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The genus *Pachylaena* (Asteraceae, Mutisieae)

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The Andean genus *Pachylaena* (Asteraceae, Mutisieae) comprises perennial, subrosulate to rosulate herbs, with wide, glaucous and crass leaves, all bilabiate corollas, the marginal ones showy, yellow and/or pink and radiating, and plumose pappus. The genus had traditionally two species: *P. atriplicifolia* and *P. rosea*. This study shows that *P. rosea* should be treated as a synonym of *P. atriplicifolia* because the two characters of distinction, the colour of the corollas and the morphology of the involucre phyllaries, are shared by both taxa. An overview of the genus *Pachylaena* and its only species *P. atriplicifolia* is performed here, which includes descriptions, synonymic lists, illustrations, a distribution map, and ecological aspects. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **157**, 373–380.

ADDITIONAL KEYWORDS: Andes – Argentina – Chile – corolla colour – taxonomy.

INTRODUCTION

The Andean genus *Pachylaena* (Asteraceae, Mutisieae) comprises perennial, subrosulate to rosulate herbs, with wide, glaucous and crass leaves, bilabiate corollas, the marginal ones radiating, yellow and/or pink and showy, and plumose pappus. The morphological features were investigated in this contribution, and it was established that *Pachylaena* is monotypic, with a single species *P. atriplicifolia*.

The genus *Pachylaena* was described by Hooker and Arnott in Hooker (1835) on the basis of a specimen collected by Gillies in Mendoza, Argentina, with the annotation ‘*Pachylaena atriplicifolia* Don’. At the end of the species description, Hooker and Arnott commented: ‘This differs from *Chaetanthera* by the non-plumose pappus, and apparently by the style of the bisexual florets not being pulverulous’. The examination of the specimens collected by Gillies, deposited in herbaria BM and K (the holotype), shows clearly that the pappus is plumose. Perhaps relying on the description of Hooker and Arnott, de Candolle (1838) redescribed the genus *Pachylaena* as non-plumose, style glabrous, and white corollas, citing the specimen of Gillies. In the same publication, de Can-

dolle (1838) established the new genus *Chionoptera*, with its only species *C. gayophyta*, for a specimen with plumose pappus and yellow corollas collected by Claude Gay in the Chilean Andes. The iconography of *C. gayophyta* (de Candolle, 1839) and the type specimens deposited at P and GH show that there are no morphological differences between Candolle’s new taxon and the specimen of *P. atriplicifolia* described by Hooker and Arnott. Further authors noticed this resemblance and established the synonymy between *Pachylaena* and *Chionoptera*. Hieronymus (1881) considered this as a distinctive species of *Pachylaena* and established the new combination *Pachylaena gayophyta* (D. Don ex Hook. & Arn.) Hieron. Weddell (1855) included *C. gayophyta* in the synonymy of *P. atriplicifolia*, a criterion followed by subsequent authors.

Philippi (1864) described the new Chilean species *Pachylaena elegans*, with a commentary at the end of the description, ‘Qua nota differt *Pachylaena* a *Tylloma*?’, establishing the resemblance between his new species and *Tylloma* (= *Chaetanthera*; Asteraceae, Mutisieae). Further authors included *P. elegans* in the synonymy of species of *Chaetanthera*, either in *Ch. splendens* (Reiche, 1905) or *Ch. flabellifolia* (Cabrera, 1937). Finally, Johnston (1929) described a new Chilean species, *Pachylaena rosea*,

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Figures 1–2. Photographs of *Pachylaena atriplicifolia* from Quebrada del Agua Negra, province of San Juan, Argentina. Fig. 1. Plant habit. Fig. 2. Detail of the capitulum showing the marginal corollas, yellow above and pink below. Photographs by Mauricio Bonifacino.

distinguishing it from *P. atriplicifolia* by ‘the ray-florets conspicuously cerise or rose-coloured, the smaller heads narrower and denser, and the undivided lower part of the involucre deeper and very sparingly provided with bracts outside’. *Pachylaena rosea* was not subject to any further taxonomic changes and thus, in its traditional circumscription, *Pachylaena* comprised two species: *P. atriplicifolia* from the Andes of Argentina and northern and central Chile, and *P. rosea* from the Andes of the Department of Vallenar in central Chile. Some floras and checklists of Chile, the country in which the two species overlap in their distribution, either accept both as distinctive species (for example, Marticorena, 1990; Hoffmann *et al.*, 1998) or recognize solely the species *P. atriplicifolia* (for example, Muñoz Pizarro, 1959; Kalin Arroyo, Marticorena & Villagrán, 1984; Squeo, Osorio & Arancio, 1994). This is mainly because the most conspicuous distinguishing character of *P. rosea*, the pink colour of the marginal corollas, is variable in the genus. My observations indicate that *P. rosea* is indistinguishable from *P. atriplicifolia*. Field observations, herbarium material examination, and label data indicate that specimens of *Pachylaena* display completely yellow marginal corollas, or yellow above and pink below (Figs 1, 2), or completely pink corollas, sometimes with variation in the same population. Other features, such as those mentioned by Johnston (1929), that is smaller size and narrow shape of the heads and the characteristics of the phyllaries of the involucre, also fail to provide any diagnostic character for *P. rosea*. Therefore, *P. rosea* is included in the synonymy of *P. atriplicifolia*, and *P. atriplicifolia* is recognized as the only species of *Pachylaena*.

The aim of this contribution is to provide an overview of the genus *Pachylaena* and its only species, which includes descriptions, synonymic lists, illustrations, ecological aspects, and a distribution map.

MATERIAL AND METHODS

This study is based on field observations and on specimens from the following herbaria: BM, GH, K, LP, P, and SGO (Holmgren, Holmgren & Barnett, 1990). For microscopic examination, dry florets and fruits were observed. The material was also boiled in water, rinsed, and stained with 2% safranin. Drawings were made by the author using a Wild M5 stereomicroscope and Olympus CH2 microscope with a camera-lucida attachment.

GENERIC RELATIONSHIPS

Cabrera (1937) associated *Pachylaena* in a generic key with the southern South American genera *Trichocline*, *Chaetanthera*, and *Brachyclados*, these genera differing from *Pachylaena* by their non-plumose pappus. Parra & Marticorena (1972) delimited the *Chaetanthera* group, with *Chaetanthera*, *Gypothamnium*, and *Pachylaena*, on the basis of pollen similarities. Bremer (1994) included *Pachylaena* in his *Chaetanthera* generic group, together with *Brachyclados* and *Chaetanthera*. He also proposed that *Pachylaena* may have its sister group within a paraphyletic *Chaetanthera*. In the molecular phylogenetic analysis of Funk *et al.* (2005), *Pachylaena* is sister to a monophyletic group which contains the genera *Chaetanthera*, *Chaptalia*, *Duidaea*, *Gerbera*, *Leibnitzia*, *Mutisia*, and *Piloselloides* (*Brachyclados* was not included in their study). A study of the genera of *Mutisieae* (Katinas *et al.*, in press) shows that *Pachylaena* morphologically resembles the monotypic *Urmenetea*, endemic to the Andes of Chile and north-western Argentina, in habit, pollen features (Tellería & Katinas, 2004), and general morphology (leaves, ray florets, style, cypselas). *Urmenetea* differs from *Pachylaena* by its

tubular-bilabiate disc florets (vs. bilabiate in *Pachylaena*), stamen's filaments papillose (vs. glabrous), and the pappus of scabrid, capillary bristles, a few inner ones flattened and wider (vs. plumose). In a molecular phylogenetic study based on the nuclear internal transcribed spacer (ITS) region and chloroplast *trnL-trnF* region (Katinas *et al.*, 2008), which includes a sampling of 20 genera of Mutisieae, *Pachylaena* is sister to the Andean-centred *Mutisia*, another of the few genera of the tribe with a plumose pappus, and both are sister to *Brachyclados*. In this tree, *Chaeantha* is sister to the genera of the subtribe Nassauviinae (Mutisieae).

GENUS DESCRIPTION

Pachylaena D. Don ex Hook. & Arn., Comp. Bot. Mag. 1: 106. 1835. Type: *Pachylaena atriplicifolia* D. Don ex Hook. & Arn.

Chionoptera DC., Prodr. 7: 14. 1838. Type: *Chionoptera gayophyta* DC. [= *Pachylaena atriplicifolia* D. Don ex Hook. & Arn.].

Description: HERBS erect to prostrate, shortly caulescent or acaulescent, perennial, with thick, vertical rhizomes. LEAVES nearly rosulate and alternate to rosulate; pseudopetiolate; blades orbicular, obovate, ovate to spatulate, obtuse at the apex, reniform, rounded to attenuate at the base, margin irregular, crenate, denticulate-mucronulate to shortly spiny, crass, rugose and glaucous above, sometimes purple below, pinnately veined, glabrous. CAPITULESCENCES monocephalous, terminal; capitula heterogamous, radiate, sessile to pedunculate; receptacle epaleate, glabrous, alveolate; involucre campanulate to hemispherical, three-four-seriate. FLORETS dimorphic, corollas bilabiate with an outer three-dentate lip, and an inner two-cleft lip; marginal florets female, with staminodes, corolla yellow, yellow above and pink below, or pink, outer lip expanded and showy; central florets bisexual, corolla yellow, outer lip not expanded; anthers caudate, apical appendage acute, tails papillose; style bilobed, dorsally papillose, papillae occasionally extending much below the bifurcation point. CYPSELAE cylindrical, truncate at the apex, subglabrous to glabrous; pappus white, persistent, two-seriate, bristles capillary, somewhat paleaceous at the base, plumose, equal in length.

Type species: *Pachylaena atriplicifolia* D. Don ex Hook. et Arn.

Distribution: Genus of one southern South American species, endemic to the Andes of Argentina and Chile (Fig. 3).

Etymology: The generic name is derived from the Greek 'pachys' (thick, stout) and 'chlæna' (cloak, overcoat, blanket) by the thick phyllaries of the involucre (Cabrera, 1971).

SPECIES DESCRIPTION

Pachylaena atriplicifolia D. Don ex Hook. & Arn., Comp. Bot. Mag. 1: 106. 1835. Type: Argentina, Prov. Mendoza. 'On loose debris, near Agua del Cerro Pelado, on the ascent to El alto de los Manantides [Manantiales], Dr. Gillies' (holotype K, digital photograph!). 'Mendoza, Dr. Gillies 222' (paratype BM, digital photograph!).

Chionoptera gayophyta DC. Prodr. 7: 14. 1838. Type: 'Chili, in arenos. sax. summ. andinum Talcaregué, loco dicto el Paraiso, February 1831, 1833, M. Gay 286' (lectotype P, digital photograph!). 'Chili, Prov. Colchagua, Talcaregoué (sic), in arenosis saxorum summ. andium loco, el Paraiso dicto, febr. 1831, Cl. Claud Gay 286' (isolectotype P, digital photograph!). 'Prov. Colchagua, Talcaregoué, in arenosis saxorum andium (Cerro de la Confusion), February 1831, Cl. Gay 286' (isolectotype P, digital photograph!). 'Cordilleres du Chili, 1833, M. Gay s.n.' (isolectotype P, digital photograph!). 'Chili, Prov. Colchagua, Cord. Talcaregue, M. Cl. Gay' (paralectotype GH, digital photograph!). Despite slight differences in the labels of the four specimens deposited at P, I consider that they belong to the same collection, and therefore they were designated as lectotype and isolectotypes. Because of the lack of date in the specimen deposited at GH, it was considered here as a paralectotype.

Pachylaena gayophyta (DC.) Hieron., Bol. Acad. Nac. Ci. 4: 48. 1881.

Pachylaena rosea I. M. Johnston., Contr. Gray Herb. 85: 171. 1929. Type: 'Chile, Northern Chile, Prov. Huasco, Potrero de Toledo, Río de la Laguna Grande, E of Vallenar, c. 28°44'–53'S, 69°57'–70°3'W, c. 2660 m alt., January 5, 1926, I. M. Johnston 5897 (holotype GH!) (Figs 4–12).

Description: HERBS 4–16 cm, erect to prostrate, shortly caulescent, stems 2–7 cm long, or acaulescent, perennial, with thick rhizomes, 4–11 cm long. LEAVES nearly rosulate and alternate to rosulate; blades 1–9 cm long, 0.8–5 cm wide, orbicular, obovate, ovate to spatulate, obtuse at the apex, reniform, rounded to attenuate at the base, margin irregular, crenate, denticulate-mucronulate to shortly spiny (occasionally spinose also on the abaxial side of the blade), crass, rugose and glaucous above, sometimes purple below, pinnately veined, glabrous; anatomically typical dorsiventral structure, with thick cuticle layer and sunken stomata; subsessile to pseudopetiolate,

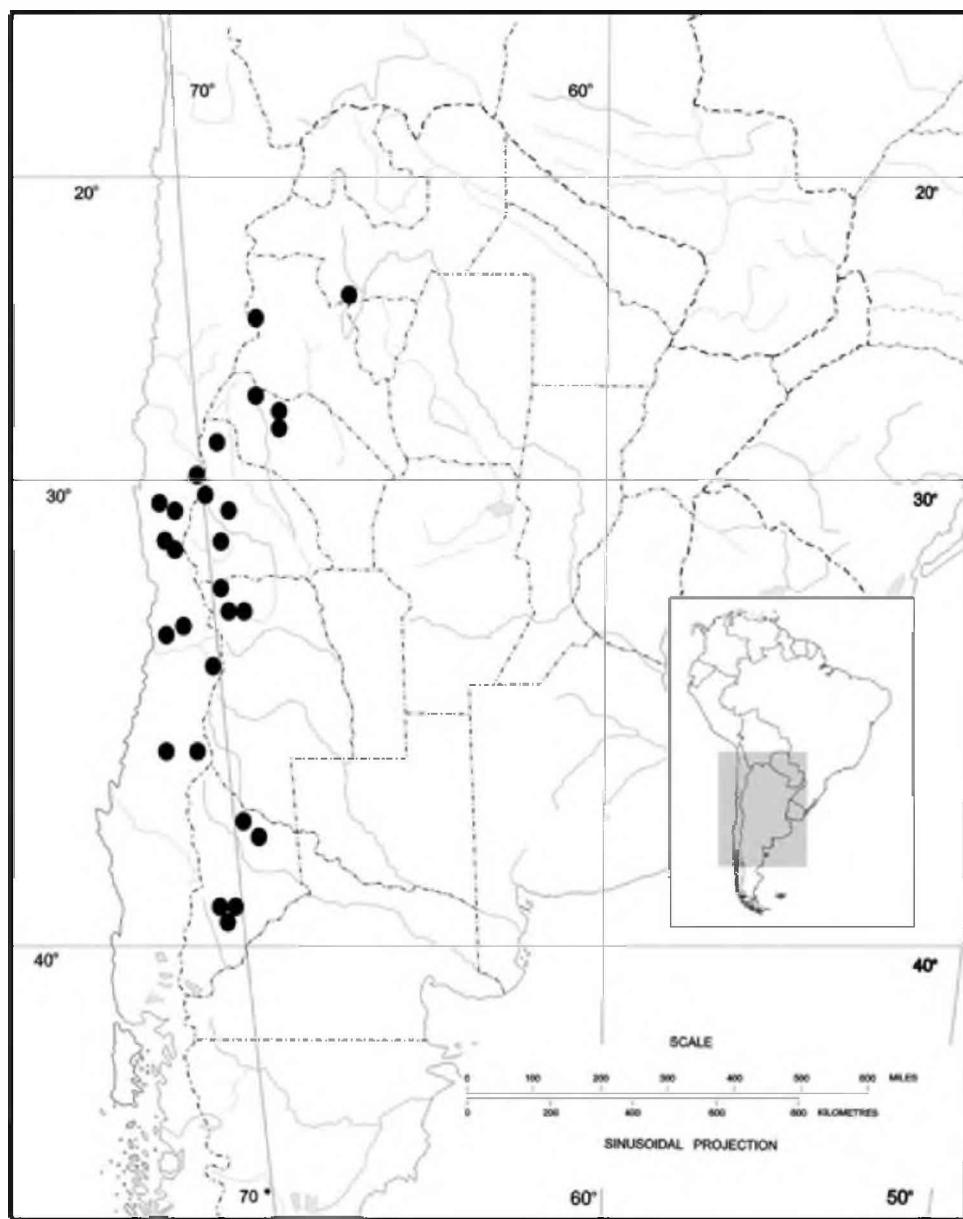
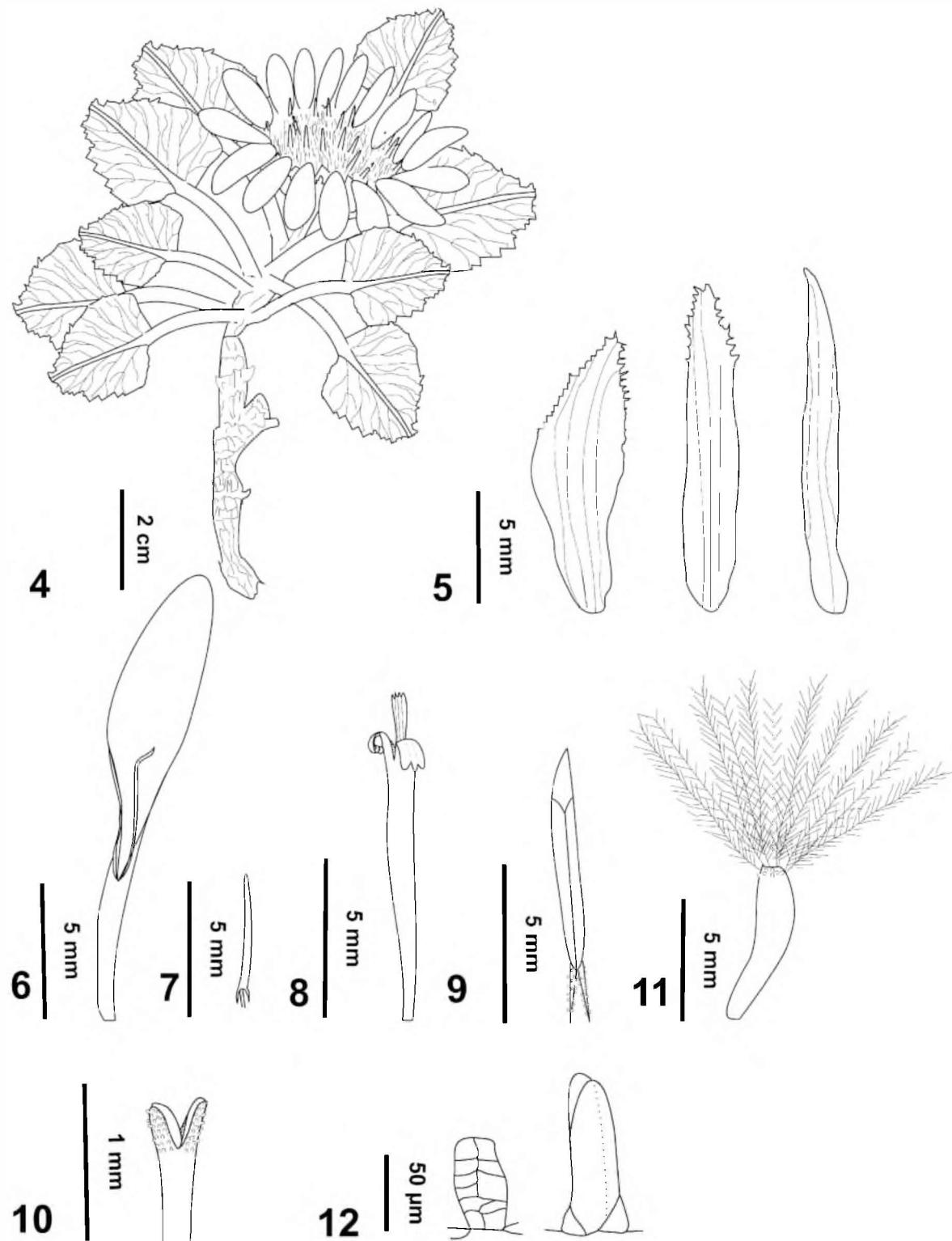


Figure 3. Distribution of *Pachylaena atriplicifolia* in Argentina and Chile.

pseudopetiole 0.13–4.5 cm long, with several parallel veins. CAPITULESCENCES monocephalous, terminal, one per plant (rarely two-headed); capitula, heterogamous, radiate, sessile to pedunculate, peduncle to 9.5 cm long; receptacle epaleate, glabrous, alveolate; involucre campanulate to hemispherical, three–four-seriate; phyllaries glabrous, first series c. ten phyllaries, 11–25 mm long, 4–12 mm wide, ovate, oblong to obovate, denticulate in the upper part; second series 14–16 phyllaries, 15–40 mm long, 4.5–7.5 mm wide, oblong or obovate, denticulate in the upper part; third series 18–22 phyllaries, 17–45 mm long, 2–3.5 mm wide, linear-oblong to oblong-ovate, margin

scarious, occasionally purple. FLORETS 80–130, dimorphic, corollas bilabiate with an outer three-dentate lip, and an inner two-cleft lip, glabrous; marginal florets 10–20, female, with staminodes 3.5–5 mm long, corolla 15–30 mm long, yellow, yellow above and pink below, or completely pink, outer lip 10–22 mm long, 3–5.5 mm wide, expanded and showy, inner lip 2–5 mm long, 0.1–0.5 mm wide, filiform; central florets 70–100, bisexual, corolla 10–20 mm long, yellow, outer lip 2–6 mm long, 1.5–3 mm wide, not expanded, inner lip 2–6 mm long, 1 mm wide; anthers 6.6–8 mm long, caudate, apical appendage acute, tails 1.2–2 mm long, papillose; style 10–22 mm long,



Figures 4–12. *Pachylaena atriplicifolia*. Fig. 4. Habit. Coll. Frenguelli s.n., LP. Fig. 5. Phyllaries of the involucre. Coll. Chicchi 67, LP. Fig. 6. Bilabiate marginal corolla. Coll. Chicchi 67, LP. Fig. 7. Staminode of marginal floret. Coll. Chicchi 67, LP. Fig. 8. Bilabiate central floret. Coll. Chicchi 67, LP. Fig. 9. Stamen of central floret. Coll. Chicchi 67, LP. Fig. 10. Upper portion of the style of the central floret. Coll. Chicchi 67, LP. Fig. 11. Cypsela with plumose pappus. Coll. Johnston 5897, GH. Fig. 12. Cypsela trichomes: glandular biseriate hair (left) and twin hair (right). Coll. Johnston 5897, GH.

apically bilobed, lobes to 1 mm, dorsally papillose, papillae occasionally extending much below the bifurcation point. CYPSELAE 3–6 mm long, 1–1.5 mm wide, cylindrical, truncate at the apex, glabrous or subgla-brous with glandular biserrate hairs and occasionally few twin hairs at the apex; pappus 7–20 mm long, white, persistent, two-seriate, bristles capillary, some-what paleaceous at the base, plumose, equal in length. $2n = 48$ (Wulff & Tombesi, 2000). Pollen spheroidal-subprolate, medium to large size, tricolporate, exine *Mutisia* type, microechinate (Parra & Marticorena, 1972; Tellería & Katinas, 2004; Zhao, Skvarla & Jansen, 2006).

Habitat and distribution: *Pachylaena atriplicifolia* grows in the Andes of Argentina (provinces of Cata-marca, Mendoza, La Rioja, Neuquén, Salta, and San Juan) and Chile (regions III, IV, V, Metropolitana, VI, and VII). It inhabits open, steppe grasslands of sandy or pebbly lithosols of the altimontane level of the Andes of Argentina and Chile, at elevations between 1400 and 4000 m. *Pachylaena atriplicifolia* grows in communities dominated by bunchgrasses of the genus *Stipa*, low compact shrubs such as *Adesmia*, and perennial herbs (for example, species of *Calandrinia*, *Cristaria*, *Chaetanthera*, *Leucheria*, *Perezia*, *Senecio*, and *Viola*).

Etymology: The specific epithet refers to the resem-blance of the leaves with those of the genus *Atriplex* (Chenopodiaceae).

Phenology and pollination: Flowering specimens have been collected from December to March. The plants have been reported to be principally visited by Lepi-doptera (butterflies), rather than Hymenoptera (bees) or Diptera (flies) (Squeo *et al.*, 2006).

Vernacular names and uses: *Pachylaena atriplicifolia* is known locally as ‘*bailagüen de papa*’ (Feresin *et al.*, 2001), ‘*bailahuen de cordillera*’ (Flores A. 226, SGO), ‘*herba santa*’ (Muñoz Pizarro, 1959), ‘*oreja de chancho*’ (Cabrera, 1971), ‘*pata de león*’ (Niemeyer s.n., SGO), ‘*rosa del parto*’, ‘*yerba del parto*’ (Ratto, 2003), ‘*yerba santa*’, and ‘*yerba santa de flores rosadas*’ (Hoffmann *et al.*, 1998). A chemical study reported the isolation of α - and β -amyrin, lupeyl acetate, and sitosterol (Hoeneisen *et al.*, 1993). The juice obtained from the roots is used to relieve tooth-ache and as a general analgesic, and is also recom-mended as a sexual stimulant (Bustos *et al.*, 1996). Assays performed to test the antifungal properties of this species do not validate its popular use as an antifungal (Feresin *et al.*, 2001).

Exsiccata: ARGENTINA. Prov. Salta. Department Cafayate, Sierra del Cajón, 20.iii.1914, Rodríguez 1378 (LP). Prov. Catamarca. Department Antofagasta de la Sierra, Paso San Francisco, 10.ii.1898, Garling s.n. (LP 6328). Department unknown, Reales Blancos, 4.ii.1930, Castellanos s.n. (LP 68469). Prov. La Rioja. Department Famatina, Sierra Famatina, above La Encrucijada, valley of Río Amarillo, $28^{\circ}58'S$, $67^{\circ}42'W$, 5.ii.1966, Hawkes *et al.* 3419 (LP); Padrero de Los Angulos, Famatina, i.1895, Vadenbenter 8271 (LP). Department General Sarmiento, Quebrada La Hedi-onda, 7.ii.1947, Hunziker 2208 (LP). Department Chilecito, camino a mina La Mejicana, entre Las Cuevas y mina, $28^{\circ}55'615"S$, $67^{\circ}40'539"W$, 22.i.2001, Simon & Bonifacino 684 (LP). Prov. San Juan. Department Iglesia, Quebrada del Agua Negra, 21.ii.1979, Cabrera 30091 (LP); camino a El Fierro, 21.i.1974, Cabrera *et al.* 24501 (LP), id., refugio El Lavadero, 21.i.1974, Cabrera *et al.* 24478 (LP). Department Cal-ingasta, Cerro Castaño, ii.1960, Fabris & Marchionni 2338 (LP); Río del Palque, ii.1960, Fabris & Marchionni 2380 (LP); Manantiales, 27.iii.1971, Volponi & Zardini 162 (LP). Department Ullún, quebrada del Salto, 15.i.1930, Pérez Moreau 213 (LP), id. 16.i.1930, Pérez Moreau 227 (LP). Prov. Mendoza. Department Luján, de Vado de Tambillos a Puente del Inca, 11.ii.1934, Pérez Moreau s.n. (LP 68414); E of Punta de Vacas, $33^{\circ}S$, 7.i.1956, Böcher *et al.* 2206 (LP); Zanjón amarillo, FCA, 18.xii.1927, King s.n. (LP 896236); Department Las Heras, pr. Quebrada de Vacas, 6/20.iii.1938, Semper 4954 (LP); Department Santa Rosa, inter Mendoza, Santa Rosa, i.1869, Philippi s.n. (SGO 76526). Prov. Neuquén. Department Catan Lil, Casa de Lata, 10.i.1972, Cabrera 21885 (LP); ladera meridional del Cerro Piedra Santa, 7.ii.1944, Frenguelli s.n. (LP); Chanahuilla, arroyo Lapa, 13.ii.1939, Chicchi 116 (LP); Cerro Lapa, 11.ii.1938, Martínez 3 (LP). Department Pehuenches, subida a la ladera occidental del Cerro Chacay-có, 5.ii.1939, Chicchi 67 (LP); Cerro Carrere, 11.i.1970, Schajovskoy 321 (LP).

CHILE. Region III. Prov. Atacama, Atacama, xi.1898, Spegazzini s.n. (LP ex LPS 1872). Prov. Copiapó, Río Piuquenes, i.1884, San Román s.n. (SGO 76525); cordillera de Copiapó, Quebrada Río Cachitos, cuenca del Copiapó, 21.ii.1977, Niemeyer s.n. (SGO 138440). Region IV. Prov. Elqui, valle del Elqui, vega Piuquenes de Baños del Toro, 19.i.1979, Osorio s.n. (SGO 134978); Cordillera de la provincia de Coquimbo, Baños del Toro, 8.i.1936, Cabrera 3526 (LP). Prov. Limari, Tulahuen, Río Torca, 1.xii.1890, Geisse s.n. (SGO 72338); Ovalle, Cerro Reluciente, without date, Geisse s.n. (SGO 76523). Prov. Choapa, Concumén, without date, Philippi s.n. (SGO 44614), id., i.1873, Landbeck s.n. (SGO 76524); Illapel, 18.xii.1971, Becket *et al.* 4601 (SGO). Region V. Prov.

Valparaíso, cordillera de Cauquenes, Cerro Las Vizcachas, i.1878, von Dessauer s.n. (SGO 44617); Lagunillas, 6.i.1982, Hoffmann & Bragg s.n. (SGO 100253). *Region Metropolitana*. Área Metropolitana, cordillera de Las Arañas, xii.1885, Germain s.n. (SGO 64673); Cajón de Los Hornos, km 54, F.C.T.A., 26.i.1981, Flores 226 (SGO); La Parva, 17.i.1980, Uslar s.n. (SGO 109547). Prov. Cordillera, cordillera de Santiago, valle del Ingenio, Maipo, i.1943, Grandjot & Grandjot 4768 (SGO); cajón del Yeso, bajando hacia el embalse del Yeso, cerca del Campamento Minero, 20.i.1995, Muñoz *et al.* 3652 (SGO). *Region VI*. Prov. Colchagua, Las Damas, Tinguirraca, i.1872, Philippi s.n. (SGO 44615), id., i.1873, Philippi s.n. (SGO 64674). *Region VII*. Prov. Curicó, Potrero Grande, Lomas Blancas, 25.i.1947, Barros 7398 (LP), id., ii.1928, Barros 2027 (LP); Lago Teno, 10 km N, 11.ii.1972, Beckett *et al.* 5112 (SGO). Region and province unknown: cordillera Los Palos, i.1884, Alamos s.n. (SGO 44616).

EXCLUDED SPECIES

Pachylaena elegans Phil., Linnaea 33: 113. 1864 (= *Chaetanthera flabellifolia* Cabrera) (Cabrera, 1937). Chile, Prov. Coquimbo, Baños del Toro, Volckmann, 1860–1861 (holotype S, not seen).

Reiche (1905) considered *P. elegans* as a synonym of *Chaetanthera splendens*. Cabrera (1937) transferred *P. elegans* to *Chaetanthera* with the new name *Ch. flabellifolia* (the name *Ch. elegans* was already in use). Cabrera (1937) distinguished *Ch. flabellifolia* from *Ch. splendens* mainly by the semicircular-flabellate shape of the leaves in the former (vs. ovate-rhombic), deeper teeth in the leaf margin, and wider involucre.

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REFERENCES

- Bremer K. 1994. *Asteraceae: cladistics and classification*. Portland, OR: Timber Press.
- Bustos DA, Tapia AA, Feresin GE, Ariza Espinar L. 1996. Ethnopharmacobotanical survey of Bauchazeta district, San Juan Province, Argentina. *Fitoterapia* 67: 411–415.
- Cabrera AL. 1937. Revisión del género *Chaetanthera* (Compositae). *Revista del Museo de la Plata, Sección Botánica* 2: 87–210.
- Cabrera AL. 1971. Compositae. In: Correa MN, ed. *Flora Patagónica*, Vol. 8. Buenos Aires: Colección Científica del Instituto Nacional de Tecnología Agropecuaria (INTA), 1–451.
- de Candolle AP. 1838. *Prodromus Systematis Naturalis Regni Vegetabilis*, Vol. 8. Paris: Treuttel et Würtz.
- de Candolle AP. 1839. *Icones Selectae Plantarum*, Vol. 4. Paris: Treuttel et Würtz.
- Feresin GE, Tapia A, López SN, Zucchini SA. 2001. Antimicrobial activity of plants used in traditional medicine of San Juan province, Argentina. *Journal of Ethnopharmacology* 78: 103–107.
- Funk VA, Bayer RJ, Keeley S, Chan R, Watson L, Gemeinholzer B, Schilling E, Panero JL, Baldwin BG, García-Jacas N, Susanna A, Jansen RK. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. *Biologiske Skrifter* 55: 343–374.
- Hieronymus G. 1881. Sertum Sanjuanicum. *Boletín de la Academia Nacional de Ciencias, Córdoba, Argentina* 4: 1–73.
- Hoeneisen M, Silva M, Jakupovic J, Papastergiou F, Peter M. 1993. Flavanones of *Lophopappus tarapacanus* and triterpenoids of *Pachylaena atriplicifolia*. *Phytochemistry* 34: 1653.
- Hoffmann A, Arroyo MK, Liberonia F, Muñoz M, Watson J. 1998. *Plantas altoandinas en la flora silvestre de Chile*. Santiago de Chile: Ediciones Fundación Claudio Gay, Empresa El Mercurio S.A.P.
- Holmgren PK, Holmgren NH, Barnett LC. 1990. *Index Herbariorum, part I: the herbaria of the world*, 8th edn. Bronx, NY: New York Botanical Garden.
- Hooker WJ. 1835. *Companion to the botanical magazine*. London: Printed by E. Couchman, for the proprietor, S. Curtis.
- Johnston IM. 1929. Undescribed species from the Cordillera of Atacama. *Contributions of the Gray Herbarium* 85: 164–172.
- Kalin Arroyo MT, Marticorena C, Villagrán C. 1984. La flora de la cordillera de los Andes en el área de Laguna Grande y Laguna Chica, III región, Chile. *Gayana, Botánica* 41: 3–46.
- Katinas L, Pruski J, Sancho G, Freire SE, Tellería MC. *in press*. The subfamily Mutisioideae (Asteraceae). *Monographs in Systematic Botany from the Missouri Botanical Garden* 107.
- Katinas L, Crisci JV, Schmidt Jabaily R, Williams C, Walker J, Drew B, Bonifacino JM, Sytsma KJ. 2008. Evolution of secondary heads in Nassauviinae (Asteraceae, Mutisieae). *American Journal of Botany* 95: 229–240.

- Marticorena C.** 1990. Contribución a la estadística de la flora vascular de Chile. *Gayana, Botánica* **47**: 85–113.
- Muñoz Pizarro C.** 1959. *Sinopsis de la flora chilena. Claves para la identificación de familias y géneros*, 2nd edn. Santiago de Chile: Ediciones de la Universidad de Chile.
- Parra O, Marticorena C.** 1972. Granos de polen de plantas chilenas, II. Compositae-Mutisieae. Chile. *Gayana, Botánica* **21**: 1–107.
- Philippi RA.** 1864. *Pachylaena elegans*. *Linnaea* **33**: 113–114.
- Ratto N.** 2003. Estrategias de caza y propiedades de registro arqueológico en la Puna de Chaschuil (Dpto. de Tinogasta, Catamarca, Argentina). Unpublished DPhil Thesis. Universidad de Buenos Aires.
- Reiche C.** 1905. *Flora de Chile*, Vol. 4. Santiago de Chile: Imprenta Cervantes.
- Squeo FA, Cepeda PJ, Olivares NC, Arroyo MTK.** 2006. Interacciones ecológicas en la alta montaña del Valle del Elqui. In: Cepeda PJ, ed. *Geoecología de Los Andes desérticos: la alta montaña del valle del Elqui*. La Serena: Ediciones de la Universidad de La Serena, 69–103.
- Squeo FA, Osorio R, Arancio G.** 1994. *Flora de Los Andes de Coquimbo: Cordillera de Doña Ana*. La Serena: Convenio Compañía Minera El Indio, Ediciones de la Universidad de La Serena.
- Tellería MC, Katinas L.** 2004. A comparative palynologic study of *Chaetanthera* (Asteraceae, Mutisieae) and allied genera. *Systematic Botany* **29**: 752–773.
- Weddell HA.** 1855. *Chloris Andina*, Vol. 1. Paris: P. Bertrand.
- Wulff AF, Tombesi TS.** 2000. Poliploides en Mutisieae andinas. *Libro de Resúmenes, III Congreso Ecuatoriano de Botánica*, Quito, Ecuador, 123.
- Zhao Z, Skvarla JJ, Jansen RK.** 2006. Mutisieae (Asteraceae) pollen ultrastructure atlas. *Lundellia* **9**: 51–76.