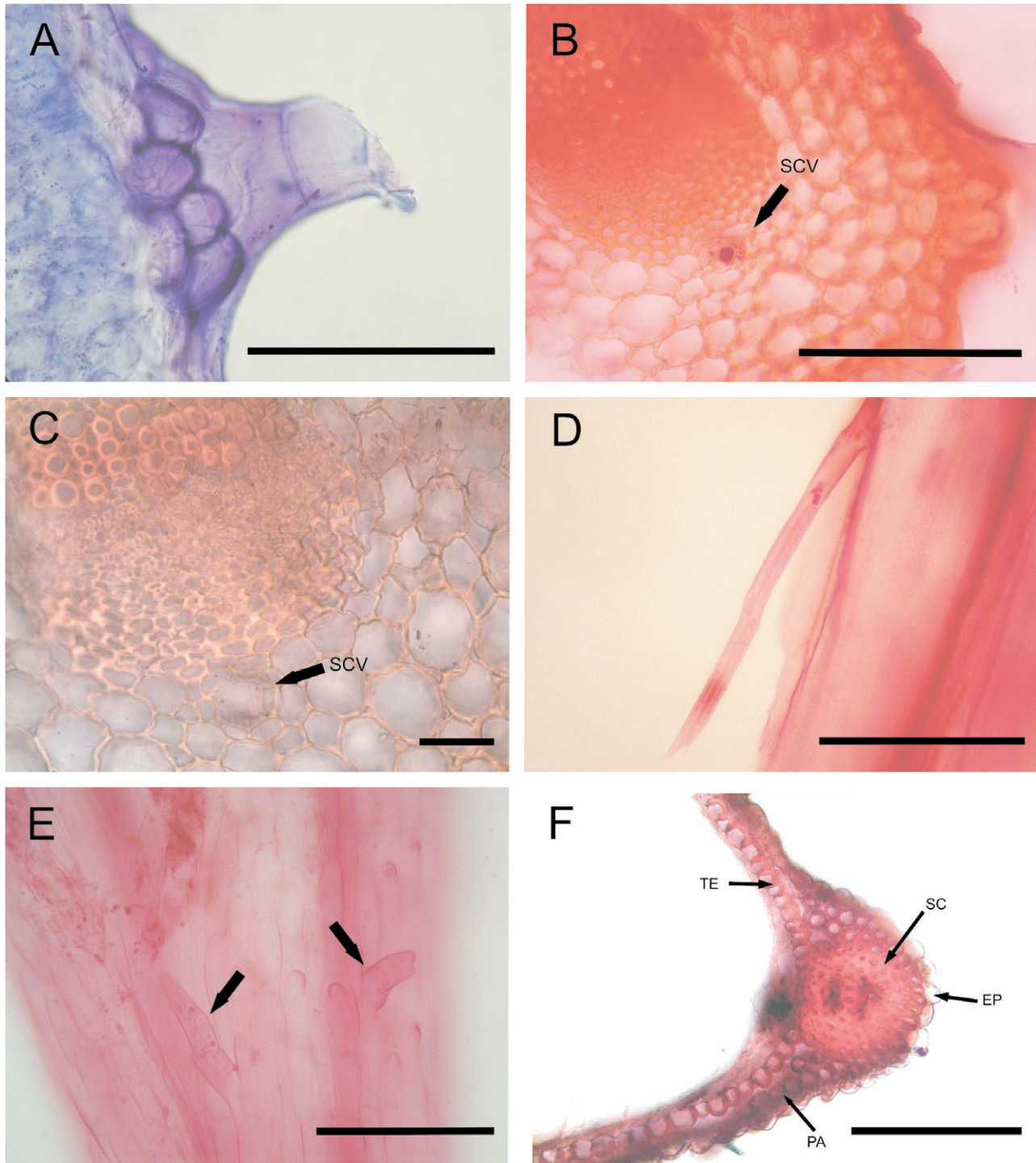


Figure 3. A, Compound base of conical trichome (*Podocoma asperrima*). B, Leaf cross-section showing the main vascular bundle and a secretory cavity filled with secretion (SCV) (*P. blanchetiana*). C, Leaf cross-section showing the epithelial cells of the secretory cavity at the base of the vascular bundle (*P. bellidifolia*). D, Twin hair on ray corolla (*P. asperrima*). E, Twin hairs at the base of the style branches (*P. bellidifolia*). F, Cypsel cross-section (*P. asperrima*) showing epicarp (EP), lateral parenchyma (PA), sclerenchyma (SC) and testa (TE). Scale bars: A, 213 μ m; B, 186 μ m; C, 58.2 μ m; D, 127.4 μ m; E, 105.35 μ m; F, 100 μ m. (*P. asperrima*, D from Dusén 17815, S and F from Sancho & Bonifacino 93, LP; *P. bellidifolia* from Dusén s.n., S; *P. blanchetiana* from Montes 3481, SI.)

phyllaries, corollas, cypselae and, rarely, on the styles (Fig. 3E); often, the apical cells of these twin hairs are transversely septate.

White ray corollas and lobes of the disc yellow corollas in *Podocoma* can turn purplish when the capitula are mature (e.g. *P. asperrima*; Fig. 13C, D). This phenomenon occurs in other Astereae (e.g. *Aster* L., Niesenbaum, Patselas & Weiner 1999; *Erigeron* L and *Myriactis* Less., Sancho & Pruski pers. observ.) and has been explained either as a pollination-induced or age-dependent pattern (Niesenbaum *et al.*, 1999).

Androecium

Anthers in *Podocoma* are those usually described for the tribe (Nesom & Robinson, [2006] 2007). The bases of the thecae are rounded (Fig. 2S) (e.g. *P. asperrima*, *P. notobellidiastrum* and *P. spgazzinii*) or slightly auriculate (Fig. 2T) (e.g. *P. blanchetiana*, *P. hirsuta* and *P. rivularis*). Apical appendages are ovate-subobtuse (e.g. *P. asperrima*, *P. hirsuta* and *P. notobellidiastrum*) or narrow-oblong (i.e. *P. blanchetiana* and *P. hieracifolia*). The distal part of the filaments has cells with thick walls that define the anther collar, which is nearly the same width as the rest of the filament. The anther collar is relatively short (i.e. equal to or shorter in length than, for instance, the apical appendage) in some species (e.g. *P. asperrima* and *P. hirsuta*) or relatively long (i.e. longer than, for instance, the apical appendage) in others (e.g. *P. bellidifolia*, *P. notobellidiastrum* and *P. rivularis*). Staminodes are absent in the ray florets.

Gynoecium

Styles of *Podocoma* are subtended by nectary with stomata. The presence of stomata on the nectary confirms the secretory function (Gopinathan & Varatharajan, 1982, Sancho & Otegui, 2000). The style bases are slightly swollen. The cells at the base of the style stain strongly and have thicker walls than the rest of the style. In ray florets, style branches are linear, subobtuse at the apex and slightly papillose dorsally (*P. asperrima*) or glabrous (*P. blanchetiana*). In disc florets, the style branches are linear-oblong and subobtuse at the apex. Dorsally, they are covered by relatively long papillae (collecting hairs) that are rounded at the apex. The collecting hairs cover the distal one-half to three-quarters of the style branches (Fig. 2U). The stigmatic surface is as described for the tribe, i.e. in two separate lines. In *Podocoma*, these two lines extend along approximately three-quarters of the style branches; the distal one-third of the style branches is sterile.

Cypselae

The cypselae are elliptic in shape and compressed in transverse section, the margins are thick ribbed. One

of the most distinct features of *Podocoma* is its rostrate cypselae, which are present in most species. The cypselae body is prolonged into a sterile neck (rostrum) of variable length. In *P. bellidifolia*, the rostrum is relatively short (1.0–1.2 mm long) and, in *P. hieracifolia*, it is relatively long (2.0–3.0 mm long) (Fig. 2V, W), with intermediates in, for example, *P. blanchetiana*. The marginal ribs of cypselae extend into the rostrum. *Podocoma notobellidiastrum* and *P. rivularis* are erostrate, albeit attenuate apically. The marginal ribs are thin (Fig. 2X). Cypselae in *Podocoma* are sericeous with short twin hairs. Glandular trichomes were not found on the fruits of *Podocoma*.

Cypselae anatomy: Cypselae transections are narrow-elliptic in outline with two prominent lateral lobes that correspond to the ribs. The pericarp consists of a single-layered epicarp. The epicarp cells are thin-walled, relatively large and covered by a distinguishable cuticle. The mesocarp is absent in the anteroposterior side of the cypselae. In the lateral lobes, the mesocarp is of sclerenchymatous bundles with a few parenchyma cells (Fig. 3F). Wide intercellular spaces are found on both sides of the parenchyma. Centrally, a vascular trace is observed. In, for example, *P. bellidifolia*, irregular spaces among the sclerenchymatous cells are distinguishable, which could represent secretory cavities. Secretory cavities in cypselae have been described in Astereae (Mukherjee & Sarkar, 2001), and they are also found in leaves of *Podocoma*. The epidermal cells of the testa are sclerenchymatous and inverted U-shaped, with outer tangential and radial walls thicker than the inner tangential walls. In some cases, a single layer of endosperm persists, although its structure is not well organized. Grau (1975) and Velez (1981) analysed the cypselae anatomy of some members of Podocominae *sensu* Nesom (1994b). The general anatomical structure of cypselae observed here for *Podocoma* is in agreement with that of *Microgyne trifurcata* Less. described by Grau (1975) and Sancho, Bonifacino & Pruski (2006), and that of *Podocoma* described by Velez (1981). Our study confirms the mesocarp structure of *Podocoma* reported by Mukherjee & Sarkar (2001).

Pappus

The pappus of *Podocoma* is white, turning brownish when dry, except in *P. notobellidiastrum* and *P. rivularis*, in which it remains whitish. The series are subequal or unequal in length, but there are no substantial differences between the shortest and the longest series. The setae are slightly wider at the base and narrower at the tapered apex. Setae are scabridulous along their whole length (Fig. 2Y, Z). In some cases, the setae are almost smooth.

Table 2. Comparison of diagnostic morphological characters in *Podocoma*

	<i>P. notobellidiastrum</i> and <i>P. rivularis</i>	<i>Podocoma s.s.</i>
Ray corollas	Filiform, subrayed to dentate	Typical true ray
Cypsela (apex)	Erostrate, attenuate distally	Rostrate
Cypsela (ribs)	Weakly two-ribbed	Strongly two-ribbed
Pappus series	One (occasionally two)	Two or three

DISCUSSION

TAXONOMIC IMPLICATIONS

The morphological and anatomical study of all species of *Podocoma* (*sensu* Nesom & Zanowiak, 1994), together with previous molecular and morphological phylogenetic analyses, led us to two main conclusions.

First, morphological discontinuities between the traditional species of *Podocoma* (*Podocoma s.s.*) and the two species recently included in *Podocoma* (*P. notobellidiastrum* and *P. rivularis*, from *Conyza*) are evident. Some of the characters that show these discontinuities are indicated in Table 2. Nesom & Zanowiak (1994) mainly supported the inclusion of these two species within *Podocoma* on the basis of the attenuate cypsela apex ('incipiently formed neck') that would be close to the rostrate cypsela of *Podocoma s.s.* From that point of view, other genera of Podocominae (*sensu* Nesom & Robinson, [2006] 2007) that have attenuate cypsela apices (i.e. *Asteropsis* and *Inulopsis*) should be included in *Podocoma* without taking into consideration their diagnostic characters different from those of *Podocoma*. This fact, added to other morphological characters that differentiate *P. notobellidiastrum* and *P. rivularis* from *Podocoma s.s.* (e.g. pappus and corollas), shows weak justification for maintaining these two species within *Podocoma*. Moreover, in agreement with morphology, the monophyly of *Podocoma* (including *P. notobellidiastrum* and *P. rivularis*) was not supported by molecular data (Sancho & Karaman-Castro, 2008), and the results suggest the segregation of these two species within a taxon distinct to *Podocoma* (G. Sancho, unpubl. data).

Second, within *Podocoma s.s.*, three groups can be distinguished, each including species that are morphologically closely related. These groups agree with those obtained, although with low support, in the recent morphological phylogenetic analysis of Sancho & Karaman-Castro (2008). The first group contains *P. asperrima* and *P. spagazzinii* with cauline linear-elliptic and denticulate leaves. The second group includes *P. hirsuta* and *P. regnellii*, characterized by their cauline, elliptic and conspicuously dentate leaves. The third group comprises a complex of three species, *P. bellidifolia*, *P. blanchetiana* and *P. hieracifolia*, mainly recognized by their oblanceolate, obovate

or broadly obovate, and denticulate leaves, usually restricted to the proximal one-third (or sometimes one-half) of the stems. Each of the three species seems to be distinct when analysing the type specimens. However, the additional specimens examined show overlap in some of the diagnostic features. The main characters used to separate the three species are leaf pubescence and cypsela neck length. The leaf pubescence is usually influenced by environmental factors, and it is problematic to define species solely on the basis of this character. With respect to cypsela neck length, *P. bellidifolia* has the shortest neck (especially in the type specimens), and *P. blanchetiana* and *P. hieracifolia* have the longest. However, some specimens with intermediate cypsela neck lengths add confusion to the identification of the three species. It seems that two equally valid answers to this problem can be considered: first, to treat the three species as synonyms, in which case the name *P. hieracifolia* would have priority; or, second, to treat the three species within a complex, but keeping them independent. In this treatment, we followed the second option.

On the basis of these two main conclusions, we propose the following taxonomy for *Podocoma*.

TAXONOMY

PODOCOMA CASS

(Greek '*podos* (ποδος) = foot, '*come* (χομη) = hair; probably refers to the pappus supported by the cypsela 'foot' or rostrum.)

Bull. Sci. Soc. Philom. Paris 1817: 137. 1817. *Type*: *P. hieracifolia* (Poir.) Cass., fide Pfeiffer, *Nomencl. Bot.* 2 (2): 770. 1874.

Podopappus Hook. & Arn., *Companion Bot. Mag.* 2 (14): 50. 1836. *Type*: *Podopappus hirsutus* Hook. & Arn., lectotype designated by Nesom & Zanowiak (1994): 109 = *Podocoma hirsuta* (Hook. & Arn.) Baker.

Description: Perennial herbs, with rhizomatous subterranean system bearing usually thick fibrous roots, stems single, erect, striate. Leaves alternate, simple, sessile, subsulate or cauline; blades broadly elliptic, oblanceolate, obovate, broadly obovate, exceptionally linear-elliptic, primary vein medial, single or with two

KEY TO *PODOCOMA* SPECIES

- | | |
|---|----------------------------------|
| 1a. Leaf blades linear-elliptic..... | 5. <i>P. spegazzinii</i> |
| 1b. Leaf blades broadly elliptic, oblanceolate, obovate or broadly obovate..... | 2 |
| 2a. Stems leafy; blades with a single, medial, primary vein and margins dentate to deeply dentate..... | 4. <i>P. hirsuta</i> |
| 2b. Stems with the leaves concentrated in the proximal third or half; blades with one medial and two lateral basal or suprabasal primary veins and margins denticulate..... | <i>P. hieracifolia</i> complex.3 |
| 3a. Rostrum of cypselae up to 1.2 mm..... | 1. <i>P. bellidifolia</i> |
| 3b. Rostrum of cypselae longer than 1.8 mm..... | 4 |
| 4a. Leaf indumentum pilose, sparse..... | 2. <i>P. blanchetiana</i> |
| 4b. Leaf indumentum pubescent, dense..... | 3. <i>P. hieracifolia</i> |

lateral basal or suprabasal veins, margins denticulate or dentate; intermediate leaves, when present, slightly clasping, distal leaves reduced, clasping. Capitula solitary or more commonly in corymbose arrays, terminal, heterogamous, short-radiate, long-pedunculate; involucre campanulate to broadly campanulate, multi-seriate, gradate, outer phyllaries ovate, acute, central and inner phyllaries linear-elliptic, acute; receptacle subconvex, epaleate. Ray florets pistillate, two- to four-seriate; corolla white often turning purplish when mature, limb short, narrow, oblong; style branches linear, glabrous or dorsally weakly papillose at apex. Disc florets hermaphrodite, corolla yellow often distally turning purplish when mature, tubular-funnelform, limb five-lobed; anther thecae rounded or auriculate at base, apical appendage ovate to oblong, subobtuse; style bifid, branches linear-oblong, subobtuse, distal three-quarters dorsally pilose, stigmatic surface in two marginal lines, distal third of style branch sterile. Cypselae compressed, margins strongly ribbed, villous (short twin trichomes), elliptic, narrowed at apex into a conspicuous neck or rostrum, sometimes cypselae of disc florets sterile; pappus of two or three series of setae, setae subequal or unequal, scabridulous, apex tapering, whitish when live, brownish when dry. $x = 9$ (*P. hirsuta*; Coleman, 1968; Hunziker *et al.*, 1989).

Distribution and habitat: *Podocoma* is endemic to southern South America and occurs in Argentina, Brazil, Bolivia, Paraguay and Uruguay up to c. 1300 m (Fig. 4). Its species inhabit open and sunny areas, and prefer high, fertile and clayish soils. For instance, in Argentina, *Podocoma* has been collected in dry grasslands (e.g. Corrientes, Chaco and Salta provinces), in *Elyonorus* Bartl. prairies (Poaceae; Chaco province), in pristine savannas with palms (*Butia yatay* Becc.; Misiones province) or on rocky slopes of relatively low mountain ranges (Buenos Aires province). *Podocoma* occurs in Brazil and Uruguay in similar habitats to those found in the Buenos Aires mountain ranges (Tandilia and Ventania). Close floristic relationships have been demonstrated among the biota of the moun-

tain ranges of these three countries (e.g. Crisci *et al.*, 2001). In Brazil and Paraguay, *Podocoma* has been found in the 'cerrado' biogeographical province, in grasslands ('campo limpio'), on rocky slopes of mountain ranges and, occasionally, in scrub with sandy soil. Some species seem to adapt more readily to variable habitats. This is the case for *P. hirsuta*, which has been found in clearings of semi-humid forest and disturbed areas, such as those close to railway tracks. Populations of *Podocoma* are not abundant and most collectors have indicated the species as locally rare or scarce. This, and the fact that many of the original habitats of *Podocoma* have been disturbed (e.g. many pristine areas of Misiones province in Argentina have been replaced by cultivation or pine forests), place some species of this genus in a vulnerable conservation status.

1. *PODOCOMA BELLIDIFOLIA* BAKER IN MARTIUS,
FL. BRAS. 6 (3): 16. 1882

Type: 'Lagoa Santa, Brazil', *Warming* s.n. (lectotype K designated here, photo LP; probable isolectotypes C photo MO, NY, S); Brazil, 'Prov. Minas Geraes Caldas', *Regnell III 730* (isosyntype US photo LP). *Notes:* 1. The specimen 'Warming s.n.' at Copenhagen indicates: '29-II-1864'; that at S indicates '2-X-1864', and that in NY indicates '9-X-1893', with a note by J. Pruski pointing out that as a probably wrong date. 2. The protologue indicates 'Habitat in prov. Minas Geraes collibus editis petrosis ad Caldas'.

= *Leucopsis podocomoides* Baker in Martius, Fl. Bras. 6 (3): 6. 1882. 'Prov. Minas Geraes: Caldas, 1845, *Widgren 219*' (lectotype K designated here; isolectotypes S × 2); 'in Brazilia australi sine loci designatione', *Sello 912* (syntype not seen).

Description: Herbs 30 to c. 50 cm tall, basal 1.0–2.5 cm of stem leafless, rest of stem leafy up to middle of plant, laxly pilose, trichomes long. Proximal leaves with blades oblanceolate, 8.0–9.5 × 1.5–2.7 cm, base attenuate, slightly auriculate and clasping, apex subacute, primary veins three, one medial and two

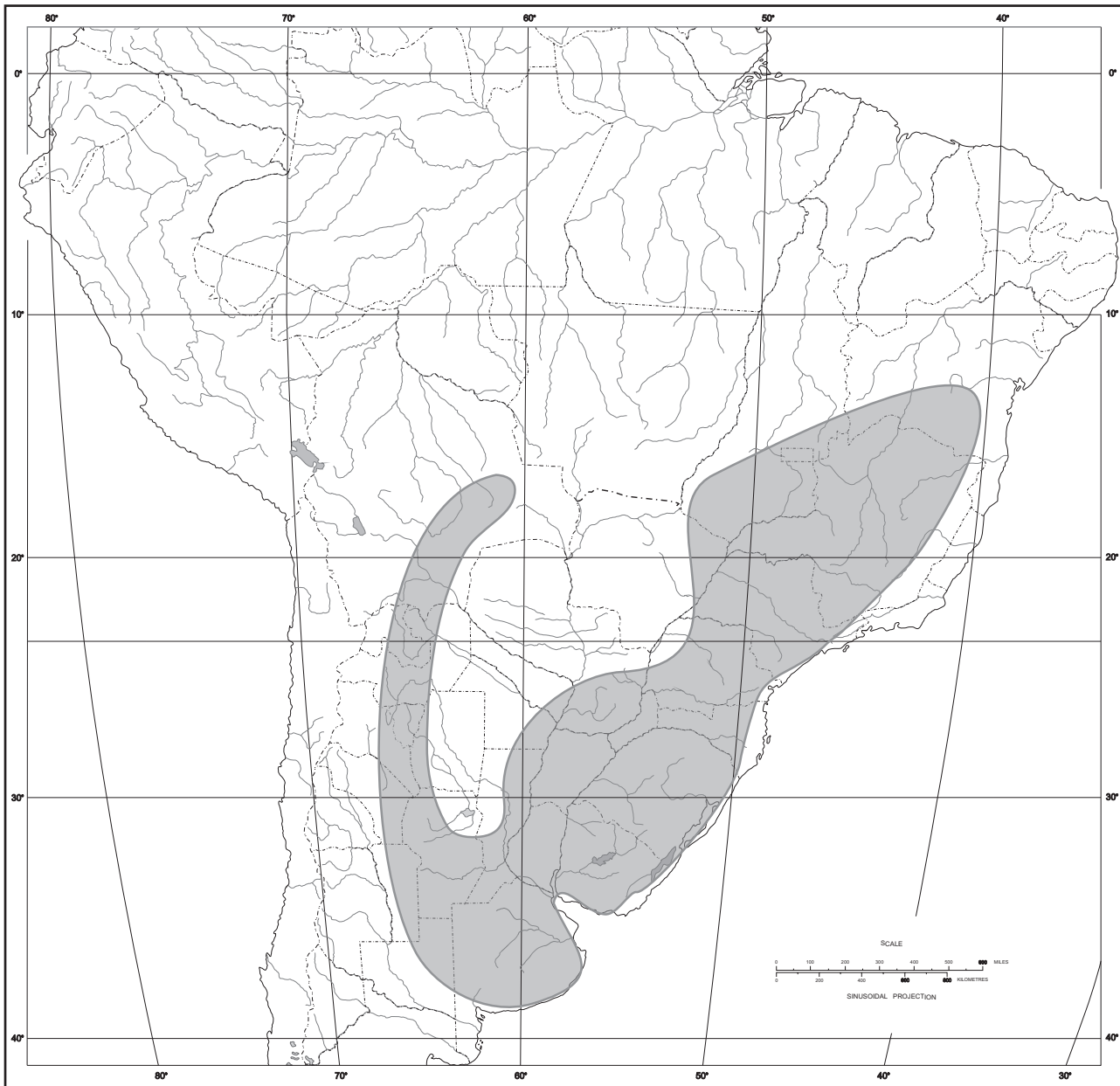


Figure 4. Distribution of *Podocoma*.

lateral basal or suprabasal, margins shortly denticulate, loosely hirsute or pilose on both surfaces, especially on main veins and margins (long conical trichomes); distal leaves reduced, 5.0–6.5 × 0.5–1.0 cm, narrowly linear or elliptic, clasping. Capitula solitary to three, peduncles 12–14 cm long, hirsute; involucre 10–12 mm high, campanulate; phyllaries three- to four-seriate, gradate, margins pale, dorsally greenish when dry, outer phyllaries 3.5 × 0.5–0.8 mm, narrow-ovate, acute, slightly pubescent (short, flagellate, filiform trichomes, twin hairs and a few conical trichomes with thin-walled cells), central and inner

phyllaries 8–9 × 1.0–1.1 mm, linear-elliptic, acute, dorsally slightly pubescent at apex, trichomes short, margins deeply fimbriate; receptacle subconvex, deeply alveolate. Ray florets, three-seriate; corolla 12 mm long, limb narrow, short, c. 4 mm, oblong, glabrous, tube narrow, densely hairy (simple, biseriate glandular trichomes); style branches dorsally glabrous. Corollas of disc florets 10.0–10.5 mm long, densely hairy (simple, biseriate glandular trichomes on tube and lobes), lobes 0.8–1.0 mm long; anthers 1.7–2.0 mm long, thecae auriculate at base, apical appendage oblong, obtuse; style branches 1.6–1.8 mm

long, distal three-quarters dorsally pilose. Cypselae 5–7 mm long, margins strongly ribbed, narrowed at apex into a short but conspicuous rostrum, rostrum 1.0–1.2 mm long, cypselae of disc florets sometimes sterile; pappus *c.* 12 mm long, setae two-seriate, unequal (Fig. 5).

Phenology: Flowering from October to February.

Distribution and habitat: Brazil (states of Goiás, Minas Geraes, Paraná and São Paulo) (Fig. 7) at 720 m. In ‘campos’, sandy peats of ‘campo-cerrado’ transition, steep rocky slopes, scrubby areas and base of ‘chapada’ escarpments, in sunny places or semi-shade. It has been indicated as locally scarce.

Notes: This species is similar to *P. blanchetiana* and *P. hieracifolia* in vegetative characters, but is recognized by its strongly ribbed cypselae with a short rostrum. Its oblanceolate leaves, often cauline with three primary veins, help to identify this species. The Brazilian specimens (including the types) have pilose leaves with long and curved trichomes. However, the Argentine and Paraguayan specimens studied here and previously determined as *P. bellidifolia*, although similar in general aspect and leaves, have shorter and denser trichomes. The rostra of cypselae in these specimens are indeed longer than those of the type specimens. This raises difficulties with respect to defining the limits of the species when other than the type specimens are analysed. A possible explanation for this situation could be hybridization, probably between *P. bellidifolia* and *P. hieracifolia*, but this could be tested only with more specific studies. In this treatment, we prefer to treat *P. bellidifolia* as distributed only in Brazil. The species is regarded here as doubtful for Argentina and Paraguay, and the Argentine and Paraguayan specimens are cited as *P. aff. bellidifolia*.

Specimens examined: BRAZIL. Goiás: Serra Caiapó, 26.x.1964, *Irwin & Soderstrom 7385* (NY, US); Alto Paraíso de Goiás, Chapada dos Veadeiros, 29.xi.1988, *Wanderley 1680, Kral 75713 & Cavalcanti* (NY). Minas Geraes: Caldas, *Regnell III 730 a* (S, three sheets). Paraná: Morungava, 5.xii.1915, *Dusén 17427* (MO); Morungava, 5.xii.1915, *Dusén 17427 a* (S); Turma, 19.x.1914, *Dusén 15642* (GH, S); Lago, 2.xii.1910, *Dusén 10893* (S); Jaguariabyra, 3.xii.1915, *Dusén s.n.* (S); Senges, Serra Mocambo, 19.ix.1975, *Hatschbach 37119* (LP). São Paulo: Jaraguá, 8.xii.1912, *Brade 5706* (LP, S, US); Butantan, i.1918, *Hoehne s.n.* (NY, ex SP 1665).

Specimens ‘affinis’ to P. bellidifolia: ARGENTINA. Corrientes: Santo Tomé, Estancia San Francisco,

5.xii.1970, *Krapovickas et al. 17205* (CTES). Jujuy: Caldera, 1.ii.1949, *Cabrera & Schwabe 194* (LP). Misiones: Loreto, 28.iii.1933, *Grüner 1352* (LP).

PARAGUAY. Caaguazú: Estancia Primera, x.1927, *Rojas 5124* (LP).

2. *PODOCOMA BLANCHETIANA* BAKER IN MARTIUS, FL. BRAS. 6 (3): 15. 1882

Type: Brazil, ‘Habitat in prov. Bahia ad Igregia Velho’, *Blanchet 3365* (lectotype BR 698188 designated here, not seen, photo at <http://www.br.fgov.br/RESEARCH/COLLECTIONS/HERBARIUM/herbariumdescription.php>; isolectotypes B probably destroyed, photo MO, BM, BR-2 not seen, K, MO, NY, P). *Note:* The specimen at K has a handwritten note by Baker saying: ‘*Haplopappus blanchetianus* Schulz Bip. in herb. Belg. *Podocoma blanchetiana* Baker’.

= *Haplopappus blanchetianus* Sch. Bip. ex Baker in Martius, Fl. Bras. 6 (3): 16. 1882, nom. nud. pro syn.

Description: Herbs 25–35 cm tall, stems leafy at base, laxly pilose, trichomes long. Leaves congested at the base; proximal leaves with blades oblanceolate, obovate or broadly obovate, 8.0–9.5 × 3.0–3.5 cm, base attenuate, slightly clasping, apex subacute, primary veins three, one medial and two lateral basal or suprabasal, margins shortly denticulate, sparse pilose on both surfaces (long conical trichomes); distal leaves reduced, 3.5–4.0 × 1.0–1.5 cm, narrowly elliptic, clasping. Capitula two or three, peduncles 2–8 cm long, pilose, trichomes long; involucre 9–11 mm high, campanulate; phyllaries three to four-seriate, gradate, margins pale, dorsally greenish and tips purplish when dry, outer phyllaries 4–5 × 0.6–0.7 mm, narrow ovate, acute, slightly pilose to subglabrous (short conical trichomes with thin-walled cells, and a few flagellate, filiform trichomes and simple, biseriate glandular trichomes), central and inner phyllaries 8.0–12 × 0.8–0.9 mm, linear-elliptic, acute, dorsally subglabrous, margins deeply fimbriate at apex; receptacle subconvex, deeply alveolate. Ray florets three-seriate; corolla purplish in mature florets, 7.0–7.5 mm long, limb narrow, short, 2.2–2.8 mm, oblong, glabrous, tube narrow, densely hairy (simple, biseriate glandular trichomes and a few conical with thin-walled cells); style branches dorsally glabrous. Corolla of disc florets 8.0–8.5 mm long, hairy (simple biseriate glandular trichomes on tube and lobes), lobes 0.5–0.8 mm long; anthers *c.* 2 mm long, thecae auriculate at base, apical appendage oblong, subobtusate; style branches 1.8–2.0 mm long, distal three-quarters dorsally pilose. Cypselae 5.5–7.5 mm long, margins ribbed, narrowed at apex into a conspicuous rostrum, rostrum 2–3 mm long; pappus *c.* 7–9 mm long, setae three-seriate, unequal (Fig. 6).

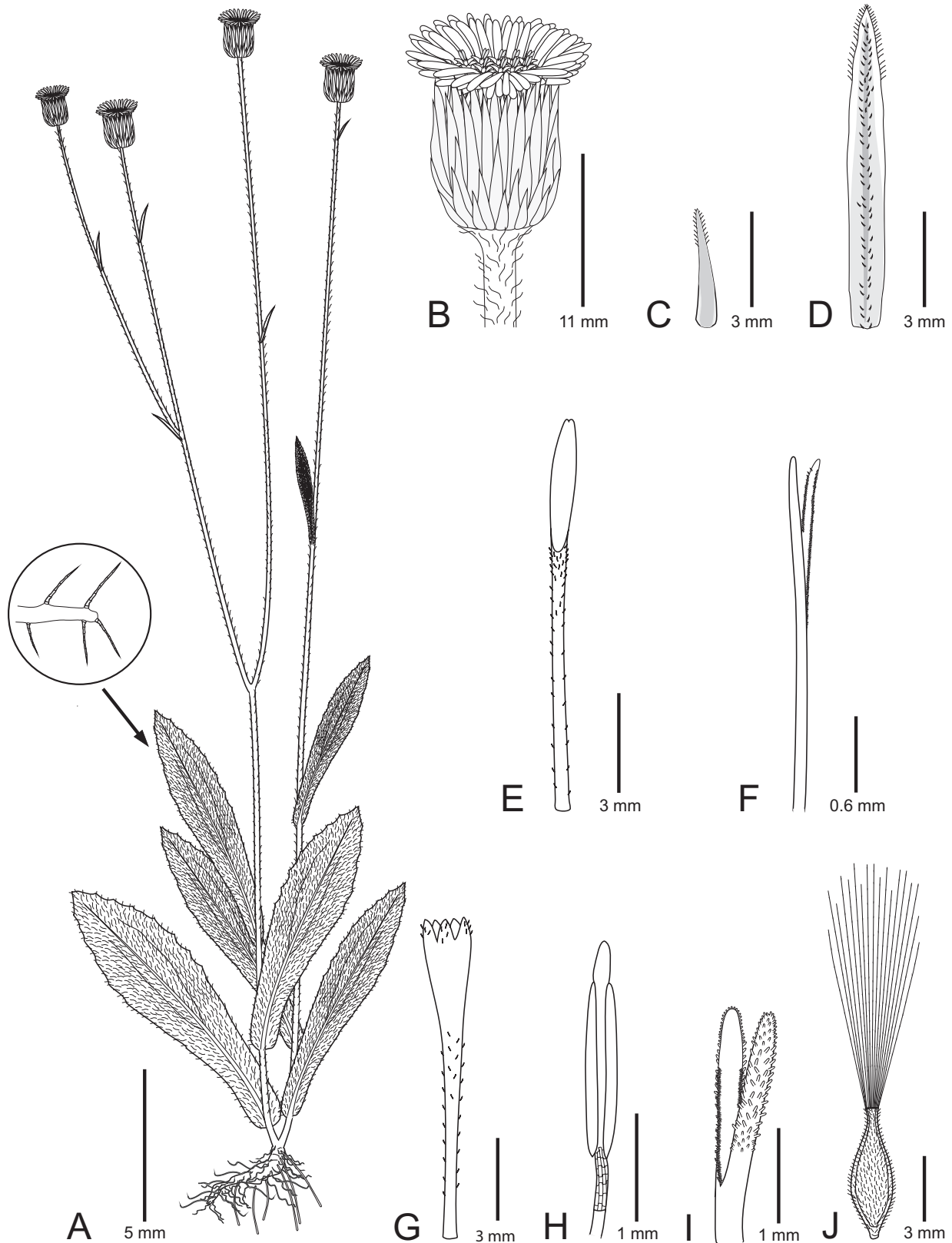


Figure 5. *Podocoma bellidifolia*: A, plant; B, capitulum; C, outer phyllary; D, inner phyllary; E, ray corolla; F, style of ray floret; G, disc corolla; H, stamen of disc floret; I, style of disc floret; J, cypsela with pappus. (A, B from Widgren 219, S; C–J from Dusén s.n., S.)



Figure 6. *Podocoma blanchetiana*: A, plant; B, capitulum; C, outer phyllary; D, inner phyllary; E, ray corolla; F, style of ray floret; G, disc corolla; H, stamen of disc floret; I, style of disc floret; J, cypsela with pappus. (From Krapovickas *et al.* 26381, CTES.)

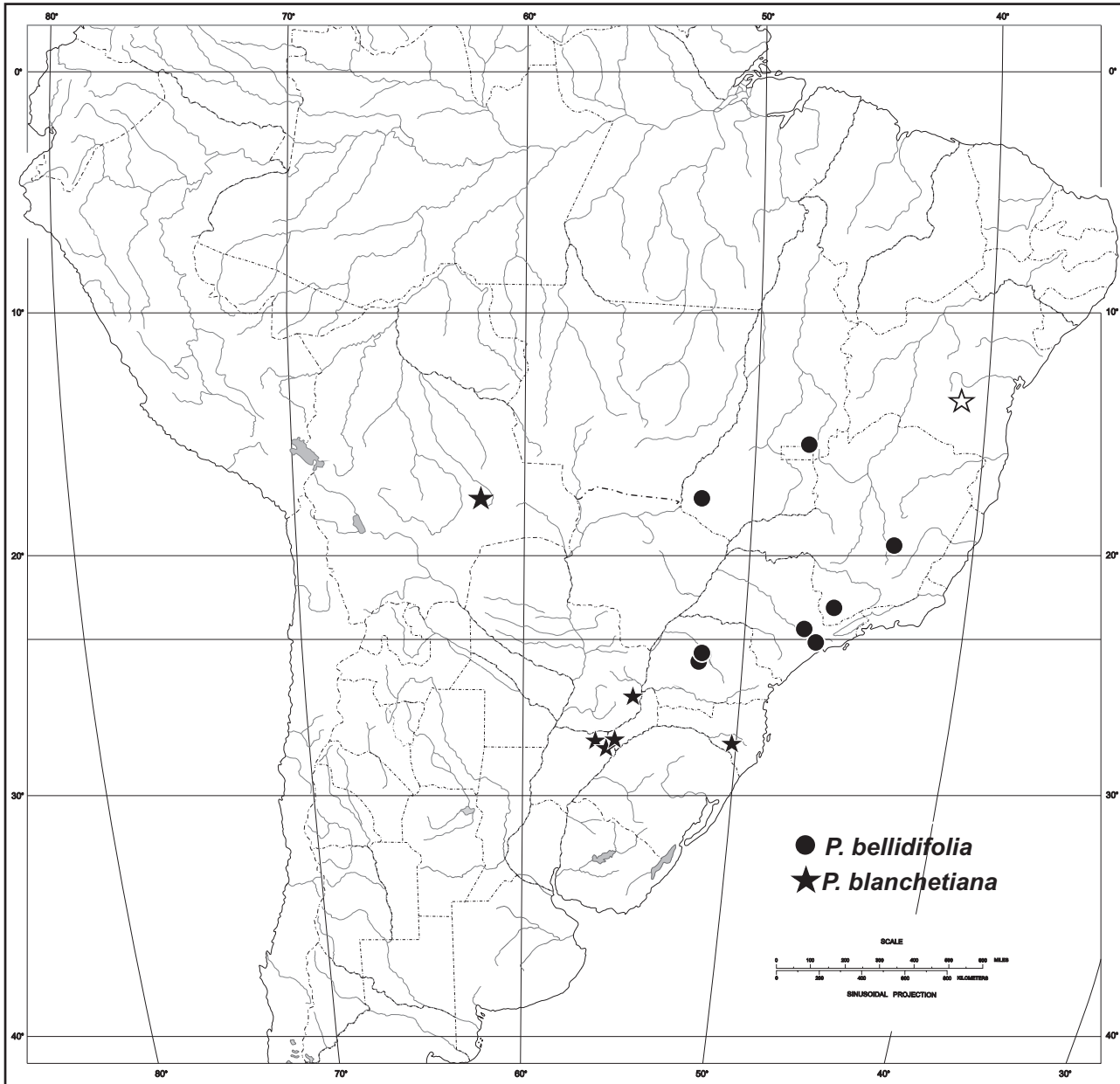


Figure 7. Distribution of *Podocoma bellidifolia* and *P. blanchetiana*. Open star indicates imprecise locality.

Phenology: Flowering from September to April.

Distribution and habitat: Argentina (Corrientes and Misiones provinces), Bolivia (Santa Cruz), Brazil (Santa Catarina, Bahia) and Paraguay (Alto Paraná) (Fig. 7). In grasslands and savannas with *Butia yatay* (Argentina). The specimen from Bolivia was collected in semi-deciduous and subhumid forest, but in rocky areas dominated by grass at 1000 m above sea level. It is indicated as locally scarce.

Notes: 1. The isoelectotype in NY has pubescent phyllaries, the inner at least pubescent at the apex.

However, the additional specimens examined show variation; indeed, some have glabrate phyllaries. Baker (1882: 15) described the phyllaries as ‘exterioribus dorso pubescentibus’. It could be the case that variation in morphological characters, e.g. phyllary pubescence, was not included in the description as Baker examined only one collection.

2. Some of the specimens from Argentina (Corrientes) have broad leaves and pubescence of long trichomes. There is a gradation in leaf trichome length throughout the specimens studied. The extreme of that gradation, specimens with leaves with long trichomes, could be treated as a variety within *P.*

blanchetiana. However, because variation is continuous, we would rather avoid the recognition of new entities.

Specimens examined: ARGENTINA. Corrientes: Santo Tomé, Garruchos, 22.xii.1954, *Burkart 19696* (SI); Ituzaingó, road to Playadito, 24.ix.1974, *Krapovickas et al. 26315* (CTES); Playadito, 24.ix.1974, *Krapovickas et al. 26381* (CTES); Santo Tomé, 5.ii.1972, *Krapovickas et al. 21001* (CTES). Misiones: San Javier, 13.iii.1969, *Krapovickas et al. 15191* (CTES, LP); Campo Grande, i.1907, *Spegazzini 103* (LP); Apóstoles, Azara, 26.xi.1987, *Zuloaga et al. 3263* (SI); Candelaria, Loreto, 3.xi.1948, *Montes 3481* (SI).

BOLIVIA. Santa Cruz: Florida, Laguna Volcanes, 3–4.iv.1994, *Fuentes 353* (MO).

BRAZIL. Santa Catarina: Lajes, Morro Pinheiro Seco, iv.1957, *Smith & Klein 10020* (US).

PARAGUAY. Alto Paraná: Ñacunday, 20.xi.1950, *Montes 9839* (CTES).

3. *PODOCOMA HIERACIFOLIA* (POIR.) CASS. IN CUVIER, DICT. SCI. NAT. 42: 60. 1826

Basionym: *Erigeron hieracifolius* (as *hieracifolium*) Poir. in Lam., *Encycl.* 8: 491. 1808.

Type: Argentina, 'Buenos-aires', *Commerson* s.n. (holotype FI not seen, photo LP).

Note: The protologue indicates '(v. s. in herb. Desfont.)'.

= *Podocoma primulifolia* (as *primulaefolia*) Cass., op. cit. 61. 1826. *Type:* Uruguay, 'Montevideo, 1767', *Commerson* s.n. (holotype P, Herb. Jussieu Catal. N°8698 p.p.). *Note:* The specimen at P has '*Erigeron? Primulaefolium*' handwritten by Jussieu on the label, as also noted by Cassini when describing *Podocoma primulifolia*.

= *Podopappus pubescens* Hook. & Arn., *Companion Bot. Mag.* 2 (14): 50. 1836. *Type:* Argentina, 'Buenos Ayres', s.d., '*Tweedie* s.n.' (holotype K).

= *Podocoma erigerifolia* (as *erigerifolium*) Steud., *Nomenc. Bot.* (ed. 2) 1: 584. 1840 (pro syn. sphalm = *P. primulifolia* Cass.).

= *Podocoma blanchetiana* var. *intermedia* Hassl., *Repert. Spec. Nov. Regni Veg.* 16 (1–4): 27. 1919. *Types:* Paraguay, Río Apa, 11/1902, *Hassler 7831* (syntype G not seen, NY, S); *Hassler 6969* (syntype not seen).

= *Podocoma foliosa* Dusén ex Malme, *Kongl. Svenska Vetensk. Acad. Handl.* 12(2): 64. 1933. *Type:* Brazil, Paraná, 'Jaguariahyba, 26/12 1915, in campo, *Dusén* s.n.' (holotype S).

Description: Herbs 20–50 cm tall, stems usually only leafy at base, exceptionally with leaves in proximal half, laxly pubescent, trichomes short. Leaves usually restricted to proximal third of stem, most distal ones reduced; proximal leaves with blades oblanceolate, or less commonly broadly obovate, 5.5–7.5 × 1.5–2.5 cm, base attenuate, slightly clasping, apex subacute, primary veins three, one medial and two lateral basal or suprabasal, margins shortly denticulate, usually dense-pubescent on both surfaces (short conical and a few small flagellate filiform trichomes); distal leaves reduced, 3.5–4.0 × 1.0–1.5 cm, narrowly elliptic, clasping and with auriculate base. Capitula two to eight, peduncle 2–8 cm long, arachnoid and pubescent, trichomes short; involucre 9–12 mm high, campanulate to broadly campanulate; phyllaries four- to five-seriate, gradate, margins pale when dry, dorsally green with purple tips when live, outer phyllaries 4–5 × 0.7–1.0 mm, narrow ovate, acute, pubescent (short conical, flagellate filiform and simple biseriate glandular trichomes), central and inner phyllaries 7.5–12.0 × 0.7–0.9 mm, linear-elliptic, acute, dorsally pubescent, trichomes short, margins fimbriate to lacerate at apex; receptacle flat, deeply alveolate. Ray florets four-seriate; corolla c. 8 mm long, limb narrow, short, 2.5–2.8 mm, oblong, glabrous, tube narrow, densely hairy (simple biseriate glandular trichomes and a few conical trichomes with thin-walled cells); style branches dorsally glabrous. Corollas of disc florets 6.0–6.5 mm long, hairy (simple, biseriate glandular trichomes and a few conical trichomes with thin-walled cells on tube and lobes), lobes 0.3–0.5 mm long; anthers c. 1.5 mm long, thecae subacute at base, apical appendage oblong, obtuse; style branches 1.8 mm long, distal three-quarters dorsally pilose. Cypselae 6–7 mm long, margins strongly ribbed, narrowed at the apex into a conspicuous rostrum, rostrum 2–3 mm long; pappus c. 7–8 mm long, setae three-seriate, unequal (Figs 8, 13A).

Phenology: Flowering from October to July.

Distribution and habitat: This species has been collected in Argentina [Buenos Aires, Catamarca, Chaco, Corrientes, Entre Ríos, Jujuy, La Pampa (Troiani & Steibel, 1999), Misiones], Brazil ('Brasilia australi', Baker, 1882; 'Paraná', Malme, 1933), Paraguay and Uruguay (Florida, Montevideo) (Fig. 9). In grasslands (e.g. with *Elyonorus* sp., Chaco, Argentina) or rocky slopes of low ranges (e.g. Buenos Aires mountain ranges, Argentina, and Montevideo mountain ranges, Uruguay). In Argentina, it was also found in fertile and clay soils, in grasslands surrounded by *Podocarpus parlatorei* Pilg. forest at 1600–1750 m (Catamarca). It has been indicated as locally scarce. We were unable to see Brazilian material.

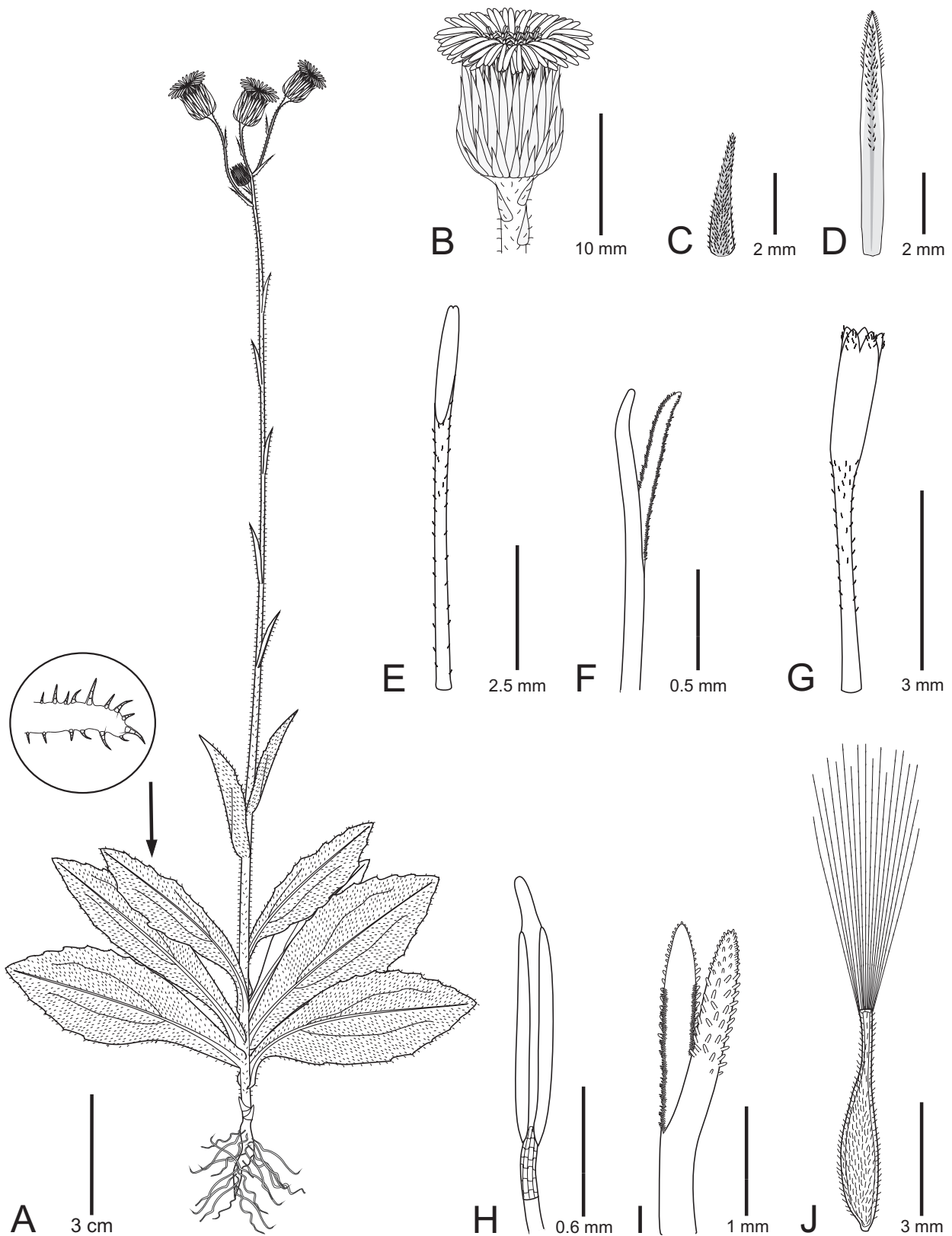


Figure 8. *Podocoma hieracifolia*: A, plant; B, capitulum; C, outer phyllary; D, inner phyllary; E, ray corolla; F, style of ray floret; G, disc corolla; H, stamen of disc floret; I, style of disc floret; J, cypsela with pappus. (A, B from *Cabrera 8119*, LP; C–E, G, J from *Schulz 256*, LP; F, H, I from *Cabrera 10275*, LP.)

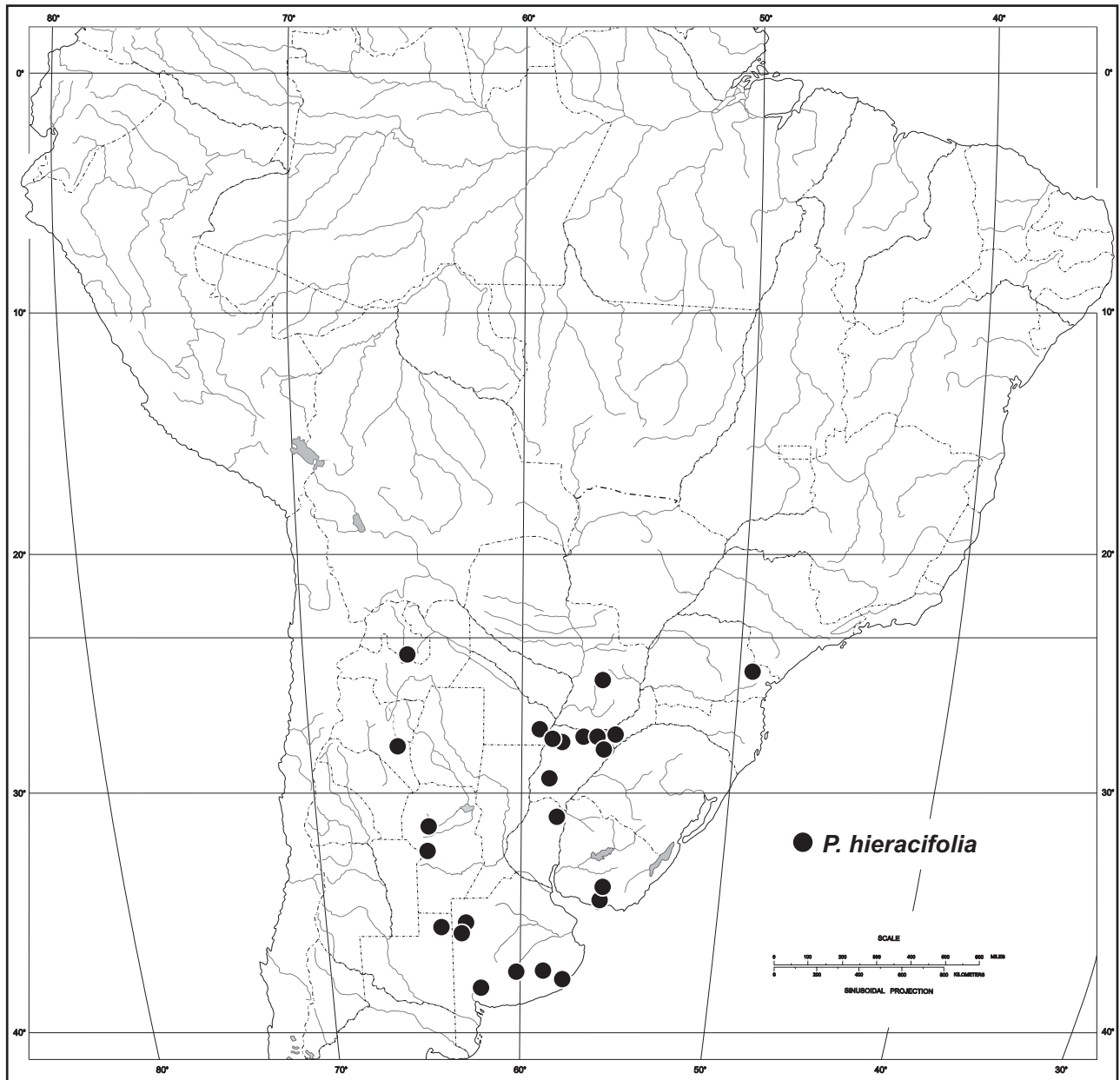


Figure 9. Distribution of *Podocoma hieracifolia*.

Notes: 1. This is a polymorphic species that usually has subsulate and oblanceolate leaves with denticulate margins, but, in some cases, it has leaves in the proximal third of the plant with dentate margins.

2. This species, together with *P. bellidifolia* and *P. blanchetiana*, constitutes a complex of species that are difficult to separate consistently. It seems that the differentiation of the three species, especially *P. hieracifolia* and *P. blanchetiana*, relies mostly on pubescence length, which may be subject to environmental variation. As pointed out by Hassler (1919:

27), the specimens of *P. blanchetiana* var. *intermedia* have features of both *P. blanchetiana* and *P. hieracifolia*. The specimens of *P. blanchetiana* var. *intermedia* have more leafy stems and are more robust plants than those of *P. hieracifolia*, although the relatively dense pubescence with short trichomes is similar. We prefer to treat this variety under the synonymy of *P. hieracifolia*, although the limits of this species are not always clear.

3. It is apparent that *P. foliosa* is not a distinct species. Indeed, it has been regarded as a synonym of

P. bellidifolia (Nesom & Zanowiak, 1994). We agree with the differences pointed out by Malme (1933: 64), when comparing it with *P. hieracifolia* and *P. bellidifolia*. Although *P. foliosa* has characters in common with both species, we prefer to consider it as a synonym of *P. hieracifolia* because of its identical pubescence (short and dense). The fact that *P. foliosa* has cauline leaves and a shorter cypsela rostrum than typical *P. hieracifolia* is not enough to separate the species. Many specimens of *P. hieracifolia* do not have strictly rosulate leaves, but some of them on the proximal third of the stem.

4. The specimen in US, cited by Nesom & Zanowiak (1994) as probably a new species, is, from our point of view, only a specimen of *P. hieracifolia* with broader leaves.

5. *Podocoma blanchetiana* var. *intermedia* and *P. foliosa* show the complexity of this group of three species (*P. bellidifolia*, *P. blanchetiana* and *P. hieracifolia*), which could, indeed, have been the subject of hybridization processes.

Specimens examined: ARGENTINA. Buenos Aires: Sierra de la Ventana, 24.v.1938, *Cabrera 4493* (LP); ib., 14.xi.1943, *Cabrera 8119* (LP); ib., 30.iii.1978, *Proyecto Ventania 87* (LP); ib., 30.iii.1978, *Proyecto Ventania 112* (LP); Pehuajó, iii.1946, *Cabrera 10275* (LP); ib., 17.iv.1988, *Delhey 6885* (LP); Sierra de Tandil, 5.iv.1972, *Frangi 440* (LP); Sierra La China, 28.v.1932, *Millán 2168* (LP); Trenquelauquen, 19.iv.1901, *Spegazzini* s.n. (LPS 11428 in LP). Catamarca: Ambato, 4.iv.1995, *Saravia et al. 13445* (CTES). Chaco: Fontana, vi.1937, *Meyer 2307* (LP); Colonia Benítez, i.1932, *Schulz 207 p.p.* (LP) [mounted on the same sheet with a specimen of *P. spegazzinii*]; ib., vi.1933, *Schulz 256* (CTES, LP); ib., s.d., *Schulz 4277* (CTES); San Fernando, v.1937, *Schulz 2678* (CTES). Córdoba: Carlos Paz, 11.ii.1939, *Bridarolli 605* (LP); Colón, Salsipuedes, iii.1935, *Dawson 16* (LP); Calamuchita, 14.xii.1946, *Hunziker 7180* (LP). Corrientes: Mburucuyá, 14.x.1954, *Cabrera 11776* (LP); ib., 4.vii.1952, *Pedersen 1765* (US) [This specimen was cited by Nesom & Zanowiak (1994) as probably belonging to a new species. From the authors point of view, it belongs to *P. hieracifolia* as part of the variability of this species, e.g. broadly obovate leaves]; Santo Tomé, 5.xii.1970, *Krapovickas et al. 17206* (CTES); Ituzaingó, 2.iii.1987, *Krapovickas et al. 41032* (CTES); ib., 5.iii.1987, *Krapovickas et al. 41197* (CTES, LP); ib., 20.ix.1970, *Krapovickas & Cristobal 16074* (CTES); Empedrado, 3.iv.1962, *Pedersen 6487* (LP); Curuzú Cuatía, 3.v.1986, *Pedersen 14554* (CTES); Barón de Astrada, 16.i.1977, *Schinini 14087* (CTES). Entre Ríos: Pedernar, iii.1934, *s.leg. 361* (LP). Jujuy: El Carmen, 23.ii.1970, *Cabrera*

& *Frangi 20729* (LP). Misiones: Candelaria, iii.1961, *Martínez Crovetto 9491* (CTES).

PARAGUAY. Caaguazú: 5.x.1905, *Hassler 9128* (BM, K, NY, S); ib. 1905, *Hassler 9357* (NY). Without precise locality: s.d., *Hassler 7831* (NY, S).

URUGUAY. Florida: Río Ti y Arroyo Mausairilla-gra, 26.xii.1936, *Rosengurt B. 762* (LP). Montevideo: v.1874, *Gibert 1309* (K); ib., i.1876 [ii/77], *Arechavaleta 4065* (K); ib., v.1877, *Frechard* s.n. (LP). Rivera: Arroyo Lunarejo, 19.ii.2004, *Sancho & Bonifacino 98* (LP) [this specimen, cited by Sancho & Karaman-Castro (2008), has features of habit and pubescence that depart from those typical of *P. hieracifolia*. It was found in forest understorey, in shade, and it may be that or potential hybridization which could have influenced these features]. Without precise locality: Campos Uruguayos, ii.1897, *Arechavaleta 31* (K) [the collection number does not appear to be correlated with the collection date].

4. *PODOCOMA HIRSUTA* (HOOK. & ARN.) BAKER IN MARTIUS FL. BRAS. 6 (3): 15. 1882

Basionym: *Podopappus hirsutus* Hook. & Arn., Companion Bot. Mag. 2 (14): 50. 1836.

Type: Brazil, 'moist ground, Rio Grande, Tweedie s.n.' (lectotype K designated here); Argentina, Guardia Argentino in North Patagonia, *Tweedie* s.n. (syntype not seen).

Note: The protologue indicates 'Rio Grande, and Guardia Argentino in North Patagonia'.

= *Podocoma regnellii* Baker in Martius Fl. Bras. 6 (3): 16. 1882. *Type:* Brazil, 'Prov. Minas Geraes, Caldas', 13-XI-1868, *Regnell III 732* (holotype C not seen, photo at LP; isotypes S, US). *Notes:* 1. We have studied four type sheets from S, three of them have date 'XI-1871', the other says '5-XI-1864'. 2. The protologue indicates 'Habitat in prov. Minas Geraes pascuis ad Angolas Velhas prope Caldas'.

= *Podocoma hirsuta* var. *macrophylla* Arechav., Fl. Urug. 3, Anales Mus. Nac. Montevideo 6 (2): 205. 1907. No type specimen cited.

Description: Herbs 50 to c. 100 cm tall, stems leafy, hirsute. Leaves cauline, progressively reduced towards stem apex; blades elliptic, 6–15 × 3.5–6.0 cm, base subauriculate, slightly clasping, apex subacute to acute, primary vein single, medial, margins dentate to deeply dentate, hirsute on both faces (long conical trichomes, a few short conical trichomes with thin-walled cells and flagellate filiform trichomes), intermediate leaves similar to most proximal ones,

distal leaves reduced, 3–4 × 0.5–1.0 cm, lanceolate, deeply dentate at apex. Capitula 3–30, peduncle 1.5–3.0 cm long, hirsute; involucre 7–9 mm high, broadly campanulate when live, campanulate when dry; phyllaries four- to five-seriate, gradate, green when live, margins pale, dorsally greenish when dry, outer phyllaries 3.0–3.5 × 0.5 mm, narrow-ovate, acute, subglabrous (simple, biseriata glandular trichomes, flagellate, filiform trichomes and a few twin hairs), central and inner phyllaries 7–8 × 0.5–0.6 mm, linear-elliptic, acute, dorsally subglabrous (simple, biseriata glandular and flagellate, filiform trichomes), margins fimbriate at apex; receptacle subconvex, deeply alveolate. Ray florets three- to four-seriate; corolla 5–8 mm long, limb narrow, relatively short, 1.5–2.5 mm, oblong, glabrous, tube narrow, hairy (simple, biseriata glandular trichomes); style branches dorsally glabrous. Corollas of disc florets 6.0–6.5 mm long, hairy (simple biseriata glandular trichomes and a few conical trichomes with thin-walled cells on tube and lobes), lobes *c.* 0.5 mm long; anthers 1.3 mm long, thecae auriculate at base, apical appendage narrowly ovate, subobtusate; style branches 0.9–1.1 mm long, distal three-quarters dorsally pilose. Cypsela 6–7 mm long, margins ribbed, densely villous, narrowed at apex into a conspicuous rostrum, rostrum 2.5–2.8 mm long; pappus *c.* 9 mm long, setae two- or three-seriate, subequal (Figs 10, 13B).

Phenology: Flowering throughout the year, especially in Brazil.

Distribution and habitat: Argentina (Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Misiones, Santa Fé and Tucumán), Bolivia, Brazil (Paraná, Rio Grande do Sul, Santa Catarina and São Paulo), Paraguay (Alto Paraná) and Uruguay (Canelones, Florida and Soriano) (Fig. 12). Collected in a wide diversity of habitats, including disturbed areas such as railway tracks. *Podocoma hirsuta* lives in grasslands, margins of forest and xerophytic forest, in sandy, high and fertile soils. In some locations it has been indicated as scarce and, in others, as frequent.

Note: The differences between *P. hirsuta* and *P. regnellii* rely only on the depth of the marginal teeth of the leaf blades, which is variable. Here, we regard *P. regnellii* as a synonym of *P. hirsuta*.

Additional specimens examined: ARGENTINA. Buenos Aires: Las Palmas, 23.iv.1952, *Boelcke* 6612 (SI); *ib.*, 23.iv.1952, *Boelcke* 6626 (SI); Delta del Paraná, Carabelas, 12.ii.1932, *Burkart* 4431 (SI); *ib.*, 28.xii.1952, *Burkart* 19028 (SI); *ib.*, Canal Arana,

21.i.1931, *Cabrera* 1630 (LP); *ib.*, Paraná de las Palmas, xii.1938, *Cabrera* 4892 (LP); Punta Lara, 14.i.1932, *Cabrera* 2020 (LP); *ib.*, 10.ii.1929, *Cabrera* 743 (GH, LP); *ib.*, 3.iii.1930, *Cabrera* 1370 (LP); *ib.*, 4.i.1940, *Dawson* 944 (LP, NY); Cerro La Peregrina, 11.xii.1938, *Eyerdam et al.* 23685 (K, SI); Los Ingleses, 20.iv.1899, *Gibson* 13 (BM); Mar del Plata, 7.i.1933, *Hicken* s.n. (SI 9708); Balcarce, 3–15.i.1943, *Hunziker* 2171 (LP, SI); Tornquist, 28.iii.2004, *Long* 2224 (LP); Isla Martín García, v.1935, *Pastore* 305 (LP); Pergamino, 8.v.1965, *Schulz* 9382 (CTES); Tornquist, 1.x.1895, *Spegazzini* s.n. (LPS 11429 in LP); La Plata, *Spegazzini* s.n. (LPS 11430 in LP); Ramallo, 22.ii.2002, *Torres R. & Trevisán* 804 (LP). Chaco: sine loc., x.1917, *Jørgensen* 2043 (GH, SI, US); Fontana, xii.1937, *Meyer* 2518 (LP); 1° de Mayo, vi.1930, *Schulz* 76 (CTES, LP); *ib.*, v.1943, *Schulz* 3920 (CTES). Córdoba: San Javier, 13.ii.1940, *Bridarolli* 1602 (LP); Ascochinga, 18.iii.1937, *Giardelli* 884 (LP, SI); *ib.*, 12.ii.1938, *Giardelli* 1210 (SI); San Justo, 3.ii.1957, *Hunziker* 13401 (LP, NY); Ascochinga, 12.ii.1938, *Nicura* 1847 (LP). Corrientes: Esquina, 2.iii.1980, *Ahumada et al.* 3483 (CTES); Santo Tomé, 21.x.1954, *Cabrera* 11955 (LP); Ituzaingó, 20.ix.1970, *Krapovickas* 16074 (LP); Esquina, 14.iii.1975, *Krapovickas et al.* 27724 (CTES, SI); Río Miriñay, 20.ii.1972, *Krapovickas & Cristóbal* 21762 (CTES, LP); Lavalle, 25.xi.1979, *Schinini et al.* 19109 (CTES). Entre Ríos: Diamante, 15.xii.1960, *Burkart* 22351 (CTES, SI); Concordia, 4.ii.1927, *Burkart* 1166 (SI); *ib.*, 21.xii.1962, *Burkart* 24039 (SI); Delta del Paraná, 25.xi.1932, *Burkart* 5106 (SI); Federación, 14.iv.1960, *Burkart & Gamarro* 21959 (SI); Parque San Martín, 22.xii.1957, *Cabrera* 12408 (LP); Río Ceibo, 23.xi.1931, *Cabrera* 1936 (LP); Pedermar, iv.1934, *Friedman* 388 (LP); Paraná, ii.1948, *Martínez Crovetto* 4773 (SI). Formosa: sine loc., iii.1898, *Jørgensen* 2903 (GH, SI, US). Misiones. Loreto, 1.i.1933, *Grüner* 1285 (LP); Caniguás, 6.vi.1949, *Montes* 4114 (LP). Santa Fé: Rafaela, 6–7.iii.1984, *Franceschi* 800 (SI). Tucumán: Capital, xii.1923, *Venturi* 2718 (GH, US). BOLIVIA. Sine loc., *Bang* 2878 (MO). BRAZIL. Paraná: Itaperussú, 17.ii.1908, *Dusén* 7165 (S, US); inter Curitiba et Pinhães, 13.xi.1909, *Dusén* 8915 (NY, US); Guajiravira, 22.xi.1909, *Dusén* 8933 (S); Jaguarihyva, 30.xii.1919, *Dusén* 16221 (GH, S); Jaguarihyva, 7.xii.1910, *Dusén* s.n. (S); sine loc., 1858, *Gibert* 69 (K); Curitiba, 26.xii.1973, *Hatschbach* 33642 (LP); Volta Grande, 29.vii.1914, *Jonsson* 763 (S). Rio Grande do Sul: Torres, 6.viii.1952, *Beetle* 1860 (US); Porto Alegre, Morro Santana, 26.vi.1979, *Bueno* 1530 (CTES); Torres, 17.i.1982, *Krapovickas & Cristóbal* 37665 (CTES); Passo do Socorro, 26.xii.1951, *Rambo* 51480 (LP, US). Santa Catarina: Rio Capinzal, 27.ii.1916, *Dusén* 17815 (MO). São Paulo: Jaraguá, 22.xii.1912, *Brade* 5493 (S, US); Campinas, 9.ix.1936,

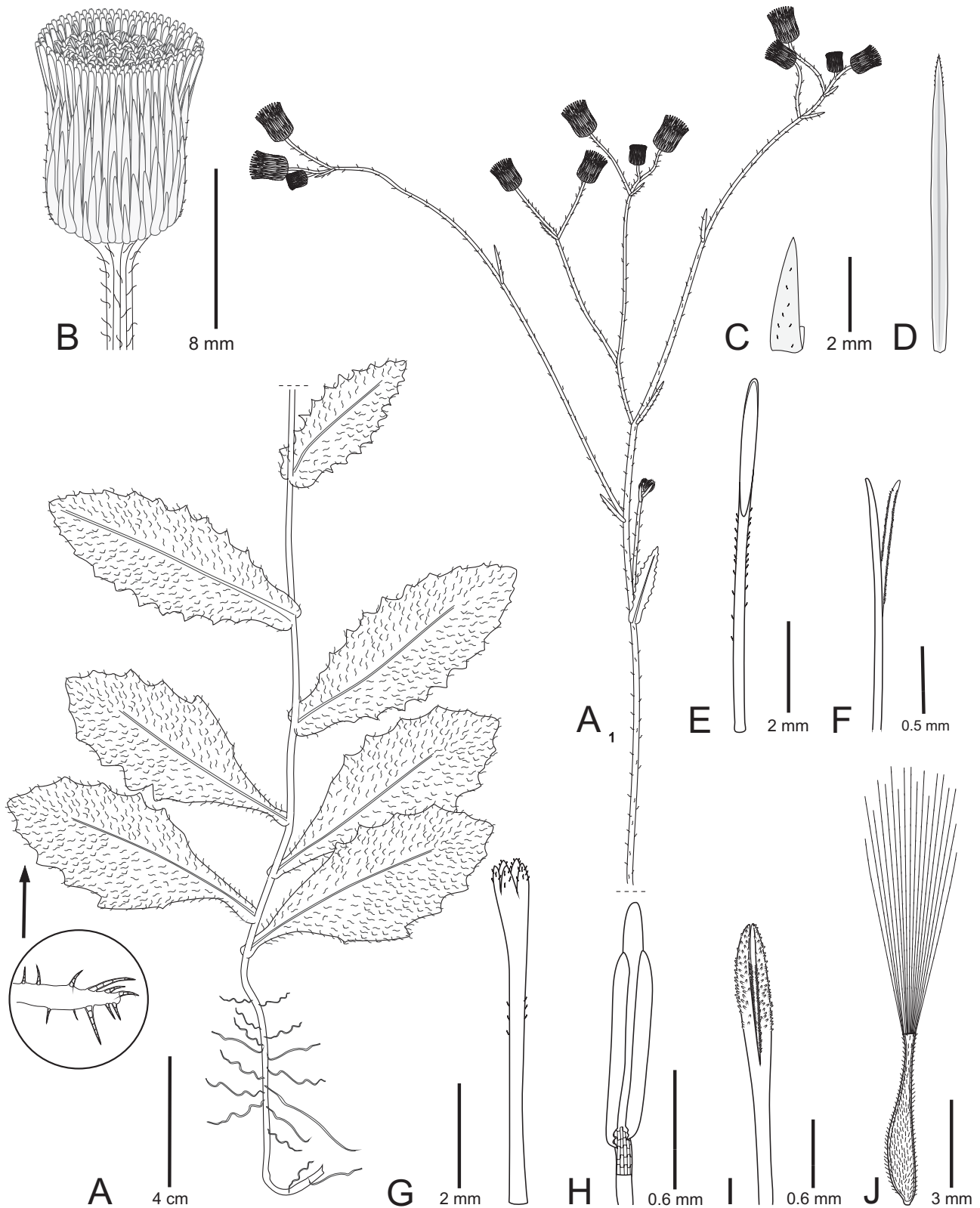


Figure 10. *Podocoma hirsuta*; A, proximal part of plant; A₁, distal part of plant; B, capitulum; C, outer phyllary; D, inner phyllary; E, ray corolla; F, style of ray floret; G, disc corolla; H, stamen of disc floret; I, style of disc floret; J, cypsela with pappus. (From Sancho & Bonifacino 73, LP.)

Santoro 725 (US); ib., 13.iii.1937, *Santoro 950* (US). PARAGUAY. Alto Paraná: Irala, 8.ii.1951, *Montes 11049* (LP, NY). URUGUAY. Canelones: Toledo, iv.1939, *Chebataroff 2963* (LP); La Floresta, 22.ii.1936, *Rosengurtt B. 291* (LP); San Luis, 18.ii.2004, *Sancho & Bonifacino 73* (LP, MVFA); ib., 74 (LP, MVFA). Florida: Cerro Colorado, 16.ii.1944, *Gallinal et al. NPE-5467* (LP, US). Montevideo: Carrasco, 22.i.1938, *Lombardo & Legrand 1331* (LP). Paisandú: vi.1882, *Ball 148* (K). Soriano: Punta Chapparro, 29.xi.1932, *Cabrera 2603* (LP). Without precise locality: 1897, *Arechavaleta 30* (K).

5. *PODOCOMA SPEGAZZINII* CABRERA, NOTAS
PRELIM. MUS. LA PLATA 1: 327. 1932

Type: Argentina, 'Salta, Pampa Grande, I-1897', *Spe-gazzini* s.n. (holotype LPS 101 in LP).

= *Podocoma asperrima* Dusén ex Malme, Kongl. Svenska Vetensk. Acad. Handl. 12(2): 63. table 3. 1933. *Type*: Brazil, 'Sta. Catharina, Rio Capinzal, 27/2 16, *Dusén 17815*' (holotype S; isotype S). *Notes*: 1. The protologue states: 'Hab non indicata verosimillime in campo'. 2. There is a specimen at MO labelled as *Dusén 17815*, but it clearly belongs to *P. hirsuta*.

Description: Herbs 30 to c. 90 cm tall, stems leafy, glabrous to laxly pilose. Leaves cauline, progressively reduced towards stem apex; blades linear-elliptic, 5.5–9.0 × 0.4–1.0 cm, base subauriculate, slightly clasping, apex subacute to acute, primary vein single, medial, margins short-denticulate, strigose to subglabrous on both surfaces (conical, flagellate filiform trichomes and a few small, biseriate glandular trichomes), intermediate leaves similar to proximal ones, distal leaves gradually reduced, 2.0–2.5 × 0.15–0.20 cm, narrowly linear. Capitula three to nine, peduncles 2.5–8.0 cm long, pilose; involucre 10–11 mm high, campanulate-globose when live, campanulate when dry; phyllaries five-seriate, sometimes with bracts of peduncle ascending to involucre, gradate, green when live, margins pale, dorsally greenish when dry, outer phyllaries 3.5 × 0.8 mm, ovate, acute, slightly pilose-arachnoid or hairy (short, flagellate filiform trichomes, simple, biseriate glandular trichomes and twin hairs), occasionally strigose (short, conical trichomes), middle and inner phyllaries 5–7 × 0.7–0.8 mm, linear-elliptic, acute, dorsally hairy, trichomes short, margins pilose at apex; receptacle subconvex, strongly alveolate. Ray florets two- to three-seriate; corolla purplish in mature florets, c. 8 mm long, limb narrow, short, 2.5–3.0 mm, oblong, glabrous, tube narrow, hairy (simple, biseriate glandular trichomes and a few twin hairs); style branches dorsally slightly papillose at apex. Corollas of disc florets 8.5–9.0 mm long, hairy (simple, biseriate glandular

trichomes on tube and lobes), lobes 0.2–0.8 mm long; anthers c. 1.3 mm long, thecae rounded at base, apical appendage narrowly ovate, subobtuse; style branches 0.8–1.2 mm long, distal three-quarters dorsally pilose. Cypselae 5–7 mm long, margins ribbed, densely villous, narrowed at apex into a conspicuous rostrum, rostrum 1.2–2.2 mm long; pappus c. 10 mm long, setae two-seriate, subequal (Figs 11, 13C, D).

Phenology: Flowering in January and February.

Distribution and habitat: This species has been collected rarely. The type collection was found in north-western Argentina in Pampa Grande and La Viña (Salta province), presumably in grasslands, although no specifics about the habitat were given. It has also been collected in eastern Argentina (humid eastern side of Chaco province), Uruguay (Rivera) and southern Brazil (Santa Catarina) (Fig. 12). It inhabits high river sides or occurs close to streams, on fertile, sandstone soils, in sunny places, mixed with other low herbaceous vegetation composed of grass and other dicotyledonous herbs, alternating with scrubby areas. It is locally rare.

Notes: 1. Nesom & Zanowiak (1994) suggested that *P. asperrima* and *P. spegazzinii* should be treated as a single species and we agree with that concept. Cabrera's name, *P. spegazzinii*, has priority over Malme's.

2. The holotype sheet of *P. asperrima* at S has three plants mounted on it. The one in the middle has wider and softer leaves than the other two and is marked on the sheet with a '?'. This plant is the one on the type sheet with leaves more similar to those of the holotype of *P. spegazzinii* which has relatively soft leaves. The paratype of *P. spegazzinii* (from Salta, La Viña), however, has coarser leaves, similar to those of the other two specimens of *P. asperrima* on the type sheet. Despite some differences between the type specimens of *P. asperrima* and *P. spegazzinii* (peduncles lanuginose-araneose immediately below the capitula, few soft trichomes on phyllaries, anthers with relatively short filament collar vs. peduncles pilose nonlanuginose-araneose immediately below the capitula, presence of conical trichomes on phyllaries, and anthers with relatively long filament collar, respectively), they were not substantial enough to justify recognition of these species as separate entities. The linear-elliptic leaves, unusual in *Podocoma*, the twin hairs on the phyllaries and the other remaining vegetative and reproductive characters justify the merging of these taxa.

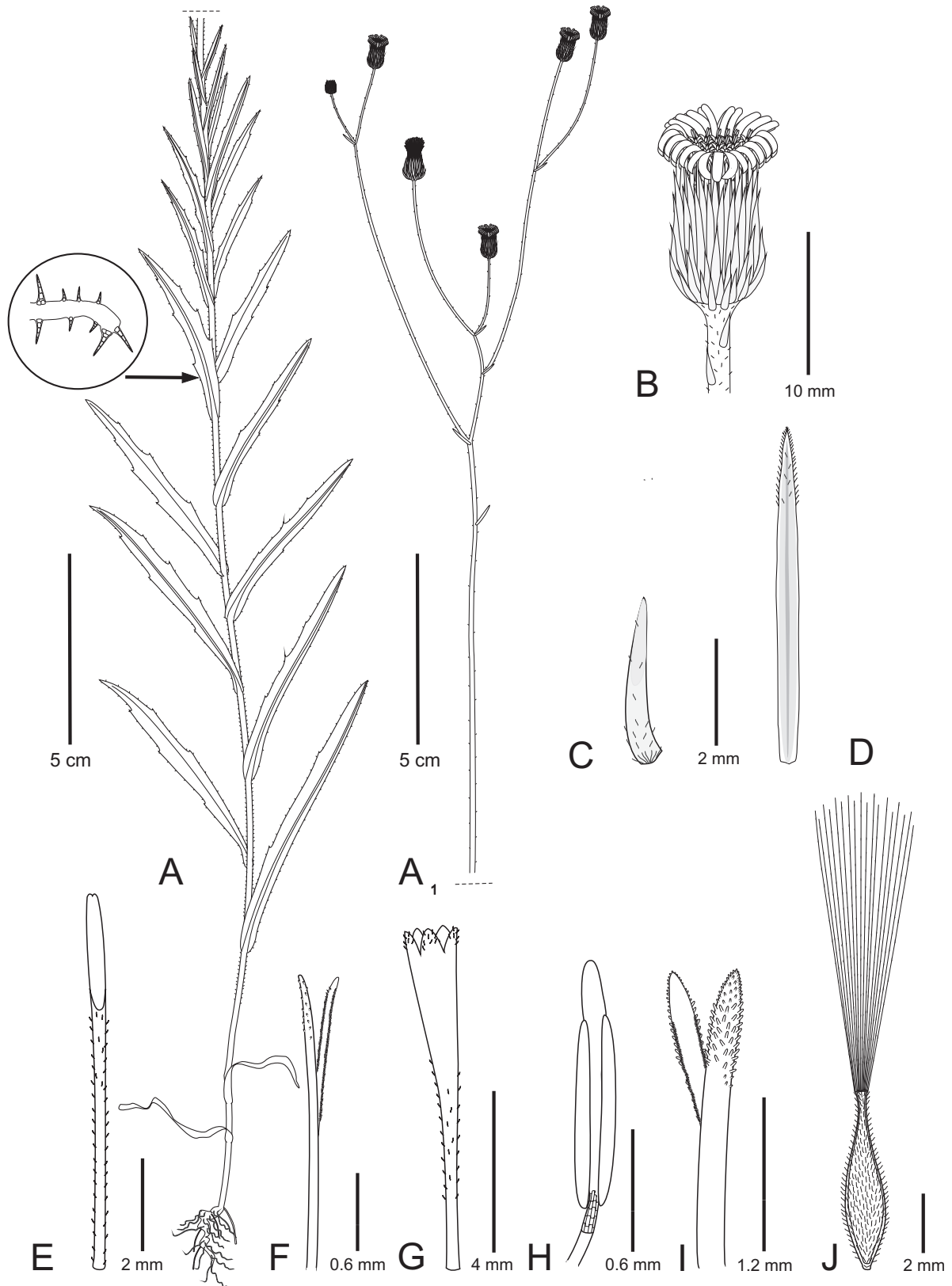


Figure 11. *Podocoma spegazzinii*: A, proximal part of plant; A₁, distal part of plant; B, capitulum; C, outer phyllary; D, inner phyllary; E, ray corolla; F, style of ray floret; G, disc corolla; H, stamen of disc floret; I, style of disc floret; J, cypsela with pappus. (From Sancho & Bonifacino 93, LP.)

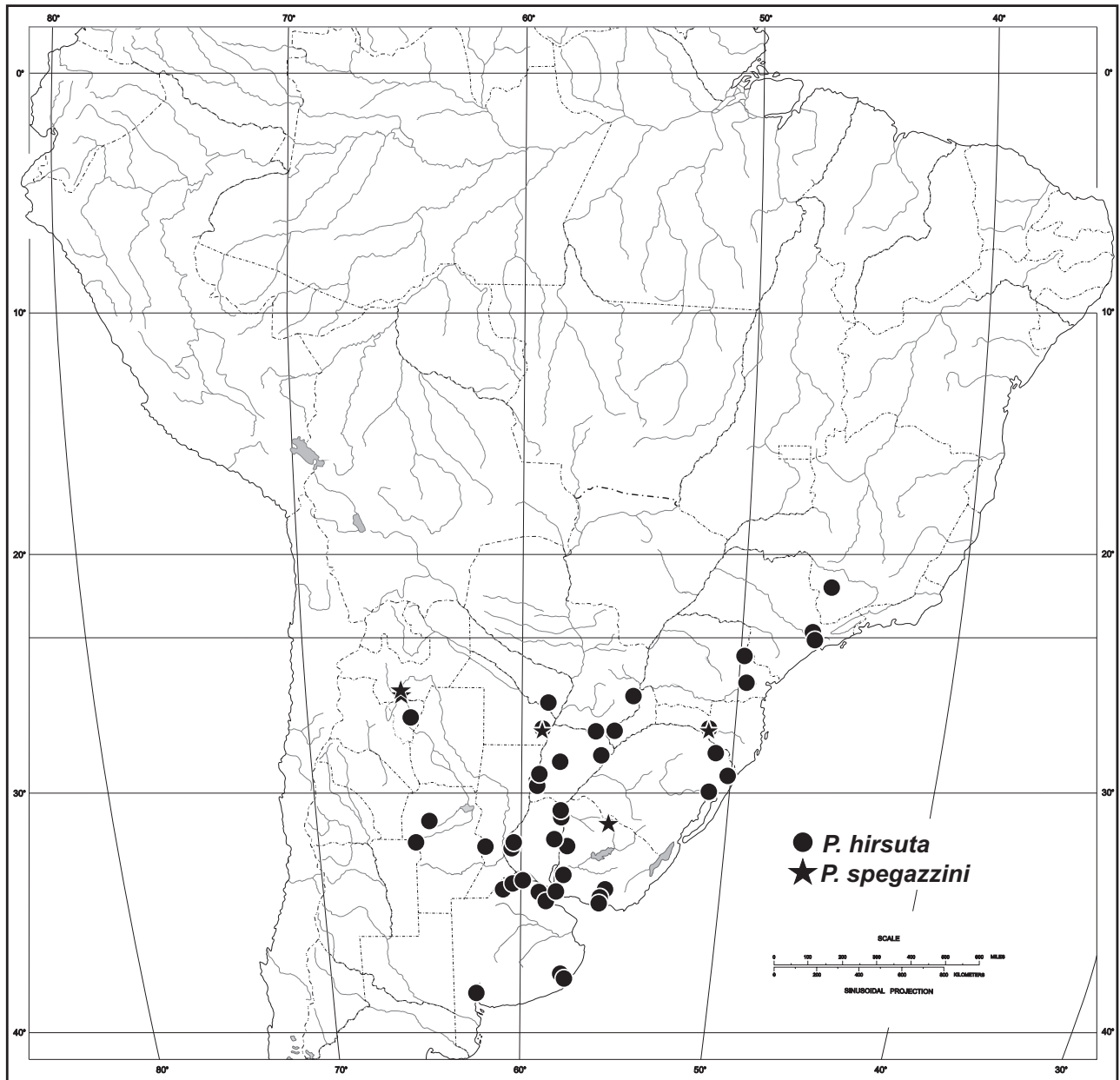


Figure 12. Distribution of *Podocoma hirsuta* and *P. spegazzinii*.

Specimens examined: ARGENTINA. Chaco: Colonia Benítez, i.1932, *Schulz 207 p.p.* (LP). Salta: La Viña, i.1897, *Spegazzini* s.n. (LPS 102 in LP). URUGUAY. Rivera: Arroyo Lunarejo, 19.ii.2004, *Sancho & Bonifacino 93* (LP, MVFA); *ib.*, 95 (LP, MVFA).

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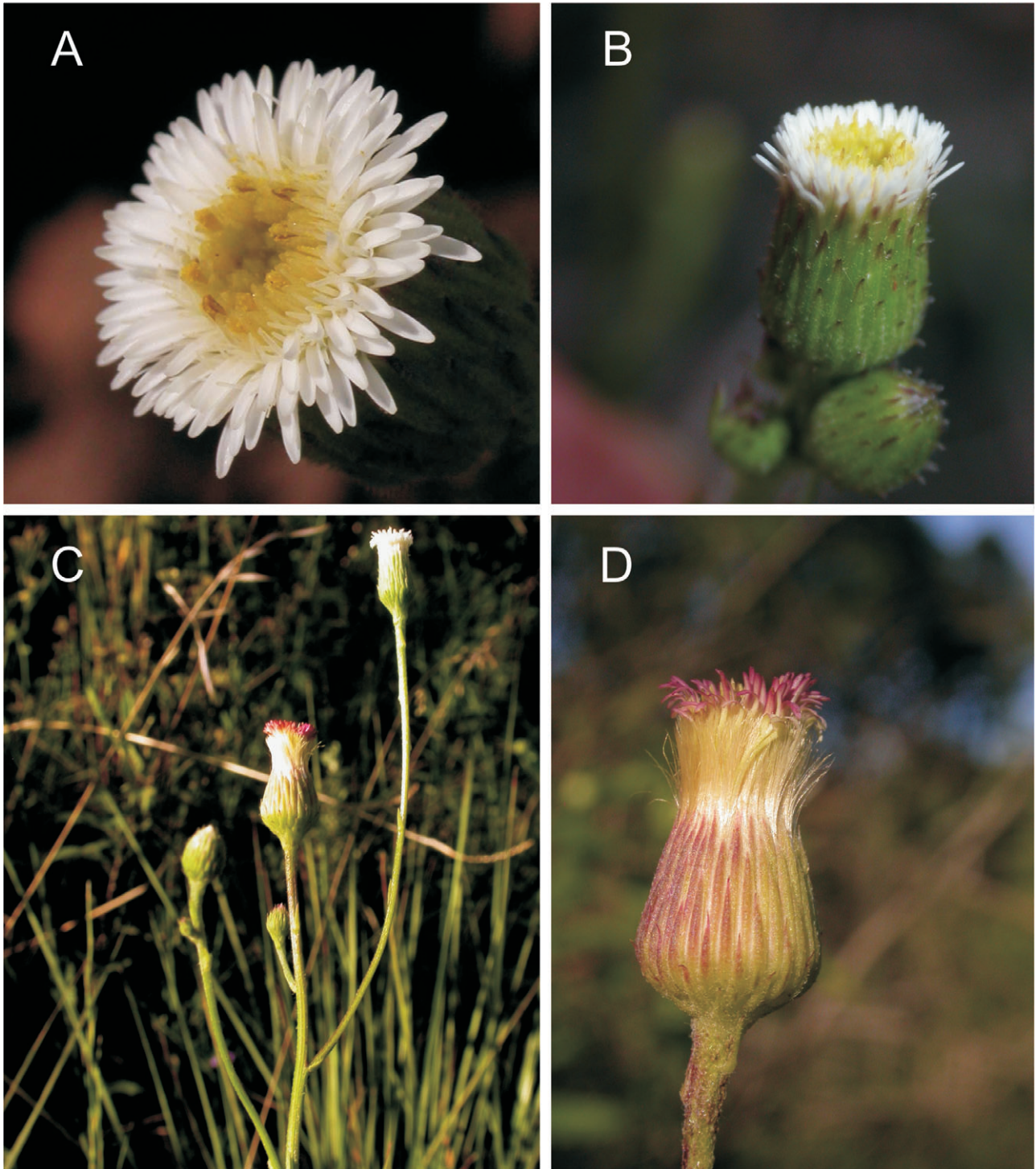


Figure 13. A, Capitulum of *Podocoma hieracifolia*. B, Capitulum of *P. hirsuta*. C, Plant apex, *P. spegazzinii*, showing one capitulum with white corollas and other with purplish corollas. D, Mature capitulum of *P. spegazzinii*.

REFERENCES

- Andreucci AC, Ciccarelli D, Desideri I, Pagni AM. 2008.** Glandular hairs and secretory ducts in *Matricaria chamomilla* (Asteraceae): morphology and histochemistry. *Annales Botanici Fennici* **45**: 11–18.
- Baker JG. 1882.** Compositae III. Asteroideae et inuloideae. In: Martius CFP, Eichler AG, eds. *Flora brasiliensis*, Vol. 6. Munich, Leipzig: Fleischer, 1–134.
- Bentham G. 1873.** Compositae. In: Bentham G, Hooker JD, eds. *Genera plantarum*, Vol. 2. London: Lovell Reeve and Co., 163–533.
- Blake SF. 1917.** New plants from Venezuela. *Contributions from the United States National Herbarium. Smithsonian Institution* **20**: 534.
- Bonifacino JM, Sancho G, Marchesi E. 2009.** New combination in *Asteropsis* (Asteraceae: Astereae). *Brittonia* **61**: 1–7.
- Bremer K. 1994.** *Asteraceae: cladistics and classification*. Portland, OR: Timber Press.
- Brouillet L, Lowrey TK, Urbatsch L, Karaman-Castro V, Sancho G, Wagstaff SJ, Semple JC. 2009.** Phylogeny and evolution of the Astereae (Asteraceae). In: Funk VA, Susanna A, Stuessy TF, Bayer RJ, eds. *Systematics, evolution, and biogeography of the Compositae*. Vienna: IAPT, 589–629.
- Cabrera AL. 1932.** Compuestas nuevas de la República Argentina. *Notas Preliminares del Museo de La Plata* **1**: 327.
- de Candolle AP. 1836.** *Prodromus systematis naturalis regni vegetabilis*, Vol. 5. Paris: Treuttel & Würtz, [Oct 1836].
- Cassini AHG. 1817.** Aperçu des genres ou sous-genres nouveaux formés par M. Henri Cassini dans la famille des Synanthérées. *Bulletin des Sciences, par la Société Philomatique* **1817**: 137–140.
- Cassini AHG. 1826.** Podocome. In: Cuvier MF, ed. *Dictionnaire des sciences naturelles dans lequel on traite méthodiquement des différents êtres de la nature*, Vol. 42. Paris: Le Normant, 60–61.
- Coleman R. 1968.** Chromosome numbers in some Brazilian Compositae. *Rhodora* **70**: 228–240.
- Crisci JV, Freire SE, Sancho G, Katinas L. 2001.** Historical biogeography of Asteraceae from Tandilia and Ventania mountain ranges (Buenos Aires, Argentina). *Caldasia* **23**: 21–41.
- Curtis JD, Lersten NR. 1986.** Development of bicellular foliar secretory cavities in white snakeroot, *Eupatorium rugosum* (Asteraceae). *American Journal of Botany* **73**: 79–86.
- Dunlop CR. 1980.** A revision of *Ixiochlamys* (Asteraceae: Astereae). *Journal of the Adelaide Botanic Gardens* **2**: 241–252.
- Ewart AJ, White J, Tovey JR. 1908.** Contributions to the flora of Australia. *Journal and Proceedings of the Royal Society of New South Wales* **42**: 184–200.
- Fiz O, Valcarcel V, Vargas P. 2002.** Phylogenetic position of Mediterranean Astereae and character evolution of daisies (*Bellis*, Asteraceae) inferred from nrDNA ITS sequences. *Molecular Phylogenetics and Evolution* **25**: 157–171.
- Freire SE, Arambarri AM, Bayón ND, Sancho G, Urtubey E, Monti C, Novoa C, Colares MN. 2005.** Epidermal characteristics of toxic plants for cattle from the Salado River Basin (Buenos Aires, Argentina). *Boletín de la Sociedad Argentina de Botánica* **40**: 241–281.
- Freire SE, Katinas L. 1995.** Morphology and ontogeny of the cypsela hairs of *Nassauviinae* (Asteraceae, Mutisieae). In: Hind DJN, Jeffrey C, Pope GV, eds. *Advances in compositae systematics*. Kew: Royal Botanic Gardens, 107–143.
- Gopinathan K, Varatharajan R. 1982.** On the morphology, topography and the significance of stomata on floral nectaries of some Compositae. *Phytomorphology* **32**: 265–269.
- Grau J. 1975.** *Podocoma* und *Vittadinia* – zwei vermeintlich bikontinentale Gattungen. *Mitteilungen (aus) der Botanischen Staatssammlung München* **12**: 181–194.
- Grau J. 1977.** Astereae – systematic review. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and chemistry of the Compositae*, Vol. 2. London: Academic Press, 539–565.
- Harris JG, Harris MW. 1994.** *Plant identification terminology. An illustrated glossary*. Spring Lake: Spring Lake Publishing.
- Hassler E. 1919.** Ex herbario Hasleriano: novitates paraguayenses. XXII. *Repertorium specierum novarum regni vegetabilis* **16**: 25–29.
- Hess R. 1938.** Vergleichende untersuchungen über die zwillingshaare der compositen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **68**: 435–496.
- Hickey LJ. 1974.** Clasificación de la arquitectura de las hojas de dicotiledoneas. *Boletín de la Sociedad Argentina de Botánica* **16**: 5–26.
- Hochreutiner G. 1899.** Compositae. In: Briquet J, Hochreutiner G, eds. VI Énumération critique des plantes du Brésil meridional récoltées par E. M. Reineck et J. Czermak. *Annuaire du Conservatoire & du Jardin Botaniques de Genève* **3**: 171.
- Hooker WJ, Arnott GAW. 1836.** Contributions towards a flora of South America and the islands of the Pacific. I. Extra-tropical South America. *Companion to the Botanical Magazine* **2**: 41–52. [Sept 1836].
- Hunziker JH, Wulff A, Xifreda CC, Escobar A. 1989.** Estudios cariológicos en Compositae V. *Darwiniana* **29**: 25–39.
- Lowrey TK, Quinn CJ, Taylor RK, Chan R, Kimball RT, De Nardi JC. 2001.** Molecular and morphological reassessment of relationships within the *Vittadinia* group of Astereae (Asteraceae). *American Journal of Botany* **88**: 1279–1289.
- Malme GO. 1933.** Compositae paranensis dusenianae. *Kongl. Svenska Vetenskaps Academiens Handlingar. Stockholm* **12**: 1–122, pl. I–VI.
- Mukherjee SK, Sarkar AK. 2001.** Morphology and structure of cypselas in thirteen species of the tribe Astereae (Asteraceae). *Phytomorphology* **51**: 17–26.
- Nesom GL. 1994a.** Comments on *Microgynella*, *Sommerfeltia*, and *Asteropsis* (Asteraceae: Astereae). *Phytologia* **76**: 101–105.

- Nesom GL. 1994b.** Subtribal classification of the Astereae (Asteraceae). *Phytologia* **76**: 193–274.
- Nesom GL, Robinson H. [2006] 2007.** Astereae. In: Kubitzki K, series ed. *The families and genera of vascular plants*, Vol. 8. Kadereit JW, Jeffrey C, eds. *Flowering plants-eudicots-Asterales*. Berlin, Heidelberg, New York: Springer-Verlag, 284–342.
- Nesom GL, Zanowiak D. 1994.** Taxonomic overview of *Podocoma* (Asteraceae, Astereae), with the incorporation of two species from *Conyza*. *Phytologia* **76**: 106–114.
- Niesenbaum RA, Patselas MG, Weiner SD. 1999.** Does flower color change in *Aster vimineus* cue pollinators? *American Midland Naturalist* **141**: 59–68.
- Noyes RD, Rieseberg LH. 1999.** ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic division in *Aster s.l.* *American Journal of Botany* **86**: 398–412.
- Ramayya N. 1962.** Studies on the trichomes of some Compositae I. General structure. *Bulletin of the Botanical Survey of India* **4**: 177–188.
- Sancho G, Bonifacino JM, Pruski JF. 2006.** Revision of *Microgyne* (Asteraceae, Astereae, Podocominae) the correct name for *Microgynella*. *Systematic Botany* **31**: 851–861.
- Sancho G, Karaman-Castro V. 2008.** A phylogenetic analysis in the subtribe Podocominae (Astereae, Asteraceae) inferred from nr ITS and plasmid *trnL-F* DNA sequences. *Systematic Botany* **33**: 762–775.
- Sancho G, Katinas L. 2002.** Are the trichomes in corollas of Mutisieae (Asteraceae) really twin hairs? *Botanical Journal of the Linnean Society* **140**: 427–433.
- Sancho G, Otegui M. 2000.** Secretory tissues in florets of *Gochnatia polymorpha* (Asteraceae, Mutisieae). Evolutionary considerations. *Phytomorphology* **50**: 172–179.
- Simón PM, Katinas L, Arambarri AM. 2002.** Secretory structures in *Tagetes minuta* (Asteraceae, Helenieae). *Boletín de la Sociedad Argentina de Botánica* **37**: 181–191.
- Stearn WT. 1992.** *Botanical Latin: history, grammar, syntax, terminology and vocabulary*. Ed. 4. Portland, OR: Timber Press.
- Troiani HO, Steibel PE. 1999.** Sinopsis de las compuestas (Compositae Giseke) de la provincia de La Pampa, República Argentina. *Revista de la Facultad de Agronomía; Universidad Nacional de La Plata* **10** (Serie Suppl. 1): 1–86.
- Velez MC. 1981.** Karpologische Untersuchungen an amerikanischen Astereae (Compositae). *Mitteilungen (aus) der Botanischen Staatssammlung München* **17**: 1–170.
- Zhang X, Bremer K. 1993.** A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. *Plant Systematics and Evolution* **184**: 259–283.

LIST OF EXCLUDED NAMES

Podocoma R.Br. Botanical appendix to Captain Sturt's expedition into central Australia **2**(App.): 80. 1849, nom. illeg., non Cass. 1817.

Podocoma bartsiiifolia S.F.Blake, Contributions from the United States National Herbarium. Smithsonian Institution **20**: 534, pl. 45. 1924 = *Blakiella bartsiiifolia* (S.F.Blake) Cuatrec.

Podocoma cuneifolia R.Br. Botanical appendix to Captain Sturt's expedition into central Australia **2**(App.): 81. 1849 = *Ixiochlamys cuneifolia* (R.Br.) F.Muell. & Sond. ex Sond.

Podocoma glandulosa Baker ex B.D.Jackson, Index Kewensis, http://www.us.ipni.org/IK_chronology.html, nom. illeg., based on *Moritzia glandulosa* Sch. Bip. in sched = *Blakiella bartsiiifolia* (S.F.Blake) Cuatrec.

Podocoma macrocephala (Less.) Herter. Estudios botánicos en la región uruguaya. IV. Florula uruguayensis. *Plantae vasculares*: 123. 1930 = *Asteropsis magapotamica* (Spreng.) Marchesi, Bonifacino & Sancho.

Podocoma notobellidiastrum (Griseb.) G.L.Nesom, *Phytologia* **76**: 112. 1994. (in nov. gen.?).

Podocoma reineckii Hochr. *Annuaire du Conservatoire & du Jardin Botaniques de Geneve* **3**: 171. 1899 = *Stenachaenium campestre* Baker.

Podocoma rivularis (Gardner) G.L.Nesom, *Phytologia* **76**: 112. 1994. (in nov. gen.?).

Podocoma nana Ewart & J.White, *Journal and Proceedings of the Royal Society of New South Wales* **42**: 192. 1908 = *Ixiochlamys nana* (Ewart & J.White) Grau.