

Taxonomic revision of the Chilean *Puya* species (Puyoideae, Bromeliaceae), with special notes on the *Puya alpestris*-*Puya berteroniana* species complex

GEORG ZIZKA^{1,2}, JULIO V. SCHNEIDER^{1,2}, KATHARINA SCHULTE³, AND PATRICIO NOVOA⁴

¹ Botanik und Molekulare Evolutionsforschung, Senckenberg Gesellschaft für Naturforschung and Johann Wolfgang Goethe-Universität, Senckenberganlage 25, 60325, Frankfurt am Main, Germany; e-mail: Georg.Zizka@senckenberg.de; e-mail: Julio.Schneider@senckenberg.de

² Biodiversity and Climate Research Center (BIK-F), Senckenberganlage 25, 60325, Frankfurt am Main, Germany

³ Australian Tropical Herbarium and Tropical Biodiversity and Climate Change Centre, James Cook University, PO Box 6811, Cairns, QLD 4870, Australia; e-mail: katharina.schulte@jcu.edu.au

⁴ Jardín Botánico Nacional, Camino El Olivar 305, El Salto, Viña del Mar, Chile

Abstract. The Chilean *Puya* species (Puyoideae, Bromeliaceae) constitute an early diverging group within the genus and thus are key taxa for the understanding of the early evolution and biogeography of *Puya*. However, a modern taxonomic treatment including information from molecular phylogenetic studies is still lacking. Here, a taxonomic revision of the Chilean species of *Puya* is presented based on morphological, molecular, and biogeographic data. A re-evaluation of the widely applied concept of *P. berteroniana* led us to the conclusion that the type of *P. berteroniana* is of hybrid origin and is maintained as ***Puya* × *berteroniana***. Our studies revealed that the name *P. berteroniana* has been widely misapplied to what in fact is the northern metapopulation of *P. alpestris*, which is here described as a new subspecies, ***Puya alpestris* subsp. *zoellneri***, a member of subgenus *Puya*. A lectotype is designated for ***Puya copiapina*** and a neotype for ***P. chilensis***. Altogether, six *Puya* species, two subspecies, four varieties and one hybrid taxon are recognized for the Chilean flora in this revision: *P. alpestris* subsp. *alpestris* and subsp. *zoellneri*; *P. boliviensis*; *P. chilensis*; *P. gilmartiniae*; *P. coerulea* var. *coerulea*, var. *intermedia*, var. *monteroana*, and var. *violacea*; *P. venusta*; and *P. × berteroniana*. A key is provided for their identification.

Key Words: Bromeliaceae, Chile, hybrid, *Puya*, *Puyopsis*.

The terrestrial bromeliad genus *Puya* Molina (Bromeliaceae) comprises 219 species (Luther, 2010) and occurs from Costa Rica to Chile and Argentina, from sea level to about 5000 m.a.s.l., and is principally confined to the Andes where the genus underwent a rapid radiation during the last 3.5 Ma (Smith & Downs, 1974; Givnish et al., 2011). Several species extend eastwards into the Guayana Shield and the Brazilian Amazon, and at the southern distribution limit of the genus, a

geographically highly isolated group is formed by the Chilean *Puya* species (Smith & Downs, 1974) occurring mainly in Central Chile which therefore represents a peculiar centre of diversity within the genus (Varadarajan, 1990; Zizka et al., 2009). The Chilean species also differ from their congeners by their unique ecology having successfully colonized not only semixerix to xeric Andean habitats but also extensive coastal habitats at low elevations.

The Chilean flora comprises approximately 5664 species of Angiosperms, of which 2727 are endemic (Marticorena, 1991). Bromeliaceae are represented in Chile with 23 species/20 endemics with the following genera: *Puya* (7 species/7 endemic; for the report of *P. alpestris* [Poepp.] Gay in Argentina [Gómez Romero & Grau, 2009] see comments below), *Tillandsia* L. (6/3), *Ochagavia* Phil. (4/4), *Greigia* Regel (4/4), *Fascicularia* Mez (1/1), and *Deuterocohnia* Mez (1/1) (Zizka et al., 2009). Although they represent only a small fraction of the overall diversity within the family (3248 spp.; Luther, 2010), recent molecular studies revealed their importance for our understanding of bromeliad evolution, in particular of the subfamily Puyoideae and its sister group Bromelioideae (Schulte et al., 2005, 2009, 2010; Horres et al., 2007; Sass & Specht, 2010).

For most of the Chilean bromeliads, updated revisions/treatments have been produced over the last few years, mainly in course of the studies for the “Flora of Chile” (*Ochagavia*: Zizka et al., 2002; *Fascicularia*: Zizka et al., 1999, the Chilean *Greigia*: Will & Zizka, 1999, *Deuterocohnia*: Schütz et al., 2009; Chilean *Tillandsia*: Zizka & Muñoz-Schick, 1993; Pinto, 2001, 2005; Pinto et al., 2006; Zizka et al., 2009). In contrast, a modern revision of the Chilean *Puya* species is lacking.

Puya was described by Ignacio Molina in 1782 in his “Saggio sulla storia naturale del Chili”. Since then, our knowledge about the diversity of the genus has increased considerably, in particular over the last century (Mez, 1896: 44 spp.; Mez, 1935: 89 spp.; Smith & Downs, 1974: 168 spp.; Smith & Till, 1998: 190; Luther, 2010: 219 spp.). Traditionally, the genus was included in the subfamily Pitcairnioideae Harms based on ovary, fruit, and seed characters (Harms, 1930; Smith & Downs, 1974, Smith & Till, 1998). Based on a comprehensive cladistic study of morphological and anatomical characters, Varadarajan and Gilmartin (1988) placed *Puya* in the tribe Puyeeae Mez together with *Abromeitiella* Mez, *Brewcaria* L. B. Sm., Steyerl. & H. Rob., *Deuterocohnia*, *Dyckia* Schult. f., *Encholirium* Mart. ex Schult., and *Hechtia* Klotzsch. Smith and Till (1998) maintained this classification, but sank *Abromeitiella* in *Deuterocohnia*. Recent molecular studies demonstrated that the

genera formerly subsumed in Puyeeae are not closely related and that *Puya* is not part of the Pitcairnioideae *s.str.*, but instead constitutes a monophyletic lineage in sister group position to subfamily Bromelioideae (Horres et al., 2000; Givnish et al., 2004, 2007, 2011; Schulte et al., 2005). Hence, Givnish et al. (2007) erected the monogeneric subfamily Puyoideae.

In his first revision of the genus, Mez (1896) discerned three subgenera within *Puya* based on inflorescence characters: *Eupuya* (compound inflorescence, inflorescence branches with sterile apices), *Pitcairniopsis* Mez (compound inflorescence, fertile throughout), and *Pourretia* Mez (inflorescence unbranched). Smith and Looser (1935) described the subgenus *Chagualia* but Smith revised the subgeneric classification later on (Smith, 1964) sinking subgen. *Chagualia* and subgen. *Pourretia* into a more broadly defined subgenus *Pitcairniopsis*, thus recognizing only two subgenera for *Puya* based on the presence or absence of sterile terminal parts on the partial inflorescences. Based on nomenclatural considerations Smith then recombined *Puya* subgen. *Pitcairniopsis* to *Puya* subgen. *Puyopsis* (Baker) L.B. Sm., and subgen. *Eupuya* to subgen. *Puya* (Smith, 1970; Smith & Downs, 1974). By far the majority of the species in the genus belongs to subgen. *Puyopsis*, only nine species have been included in subgen. *Puya* (Smith & Downs, 1974; Homung-Leoni & Sosa, 2008).

This subgeneric classification has recently been challenged by molecular phylogenetic studies that demonstrated the paraphyly of the two subgenera (Jabaly & Sytsma, 2010). In this study, two principal lineages within the genus were identified, the Core *Puya* (comprising the majority of the species), and sister to this the Chilean *Puya* which thus represent an early diverging group within the genus. The Core *Puya* clade comprises the majority of species traditionally placed in subgen. *Puyopsis*, whereas the Chilean *Puya* harbor the majority of the species placed in subgen. *Puya*. Of the seven Chilean *Puya* species five belong to subgen. *Puya* (*P. alpestris*, *P. berteroniana* Mez, *P. boliviensis* Baker, *P. chilensis* Molina, *P. gilmartiniae* G.S. Varad. & A.R. Flores) and two to subgen. *Puyopsis* (*P. coerulea* Lindl., *P. venusta* Phil.) (Smith & Downs, 1974). Besides the Chilean representatives of subgen. *Puya*,

three additional species were traditionally placed in the subgenus (*P. castellanosii* L.B. Sm.: Argentina; *P. weddelliana* Mez: Bolivia; and *P. raimondii* Harms: Peru, Bolivia; Smith & Downs, 1974; Hornung-Leoni & Sosa, 2008). In the light of the molecular data, the subgenus concept of *Puya* probably will have to be revised. Nevertheless, this is beyond the scope of our treatment here, therefore we keep the presently accepted concept of the two subgenera *Puya* and *Puyopsis*.

The most extensive revisions of this large genus are still those of Mez (1896, 1935) and Smith and Downs (1974). Other important contributions to our understanding of the systematics and evolution of the genus have been made by Varadarajan (1990), Varadarajan and Flores (1990), Hornung-Leoni and Sosa (2005, 2008) based on morphological studies, and Jabaly and Sytsma (2010) and Schulte et al. (2010) based on molecular phylogenetic analyses.

For the systematics and taxonomy of the Chilean species the important contribution of Smith and Looser (1935) is especially noteworthy. More recently, Gourlay (1952), Zizka (1992), Ravenna (2000), Echenique et al. (2003), and Muñoz-Schick (2003) have dealt briefly with some of the Chilean species, Trumpler (1998) provided an extensive analysis of morphology and distribution of the Chilean species, and Zizka et al. (2009) on their distribution and conservation status.

Most of the Chilean *Puya* species are comparatively well circumscribed but morphological variability across the distribution of the species as well as occasional aberrant plants that may constitute hybrids can blur the morphological boundaries between taxa. The most problematic group within the Chilean *Puya* is the *Puya alpestris*-*P. berteroniana* species complex. As already described by Gourlay (1952), the fragmentary type specimen of *Puya berteroniana* Mez has been a matter of conflicting interpretations and species concepts. In particular, the type differs considerably from the plants Smith and Downs (1974) and other authors have applied the name to.

Recently, an AFLP study of the Chilean *Puya* species revealed that they represent three main genetic groups, with the purple flowered *coerulea* group (*P. coerulea*, *P. venusta*) and the

blue flowered *alpestris* group (*P. alpestris*, “*P. berteroniana*”) in sister group position to each other (Schulte et al., 2010), and the yellow flowered *chilensis* group (*P. boliviensis*, *P. chilensis*, *P. gilmartiniae*) as sister to both. Whereas *P. boliviensis*, *P. chilensis*, *P. coerulea*, *P. gilmartiniae*, and *P. venusta* were resolved as monophyletic clades in that study, this was not the case for the members of the *P. alpestris*-*P. berteroniana* species complex which again highlights the need of a revision of this group. Furthermore, the AFLP study confirmed the recent hybrid origin of morphologically intermediate individuals, and detected several additional hybrids. Hybrids were found in sympatric populations and were detected between the *chilensis* and the *alpestris* group as well as between the *alpestris* and the *coerulea* group (Schulte et al., 2010).

In the following we present an updated taxonomic revision of the Chilean *Puya* species based on our morphological, biogeographic, and genetic studies.

Material and methods

Collections of *Puya* from the herbaria B, BM, CONC, E, FR, FRP, G, GH, HAL, HBG, MO, NY, SGO, US, WU were studied. Additionally, species were studied during field trips in 2006–2007. Measurements of plant size were taken from living plants in their habitat, those of leaf length and width principally from herbarium specimens. Authors were abbreviated following Brummit and Powell (1992), descriptive terminology is based on Stearn (1992). The rank of the subspecies was used for taxa that show minor, but geographically structured discontinuities; if discontinuities are not geographically structured, then the rank of variety was used.

Taxonomic treatment

***Puya* Molina, Sag. Stor. Nat. Chili: 160, 351. 1782. Type: *Puya chilensis* Molina.**

Renealmia Feuillée, J. Obs. Phys. Math. Bot. 3: 59, t. 39. 1725. Type: *Renealmia paniculata* L.

Pourretia Ruiz & Pav., Fl. Peruv. Prodr.: 46, t. 7. 1794. Type: *Pourretia lanuginosa* Ruiz & Pav.

Plants perennial, acaulescent or long caulescent, simple or branched, stout, often with a tall inflorescence. Leaves densely rosulate, coriaceous; sheath distinct, generally wide; blade narrowly triangular, the base not narrowed, mostly succulent and spinose-serrate. Inflorescence simple or paniculate. Flowers perfect, showy; sepals convolute, free, shorter than the petals, glabrous, tomentose, or lanate; petals free, with or without appendages, the blades tightly spiraled together after anthesis, distinct from claw; stamens generally shorter than the petals, the filament bases separate from each other after anthesis; ovary superior or slightly inferior, glabrous, style long, slender. Capsule loculicidal and often tardily septicial as well; seeds appendaged, with a dorso-apical wing.

Distribution.—About 219 species distributed from Costa Rica to Chile and Argentina, principally Andean; seven species in Chile.

The genus *Puya* is easily distinguished from other closely related genera by the petal blades that are distinct from the claw and

spiraled together after anthesis, the appendaged seeds, the narrowly triangular leaf blades that are never contracted at base, and the superior to slightly inferior ovary.

Petal color is the most consistent character to distinguish species groups among Chilean *Puya*: petals are (greenish-) yellow in the *P. chilensis* group (*P. boliviensis*, *P. chilensis*, *P. gilmartiniae*), blue-green in the *P. alpestris*, and blue in the *P. coerulea* group (*P. coerulea*, *P. venusta*); in *P. × berteroniana* the petal color is unknown.

Some earlier works (e.g., Kunth, 1815: 296) cited *Achupalla* Kunth, originally published in Humboldt's (1810–13: 221, pl. 30: "Le premier plan du dessin présente un groupe de *Pourretia pyramidata*, plante voisine du *Pitcairnia*, connue dans les Cordillères sous le nom d'*achupallas*.")) *Vues des Cordillères*, as a synonym of *Puya*. However, this name refers to a plant denominated *Pourretia pyramidata* Ruiz & Pav. and locally known by the Indians under the vernacular name of achupalla. Thus, achupalla was not intended as a scientific name.

Key to the Chilean species of *Puya*

1. Inflorescence compound, major portion of the branch apices sterile (subgen. *Puya*).
 2. Flowers metallic blue-green; leaf blades with contrasting sides (densely lepidote below).
 3. Flowering shoot 1.2–1.5(–2) m high; leaf-blades 15–25(–32) mm wide; inflorescence of up to 20(–40) branches, lax, the branches laxly few-flowered *Puya alpestris* ssp. *alpestris*
 3. Flowering shoot to (2–)2.5–5 m high; leaf-blades to 50 mm wide; inflorescence of (40–)50–80 (–100) branches, the branches densely many-flowered *Puya alpestris* ssp. *zoellneri*
 2. Flowers yellow to greenish; leaf blades concolourous.
 4. Flowers about 3 cm long, leaf-blades lepidote on both sides *Puya gilmartiniae*
 4. Flowers 4.5–7.3 cm long, leaf blades glabrous above.
 5. Inflorescence >0.8 m long, with 80–100 branches, dense *Puya chilensis*
 5. Inflorescence up to 0.5 m long, with few branches, lax *Puya boliviensis*
1. Inflorescence compound, the branches fertile throughout or nearly so (subgen. *Puyopsis*).
 6. Flowers congested in apical part of inflorescence branches, inflorescence dense; floral bracts serrate *Puya venusta*
 6. Flowers not congested in apical part of inflorescence branches, inflorescence lax to ± dense; floral bracts entire.
 7. Inflorescence ± dense; plants very rare *Puya × berteroniana*
 7. Inflorescence lax to ± dense.....(*Puya coerulea*).
 8. Floral bracts shorter than the pedicels, narrow *Puya coerulea* var. *violacea*
 8. Floral bracts about as long as or longer than the pedicels.
 9. Floral bracts exceeding the middle of the sepals; branches ± densely flowered.....*Puya coerulea* var. *coerulea*
 9. Floral bracts shorter than the middle of the sepals; branches laxly flowered.
 10. Inflorescence densely and persistently white-tomentose *Puya coerulea* var. *intermedia*
 10. Inflorescence glabrous by anthesis *Puya coerulea* var. *monteroana*

Puya* subgen. *Puya Molina, Sag. Stor. Nat. Chili: 160, 351. 1782. *Puya* subgen. *Eupuya* Mez, Monogr. Phaner. [DC.] 9: 472. 1896. nom. illeg. Type: *Puya chilensis* Molina.

Inflorescence compound, the lateral branches sterile toward apex (approximately upper third).

Puya alpestris (Poepp.) Gay, Fl. Chil. 6: 12. 1853.

Plants caulescent, in flower 1.2–5 m high, stems prostrate, branched. Leaves in a dense rosette 1–2 m in diameter; sheath 2.5–9.5×(0.9–)1.8–10 cm; blade 36–120×

0.35–4.6 cm, green above, yellowish-brown when dried, \pm glabrous (to sparsely lepidote), densely whitish lepidote below; spines \pm curved, 2–10 mm long, brown, becoming further spaced apart from base to apex. Inflorescence (above the scape) 0.25–1 m long, with 15–100 racemose branches (partial inflorescences), these 6.5–32 cm long, in the lower third (to two thirds) fertile, the flowers densely spaced, sterile above with reduced bracts, these \pm hairy with stellate hairs, glabrescent when fruiting; scape 5.5–8 cm in diameter at base, densely hairy with stellate hairs when young, \pm glabrescent; scape bracts caducous, broadly oblong, acuminate, 4.2–6 \times 1.5–2 cm, with stellate trichomes, membranous, entire, conspicuously nerved; primary bracts ovate to oblong, 4–20 \times 1.3–9.5 cm, dark brown when dried, membranous, densely lepidote, entire, \pm serrate only toward apex; floral bracts elliptical, acuminate to mucronate, 1.2–2.7(–5) \times 0.4–2.2 cm, reaching up to about the middle of the sepals, whitish or brownish when dried, thinly membranous, \pm hairy with stellate hairs, inconspicuously nerved, entire; pedicel 3–17 \times 1–2 mm, green. Flowers 3.5–6 cm long; sepals oblong, apex rounded, sometimes with a mucro, 1.8–3.7 \times 0.3–1 cm, green with whitish margin (fresh material), \pm with stellate hairs, coriaceous, with membranous margin, nerved; petals elliptical, rounded to rarely acute, 3.6–5.7 \times 1.3–2.5 cm, naked, metallic blue-green; stamens 6, filaments 2.3–3.5 cm long, anthers 5–9.3 \times 1–1.5 mm, pollen orange; ovary 4 \times 8 mm, style 3.1 cm long, stigmas 8 mm long. Fruit 1.5–2.2 \times 1.3–1.8 cm; seeds 3–4 \times 1.5–2.5 mm, \pm triangular in outline, with membranous wing.

Distribution and ecology.—Endemic to Chile, occurring from Region IV to Region IX, between sea level and 2000 m. Its report from Argentina (Gómez Romero & Grau, 2009) remains doubtful since the cited plant was described as having violet petals, a state not known from *P. alpestris*. However, the cited collection could not be verified by us so far. *Puya alpestris* grows in stony, arid to semi-humid habitats.

Phenology.—Flowering between October and December.

Vernacular names.—Chagual.

Additional specimens examined (not assigned to subspecies): Chile. Región IV: Prov. Coquimbo, Dept. Ovalle, Fray Jorge, 15 Oct 1947, *Sparre 3071* (SGO). **Región V:** Cuesta El Melón, subida Cuesta Alicahue, 13 Nov 1993, *Muñoz Schick 3334* (SGO). **Región Metropolitana:** Filo del cerro entre cerro El Toro y cerro El Tollo, 5 Mar 2000, *Arroyo & Humaña 201498* (SGO); Caleu, desde Carabineros hacia el Norte, 29 Nov 1993, *Muñoz Schick 3349* (SGO). **Región VII:** Km 94 a Laguna del Maule, 20 Jan 2003, *Muñoz Schick 4342* (SGO). **Región IX:** Primeros km subida a Parque Nacional Nahuelbuta, 18 Jan 2003, *Muñoz Schick 4317* (SGO); Cautin, Near La Paz, Oct 1885, *Rusby 2850* (NY, US).

Puya alpestris* (Poepp.) Gay ssp. *alpestris, Fl. Chil. 6: 12. 1853. *Pourettia alpestris* Poepp., Fragm. Syn. Pl.: 8. 1833. Type: Chile, Biobío: in der Nähe von Antuco, Cuesta del Prado, Feb 1829, *E. F. Poeppig 93* (holotype: W, destroyed; lectotype, designated by Smith & Downs, 1974: BM; isotypes: B, G, HAL). (Fig. 1)

Puya whytei Hook.f., Curtis's Bot. Mag. 94: t. 5732. 1868. Type: Chile, s.loc., 1864, *M. Whyte 171/1* (holotype: K).

Puya pumila Ravenna, Onira 4(15): 57. 2000. Type: Chile. Región IX: In decliviis secus fluminem Bio-Bio, inter Santa Juana et Tanaollín, Dec 1999, *Ravenna 3903* (holotype: Herb. Ravenna n.v.; isotypes: BA n.v., CONC n.v., SGO n.v.; see notes below).

"*Pitcairnia coerulea*" auct. non Benth.: Baker pro parte (not the *Puya coerulea* Lindl. element), Handb. Bromel.: 121. 1889 (see notes under *Puya coerulea* var. *coerulea*).

Plants in flower 1.2–2.5 m high. Leaves in comparatively low number; sheath 2.5–4.5 (–9) \times 0.9–5.3(–9) cm; blade 36–65(–98) \times 0.35–2.5(–3.2) cm, spines 2–8 mm long. Inflorescence (above the scape) 0.25–0.72 m long, with 15–20(–40) lateral branches, lower third to lower half of lateral braches fertile, the flowers \pm laxly disposed, rachis glabrous to densely lepidote; primary bracts 4–11 \times 1.3–4.5 cm; floral bracts whitish when dry, thin-membranous; pedicel 3–15 \times 1–2 mm.

Distribution and ecology.—Endemic to Chile; distributed from Central Chile, Region VII (approx. 50 km E of Linares, Paso Pehuenche, 35°42'S) to Region IX (E of Temuco, Lonquimay, 38°27'S); from sea level to 2000 m. Abundant in Regions VIII and IX

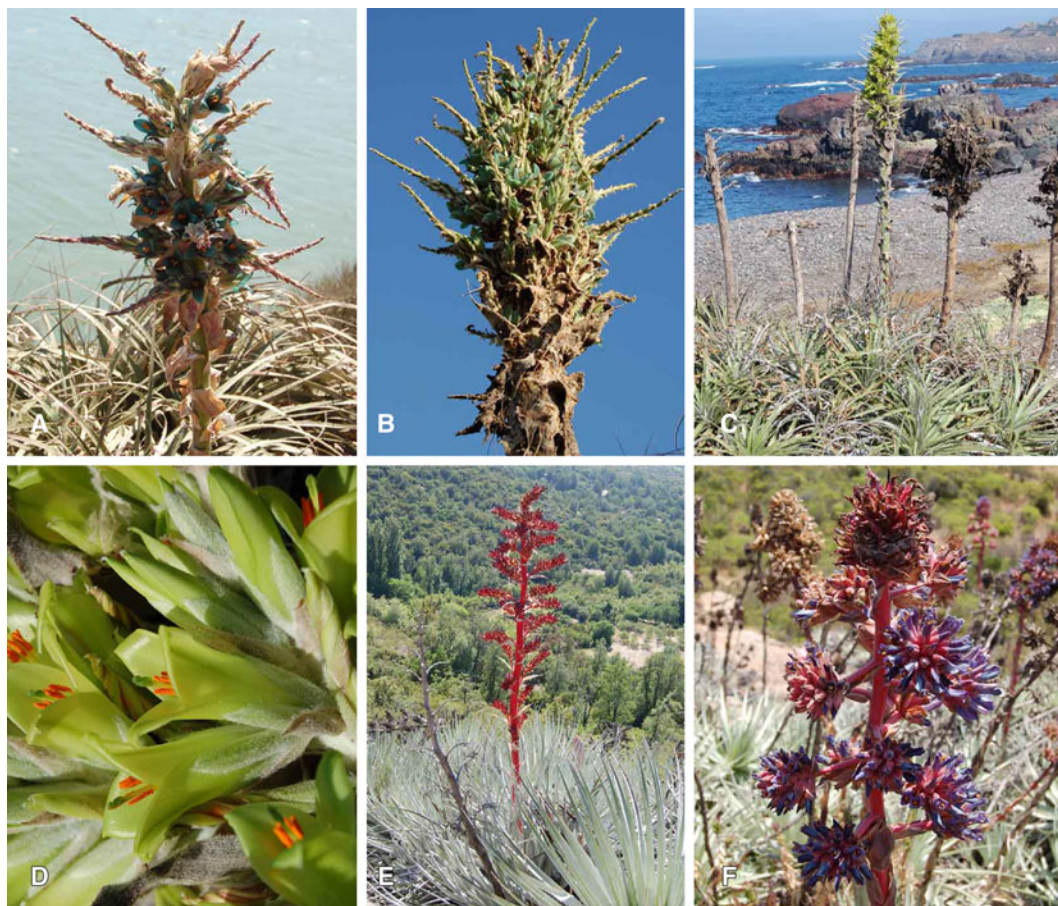


FIG. 1. Chilean *Puya* species. A. *Puya alpestris* subsp. *alpestris*. B. Inflorescence of *Puya alpestris* subsp. *zoellneri*. C. *Puya chilensis*. D. *Puya chilensis*, close-up of lateral inflorescence with yellow-greenish flowers. E. *Puya coerulea* var. *coerulea*. F. *Puya venusta*.

(Concepción – Angol, 36°–37° S). Frequent in the more humid, seasonal mediterranean bioclimate types and the areas of sclerophyllous forest.

Phenology.—Flowering between October and December.

Conservation.—Least concern (Zizka et al., 2009).

Vernacular names.—Chagual.

Additional specimens examined. Chile. Región Metropolitana: Santiago, Prov. Santiago, *N.N. s.n.* (G-8456/3). **Región VII:** Constitución, am Strand in der Nähe einer Zellulosefabrik, 14 Dec 2006, *Zizka 8066* (FR, SGO); RN Los Ruiles, 15 Dec 2006, *Zizka 8086* (FR, SGO); Talca, Constitución, 10 Feb 1921, *Hollerlmayer 467* (CONC); Talca, Valle del Río Maule, Río Cipreses, Laguna de la Invernada, al noreste del dique, 18 Dec 1990, *Leuenberger et al. 4067* (B); Talca, Paso Pehuenche (o del Maule), 2,5 km E (above) of

Amarillo, 11 Jan 1996, *Nyffeler & Eggli 396* (B, SGO); Talca, Constitución, Dec 1891, *Reiche s.n.* (SGO-61083); Talca, P. Linares, La Mina, Camino al Melado, 17 Dec 1953, *Ricardi 2786* (CONC); Curicó, Hacienda Monte Grande, Dec 1924, *Werdermann 563* (BM, E, G, HBG, NY, US); Cauquenes, Hualqui-Pichaco, 12 Dec 1936, *Yunge s.n.* (CONC-5894). **Región VIII:** Puente Abanico, auf dem Weg von PN Laguna del Laja nach Antuco, am Straßenrand, 16 Dec 2006, *Zizka 8087* (CONC, FR); Antuco, an der Straße von Antuco nach Los Angeles, 16 Dec 2006, *Zizka 8093* (CONC, FR). Concepción, Dec 1825, *D'Urville s.n.* (B-40/98-4); Concepción, Nov 1891?, *D'Urville 101* (P); Ñuble, Cordillera Proladura, 22 Feb 1955, *Ledezma 733* (CONC); Concepción, 25 Dec 1934, *Looser 3182* (GH); Concepción, San Rosendo-cerros, 23 Dec 1957, *Montero 5555* (CONC); BioBio, Los Angeles, Antuco, 30 Nov 1959, *Montero 6152* (CONC, US); BioBio, Antuco, cerros, 28 Dec 1937, *Montero 3450* (CONC); BioBio, Antuco, 21 Dec 1964, *Montero 7036* (CONC); Nuble, Ataculco, El Mirador, 21 Dec 1948, *Pfister s.n.* (CONC-8791); Concepción, Cerro Caracol, *Pfister s.n.* (CONC-1136);

BioBio, Cord. d. Colchagua, *Philippi s.n.* (SGO-46425); BioBio, Chile australis, in montibus andis at Antuco, Feb 1829, *Poeppig 891* (B, BM, G, HAL); BioBio, La junta entre los Rios BioBio y Mininco, 5 Dec 1953, *Sparre & Smith 88* (CONC); Concepción, Hills of Concepción, near summit, overlooking University grounds, 3 Jan 1936, *West 4981* (B, GH); Concepción, Cerros de la Toma-Concepción, *Yunge s.n.* (CONC-5261); Concepción, Cerros de la Toma, Nov 1928, *Yunge 2574* (NY); BioBio, Antuco, Risco detrás del pueblo, 13 Dec 1941, *Yunge s.n.* (CONC-6813). **Región IX:** Malleco, Angol, *Ball, J. s.n.* (E); Malleco, Angol, Road to Parque Nacional Nahuelbuta; shrubby road side verge, 28 Nov 1999, *Gardner & Knees 6133* (E); Malleco, Cordillera Lonquimay, *Hollermer 3897* (CONC); Malleco, Entre Angol et P.N. Nahuelbuta, 12 Jan 1985, *Billiet 3650* (BM); Malleco, Angol, 9 Jan 1942, *Gunckel 12009* (CONC); Malleco, Cord. Lonquimay, 10 Mar 1923, *Hollermer 467* (CONC); Malleco, Mininco/Malleco, 23 Nov 1952, *Kunckel 341* (HBG); Malleco, Angol, Cerros, 2 Dec 1935, *Montero 2481* (CONC, GH); Malleco, Angol, Cerros Sur, 1 Jan 1941, *Montero 3906* (CONC); Malleco, Angol, Cerros N, 25 Nov 1959, *Montero 5876* (CONC); Malleco, Angol, Deuko, 25 Dec 1959, *Montero 5932* (CONC); Malleco, Deuco-Cerros lado oriente, 6 Nov 1976, *Montero 10256* (CONC); Malleco, Angol, Cordillera de Nahuelbuta "El Guon", 19 Nov 1982, *Montero 12327* (CONC); Malleco, Angol, Jan 1877, *N.N. s.n.* (SGO-46422); Malleco, Near El Vergel, 10 km south of Angol, Dec 1935, *West 4926* (GH, MO); Malleco, Near El Vergel, 10 km south of Angol, 30 Dec 1935, *West 4927* (MO). **Without precise locality/region:** *Hollermer 5802* (CONC); 1 Oct 1868, *Hooker BM 94* (GH); 14 Aug 1937, *Johnston s.n.* (GH); *Poeppig s.n.* (GH); May 1984, *Smith, L.B. s.n.* (MO, NY); 22 Apr 1981, *Weber s.n.* (B). **Cultivated plants:** 10 Sep 1944, *Bracelin 2802* (NY); 29 Aug 1932, *Ginzberger 879* (WU); 17 Jul 1922, *N.N. s.n.* (HBG-2/1737).

As noted by Weber (1984: 576) the collection number of the type is *Poeppig 93*, not 891 (or Diar. 891). The latter refers to the page of his diary.

The type of *Puya pumila* Ravenna could not be traced in the public herbaria (BA, CONC, SGO) indicated in the protologue. We therefore assume that all the material is still held at Ravenna's private herbarium. Nevertheless, the description clearly shows its synonymy with *Puya alpestris* subsp. *alpestris*.

Puya alpestris has been reported to contain pale pink to red-wine-like or blue nectar (Hansen et al., 2007).

***Puya alpestris* subsp. *zoellneri* (Mez) Zizka, J.V. Schneid. & Novoa, subsp. nov.** Type: Chile. Region V: Viña del Mar, Camino El Olivar, 70°65015'W, 33°43773'S, 300 m a.s.l., 10 Dec 2006, *G. Zizka 8004* (holotype: FR-0028991). (Figs. 1, 2)

"*Puya coarctata*" auct. non Fischer: Philippi, J. Bot. 22: 208. 1884.

"*Puya coerulea*" auct. non Lindl.: Johow, Anales Univ. Chile 126: 36. 1910.

"*Puya whytei*" auct. non Hook.f.: Gourlay, Trans. & Proc. Bot. Soc. Edinburgh 24: 72, pl. 8. 1910.

Pitcairnia alpestris L.H. Bailey, Stand. Cycl. Hort: 2863. 1916, nom. nud.

"*Puya berteroniana*" auct. non Mez: Gourlay, Kew Bull. 7: 501. 1952; Sealy, Bot. Mag. 176: t. 495. 1967; Navas, Flora Cuenca Chile 1: 139. 1973; Smith & Downs, Fl. Neotrop. 14(1): 186. 1974; Rauh, J. Bromeliad Soc. 35(4): 165. 1985; Read, J. Bromeliad. Soc. 38(3): 101. 1988; Benoit, Red Book Chil. Fl. 1: 120. 1989; Varadarajan, J. Bromeliad Soc. 39(1): 6. 1989; Zizka, Palmengarten 19: 98. 1992.

Plants in flower (2–)2.5–4.5 m high. Leaves numerous, in a dense rosette; sheath 3.8–9.5 × 4–10 cm; blade 54.5–120 × 1.4–4.6 cm, with spines 8–10 mm long. Inflorescence (fertile part) c. 1 m long, with (40–)50–80(–100) lateral branches, these at least 20 cm long, the lower third to half of lateral braches fertile, the flowers ± dense, rachis ± densely hairy with stellate trichomes; primary bracts 8–20 × 2.4–9.5 cm; floral bracts brownish when dry, ± membranous; pedicel 5–17 × 1–2 mm.

Distribution and ecology.—Endemic to Chile; distributed from North and Central Chile, Region IV (ca. 75 km N of La Serena, Incahuasi, 29°15'S) to Region VII (ca. 80 km E of Cúrico, Termas del Flaco, 34°56'S); from sea level to 2200 m. Abundant in Region V and Región Metropolitana (between Valparaiso and Santiago, ca. 33°–34° S). Grows in stony, arid habitats.

Phenology.—Flowering between October and December.

Conservation.—Least concern (Zizka et al., 2009; therein discussed under *P. berteroniana* sensu Smith & Downs, 1974).

Etymology.—This species is named in honor of the german-born botanist and specialist of the Chilean flora Otto Zöllner (1909–2007).

Additional specimens examined. Chile. Región IV: Limari, Fundo Fray Jorge, cerca de las casas del fundo y la quebrada de Las Vacas; entre los penascos, 10 Mar 1947, *Carrigo s.n.* (SGO-60188); Choapa, Coast at Pichidangui, 5 Oct 1995, *Gardner & Knees 5949* (E); Ovalle, Totoralillo, 18 Nov 1961, *Jiles 4027* (CONC); Choapa, Pichidangui, overlooking rocky beach just south of the village, 18 Jan 1989, *Lammers et al. 6391* (CONC); Elqui, Hacienda Pangue, como a 23 km al sur de Vicuña, en el camino a Hurtado, 13 Oct 1940, *Looser 4227* (GH); Elqui, Corral de Julio; camino a exclusión la

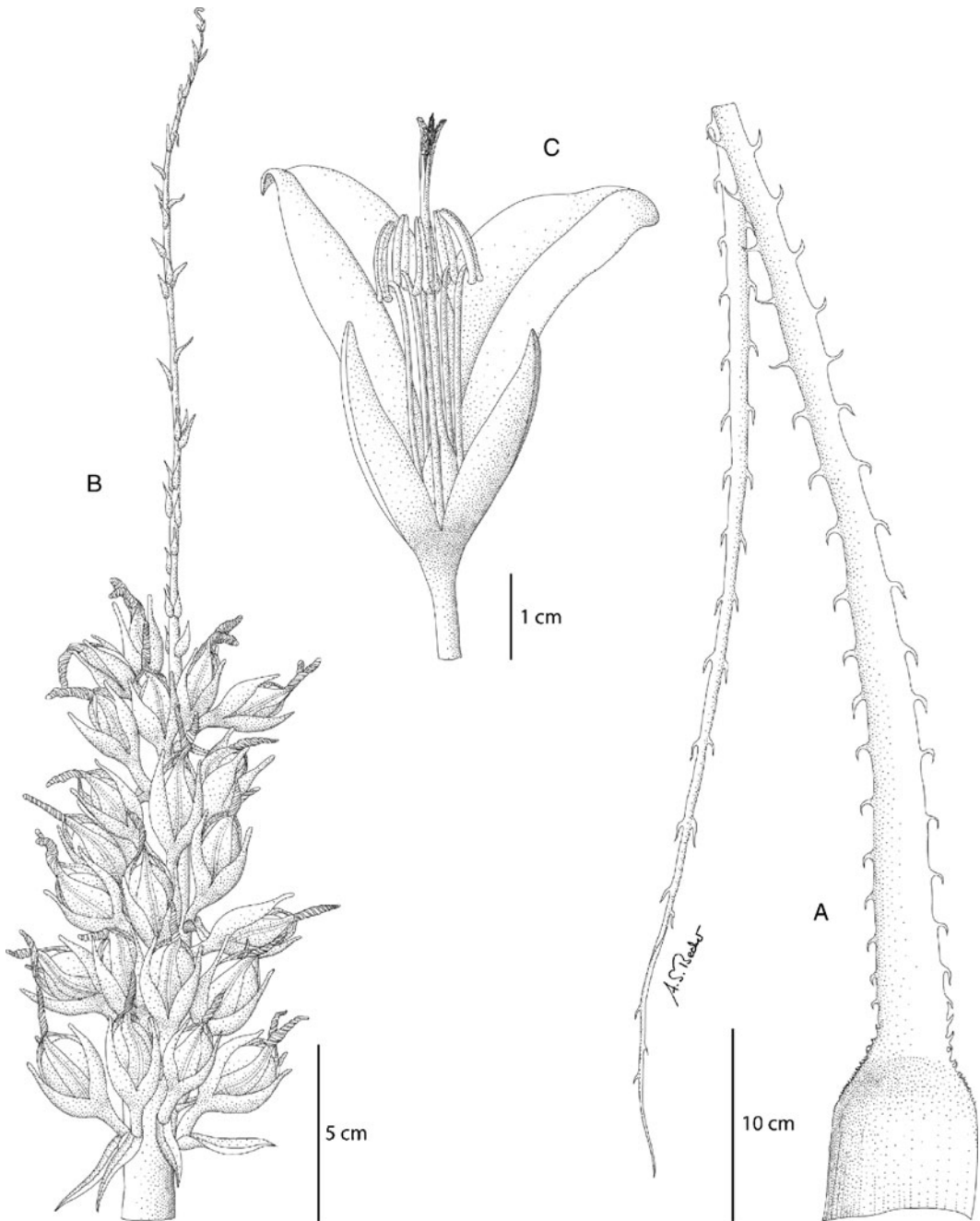


FIG. 2. *Puya alpestris* subsp. *zoellneri*. A. Basal leaf (*Zizka* 8004 [FR]). B. Inflorescence branch with sterile apical part (*Zizka* 8036 [FR]). C. Flower (*Zizka* 8036 [FR]).

Rojadilla, 6 Nov 1976, *Muñoz* 908 (SGO); Limarí, Fray Jorge, 15 Oct 1947, *Sparre* 3071 (SGO); Huasco, about 5 km S of Atacama-La Serena boundary, 15 km S of Incaguasi, 20 May 1987, *Varadarajan et al.* 1480 (GH, MO); Elqui, about 60 km N of la Serena, on the way to Pta. Totorallito, near El Oliva, Isla Tilgo, 22 May 1987,

Varadarajan et al. 1482 (GH); Elqui, Playa las Tacas (Cerro Zoraida), about 20 km S of Coquimbo, and about 5 km E of the ocean, 22 May 1987, *Varadarajan et al.* 1486 (GH); Los Hornos nach Chungungo, ca. 2 km hinter Abzweigung von Panamericana, 22 Dec 2006, *Zizka* 8126 (FR); PN Fray Jorge, an der Straße zum Berggipfel, ca.

500 m an der Abzweigung zum Forschungssektor, 23 Dec 2006, *Zizka 8139* (CONC, FR); PN Fray Jorge, 24 Dec 2006, *Zizka 8140* (FR, SGO). **Región V:** Quillota, Limache, Cerros al Norte, 10 Dec 1917, *Behn s.n.* (CONC-20622); Valparaíso, Viña del Mar, Cerros del Tranque, 16 Dec 1923, *Behn s.n.* (CONC-20618); Los Andes, Valley of the Rio Aconcagua, some 3–5 km upwards Guardia Vieja following the tracks of the now disused Transandean railway, 5 Feb 1993, *Eggl & Leuenberger 2312* (B); Quillota, Parque Nacional de La Campana, 9 Oct 1995, *Gardner & Knees 5987* (E); Valparaíso, Laguna Verde, 25 km south of Valparaíso on coast, 7 Jan 1939, *Goodspeed 23329* (GH); Valparaíso, 4 km southwest of Valparaíso, 15 Nov 1951, *Hutchinson 22* (SGO, US); San Felipe de Aconcagua, between Calera and San Felipe, 5 Nov 1948, *Killip & Pisano 39780* (US); Quillota, Estación Palos Quemados, 27 Jan 1933, *Looser 2666* (GH); San Felipe de Aconcagua, Punta Teatinas, c. de la Serena, 17–20 Sep 1933, *Looser 2903* (GH); Quillota, Limache, Cerro Cruz, 29 Sep 1932, *Looser 2488* (GH); Quillota, Limache, 2 Feb 1921, *Looser s.n.* (CONC-65505); Quillota, Cerros Caquis, 15 km east of Melon, 15 Dec 1938, *Morrison 16916* (G, MO); Valparaíso, Valparaíso, *N.N. 3252* (KIEL); Valparaíso, Valparaíso, *N.N. s.n.* (SGO-46427); Valparaíso, prope urbem Valparaíso, Dec 1851, *Philippi & Hohenacker 386* (P); Valparaíso, prope urbem Valparaíso, Dec 1851, *Philippi & Hohenacker 1861* (G); Valparaíso, Concón, *R.B. 347* (BM); Valparaíso, near Valparaíso, 22 Sep 1914, *Rose 19160* (NY, US); Quillota, Cerro Marga-Marga, Coliguay-El Molino, 23 May 1987, *Varadarajan et al. 1490* (GH); Viña del Mar, Camino el Olivar, arriba del entrada J. Bot. Nac., 10 Dec 2006, *Zizka 8003* (CONC, FR); Carretera, Olmue a Caleu, Cuesta la Dormida, 10 Dec 2006, *Zizka 8005* (FR, SGO); Concón, *Miers 347* (CONC). **Región Metropolitana:** Santiago, Santiago, Jan 1919, *Claude-Joseph 926* (US); Santiago, Mts. east of Santiago, 23 Nov 1900, *Hastings 218* (NY); Santiago, Mts. east of Santiago, 21 Dec 1906, *Hastings 313* (US); Santiago, La Hermida, cerca de Santiago, Sep 1931, *Looser 2104* (CONC, GH, US); Maipo, Angostura de Paine, límite entre Santiago y Colchagua, 4 Dec 1933, *Looser 2557* (GH); Santiago, Tiltill, 5 Nov 1932, *Looser 2556* (GH); Santiago, Tiltill, 18 Feb 1933, *Looser 2667* (GH); Santiago, Peñaflo, 21 Dec 1927, *Montero 768* (GH); Santiago, Peñaflo, 29 Jan 1935, *Montero 2112* (CONC); Santiago, Prov. Santiago, *Philippi 249* (B); Santiago, Santiago, *Philippi s.n.* (WU-205); Santiago, Prov. Santiago, *Philippi s.n.* (B-40/98/2); Santiago, San Cristóbal, Santiago, Oct 1879, *Philippi, A. s.n.* (SGO-46426); Santiago, Rinconada de La Cerda, Quebrada La Plata, 6 Sep 1958, *Schlegel 1664* (CONC, SGO); Santiago, Quebrada La Plata, 15 Dec 1960, *Schlegel 3320* (CONC); Santiago, between cuesta de la Dormida and Tiltill, 23 May 1987, *Varadarajan et al. 1492* (GH); Santiago, Reserva Forestal Río Clarillo, 3 Aug 1983, *Yané s.n.* (SGO-102431); **Región VI:** Reserva Nacional Río de Los Cipresses, Zona des los Pumas, 12 Dec 2006, *Zizka 8036* (FR, SGO); Termas de Cauquenes, Ruta del Acido, 12 Dec 2006, *Zizka 8042* (CONC, FR); Cachapoal, Quebrada camino, Viña del Flaco, Huerteillas, 8 Jan 1951, *Ricardi s.n.* (CONC-10207/1). **Región VII:** Colchagua, Cerro, sur Baños Flaco, Dec 1937, *Espinosa s.n.* (SGO-46424); Colchagua, San Fernando, Termas del Flaco, 22 Dec 1965, *Montero 7415* (CONC); Colchagua, Cord. de la Dehesa, Nov 1861, *N.N. s.n.* (SGO-46429); Colchagua, Cord. de la Dehesa, Nov 1861, *N.N. s.n.* (SGO-46428). **Without precise locality:** Costa, 4 Nov 1920, *Claude-Joseph 1208* (US); *Looser 2554* (GH). **Cultivated**

plant: grown near Hutchin, England, 12 Nov 1951, *Gourlay s.n.* (US-2048519).

As first noted by Smith and Looser (1935), *Puya alpestris* is a highly variable species showing two different forms across a north–south gradient, a large one with dense spikes and a northern distribution and a small one with laxly disposed lateral inflorescences and a southern distribution. Gourlay (1952) discussed this variation in more detail and noted that *Puya whytei* corresponds to the small form originally described as *P. alpestris* by Poeppig. Following a letter from L. B. Smith, Gourlay agreed on using the name *P. berteroniana* for the large form, although he was aware of the problematic concept of that species (see notes under *P. × berteroniana*). Smith and Downs (1974) continued to use the name *P. berteroniana* for the larger northern form. However, the original description of *P. berteroniana*, based on the fragmentary specimen *Bertero 115*, does not correspond with the plants of the northern form due to their different inflorescences. Therefore, we describe the new subspecies for all plants corresponding to the northern form, while *P. berteroniana* is considered a very rarely collected (and presumably rare) species of putative hybrid origin (see below).

Puya alpestris subsp. *zoellneri* differs from subsp. *alpestris* in having leaf blades to 4.6 cm broad (0.35–2.5[–3.2] cm in subsp. *alpestris*) and inflorescences with at least 40 lateral branches (up to 20 in subsp. *alpestris*). Additionally, the flowering plants are (2–)2.5–4.5 m tall (to 2.5 m in subsp. *alpestris*).

Puya boliviensis Baker, Handb. Bromel.: 126. 1889. Type: Chile, Region II: Antofagasta, Cobija, Jul 1836, *C. Gaudichaud s.n.* (holotype: P; isotypes: B, F, US).

Puya copiapina Phil., Anales Univ. Chile 91: 613. 1895. Type: Chile, Region III (Atacama): Morro de Caldera, 1888, *W. Geisse s.n.* (lectotype, here designated: SGO 46420).

Plants ± caulescent, in flower 1–2 m high, stems ± prostrate. Leaves numerous, in a dense rosette, ± erect; sheath (1.2–)2–5 × 1.6–6.5 cm, ± ovate, brown, margin spinose apically, entire towards base, below lepidote, glabrescent towards base, above glabrous, shining; blade 16–45.3(>100) × (1–)2.3–

3.5(–6) cm, ± green, sparsely lepidote and glabrescent above, lepidote to glabrous below (scales only persistent in the furrows), spines ± hook-shaped, 6–8(–10) mm long, brown, approx. 2 cm apart. Inflorescence (above the scape) c. 50 cm long, usually lepidote, with c. 20 racemose branches (partial inflorescences), these 13–21 cm long, axis of partial inflorescence densely covered with stellate trichomes, the lower half fertile, the flowers laxly spaced, sterile above with reduced bracts, the sterile bracts similar to the floral bracts but smaller; scape bracts narrowly triangular (lower ones) to broadly ovate (upper ones), acuminate, 9.2×2.5 cm, brown, with stellate trichomes, membranous, nerved, margin ± spinose, becoming entire towards flowering part; primary bracts ovate, 1.9–2.5×4.2–5.7 cm, brown when dried, ± membranous, lepidote, inconspicuously nerved, entire; floral bracts elliptical to ovate, acuminate, rarely rounded with a mucro, 2.1–3.5×0.6–1.8 cm, reaching up to about the middle of the sepals, rarely up to about as long as the sepals, dark brown, membranous, ± lepidote with stellate hairs, conspicuously nerved, entire; pedicel 8–15×1–2 mm. Flowers 4.5–6.1 cm long; sepals lanceolate, apex rounded, sometimes with mucro or acute, 1.8–3.5×0.4–0.7 cm, light brown, ± hairy with stellate hairs, coriaceous, longitudinally striate, margin entire, nerved; petals elliptical to spatulate, rounded with inconspicuous mucro, 4.5–5×1.9–2.1 cm, yellow to greenish, naked, with green spot at base; stamens 6, filaments 2.4–3 cm long, anthers 7.5–11×1–1.5 mm, pollen yellow to orange; ovary 8.5×2 cm, style 2–2.8 cm long, stigmas 6 mm long. Fruit 1.5–2.4×1.3–2 cm; seeds 3–4×3 mm, broadly triangular in outline, with membranous wing.

Distribution and Ecology.—Endemic to northern Chile; distributed in Region II (Antofagasta, 22°30'–26° S), up to about 670 m. Grows in rocky, arid areas of the coastal cordillera.

Phenology.—Flowering between November and February.

Conservation.—Endangered (Zizka et al., 2009).

Vernacular name.—None reported.

Additional specimens examined. CHILE. Región II: Tocopilla, Cobija, *Gaudichaud s.n.* (US-2144942); Tocopilla, Cobija, Jul 1836, *Gaudichaud s.n.* (F-1435100, GH, P); Antofagasta, Taltal, 1 Nov 1940, *Grandjot 4224* (GH); Antofagasta, Quebrada Metancilla, 3 Dec 1988, *Hoffmann 280* (CONC); Antofagasta,

Quebrada El Rincón, Peña Grande, 2 Dec 1988, *Hoffmann s.n.* (CONC-99116); Antofagasta, Hills south-east of Taltal, 25 Nov 1925, *Johnston 5107* (GH, US); Antofagasta, Vicinity of Aguada de Miguel Diaz, 1–4 Dec 1925, *Johnston 5321* (GH, US); Antofagasta, Huanchillo, Quebrada La Esmeralda, N Grenze des Nationalparks Pan de Azucar, 6 Feb 1991, *Zizka 1559* (FRP); Antofagasta, Schlucht ca. 200 mS von Quebrada Rincon, 4 Feb 1991, *Zizka 1521* (FRP); *Zizka 1522* (FRP); ca. 20 kmN of Taltal, Quebrada Palo Barao, 5 Feb 1991, *Zizka 1560* (FRP); Paposo, Quebrada Peralita, 29 Dec 2006, *Zizka 8161* (CONC, FR); *Zizka 8162* (CONC, FR); *Zizka 8163* (CONC, FR); *Zizka 8164* (FR).

Puya boliviensis is morphologically closest to *P. chilensis* and *P. gilmartiniae*. It differs from the first in its shorter inflorescence with about 20 lateral branches (80 or more in *P. chilensis*), and from the latter by the larger flowers (4.5–6.1 cm long compared to about 3 cm in *P. gilmartiniae*) and glabrous adaxial leaf surface (lepidote in *P. gilmartiniae*). *Puya boliviensis* is also geographically the most isolated of all Chilean *Puya* species.

Muñoz (1960) identified two specimens collected by Geisse *s.n.* as the types of *Puya copiapina* Phil., SGO 46420 and SGO 71679, among which we chose the first as the lectotype.

Puya chilensis Molina, Sag. Stor. Nat. Chili: 160, 351. 1782. Type: Description (herbarium and types of Molina unknown [Stafleu & Cowan, 1981]); Chile. Región VIII: Prov. Concepción, Los Perones, acantilado frente al mar, detrás del Cerro Teta Sur, 30 m s. m., 36° 45'S, 73°11'W, 20 Nov 1975, *M. Quezada 174* (neotype, **here designated**: CONC 45034, two sheets; photocopy of CONC specimens: FR-5364, FR-5365). (Fig. 1)

Renealmia ramosa, lutea, foliis spinosis, vulgo *Puya* Feuillée, J. Obs. Phys. Math. Bot. 3: pl. 39. 1725. Type: Description and plate.

Pourretia coarctata Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 81. 1798. Type: Chile. *H. R. Ruiz & J. A. Pavon s.n.* (MA? n.v.).

Puya (“*Puja*”) *suberosa* Molina, Sag. Stor. Nat. Chili, ed. 2: 153. 1810. Type: Description (herbarium and types of Molina unknown [Stafleu & Cowan, 1981]).

Pitcairnia chilensis Lodd. Cat. ex Loudon, Hort. Brit.: 118. 1830, nom. nud.

Puya gigantea Phil., Linnaea 33: 246. 1864; *Puya chilensis* “var. *P. gigantea*” (Phil.) Baker, Handb. Bromel.: 127. 1889, comb. illeg.; *Puya chilensis* var. *gigantea* Baker ex Mez, Monogr. Phaner. [DC.] 9: 473. 1896. Type: Chile. Aconcagua, Los Molles, Nov 1862, *C. L. Landbeck s.n.* (lectotype, designated by Muñoz, 1960: SGO 46417).

Puya quillotana Weber, Feddes Repert. 95(9–10): 577. 1984. Type: Chile. Prope Quillota, C. Bertero 1261 (holotype: HAL; isotypes: KIEL, WU [photo]).

Plants caulescent, in flower up to 4(–5) m high, stems prostrate, branched, 15–20 cm in diameter. Leaves numerous, in a dense rosette approx. 1 m high; sheath 7–10×4.4–10 cm, ovate, dark brown, margin apically spinose, entire toward base, above glabrous, below densely lepidote, glabrescent towards base; blade 55–107×2.3–5.7 cm, yellowish-green when dried, soon glabrous on both sides, the scales usually persistent in the longitudinal furrows of the leaf, spines 7–15 mm long, brown, several cm apart, becoming more distant from base to apex. Inflorescence ≥1 m high, triangular in outline; scape bracts ovate, acuminate, 9.8×2.8 cm, ± lepidote, membranous, nerved, entire or spinose-serrate towards apex; with 80–100 racemose branches (partial inflorescences), these 21–30 cm long, axis of partial inflorescence densely covered with stellate trichomes, glabrescent after anthesis, in lower third to half fertile, the flowers densely spaced, sterile above with reduced bracts, these ± hairy with stellate hairs, glabrescent at fruiting time, sterile bracts similar to floral bracts but smaller; primary bracts ovate to broadly ovate, 6.5–15.5×2.5–6.8 cm, dark brown when dried, membranous, densely lepidote, ± prominently nerved, margin basally entire, ± serrate towards apex; floral bracts variable, elliptical to lanceolate or ovate, acuminate, (1.5–)2.5–4.5×0.7–2.1 cm, often exceeding the sepals, at least reaching up to about the middle of the sepals, dark brown, thin membranous, ± hairy with stellate hairs, inconspicuously nerved, entire; pedicel 7–15×1.5–3 mm. Flowers 5–7.3 cm long; sepals narrowly elliptical to lanceolate, apex rounded, sometimes with a mucro or acute, 2.1–4×0.3–0.9 cm, ± hairy with stellate hairs, coriaceous, entire, nerved; petals narrowly elliptical, rounded to rarely acute, 4–7×0.8–2.1 cm, yellow to green, naked; stamens 6, filaments 3–4.5 cm long, anthers 7–15×1.5 mm, pollen yellow; ovary 7–11×3–5 mm, style 3.4–4.5 cm long, stigmas 7–10 mm long. Fruit 1.7–2.7×1–2.5 cm; seeds 2.5–5×2–3 mm, ± triangular in outline, with membranous wing.

Distribution and ecology.—Endemic to Chile; distributed from Central Chile, Region IV (La Serena, 30°S) to Region VIII (S of Concepción-Estación El Fuente, 37°11'S), abundant in Region IV and V (La Serena, 30°S – Valparaíso, 33°S); between sea level and 900 m. Grows in stony terrain close to the coast and in interior mountains.

Phenology.—Flowering from August to November.

Conservation.—Least concern (Zizka et al., 2009).

Vernacular names.—Cardón, Chagual, Puya.

Additional specimens examined. Chile. Región IV:

Elqui, Prov. Coquimbo, La Serena, 1838, *Gay 17 or 19* (P); Elqui, Quebrada Honda, 19 Sep 1952, *Jiles 2202* (CONC); Limarí, Lumi-Lumi, 31 Aug 1947, *Jiles 249* (CONC); Limarí, Fray Jorge, 15 Aug 1947, *Jiles 224* (CONC); Limarí, Fray Jorge, parte baja, Sep 1958, *Kummerow s.n.* (CONC-51332); Choapa, Pichidangué, 21 Aug 1977, *Montero 10797* (CONC); Choapa, Los Vilos, 8 Oct 1965, *Montero 7188* (CONC); Quebrada Honda, *Morrison 16916* (MO); Elqui, Corral de Julio, camino a exclusión la Rojadilla, 6 Nov 1976, *Muñoz 909* (SGO); Limarí, Lomajes orientales de Talinay, 18–21 Nov 1940, *Muñoz & Coronel 1302* (SGO); *Muñoz & Coronel 1552* (SGO); Limarí, desembocadura del Río Limarí cerca del Bosque de Fray Jorge, Sep 1936, *Muñoz s.n.* (GH); Elqui, Corral de Julio, exclusión Aguas Malas Escasa, 6 Nov 1976, *Muñoz, M. 896* (SGO); Choapa, Illapel, Dec 1862, *Philippi s.n.* (SGO-46419); Limarí, Fray Jorge, Jan 1883, *Philippi, F. s.n.* (SGO-46406); Choapa, Coast at Los Vilos, 6 Oct 1914, *Rose 19229* (US); Limarí, Bahía Fray Jorge, 22 Sep 1960, *Schlegel 2875* (CONC); Prov. Coquimbo, Dept. Ovalle, Fray Jorge, 13 Oct 1947, *Sparre 3039* (SGO); Choapa, Prov. Choapa, Chigualoco, between Socos and Los Vilos, 22 May 1987, *Varadarajan et al. 1487* (GH, MO); Elqui, Playa las Tacas (Cerro Zoraida), about 20 km S of Coquimbo and about 5 km E of the ocean, 22 May 1987, *Varadarajan et al. 1484* (GH, MO); Choapa, Angostura de Gálvez, al sur de Puerto Oscuro en la costa de la Provincia Coquimbo, 24 Feb 1966, *Villalón s.n.* (US-2470568); Choapa, west of Illapel, on road to Mincha, 23 Nov 1935, *West 3936* (MO). **Región V:** Quillota, Friseo, Limache, Cerros al Norte, 18 Aug 1917, *Behn s.n.* (CONC-20619); Valparaíso, Valparaíso-salto, 1 Oct 1933, *Behn s.n.* (CONC-26810); Valparaíso, Viña del Mar, 7 Sep 1922, *Behn s.n.* (CONC-20620); Quillota, Quillota, *Bertero 1261* (G, HAL, KIEL); Quillota, Limache, Cerro Cruz, 4 Oct 1931, *Garaventa 1969* (CONC); Quillota, Limache, Cerro Cruz, 4 Oct 1931, *Garaventa 2103* (GH); Valparaíso, Valparaíso, 1932, *Gaudichaud 69* (G); Valparaíso, Valparaíso, *Gaudichaud 75* (P); Valparaíso, Quintero, Loma de la Cruz, Nov 1953, *Gunckel 43.244* (CONC); Valparaíso, Valle de Marga-Marga (coast ranges southeasterly from Valparaíso), *Jaffuel & Pirion 3025a* (GH); Quilpue, 1 Nov 1866, *King s.n.* (E); Quillota, Monte Mar, 16 Sep 1953, *Kunckel 831* (HBG); Quillota, *Looser 268* (CONC); Quillota, Limache,

Cerro Cruz, 19 Sep 1932, *Looser 2484* (GH); Quillota, Limache, Cerro Cruz, 19 Sep 1932, *Looser 2487* (GH); Papudo Cerros, *Montero 3202* (CONC); Petorca, Papudo, Cerro, 15 Sep 1967, *Montero 8009* (CONC); Valparaíso, Concon, 1885, *Philippi & Borchers 103* (BM); Valparaíso, Concon, 1885, *Philippi & Borchers 113* (BM); Cerros Agorta, 1882, *Philippi & Borchers s.n.* (BM-541656, GH); Valparaíso, Valparaíso, 1885, *Philippi & Borchers s.n.* (BM-541657c); Petorca, between La Ligua and Los Molles, 22 Oct 1914, *Rose 19403* (US); Viña del Mar, Jardín Bot., Lote B, 10 Dec 2006, *Zizka 8001* (CONC, FR). **Región Metropolitana:** Santiago, Prov. Santiago, Arcuquén, *Philippi s.n.* (SGO-66008). **Región VII:** Cauquenes, Constitución, Oct 1893, *Reiche s.n.* (SGO-61088). **Región VIII:** Concepción, Boca del Bio-Bio, 29 Sep 1946, *Behn s.n.* (CONC-7039); Concepción, Prope la Concepción, Oct 1825, *Macrae 102* (G); Concepción, Estación El Fuente, 2 Nov 1935, *Montero 2145* (CONC); Concepción, Los Perones detrás del Cerro Teta Sur, 20 Sep 1975, *Quezada 175* (CONC); Concepción, Hills back of Talcahuano, 22 Nov 1916, *Skottsberg 1376* (NY). **Without locality:** 1857, *H.P.? s.n.* (P); *Frömbing 433* (M); *Kubitzki 76* (WU); Mar 1849, *N.N. 4745* (P); *Rechinger 63037* (WU); *Rose 19160* (NY); *Weber s.n.* (B). **Cultivated plant:** 21 May 1957, *Hutchinson 57.444-1* (US).

Recent molecular studies (Schulte et al., 2010) confirmed the view that *Puya chilensis* is most closely related to *P. boliviensis* and *P. gilmartiniae*. All three species share the yellow to greenish flowers, a characteristic not found in the other Chilean *Puya* species.

A type specimen could not be traced for *P. chilensis* (the herbarium and types of Molina are unknown [Stafleu & Cowan, 1981]) and the protologue provides only a short diagnosis. Therefore, a neotype has been designated here.

Philippi cited a collection of *Landbeck s.n.* from Los Molles, Prov. Aconcagua as the type of *Puya gigantea* Phil. Among the collections held at SGO, Muñoz (1960) identified the specimen SGO 46417 as the type, which we here consider an indirect lectotypification.

Puya quillotana was described by Weber (1984), but has been shown to be conspecific with *P. chilensis* by Trumpler (1998) and Hornung-Leoni & Sosa (2008).

Puya gilmartiniae G.S. Varad. & A.R. Flores, J. Bromeliad Soc. 40(4): 161. 1990. Type: Chile, Region IV (Coquimbo): Elqui, about 60 km N of La Serena, on the way to Punta Totalillo, near El Olivo, Isla Tilgo, 22 May 1987, G.

S. Varadarajan et al. 1481 (holotype: GH; isotypes: MO, WS n.v.).

Plants caulescent, in flower 1.5–2 m high, stems prostrate, branched, 30–50 cm long. Leaves 15–20 in a dense rosette, arching; sheath 2–5×3.7–6 cm; blade 26–60×1.5–2.5 cm, lepidote above and beneath, more densely towards the margin and near the spines, the spines 7–10 mm long, 1.2–2 cm apart. Inflorescence (above the scape) 37–60 cm long, with up to 24 racemose branches (partial inflorescences), these 15.5–38 cm long, the axis woolly, glabrescent after anthesis, the lower third fertile, the flowers densely spaced, sterile above with reduced bracts, these similar to the floral bracts but smaller; scape bracts narrowly triangular to broadly lanceolate, acuminate, membranous, nerved, entire; primary bracts ovate to lanceolate, 13×3.5 cm, brown when dried, membranous, ± veined, margin entire; floral bracts elliptical to ovate, acuminate, 2.4×1.2 cm, equalling or exceeding the sepals, brown, membranous, inconspicuously nerved, entire; pedicel 7–10×2 mm. Flowers 3 cm long; sepals elliptical to lanceolate, apex rounded, ± mucronate, 1.5–2.3×0.4–0.6 cm, subcoriaceous, nerved, entire; petals elliptical, 2.6–3×0.9 cm, yellow, naked; stamens and ovary not seen. Fruit 2.3–3.5×2–2.3 cm; seeds 2–3.3×3 mm, broadly triangular in outline, with a membranous wing.

Distribution and ecology.—Endemic to central Chile, known only from Region IV (29°16'–29°39'S). Grows in coastal scrub vegetation between 50 and 520 m.

Conservation.—Critically endangered (Zizka et al., 2009).

Additional specimens examined. CHILE. Región IV: Elqui, La Serena: Puente Juan Soldado, just before Cuesta Buenos Aires, 30 Nov 2004, *Baxter et al. DCI 1753* (E); Chungungo, Straße von Chungungo zur Mine El Tolfo, ca. 5 km von Chungungo entfernt, 22 Dec 2006, *Zizka 8128* (CONC, FR).

This species is morphologically most similar to *P. boliviensis* and *P. chilensis* from which it differs by its smaller flowers. Varadarajan and Flores (1990) suggested that *P. gilmartiniae* might be a hybrid derived from a crossing between *P.*

boliviensis and *P. chilensis* because some features appear to be intermediate between the putative parental species and because the rather narrowly distributed *P. gilmartinae* occurs at the northern limit of *P. chilensis* and south of the area of *P. boliviensis*. The actual distribution area of the latter lies about 200–300 km north of the area of the other two species but the areas of all three species might have been confluent during former more humid periods. Interestingly, molecular studies (Schulte et al., 2010) support the idea of a hybrid origin involving the mentioned species.

Puya gilmartinii was named in honor of Amy Jean Gilmartin and therefore is to be changed to *P. gilmartinae* according to ICBN (McNeill et al., 2007), art. 60.11., ex. 30.

Puya subgen. Puyopsis (Baker) L.B. Sm. & Looser, *Phytologia* 19: 286. 1970. *Pitcairnia* subgen. *Puyopsis* Baker, *Handb. Bromel.*: 91, 117. 1889. Lectotype, designated by L.B. Smith, 1970: *Pitcairnia brachystachya* Baker (= *Puya brachystachya* [Baker] Mez).

Puya subgen. *Pitcairniopsis* Mez, *Monogr. Phaner.* [DC.] 9: 475. 1896. Type: *Pourretia floccosa* Linden.

Puya subgen. *Pourretia* Mez, *Monogr. Phaner.* [DC.] 9: 489. 1896, comb. illeg. Type: *Pourretia lanuginosa* Ruiz & Pav.

Puya subgen. *Chagualia* L.B. Sm. & Looser, *Revista Univ. (Santiago)* 20: 243. 1935. Type: *Puya coerulea* Lindl.

Inflorescence and its branches fertile throughout.

Puya × berteroniana Mez, *Monogr. Phaner.* [DC.] 9: 477. 1896. Type: Chile, Region V: Quillota, La Quinta, 1818, *C. L. G. Bertero 115* (holotype: P; isotypes: B, G).

Habit, leaves, and inflorescence unknown. Partial inflorescences basally for 1.6–3.2 cm sterile, broadly triangular in outline, 19.5–28 cm long; rachis densely covered with stellate trichomes, flowers ± dense, fertile throughout, bracts reduced in size towards apex; primary bracts ovate, 8.5–12.5 × ca. 3.5 cm, brown, lepidote, membranous,

nerved, serrate; floral bracts elliptical to rarely ovate, acute to acuminate, 2–5 × 0.7–1.4 cm, exceeding the sepals, reddish below, lepidote, ± membranous, nerved, entire; pedicel 5–12 × 1.5–2.5 mm. Flowers 2.7–5.2 cm long; sepals rounded and rarely mucronate to acuminate, 1.8–4 × 0.4–0.6 cm, coriaceous, prominently nerved, entire; petals 4.5 cm long; filaments 3 cm long, pollen yellow; ovary 6 × 3 mm, style and stigma not seen. Fruit and seeds not known.

Distribution and ecology.—Only known from the type.

Puya berteroniana has been the most problematic species of the genus in Chile (Smith & Looser, 1935; Gourlay, 1952) for its identity and taxonomic rank have remained unclear up to now. Mez (1896) based the species on a fragmentary specimen collected by Carlos Bertero (no. 115) in the region of Valparaiso, kept at Paris (P). The specimen is similar to *P. alpestris* but lacks the extensive terminal sterile parts of the partial inflorescences (although few presumably sterile floral bracts are found densely spaced at the terminal end). Consequently, Mez placed his new species in the subgenus *Pitcairniopsis* Mez [= *Puya* subgen. *Puyopsis* (Baker) L.B. Sm.], characterized by partial inflorescences without sterile terminal parts. No similar plants were reported until recently and Smith and Looser (1935), based on personal communication from Prof. Benoist who had been able to study the type specimen at P and reported sterile bracts for the tip of the branches, declared *P. berteroniana* to be synonymous with *P. alpestris*. Later, Smith and Downs (1974) revised the material and kept both as separate species in *Puya* subgenus *Puya*. They applied the name *P. berteroniana* for plants with bluish flowers very similar to *P. alpestris*, but larger in all parts, with more branches per inflorescence and more northerly distributed. This taxonomic concept was commonly applied until now, although the differences between the type specimen of *P. berteroniana* and the plants usually named so, remained (a problem already recognized by Gourlay [1952]). Moreover, the species rank of the two groups (*P. alpestris* and *P. berteroniana* sensu Smith and Downs 1974) has never been thoroughly assessed. The fact that the northern and the southern taxa are obviously very similar

and the plants apparently become gradually taller from south to north cast doubt on their status as distinct species.

As far as *Puya berteroniana* Mez is concerned, our analysis of the inflorescence confirmed Mez' view that the terminal sterile parts characteristic for subgenus *Puya* are not found on the plant documented by the holotype (P) and the isotypes (B, G) of this taxon. As already argued by Smith and Looser (1935), no plants similar to the type have been collected, which makes it highly probable to regard *P. berteroniana* Mez as i) a very rare, by now extinct species, ii) based on a teratological specimen or iii) a product of hybridisation.

In 2006, a plant could be observed at Pichidangui (*Zizka 8119* [CONC, FR]) that appeared to be intermediate between *P. alpestris* subsp. *zoellneri* and *P. venusta*, both occurring sympatrically in the area. The Pichidangui plant resembled the type specimen of *P. berteroniana* in having an inflorescence similar to *P. alpestris* but lacking the sterile terminal parts; the leaves also resembled those of *P. alpestris*. Interestingly, the further investigation of this specimen revealed it to be genetically intermediate between *P. alpestris* and the *P. coerulea* group (Schulte et al., 2010). Nonetheless, for *P. coerulea* does not occur in the area of Pichidangui, considering it as one of the parental species is not yet convincing. Among the material studied, there is also a specimen (*Flores s.n.* [SGO 119847]) from Playa Las Tacas in the Coquimbo region that is similar to *Zizka 8119* and *P. × berteroniana*. Since the extent of hybrid formation and the putative parental species are still unclear, we refrain from assigning them to a taxon. However, *Puya berteroniana* Mez is here regarded to be a very rare taxon of hybrid origin. Up to now, *Puya* hybrids have been only reported by Luther (2010) who listed two species of hybrid origin (*P. × loxensis* Manzanares & W. Till, *P. × pichinchae* Mez & Sodiro), but no hybrids between representatives of different subgenera have been recorded up to now. However, a hybrid between the genera *Puya* and *Deuterocohnia*, *× Pucohnia* G.H. Anderson ex D.A. Beadle, was published by Beadle (1991).

Among the type collections (*Bertero 115*) the specimen labels bear heterogeneous in-

formation concerning collection sites and dates. They were either collected in La Quinta in 1818 or close to Rancagua in 1824. As pointed out by Smith and Looser (1935), La Quinta lies west of Requínoa, close to Coínco, in the province of Colchagua, and is a locality quite far away from Quillota; the Quinta collection corresponds with the one collected close to Rancagua. Whether one of the collection sites is erroneous – as suspected by Smith and Looser (1935) – or whether *Bertero 115* is a heterogeneous collection remains unclear.

There has been some confusion about the correct epithet of *P. berteroniana*. Stuessy and Marticorena (1990) proposed to change the original name to *P. berteroaana*. However, *P. berteroniana* is the correct spelling according to the ICBN (McNeill et al., 2007), art. 60.6., ex. 14.

***Puya coerulea* Lindl.**

Plants in flower 1–2.7 m high, caulescent, stems prostrate or erect, branched, 3 cm in diameter, covered by the old leaf bases. Leaves numerous, ± 25 , in a dense rosette 0.75–1 m in diameter; sheath 2–12 \times 1.5–13 cm; blade 11–62 \times 0.4–5 cm, whitish to glaucous, densely lepidote, spinose, the spines \pm hook-shaped, 2–5 mm long, reddish to brown, 0.3–1.5 cm apart at base, 3.5 cm apart towards apex. Scape up to 1 m high, 0.9–2 cm in diameter, greyish-green to reddish, inconspicuously longitudinally striate, woolly when young, becoming glabrous; scape bracts triangular or ovate, acuminate, 3.9–9.7 \times 0.8–1.3 cm, \pm lepidote, inconspicuously nerved, serrate. Inflorescence (above the scape) 0.5–1.1 m long, with racemose partial inflorescences, these 5–17.5 cm long (terminal inflorescence 19.5–28.5 cm); axis of partial inflorescence densely woolly-lepidote, glabrescent; primary bracts triangular to ovate, 1.4–10 \times 0.4–2.5 cm, shorter than the lateral branches, \pm lepidote, chartaceous to membranous, inconspicuously nerved, serrate; floral bracts highly variable, elliptical to ovate, acute to acuminate, 0.3–4.4 \times 0.1–2 cm, thinly membranous, inconspicuously nerved, entire or serrate; pedicel 3–24 \times 1.5–2.5 mm. Flowers 3.2–6 cm long; sepals triangular to lanceolate, apex rounded, sometimes with a mucro or rarely acuminate, 1.2–3 \times 0.2–0.9 cm, green

(fresh material), membranous to coriaceous, thinly membranous at margin, entire or inconspicuously serrate; petals elliptical, rounded, 2.8–5.2 × 1.3–2.5 cm, blue to blue-violet, with 2 appendages at base; stamens 6, filaments 3.4–4.7 cm long, anthers 4–8 × 1–1.5 mm, pollen yellow to orange; ovary pyramidal, 7–8 × 4 mm, style 2.7–3 cm long, stigmas 3-parted, 3–6 mm long. Fruit 1–1.8 × 1–1.5 cm; seeds 2–3 × 1–2.5 mm, narrowly triangular in outline, flattened, with membranous wing.

Distribution and ecology.—Endemic to Chile; distributed from Region IV to Region IX (30°05'–36°38'S), between (20–)100 and 2200 m. Grows in stony, arid areas.

Phenology.—Flowering from October to March.

Vernacular names.—Chagual chico, Chagualillo, Pipolle.

Puya coerulea is a morphologically highly variable species that was subdivided into four varieties by Smith and Looser (Smith, 1970), principally based on differences in relative lengths of floral bracts, pedicels, and sepals. Here, we adopt this widely accepted classification, although numerous morphologically intermediate plants exist, blurring the boundaries between the varieties. *Puya coerulea* var. *coerulea* appears to be the only group that is confined to the Chilean Coastal Cordillera, while the others are found on the western slopes of the Andes, the Central Valley and the coastal border. The varieties *violacea* and *intermedia* occur sympatrically as do var. *monteroana* and var. *intermedia*.

Interestingly, a molecular study revealed two subgroups within *P. coerulea* that apparently reflect geographical differences, one being a moderately supported *Puya coerulea* var. *coerulea*, the other one uniting the remaining three varieties, with the exception of one accession of var. *intermedia* (Schulte et al., 2010). The last varieties seem to be especially subject to gene flow, explaining their poorly defined taxonomic boundaries.

P. coerulea Lindl. var. **coerulea**, Edwards's Bot. Reg. 26: pl. 11. 1840. Type: Typified by original description and figure. (Fig. 1)

Pourretia coerulea Miers, Trav. Chile 2: 531. 1826, nom. nud.

Pitcairnia coerulea (Lindl.) Benth., Gen. Pl. [Bentham & Hooker f.] 3(2): 666. 1883 (see notes).

"*Pitcairnia coerulea*" auct. non Benth.: Baker pro parte (not the *Puya alpestris* element), Handb. Bromel.: 121. 1889 (see notes).

"*Puya violacea*" auct. non Mez: Watson, Curtis's Bot. Mag. 134: pl. 8194. 1908.

Plants in flower to 2.5 m high. Leaf sheath 4.5–12 × 5.3–13 cm; blade 36–62 × 1.5–3.5(–5) cm. Inflorescence woolly, the partial inflorescences fertile throughout, flowers densely spaced; primary bracts 4.7–10 × 1–3 cm; floral bracts 1–4.4 × 0.4–1.5 cm, membranous, reaching about the lower third of the sepals, rarely about as long as these; pedicel 3–15 × 1.5–2.5 mm.

Distribution and ecology.—Endemic to Chile; distributed from the Region IV (Playa Las Tacas, 30°05'S) to Region VI (Cachapoal, 33°55'S), between (20–)500 and 2000 m; confined to the Coastal Cordillera. Grows in stony, semiarid areas.

Phenology.—Flowering between October and February.

Conservation.—Near threatened (Zizka et al., 2009).

Vernacular names.—Chagual, Chagualillo.

Additional specimens examined. Chile. Región IV: Elqui, Playa las Tacas (Cerro Zoraida), about 20 km S of Coquimbo, and about 5 km E of the ocean, 22 May 1987, *Varadarajan et al. 1485* (GH). **Región V:** Quillota, Quillota, *Bertero 859* (HAL, KIEL); Valparaíso, *Cumming 388* (E); Quillota, Cerro Campana, 13 Jan 1928, *Garaventa 1334* (CONC); Quillota, El Robb?, 11 Jan 1932, *Garaventa 2282* (CONC); Tiltil, *Garaventa & Looser 2554* (GH); Quillota, Cerro Campana, Cajón de la Gloria, Palmas de Ocos, 2 Nov 1973, *Garaventa 6096* (CONC); Valparaíso, in petroflis apricis montanis Valparaíso, Jul 1830, *Bertero 571* (NY); San Felipe de Aconcagua, above Ramayama Copper Mine, Cerro Las Vizcachitas, 7 Dec 1951, *Hutchinson 93* (US); Cerro Campana, 15 Feb 1884, *Philippi & Borchers s.n.* (BM-541658); Quillota, between cuesta de la Dormida and Tiltil, 20 May 1987, *Varadarajan et al. 1491* (GH); Cerro La Campana, desde la placa Darwin a la cima, 4 Dec 1981, *Villagrán & Meza 3231* (SGO); San Felipe de Aconcagua, upper south slopes and near summit Cerro de las Vizcachas, 14–15 Jan 1936, *West 5143* (GH, MO); *Zizka 8025* (FR, SGO); Petorca, Los Molles, 20 Oct 1965, *Behn s.n.* (CONC-36827). **Región Metropolitana:** Caleu, Lo Marin, falda sur de Cerro Roble, 11 Dec 2006, *Zizka 8008* (CONC, FR); Maipo, Río Clarillo, Fundo El Principal, 1000 m, 10 Nov 1940, *Grandjot 4225* (GH); Maipo, Pan American highway just south of Santiago enroute to Rancagua, 28 Dec 1951,

Hutchinson 202 (B, G, NY, US); Chacabuco, entre Rungue y La Capilla (Caleu), 6 Nov 1927, *Looser 2026* (GH); Maipo, Angostura de Paine, limite entre los provincios de Santiago y Colchagua, 4 Dec 1932, *Looser 2549* (GH, US); Maipo, Angostura de Paine, limite entre las Prov. Santiago y Colchagua, 4 Dec 1932, *Looser 2550=2553* (US); Maipo, Angostura de Paine, limite entre las Prov. Santiago y Colchagua, *Looser 2551=2553* (US); Maipo, Angostura de Paine, limite entre las Prov. Santiago y Colchagua, 4 Dec 1932, *Looser 2553* (GH); Santiago, Tiltil, 5 Nov 1932, *Looser 9554* (GH); Santiago, Hospital, San Francisco de Aculeo, 29 Oct 1976, *Montero 10242* (CONC); Santiago, Altos de Tiltil, 1 Nov 1897, *Reiche s.n.* (SGO-46400). **Región VI:** Cachapoal, Rancagua, Angostura de Paine (cerros), 8 Nov 1961, *Montero 6489* (CONC). **Without locality:** *Bertero 859* (HAL, B [drawing]), *Shuttleworth 388* (BM); s.loc., 33°02'38.6"S, 70°98'42.7"W, 11 Dec 2006, *Zizka 8020* (FR, SGO).

Lindley referred the name *Puya coerulea* to Miers (1826) who published the name *Pourretia coerulea* without a description. The plant used for Lindley's description was the same as used by Miers (Lindley, 1840). Smith and Looser (1935) searched the type collections of Lindley held at CGE but did not find a specimen corresponding to *Puya coerulea*. Therefore, they concluded that Lindley had not preserved a herbarium specimen made from the cultivated plant used for his original description and drawing. Since this description is sufficiently detailed to recognize unambiguously the species, we refrained from designating an epitype.

In his publication of *Pitcairnia coerulea* Bentham (1883: 666) referred to Lindley's *Puya coerulea*: "*P. caerulea* (*Puya caerulea*). Miers in Lindl. Bot. Reg. 1840, t. 11)." Therefore, he made a new combination. Baker's (1889) description of *Pitcairnia coerulea* contained two elements, one of them corresponding to *Puya coerulea* Lindl., the other one to *Puya alpestris* Poepp. (including *P. whytei* Hook.f.).

Puya coerulea* var. *intermedia (L.B. Sm. & Looser) L.B. Sm. & Looser, *Phytologia* 19: 287. 1970. *Puya violacea* var. *intermedia* L.B. Sm. & Looser, *Revista Univ. (Santiago)* 20: 252. 1935. Type: Chile, Colchagua, Baños de Cauquenes, 3–4 Apr 1931, *G. Looser 2015* (holotype: GH).

Puya paniculata Phil., *Linnaea* 33: 247. 1864.
Pitcairnia philippii Baker, *Handb. Bromel.*: 122. 1889, nom. nov., non *Pitcairnia paniculata* Ruiz

& Pav. Type: Chile, Colchagua, *R. A. Philippi s.n.* (lectotype, designated by Smith & Looser, 1935: B n.v.; isotype: BM).

Puya glabrata Phil. ex Baker, *Handb. Bromel.*: 122. 1889; nom. nud.

Plants in flower up to 2.3 m high. Leaf sheath 2.6–8.5×3.4–5.7 cm; blade 45–47×1–1.9 cm. Partial inflorescence basally sterile for 3–5 cm, flowers loosely spaced, whitish woolly, glabrescent; floral bracts 1.2–1.8(–2.7)×0.3–0.6 cm, thinly membranous, reaching the base or rarely up to the upper third of the sepals; pedicel 5–15×1.5–2 mm.

Distribution and ecology.—Endemic to Chile; distributed from Region V (Quillota, 32°59'S) to Region VII (Constitución, 35°20' S), between sea level and 1100 m. Grows on stony hills.

Conservation.—Near threatened (Zizka et al., 2009).

Additional specimens examined. **Chile. Región V:** Valparaíso, Valle de Marga-Marga (coast ranges south-easterly from Valparaíso), *Jaffuel & Pirion 3276* (GH). **Región Metropolitana:** Santiago, Quinta Normal de Agricultura, 23 Nov 1960; Camino Rungue a Caleu, 28 Nov 1993, *Muñoz Schick 3345* (SGO). **Región VI:** *Schlegel 3108* (CONC); Rancagua, Angostura, direkt an der Panamericana nach Rancagua, 11 Dec 2006, *Zizka 8026* (CONC, FR, SGO); PN Los Cipresses, El Ranchillo, 12 Dec 2006, *Zizka 8027* (CONC, FR); PN Los Cipresses, Las Apas, 12 Dec 2006, *Zizka 8034* (CONC, FR); Termas de Cauquenes, Ruta del Acido, am Río Claro, 200 m flüßaufwärts von der Ruta, 12 Dec 2006, *Zizka 8045* (FR, SGO); Cachapoal, Termas de Cauquenes, 23 Jan 1927, *Behn s.n.* (CONC-20623); Cachapoal, Baños de Cauquenes, 3–4 Apr 1931, *Looser 2015* (GH); Cachapoal, Baños de Cachantún, Prov. de Colchagua, 21 Jan 1934, *Looser 2892* (GH); Cachapoal, Complejo turístico La Leonera, 5 Nov 1989, *Muñoz & Morera 2394* (SGO); Cachapoal, Termas de Cauquenes en el cerro, 1 Nov 1952, *Pfister s.n.* (CONC-13060); Colchagua, *Philippi s.n.* (B n.v., BM). **Región VII:** Constitución, zwischen Constitución und Putu, 13 Dec 2006, *Zizka 8050* (CONC, FR); *Zizka 8052* (CONC, FR); Constitución, am Strand in der Nähe einer Zellulosefabrik, 14 Dec 2006, *Zizka 8073* (CONC, FR).

Philippi did neither specify a holotype, nor a collector in the protologue of *Puya paniculata*, and specified only that the species is frequent in the Colchagua province ("in prov. Colchagua satis frequens est"). Among the collections held at SGO, Muñoz (1960) identified two specimens collected by Landbeck in 1860 as the

types, SGO-46411 and SGO-46414. However, Smith and Looser (1935) mentioned *Philippi s.n.* (B), collected in Colchagua, as the type, therefore providing an indirect lectotypification.

Puya coerulea var. monteroana (L.B. Sm. & Looser) L.B. Sm. & Looser, *Phytologia* 19: 287. 1970. *Puya violacea* var. *monteroana* L.B. Sm. & Looser, *Revista Univ.* (Santiago) 20: 252. 1935. Type: Chile, Colchagua, Cerro Centinela (San Fernando), Oct 1925, *G. Montero 26* (holotype: GH).

Plants in flower ca. 1–1.4 m high. Leaf sheath 2–4.7×2.2–3.3 cm; blade 19–48×0.8–1.1 cm. Partial inflorescence basally sterile for 6–6.5 cm, flowers loosely spaced, rachis whitish woolly, glabrescent; floral bracts 0.5–2.5×0.25–0.6 cm, thinly membranous, reaching to the base, rarely to the middle of the sepals; pedicel 9–12(–19)×1.5–2 mm.

Distribution and Ecology.—Endemic to Chile; distributed in Regions VI and VII (34°–35°S), between 400 and 1200 m.

Conservation.—Vulnerable (Zizka et al., 2009).

Additional specimens examined. Chile. Región VI: PN Los Cipresses, Las Aspas, 12 Dec 2006, *Zizka 8030* (CONC, FR); *Zizka 8035* (CONC, FR); Cachapoa, Baños de Requinoa, al puente del Requinoa, 21 Jan 1934, *Looser 2891* (US); Colchagua, Cerro Centinela (San Fernando), Oct 1925, *Montero 26* (GH); Colchagua, Río Claro (Sierra Bellavista), 25 Oct 1969, *Zöllner 4524* (CONC); Colchagua, *Philippi s.n.* (HBG-11/1737). **Región VII:** Constitución, zwischen Constitución und Putu, 13 Dec 2006, *Zizka 8051* (FR, SGO).

Puya coerulea var. violacea (Brongn.) L.B. Sm. & Looser, *Phytologia* 19: 287. 1970. *Pitcairnia violacea* Brongn., *Ann. Fl. Pomone* 3(1): 116. 1847 and in *Allg. Gartenzeitung* (Otto & Dietrich) 15: 299. 1847. *Puya violacea* (Brongn.) Mez, *Monogr. Phaner.* [DC.] 9: 476. 1896. Type: Paris Hort., s.loc., Mar 1847 (holotype: P, n.v.).

Pourretia rubricaulis Miers, *Trav. Chile* 2: 531. 1826, nom. nud.

Puya rubricaulis Steud., *Nomenclat. Bot.*, ed. 2(2): 419. 1841, nom. nud.

Pourretia violacea Linden, *Bot. Zeitung* (Berlin) 11: 718. 1853. Type: Description.

Plants in flower 1–2.7 m high. Leaf sheath 3–6.5×1.5–7 cm; blade 11–56×0.4–1.6 cm. Scape red below fertile part. Inflorescence with a red axis; partial inflorescence basally sterile for 4.5–9 cm, with the flowers loosely spaced, whitish woolly, glabrescent; primary bracts 1.4–3×0.4–1.2 cm; floral bracts 0.3–1.2×0.1–0.3 cm, thinly membranous, much shorter than the pedicels; pedicel 10–24×1.5–2 mm, black-violet.

Distribution and ecology.—Endemic to Chile; distributed from Region VI (Termas de Cauquenes, 34° 14' S) to Region VIII (Chillán, 36°38'S), between 100 and 1300 m. Grows in stony areas.

Phenology.—Flowering from December to March.

Conservation.—Vulnerable (Zizka et al., 2009).

Vernacular names.—Chagual chico, Chagualillo, Pilpolle.

Additional specimens examined. Chile. Región VI: Cordillera de Popeta, Jan 1887, *N.N. s.n.* (SGO-46413); Pichilemu, Quebrada El Roble, 29–30 Sep 1981, *Villagrán & Pérez 3149* (SGO); Termas de Cauquenes, Ruta del Acido, am Río Claro, 200 m flufaufwärts von der Ruta, 12 Dec 2006, *Zizka 8046* (CONC, FR, SGO); Colchagua, Colchagua, 1862, *Philippi s.n.* (G-8456/17); entre Población y Cueva, *Philippi s.n.* (SGO-46407); Colchagua, La Rufina, Fundo Bellavista, P. de Colchagua, 4 Jan 1951, *Ricardi s.n.* (CONC-10075). **Región VII:** Talca, Upper Valley of Río Maule, 5 km W of Cipreses, 27 Jan 1990, *Gardner et al. 4594* (E); Cauquenes, Mar 1871, *King s.n.* (E, 3 sheets); km 94 a Laguna del Maule, 20 Jan 2003, *Muñoz Schick 4340* (SGO); *Muñoz Schick 4341* (SGO); Camino La Montaña pasado Los Queñes, 21 Jan 2003, *Muñoz Schick 4345* (SGO); Talca, Junquillar Norte, Constitución, 14 Dec 2001, *Solervicens s.n.* (SGO-150460) (SGO); Talca, dry hills above Río Claro, Talca, 5 Jan 1904, *Elliot 369* (BM); Maule, 8 Feb 1892, *Kuntze s.n.* (US-701207); Maule, 8 Feb 1892, *Kuntze, s.n.* (NY); Talca, Río Maule-Canal Boca Sur, 8 Dec 1957, *Montero 5412* (CONC); Talca, Paso Pehuenche (o del Maule), 6 km W (below) customs station at La Mina (=8.3 km E of bridge over the Río Maule, =33.4 km E of Armerillo), 11 Jan 1996, *Nyffeler & Eggl 394* (B, SGO); Cauquenes, Constitución, Dec 1891, *Reiche s.n.* (SGO-61087); Talca, Camino de Talca a Putu, Fundo El Trapiche, 4 Jan 1964, *Schlegel 4928* (CONC); Talca, La Escuadra, camino a Laguna del Maule, 8 Jan 1961, *Schlegel 3452* (CONC); Curicó, Hacienda Monte Grande, Dec 1924, *Werdermann 539* (B, BM, E, G, HBG, NY, US); Curicó, Hcd. Monte Grande al interior de esta Hacienda, 15 Jan 1943, *N.N. 32* (SGO). **Región VIII:** Nuble, Prov.

Chillan, Dec 1869, *N.N. s.n.* (SGO-46415); Nuble, Chillan prov., Dec 1869, *Philippi s.n.* (SGO-46397).

Puya venusta Phil., *Reise Atacama*: 4. 1860; Phil., *Anales Univ. Chile* 91: 613. 1895. Type: Chile, Región IV: in der Nähe von Coquimbo, without date, *Philippi 940* (lectotype [see comments below], designated by Smith & Looser, 1935: B; photo of B specimen: G, GH). (Fig. 1)

Pitcairnia venusta (Phil.) Baker, *Handb. Bromel.*: 123. 1889. Type: Chile, Coquimbo, in der Nähe von Coquimbo, without date, *Philippi 940* (lectotype, designated by Smith & Looser, 1935: B; photo of B specimen: G, GH).

Pitcairnia sphaerocephala Baker, *Hand. Bromel.*: 123. 1889. Type: Chile, Region IV: Coquimbo, C. *Gaudichaud 55* (holotype: P).

Puya gaudichaudii Mez, *Monogr. Phaner.* [DC.] 9: 496. 1896. Type: Chile, Region IV: Coquimbo, C. *Gaudichaud 56* (holotype: P; photos of holotype: NY, GH).

Puya coquimbensis Mez, *Monogr. Phaner.* [DC.] 9: 492. 1896. Type: Chile, Region IV: Coquimbo, 1835, C. *Gaudichaud 52* (lectotype, designated by Smith & Downs, 1974: B).

Plants caulescent, in flower 1.2–1.8 m high, stems prostrate, branched, over 40 cm long. Leaves numerous, in a dense rosette of approx. 60 cm in diameter, arching; sheath (1.3–)3–9×(1.3–)3.2–9 cm, ovate to orbicular, clearly distinct from blade, below dark castaneous and lepidote in upper third, straw coloured and glabrous towards base; blade 10–46×1–3.5 cm, greyish-green, densely lepidote on both surfaces, spinose, the spines 3–5 mm long, brown to reddish, 0.1–0.7 cm apart at leaf base, 2 cm apart towards apex. Scape 56–150×1–1.5 cm, red, hairy with stellate hairs when young, glabrescent; scape bracts triangular to ovate, acute to acuminate, 3.5–6×1.4–3.5 cm, violet to brown, lepidote, chartaceous to membranous, inconspicuously nerved, serrate. Inflorescence simple and a raceme or compound of racemose partial inflorescences, these ± ovate in outline, 7–14 cm long, the axis lepidote, basally sterile for 3–7 cm, flowers very densely spaced above; primary bracts ovate, 3.7–7.2×1.5–3.7 cm, violet to brown when dried, chartaceous to membranous, inconspicuously nerved, ± serrate;

floral bracts imbricate, elliptical to obovate, acute to acuminate, 2.2–4.3(–7.2)×0.8–2(–3.5) cm, ± exceeding the sepals, violet, membranous, inconspicuously nerved, margin±serrate; pedicel 5–15×2 mm. Flowers 3–4.5 cm long; sepals lanceolate, apex rounded, sometimes with a mucro, 1.2–2.3×0.2–0.7 cm, light brown, often tinged with violet, membranous to coriaceous, nerved, entire; petals elliptical to obovate, rounded to rarely acute, 2.3–3.6×0.5–1 cm, dark blue to dark violet, black when dried, with 2 appendages at base; stamens 6, filaments 2.2–3 cm long, anthers 3.5–8.5×1–1.5 mm, pollen yellow to orange; ovary 5–7×3–4 mm, style 1.9–2.9 cm long, stigmas 3–8 mm long. Fruit 1–2×1.5–2 cm; seeds 2.7–4.3×1.7–2.2 mm, ± triangular in outline, with membranous wing.

Distribution and ecology.—Endemic to Chile; distributed from Region IV (Coquimbo, 29°57'S) to Region V (Islote "Cerro de la Cruz" de Zapallar, 32°34'S), between 5 and 250(–750) m; grows in sandy or rocky areas, forming dense stands.

Phenology.—Flowering between August and December.

Conservation.—Vulnerable (Zizka et al., 2009)

Vernacular names.—Chagual chico, Chagualillo.

Additional specimens examined. Chile. Región IV: Choapa, Coast at Pichidangui, 9 Mar 1996, *Brownless et al. IIECH-631* (E); Coquimbo, Nov 1929, *Elliott 543* (GH); Prov. Coquimbo, Playa Las Tacas, a 20 km al Sur de Coquimbo, 15 Aug 1986, *Flores s.n.* (SGO 119854 & 119855); Choapa, Coast at Pichidangui, 5 Oct 1995, *Gardner & Knees 5948* (E); Elqui, Coquimbo, 1831–33, *Gaudichaud 52* (P); *Gaudichaud 53* (photo GH, P); *Gaudichaud 54* (P); *Gaudichaud 55* (P); *Gaudichaud 56* (photo GH, P); 1835, *Gaudichaud & Mandner 11393* (F, photo GH); 1835, *Gaudichaud s.n.* (B-40/98-18); *Gaudichaud s.n.* (B-40/98-17); Limarí, Las Pajas, 1 Oct 1947, *Jiles 377* (CONC); Limarí, Talinay, cerca del mar, 16 Sep 1951, *Jiles 2046* (CONC); Limarí, Estancia Talca, 16 Jun 1949, *Jiles 1268* (CONC); Elqui, Cruz Grande, bajada a la caleta, 25 Feb 1972, *Jiles 5962* (CONC); Choapa, Quebrada de Buitre (salida), 1.1/2 km del mar, al oriente de la Estación Ingeniero Barriga, unos 10 km al N de Quilimarí, 14 Oct 1948, *Looser 5498* (US); Choapa, Pichidangui, 13 Sep 1968, *Montero 8143* (CONC); Choapa, Pichidangui, estanque "Aqua Potable", 14 Sep 1972, *Montero 8738* (CONC); Choapa, Pichidangui, Playa entre Pichidangui y Quilimarí, 21 Sep 1977, *Montero 10514* (CONC); Prov. Coquimbo, Las Tacas, 20 Oct 1984, *Muñoz Schick 1901* (SGO); Elqui,

Coquimbo, *Philippi s.n.* (B); Coquimbo, Nov 1853, *Philippi s.n.* (SGO 46405); Choapa, Carretera Panamericana, 20 km al sur de Los Vilos, 14 Sep 1957, *Ricardi & Marticorena 4231/616* (CONC); Choapa, Los Molles, 2 Oct 1960, *Schlegel 2984* (CONC); Elqui, Playa las Tacas (Cerro Zoraida), about 20 km S of Coquimbo, and about 5 km e. of the ocean, 22 May 1987, *Varadarajan et al. 1483/2* (GH); Choapa, Los Vilos, 15 km south, 22 May 1987, *Varadarajan et al. 1488/1* (GH); Pichidangui, Panamericana nach Los Vilos, ca. 300 m hinter der Peaje Pichidangui, 20 Dec 2006, *Zizka 8120* (CONC, FR, SGO); *Zizka 8124* (FR). **Región V:** Petorca, La Ligua: Ruta 5 at Puente Chivato, 29 Nov 2004, *Baxter et al. DCI 1711* (E); Petorca, Zapallar, 12 Oct 1935, *Behn s.n.* (CONC-24433); Petorca, Zapallar, Cerro de la Cruz, 29 Jul 1917, *Behn s.n.* (CONC-20617); Petorca, Zapallar, 12 Oct 1933, *Behn s.n.* (CONC-26811); Petorca, Zapallar, Punta Pite, 12 Jan 1950, *Garaventa 4941* (CONC); Petorca, Zapallar, 20 Sep 1953, *Kunkel 830* (HBG); San Felipe de Aconcagua, Los Molles, Nov 1861, *Landbeck s.n.* (SGO-46401); Petorca, Zapallar, 20 Nov 1932, *Looser 2542* (GH); *Looser 2537* (GH); *Looser 2542*(=2548) (US); *Looser 2543* (GH); *Looser 2544* (GH); *Looser 2545* (US); Petorca, Zapallar, 20 Nov 1932, *Looser 2548* (GH, US); *Looser s.n.* (GH); Petorca, Zapallar, Sep 1950, *Morales 22355* (CONC); San Felipe de Aconcagua, Prov. Aconcagua, *Philippi 247* (B); Petorca, Zapallar, Sep 1875, *Philippi s.n.* (SGO-46404); Petorca, Zapallar, Sep 1865, *Philippi s.n.* (SGO-66018); Petorca, Halbinsel von Zapallar, 18 Nov 1987, *Rechinger 63777* (WU); Petorca, Zapallar, 1 Dec 1935, *West 4573* (US); Petorca, Zapallar, Jul 1975, *Zöllner 8311* (MO); Valparaíso, Los Molles, Prov. Aconcagua, 27 Oct 1979, *Zöllner 10577* (MO); Valparaíso, Los Molles, Prov. Aconcagua, 23 Oct 1979, *Zöllner 10568* (MO); Petorca, Zapallar, 5 Apr 1996, *Zöllner s.n.* (HBG-12/1737). **Without locality:** *Philippi 940* (photo GH); *Philippi 11421* (photo NY); *West 4573* (GH). **Cultivated plant:** Jun 1962, *Marnier-Lapostolle s.n.* (US-2520954).

Philippi (1860: 4) in his “Reise durch die Wüste Atacama” published the name *Puya venusta* including a short diagnosis: “An ein paar Stellen fand ich auf dem Felsen eine prachtvolle Pourretia (oder *Puya*, *P. venusta* Ph.), Sie hat graue Blätter, einen 3–4 Fuss hohen, hochkermesinrothen Blütenstiel, graue Brakteen, und lavendelblaue Blumen mit saffrangelben Staubgefäßen [At some places on the rock I found a splendid Pourretia (or *Puya*, *P. venusta* Ph.), that has grey leaves, a 3–4 feet high, strongly carmine peduncle, grey bracts, and lavender flowers with saffron-yellow anthers].” This publication is valid following the ICBN (McNeill et al., 2007), Art. 34.1(a), since Philippi expressed his doubts about the taxonomic identity (*Pourretia* or *Puya*), but accepted the species. Hence Baker (1889), when describing *Pitcairnia venusta*, referring to *Puya venusta* Phil. inedit. as a “basionym” produced a new combination. Philippi’s description of *Puya venusta* (Philippi 1895) was obviously intended

by him as the original publication of that species. Therein he specified the vicinities of Coquimbo as the type locality (“jam. 1860 in itinere atacamensi indicata, sed non descripta. Habitat prope Coquimbo”). Later, Smith and Looser (1935) cited the Berlin specimen of *Philippi 940* – a specimen without collection date – as the holotype of that species, which is here considered an indirect lectotypification. Although, Muñoz (1960) identified among Philippi’s collections held at SGO the specimen *Philippi s.n.* (SGO-46405, collected near Coquimbo in 1853) as the type of *P. venusta*, there is no reason to reject Smith and Looser’s indirect lectotypification.

Puya venusta is well circumscribed and is easily recognized by its blue flowers that are apically congested in the lateral inflorescences. Putative hybrids between *P. venusta* and *P. chilensis* have been observed in the region of Zapallar (Zizka et al., 2009).

Acknowledgments

We thank the Chilean authorities, especially the Corporación Nacional Forestal (CONAF) for various support and permission to collect plant material. We are grateful to the directors of herbaria B, BM, CONC, E, FR, FRP, G, GH, HAL, HBG, MO, NY, SGO, US, and WU for providing material. Special thanks are due to the herbaria and staff of CONC and SGO for their support. We thank Chilean botanists, conservationists, and friends for important informations about collections, bromeliad habitats, companionship, and support during field trips, especially Otto Zoellner, Roberto R. Rodriguez, Melica Muñoz-Schick, Andrés Moreira-Muñoz, and Carlos Trabold. We also thank Claudia Hornung and an anonymous reviewer for helpful comments. The drawings were done by Anna Sarah Becker. The studies were financially supported by the Deutsche Forschungsgemeinschaft (DFG ZI 557/6, 7–1, SCHU 2426/1-1). The authors also acknowledge funding from the research funding program “LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” of the Hesse’s Ministry of Higher Education, Research, and the Arts (Biodiversity and Climate Research Center, BiK-F).

Literature Cited

- Baker, J. G.** 1889. Handbook of the Bromeliaceae. G. Bell & Sons, London.
- Beadle, D. A.** 1991. A preliminary listing of all the known cultivar and grex names for the Bromeliaceae. The Bromeliad Society, Los Angeles.
- Bentham, G.** 1883. Bromeliaceae. In: G. Bentham & J. D. Hooker (eds), *Genera plantarum* 3(2): 657–670. Reeve, London.
- Brummit, R. K. & C. E. Powell.** 1992. Authors of plant names. Royal Botanic Gardens, Kew.
- Echenique, A., C. Kenrick, M. V. Legassa.** 2003. El Jardín Botánico Chagual: un jardín de plantas nativas de la zona de clima mediterráneo de Chile. *Chagual* 1(1):4–11.
- Givnish, T. J., K. C. Millam, T. M. Evans, J. C. Hall, J. C. Pires, P. E. Berry & K. J. Sytsma.** 2004. Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and South American-African disjunctions in Rapateaceae and Bromeliaceae based on *ndhF* sequence data. *International Journal of Plant Sciences* 165: 35–54.
- , ———, ———, **J. C. Pires, P. E. Berry & K. J. Sytsma.** 2007. Phylogeny, biogeography, and ecological evolution in Bromeliaceae - insights from *ndhF* sequences. *Aliso* 23: 3–26.
- , **M. H. J. Barfuss, B. Van Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, R. S. Jabaily, D. M. Crayn, J. A. C. Smith, K. Winter, G. K. Brown, T. M. Evans, B. K. Holst, H. Luther, W. Till, G. Zizka, P. E. Berry & K. J. Sytsma.** 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: Insights from an eight-locus plastid phylogeny. *American Journal of Botany* 98: 872–895.
- Gómez Romero, S. E. & A. Grau.** 2009. Las especies de *Puya* (Bromeliaceae) en la Argentina. *Boletín de la Sociedad Argentina de Botánica* 44: 175–208.
- Gourlay, W. B.** 1952. *Puya berteroniana*. *Kew Bulletin* 7: 501–506.
- Hansen, D. M., J. M. Olesen, T. Mione, S. D. Johnson & C. B. Müller.** 2007. Coloured nectar: distribution, ecology, and evolution of an enigmatic floral trait. *Biological Reviews* 82: 81–111.
- Harms, H.** 1930. Bromeliaceae. In: A. Engler (ed.), *Die Natürlichen Pflanzenfamilien*, ed. 2, 15a: 65–159. Wilhelm Engelmann, Leipzig.
- Hornung-Leoni, C. & V. Sosa.** 2005. Morphological variation in *Puya* (Bromeliaceae): an allometric study. *Plant Systematics and Evolution* 256: 35–53.
- & ———. 2008. Morphological phylogenetics of *Puya* subgenus *Puya* (Bromeliaceae). *Botanical Journal of the Linnean Society* 156: 93–110.
- Horres, R., K. Schulte, K. Weising & G. Zizka.** 2007. Systematics of Bromelioideae (Bromeliaceae) – evidence from molecular and anatomical studies. *Aliso* 23: 27–43.
- , **G. Zizka, G. Kahl & K. Weising.** 2000. Molecular phylogenetics of Bromeliaceae: Evidence from *trnL*(UAA) intron sequences of the chloroplast genome. *Plant Biology* 2: 306–315.
- Jabaly, R. S. & K. J. Sytsma.** 2010. Phylogenetics of *Puya* (Bromeliaceae): Placement, major lineages, and evolution of Chilean species. *American Journal of Botany* 97: 337–356.
- Kunth, K. S.** 1815. *Voyage de Humboldt et Bonpland, sixième partie - Botanique: Nova genera et species plantarum*, vol. 1. Librairie Grecque-Latine-Allemande, Paris.
- Lindley, J.** 1840. *Puya caerulea*. In: *Edwards's Botanical Register* 3: 11. Ridgway, London.
- Luther, H. E.** 2010. An alphabetical list of bromeliad binomials, ed. 12: 1–45. The Sarasota Bromeliad Society and Marie Selby Botanical Garden.
- Marticorena, C.** 1991. Contribución a la estadística de la flora vascular de Chile. *Gayana Botánica* 47: 85–113.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicholson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema & N. J. Turland (eds.)** 2007. *International Code of Botanical Nomenclature (Vienna Code)*. Regnum Vegetabile 146. Ruggell: Gantner Verlag.
- Mez, C.** 1896. Bromeliaceae. In: A. L. P. P. de Candolle & A. C. P. de Candolle (eds.), *Monographiae Phanerogamarum Prodrumi nunc Continuato, nunc Revisio Auctoribus Alphonso et Casimir de Candolle Aliisque Botanicis Ultra Memoratis* 9: 466–499. Paris.
- . 1935. Bromeliaceae. In: A. Engler (ed.), *Das Pflanzenreich* 100: 284–315. W. Engelmann, Leipzig.
- Miers, J.** 1826. *Travels in Chile and La Plata*. Vol. 2. Baldwin, London.
- Muñoz, C.** 1960. Especies de plantas descritas por R. A. Philippi en el siglo XIX; estudio crítico en la identificación de sus tipos nomenclaturales. Ediciones de la Universidad de Chile, Santiago.
- Muñoz-Schick, M.** 2003. Acerca del nombre “Chagual”. *Chagual* 1(1): 74–75.
- Philippi, R. A.** 1860. *Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853–54*. Eduard Anton, Halle.
- . 1895. Plantas nuevas chilenas : Bromeliáceas. *Anales de la Universidad de Chile* 91: 607–615.
- Pinto, R.** 2001. Presencia de *Tillandsia virescens* en el sistema de tillandsiales de la cordillera de la costa de Iquique, norte de Chile. *Gayana Botánica* 58(1): 90.
- . 2005. *Tillandsia* del norte de Chile y del extremo sur de Perú. A. Molina Flores, Santiago.
- , **I. Barria & B. A. Marquet.** 2006. Geographical distribution of *Tillandsia* lomas in the Atacama Desert, northern Chile. *Journal of Arid Environments* 65: 543–552.
- Ravenna, P.** 2000. A new *Puya* species from central Chile (Bromeliaceae). *Onira* 4(15): 57–61.
- Sass, C. & C. D. Specht.** 2010. Phylogenetic estimation of the core Bromelioids with an emphasis on the genus *Aechmea* (Bromeliaceae). *Molecular Phylogenetics and Evolution* 55: 559–571.
- Schütz, N., M. Barfuss, K. Weising & G. Zizka.** 2009. The genus *Deuterocohnia* Mez (Bromeliaceae): Conflicting data in phylogenetic analysis. *Systematics 2009, Program and abstracts volume*: 118, National Herbarium of the Netherlands and National Museum of Natural History Naturalis, Leiden.
- Schulte, K., M. H. J. Barfuss & G. Zizka.** 2009. Phylogeny of Bromelioideae (Bromeliaceae) inferred

- from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molecular Phylogenetics and Evolution* 51: 327–339.
- , **R. Horres** & **G. Zizka**. 2005. Molecular phylogeny of Bromelioideae and its implications on biogeography and the evolution of CAM in the family (Poales, Bromeliaceae). *Senckenbergiana Biologica* 85:113–125.
- , **D. Silvestro**, **E. Kiehlmann**, **S. Vesely**, **P. Novoa** & **G. Zizka**. 2010. Detection of recent hybridization between sympatric Chilean *Puya* species (Bromeliaceae) using AFLP markers and reconstruction of complex relationships. *Molecular Phylogenetics and Evolution* 57: 1105–1119.
- Smith, L. B.** 1964. Notes on Bromeliaceae XXII. *Phytologia* 10: 454–484.
- . 1970. Notes on Bromeliaceae XXX. *Phytologia* 19: 281–291.
- & **R. J. Downs**. 1974. Pitcairnioideae. *Flora Neotropica Monographs* 14(1). Hafner, New York.
- & **G. Looser**. 1935. Las especies chilenas del género *Puya*. *Revista Universitaria (Santiago)* 3: 241–279.
- & **W. Till**. 1998. Bromeliaceae. *In*: K. Kubitzki (ed.), *The families and genera of vascular plants*, vol. 4: 74–99. Springer, Berlin.
- Staffeu, F. A. & R. S. Cowan**. 1981. *Taxonomic Literature*, Vol. 3. *Regnum Vegetabile* 105. Bohn, Scheltema & Holkema, Utrecht.
- Stearn, W. T.** 1992. *Botanical Latin*. 4. ed. David and Charles, Newton Abbot.
- Stuessy, T. & C. Marticorena**. 1990. Orthography of some epithets honoring Bertero in the vascular flora of the Juan Fernandez Islands and Continental Chile. *Gayana Botanica* 47(3–4): 77–81.
- Trumpler, K.** 1998. Systematisch-taxonomische Untersuchungen chilenischer Pitcairnioideae (Bromeliaceae). Unpublished diploma thesis, Goethe-University, Frankfurt am Main, Germany.
- Varadarajan, G. S.** 1990. Patterns of geographic distribution and their implications on the phylogeny of *Puya* (Bromeliaceae). *Journal of the Arnold Arboretum* 71: 527–552.
- & **A. Flores**. 1990. Novelty of *Puya* Molina (Pitcairnioideae), II: A new species from Chile. *Journal of the Bromeliad Society* 40: 161–165.
- & **A. J. Gilmartin**. 1988. Taxonomic realignments within the subfamily Pitcairnioideae (Bromeliaceae). *Systematic Botany* 13: 294–299.
- Weber, W.** 1984. Die Bromeliaceae im Herbarium D.F.L. von Schlechtendals. *Feddes Repertorium* 95: 573–600.
- Will, B. & G. Zizka**. 1999. A review of the genus *Greigia* Regel (Bromeliaceae) in Chile. *Harvard Papers in Botany* 4(1): 225–240.
- Zizka, G.** 1992. Bromeliáceas. *In*: Grau J, Zizka G (eds) *Flora silvestre de Chile*. Palmengarten Sonderheft 19: 101–107.
- , & **M. Muñoz-Schick**. 1993. *Tillandsia marconae* Till & Vitek, a Bromeliad species new to Chile. *Boletín del Museo Nacional de Historia Natural de Chile* 44: 11–17.
- , **R. Horres**, **E. C. Nelson** & **K. Weising**. 1999. Revision of the genus *Fascicularia* Mez (Bromeliaceae). *Botanical Journal of the Linnean Society* 129: 315–322.
- , **M. Schmidt**, **K. Schulte**, **P. Novoa**, **R. Pinto** & **K. König**. 2009. Chilean Bromeliaceae: diversity, distribution and evaluation of conservation status. *Biodiversity and Conservation* 18: 2449–2471.
- , **K. Trumpler** & **O. Zöllner**. 2002. Revision of the genus *Ochagavia* (Bromeliaceae, Bromelioideae). *Willdenowia* 32: 331–350.