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Revalidation of *Chusquea argentina* (Poaceae, Bambusoideae, Bambuseae) on the basis of morphological, anatomical and phenological characters

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Abstract

Chusquea (Poaceae, Bambusoideae, Bambuseae) is the most diverse genus of woody bamboos in the world. In Andean Patagonian forests of southern Argentina and Chile, several species of *Chusquea* are the dominant components of the understory. *Chusquea argentina* and *C. culeou* fo. *longiramea* were described from that area on the basis of morphological characters. Some authors have considered *C. argentina* to be a valid species and others have treated this and *C. culeou* fo. *longiramea* as synonyms of *C. culeou*. This study contributes to the delimitation of these taxa. Based on morphology and anatomy, we clarify differential characters between *C. culeou* and *C. argentina* and restore the latter as a valid species. *Chusquea culeou* fo. *longiramea* is synonymized under *C. argentina*. According to data of mass flowering events recorded in southern Argentina and Chile, *C. culeou* and *C. argentina* become reproductive at different times. Anatomical descriptions of culm and foliage leaf blade epidermis and cross sections are provided for each species. Comparative tables based on diagnostic characters are also included.

Key words: Anatomy, Argentina, Chile, *Chusquea*, mass flowering, morphology, taxonomy

Resumen

Chusquea (Poaceae, Bambusoideae, Bambuseae) es el género de bambúes leñosos más diverso del mundo. En los bosques andino-patagónicos de la Argentina y Chile, varias especies de *Chusquea* son el componente dominante del sotobosque. *Chusquea argentina* y *C. culeou* fo. *longiramea* fueron descritas para ese área sobre la base de caracteres morfológicos. Algunos autores han considerado a *C. argentina* como una especie válida y otros la han tratado junto con *C. culeou* fo. *longiramea* como sinónimo de *C. culeou*. Este estudio contribuye a la delimitación de estos taxones. Considerando aspectos morfológicos y anatómicos, se dan a conocer caracteres diferenciales de *C. culeou* y *C. argentina* y se restablece esta última como especie válida. *Chusquea culeou* fo. *longiramea* se considera sinónimo de *C. argentina*. Según información de eventos de floración masiva registrados en el sur de la Argentina y Chile, *C. culeou* y *C. argentina* florecieron en distintos momentos. Se proporciona una descripción anatómica de la caña y la lámina foliar a nivel de epidermis y sección transversal para cada especie. Se incluyen tablas comparativas basadas en caracteres diagnósticos.

Palabras clave: Anatomía, Argentina, Chile, floraciones masivas, morfología, taxonomía

Introduction

Chusquea Kunth (1822: 151) is the most diverse woody bamboo genus in the world; it comprises ca. 163 species (Bamboo Phylogeny Group 2012, Costa da Mota *et al*. 2013, Guerreiro & Rúgolo de Agrasar 2013). The genus is distributed from Mexico to Argentina and Chile from sea level to over 4000 m. The species of *Chusquea* are often significant, sometimes dominant, components of montane forest and high altitude grassland vegetation, where they can be aggressive colonizers (Judziewicz *et al*. 1999). Woody bamboos are also well known as understory dominants in cool temperate southern South America, in Andean Patagonian beech forests of Argentina and Chile. Clark (1995) cited ca. 15 endemic species in this area.

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Chusquea argentina Parodi (1941: 339) was described on the basis of specimens collected in the thick rainforest of Puerto Blest, Río Negro Province, Argentina. *Chusquea culeou* Desvaux (1853: 450) fo. *longiramea* Parodi (1941: 343) was described from this same area. This form differs from *C. culeou* by its longer flowering branches up to 35 cm in length. Diagnostic characters of *C. argentina, C. culeou,* and *C. culeou* fo. *longiramea* were stated by Parodi (1945) in a revision of the *Chusquea* species native to Chile. These included length of flowering branches, size and consistency of foliage leaf blades, presence of transverse veins and length of spikelets.

Nicora (1978), following the criteria of Parodi (1941, 1945), recognized *C. argentina* as a valid species and distinguished it from *C. culeou* based on morphological characters, and considered *C. culeou* fo. *longiramea* as a synonym of *C. culeou*. However, Nicora noticed that *C. culeou* fo. *longiramea* was difficult to distinguish from *C. argentina*, stressing the need for further studies to clarify whether the named entities are variants within a species or independent lineages that should be considered distinct species.

Several authors have considered *C. argentina* as a synonym of *C. culeou* (Zuloaga *et al*. 1994, 2012, Judziewicz *et al*. 1999, Triplett & Clark 2003, Morrone *et al*. 2008). However, Matthei (1997) and Clark (2000) treated *C. argentina* as a valid species for Argentina and Chile. According to Triplett & Clark (2003), *C. argentina* is part of a group of closely related woody bamboos native to the Andes of Argentina and Chile. Their study using principal components analysis revealed that variation in vegetative and floral characters is continuous, thus Triplett & Clark (2003) emphasized the fact that additional studies are necessary to resolve the classification of this group. The taxonomic treatment of *C. culeou* fo. *longiramea* as a synonym of *C. culeou* has been adopted by several authors (Zuloaga *et al*. 1994, 2012, Clark 2000, Morrone *et al*. 2008).

The goal of the present paper is to contribute to the delimitation of the *Chusquea* of southern Argentina and Chile considering morphological, anatomical and phenological characters. In this paper, *C. culeou* is distinguished from *C. argentina* and the latter is restored as a valid species for Argentina and Chile. *Chusquea culeou* fo. *longiramea* is synonymized under *C. argentina*. Detailed morphological descriptions, illustrations and descriptions of culm and foliage leaf blade epidermal and cross section characters are provided for each species. Evidence of the existence of different flowering cycles in *C. culeou* and *C. argentina* is presented. Comparative tables including characters of taxonomic value are also provided.

Material and Methods

Morphological descriptions followed Clark (1989). Vegetative and reproductive characters were analyzed in specimens belonging to the following herbaria: BA, BAA, BAB, BM, CONC, CORD, CTES, JUA, K, LIL, MCNS, MERL, MVM, NY, P, SGO, SI, US, and W (Thiers 2013). We examined 62 specimens, which are listed below. In the specimen citations, "veg." indicates a vegetative specimen and "fl." indicates a reproductive specimen.

For anatomical studies the middle portion of foliage leaf blades and the middle third of the internodes of developed culms were selected. Small epidermal fragments of culms and small fragments of foliage leaves were placed in glass tubes with xylene and exposed to ultrasound for approximately two hours to eliminate superficial wax and impurities. The material was dehydrated, coated with a gold–palladium alloy and photographed using a Scanning Electron Microscope Philips XL30 TMP at the Museo de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires, Argentina. Selected characters and terminology follow Ellis (1979), Rúgolo de Agrasar & Rodríguez (2002) and Guerreiro *et al*. (2013a, 2013b).

To obtain foliage leaf blade cross sections, herbarium material was boiled in water with commercial use detergent for several hours before making the sections manually. The histological sections were stained with safranin and mounted in glycerine-gelatine (D’Ambrogio de Argüeso 1986). The culm material was placed in plastic tubes with ethylenediamine 4% for two weeks at room temperature, before preparing anatomical sections using a sliding microtome. The histological sections were stained with safranin and fast-green and mounted in a synthetic mounting medium (D’Ambrogio de Argüeso 1986). Leaf and culm cross sections were observed and photographed with a light microscope Nikon Microphot FXA at Instituto de Botánica Darwinion, San Isidro, Argentina. Selected characters and terminology follow Ellis (1976), Xishen *et al*. (2002), Rúgolo de Agrasar & Rodríguez (2003) and Guerreiro *et al*. (2013a, 2013b).

Results

Chusquea argentina Parodi (1941: 339). Type:—ARGENTINA. Río Negro: Puerto Blest, 12 January 1935, *Cabrera & Job 253* (holotype BAA!, isotypes LP, US-1815752!). Fig. 1.

Chusquea culeou Desvaux (1853: 450) fo. *longiramea* Parodi (1941: 343). Type:—ARGENTINA. Río Negro: Puerto Blest, 6 February 1934, *Parodi 11737* (holotype BAA!, isotypes BA!, US-1539670!). *Syn. nov.*

Culms 3–6 m tall, 0.5–3.5 cm diameter, solid, flexible, arching. Nodes glabrous, with one central bud flanked by numerous subsidiary buds, linearly arranged. Culm leaves: sheaths 14–18 cm long, longer than internode, obtuse, glabrous, distal margin pubescent, basal margins overlapping; outer ligule a small rim; inner ligule 0.5–0.6 mm long, membranous; blades 1–3 cm long, erect, triangular, abaxially glabrous. Mature branch complement with 15–25 branches, 30–35 cm long, flexible. Foliage leaves: sheaths glabrous; outer ligule 0.1–0.2 mm long, glabrous or ciliate; inner ligule 1.2–2.5 mm long, membranous, abaxially pubescent; pseudopetiole 3–5 mm long, glabrous; blades 6–13 × 0.5–1 cm, linear, acuminate, membranous, somewhat flaccid, midrib prominent, transverse veins hardly distinguishable. Flowering branch complement with 10–15 leafy branches, 30–35 cm long, flexible, unilateral. Inflorescence 5–6.5 × 1–1.5 cm, dense, ovate, terminal. Pedicels 2–3 mm long, pubescent. Spikelets 8–9 mm long, linear, greenish. Glumes 2, persistent, obtuse, 1-nerved, margin ciliate, scabrous; lower glume 1–2 mm long, sometimes bilobate; upper glume 1.5–3 mm long. Sterile lemmas 2, mucronate, 1-3-nerved, diverging from the spikelet, distal third pubescent; lower sterile lemma 4.5–5.5 mm long, ½ the length of the fertile lemma; upper sterile lemma 6–6.8 mm long, ¾ the length of the fertile lemma. Fertile lemma 5–7.5 mm long, 7-nerved, mucronate, pubescent in distal third. Palea 5–6.5 mm long, subequal to the fertile lemma, 2-nerved, nerves scabrous, apex ciliate, pubescent in distal third. Lodicules 3, 1.1–1.3 mm long, ovate, both anterior ones with base 0.5–0.6 mm wide and acute apex, scabrous; posterior one wider, apex ciliate. Stamens 3, anthers 3–4 mm long. Gynoecium fusiform, stylar branches 2. Caryopses not seen.

Geographic distribution and habitat:—This species inhabits a narrow strip along the eastern Andean slopes of Neuquén, Río Negro and northern Chubut Provinces in southern Argentina, near the Chilean border, where it occurs beneath the dense canopy of *Nothofagus* Blume (1850: 307) forests. *Chusquea argentina* is also distributed in Chile, where it is found in the central valley and lower foothills, in the very humid forest, from Ñuble Province in the VIII Región de Biobío up to Llanquihue Province in the X Región de Los Lagos (36º–42ºS). On both sides of the Andes, it occurs up to 1450 m above sea level (Parodi 1945, Nicora 1978, Matthei 1997).

Anatomical characters:—Culm cross section (Fig. 2A–B): Epidermis formed by a layer of sclerified cells with thick external wall. Hypodermis formed by 5–7 layers of thick walled cells. Vascular bundles in 5–6 cycles. Phloem facing different directions. Peripheral vascular bundles ovate, completely surrounded by a thick sheath of sclerenchyma. Transitional and central vascular bundles ovate, elliptical, surrounded by a discontinuous sclerenchymatic sheath more developed in relation to the phloem and protoxylem. Central vascular bundles 190–200 × 180–190 µm.

Culm epidermis (Fig. 2C): Ribs and furrows not evident. Long cells with straight walls, without papillae. Abundant stomatal complexes, 10–16 × 1–4 µm, long and narrow, irregularly arranged, slightly sunken. Silica bodies, prickle hairs, microhairs and macrohairs absent.

Foliage leaf blade cross section (Fig. 2D–F): Rounded adaxial ribs and shallow furrows. Developed midrib with sclerenchyma projecting abaxially. Outer walls thickened and covered by a distinct, thick cuticle continuous over the epidermal cells. Fan-shaped bulliform cells situated at level with the general epidermal surface or at the base of shallow furrows. Fusoid cells present, successive, separated by numerous chlorenchyma cells. Well-developed caps of sclerenchyma at margins, not in contact with lateral bundle; on one margin pointed, the other rounded.

Foliage leaf blade abaxial epidermis (Fig. 2G–H): Long cells with straight walls and rounded, large papillae, arranged in one or two rows. Stomatal complex 12–16 × 7–11 µm, arranged in rows in intercostal zones; subsidiary cells rectangular in outline with simple papillae. Dumb-bell shaped silica bodies with rounded ends and narrow central portion, arranged in short rows associated with prickle hairs in costal zones; rounded silica bodies found only on midrib and leaf margins. Abundant prickle hairs with medium base and brief apex, arranged in rows in costal zones. One row of angular prickles on leaf margin. Scarce elongated bicellular microhairs with parallel-sided basal cell, irregularly arranged. Scarce macrohairs near leaf margins or midrib.

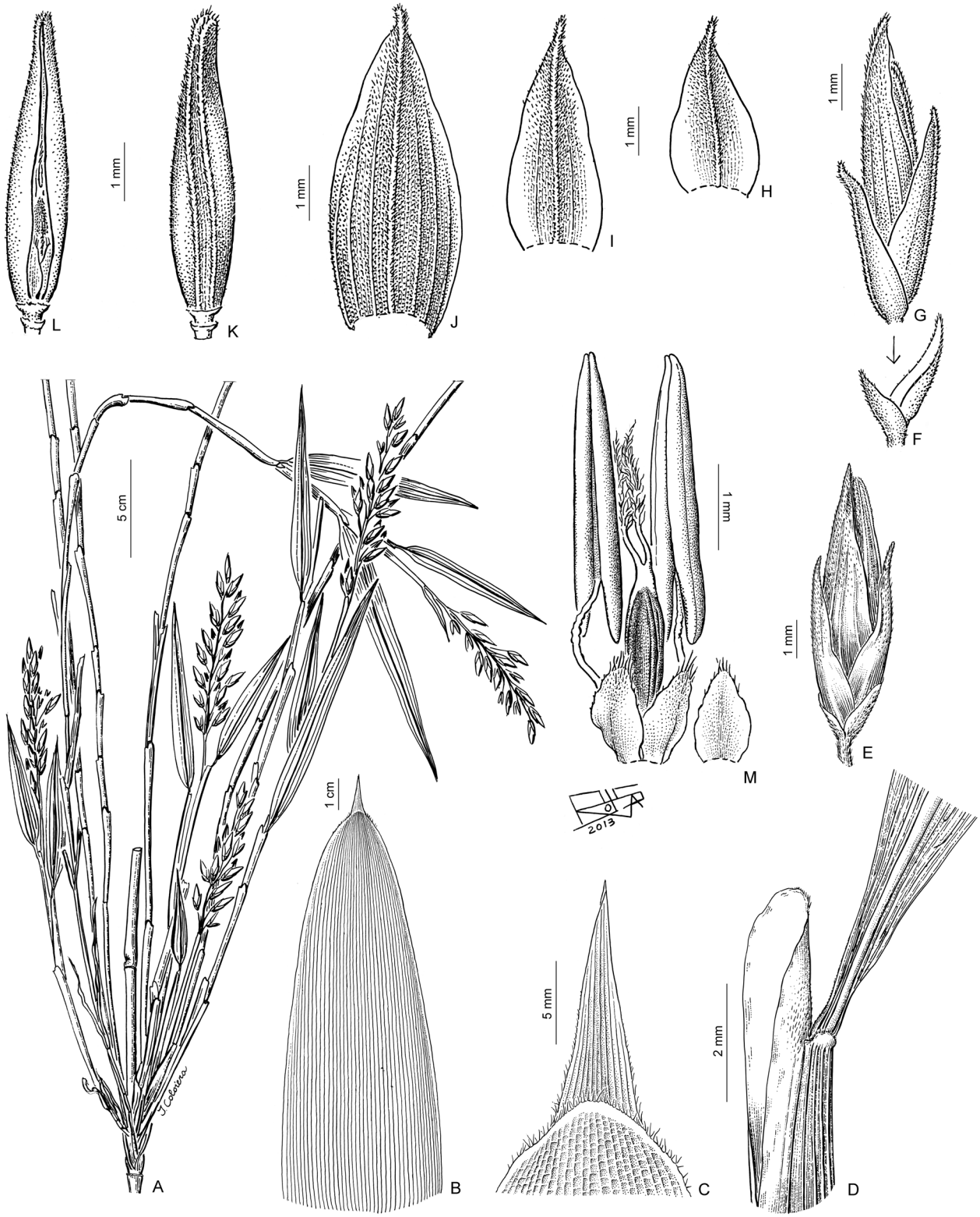

FIGURE 1. *Chusquea argentina.* A. Fragment of culm with a flowering branch complement. B. Culm leaf. C. Culm leaf blade and inner ligule**.** D. Foliage leaf inner ligule and pseudopetiole. E. Spikelet. F. Glumes. G. Sterile lemmas and anthecium. H. Lower sterile lemma. I. Upper sterile lemma. J. Fertile lemma. K. Palea, dorsal view. L. Palea, ventral view. M. Lodicules, gynoecium and anthers. A, D and E from *Caso 15187* (BAB), illustrated by Irene Coloiera, reproduced from Nicora (1978), with permission of the copyright holder, INTA; B and C from *Roig 13919* (BAB), all others from *Cabrera 253* (BAA), illustrated by Francisco Rojas.

Phenology:—In the southern hemisphere summer of 2010–2011, a mass flowering event of *C. argentina* was recorded in the western portion of Nahuel Huapi National Park, Argentina, near Puerto Blest (type locality of *C. argentina* and *C. culeou* fo. *longiramea*), and extended southward to northern Chubut. This flowering event continued until summer of 2012–2013 (Sampedro del Río, pers. comm.).

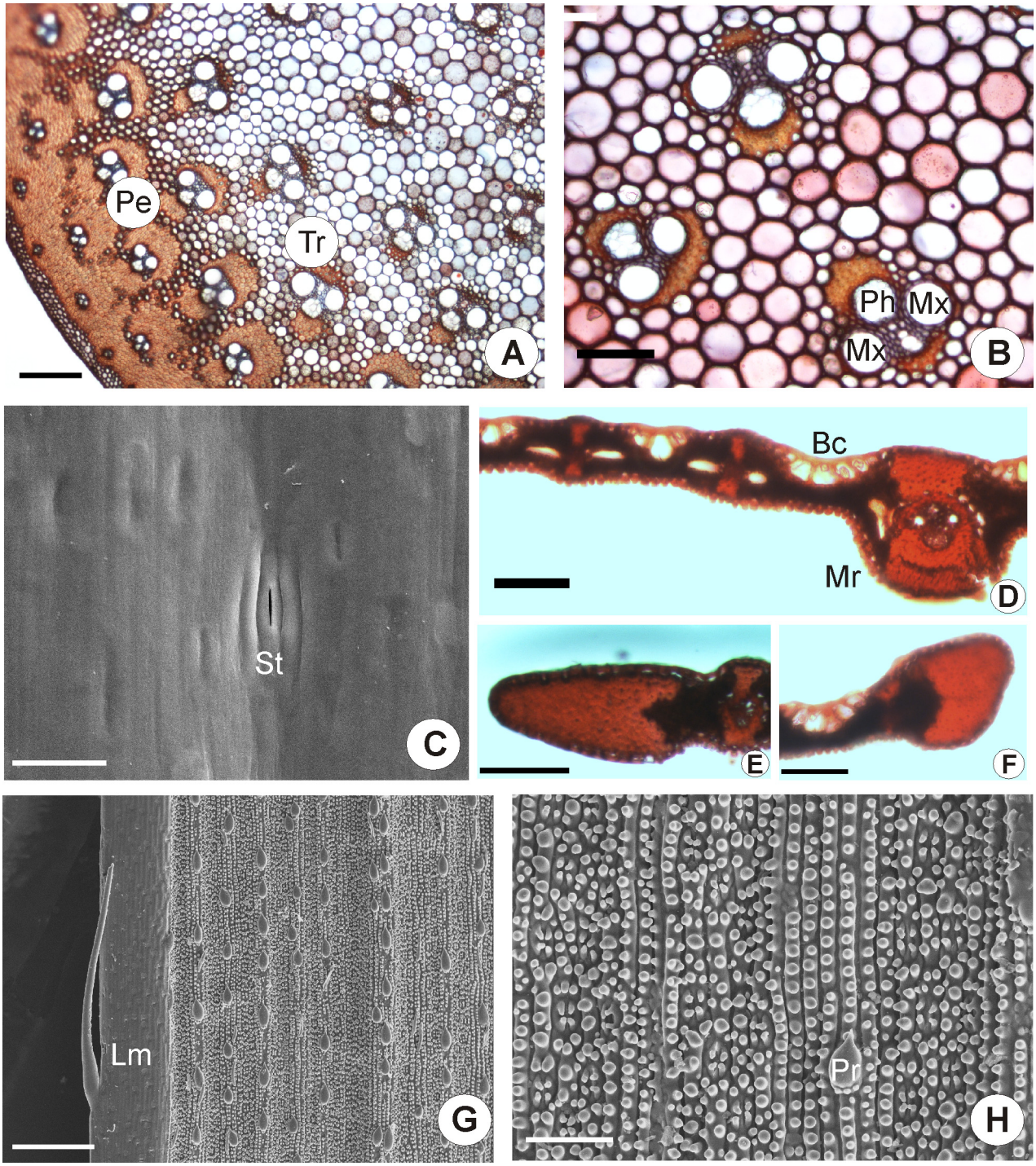

FIGURE 2. *Chusquea argentina* anatomical characters. A. Culm cross section showing epidermis, hypodermis, peripheral and transitional vascular bundles. B. Central vascular bundles. C. Culm epidermis, general view with stomata. D. Leaf blade cross section, developed midrib, projecting abaxially. E. Leaf margin with pointed cap of sclerenchyma. F. Leaf margin with rounded cap of sclerenchyma G. Leaf blade abaxial epidermis, leaf margin and macrohair. H. Leaf blade abaxial epidermis, general view. Abbreviations: Bc, bulliform cells; Lm, leaf margin; Mr, midrib; Mx, metaxylem; Pe, peripheral vascular bundle; Ph, phloem; Pr, prickle hair; St, stomata; Tr, transitional vascular bundle. Scale bars = 200 µm for A and G, 100 µm for B, D–F, 50 µm for H and 20 µm for C.

Additional specimens examined:—ARGENTINA. Chubut: Cushamen, Lago Puelo National Park, 26 February 1950, fl., *Soriano 4305* (BAB); ditto, 253 m, 42º6'10''S, 71º43'31''W, 3 February 2010, fl., *Yormann 13* (SI); Futaleufú: Los Alerces National Park, no date, fl., *Roig 13919* (BAB, MERL). Neuquén: Los Lagos, Traful, February 1943, fl., *Soriano 105* (BAA); Huiliches, Lanín National Park, 15 February 1983, fl., *Tarak s.n.* (BAA).

Río Negro: Bariloche, Frias lake, February 1943, fl., *Soriano 306* (BAB); ditto, 4 February 1948, fl., *Caso 15187* (BAA, BAB, SI); ditto, 10 January 1952, fl., *Boelcke 5422* (BAA); Nahuel Huapi lake, 2 November 1940, fl., *Diem 282* (BAB); Nahuel Huapi National Park, 14 January 1952, fl., *Boelcke 5596* (BAA, BAB, P); Puerto Blest, 779 m, 41° 2'21''S, 71°48'25''W, 10 January 2012, fl., *Guerreiro 12* (SI); ditto, 766 m, 41°1'22''S, 71°49'19''W, 10 January 2012, fl., *Guerreiro 17* (SI).

CHILE. VIII Región del Biobío: Ñuble, Yungay, 1000–1500 m, February 1943, fl., *Ruisaco 2* (SGO). IX Región de La Araucanía: Cautín, Conguilio National Park, Truful-truful, 26 January 1928, fl., *Gunckel 2124* (BAA); Malleco, 9 February 1945, fl., *Montero 4395* (BAA); Temuco, Nielol peak, 26 November 1947, fl., *Sparre 3205* (SGO); ditto, 120 m, 38°40'S, 72°35'W, 15 March 1978, fl., *Landrum 3362* (SGO). X Región de Los Lagos: Osorno, January 1933, fl., *Rudolph s.n.* (SGO); ñadi de Caipulli, 10 February 1948, fl., *Sparre 4438* (SGO); Puyehue National Park, El Toro lake, November 1975, veg., *Briones s.n.* (SGO); Aguas Calientes, November 1975, veg., *Briones s.n.* (SGO); ditto, 440m, 40°44'S, 72°18'W, 13 January 1996, fl., *Matthei 403* (CONC). XIV Región de Los Ríos: Valdivia, Corral, 8 February 1930, fl., *Gunckel 18590* (CONC); Huahum river valley, 900 m, February 1941, fl., *Bernath 257* (SGO); Trafun, 21 January 1957, fl., *Pfister 19538* (BAA).

Chusquea culeou Desvaux (1853: 450, t. 83, f. 2). Type:—CHILE. Valdivia: selvas húmedas, 1835, *Gay 293* (holotype P!, isotypes BAA!, SGO-157!, US-2874609!). Fig. 3.

Chusquea andina Philippi (1858: 103). Type:—CHILE. Andes de Chillán, December 1855, *Germain s.n.* (holotype SGO-152!, isotypes BAA!, US-556439!, W-1916-0039877!).

Chusquea breviglumis Philippi (1858: 103). Type:—CHILE. Cordillera de Chillán, 1855, *Germain de Saint-Pierre s.n.* (holotype SGO-153!, isotypes BAA!, K!, P!, US-2874604!, W-1889-0028049!, W-1889-0362891!).

Culms 1–7 m tall, 1–2.5 cm diameter, solid. Nodes glabrous, one central bud flanked by numerous subsidiary buds, linearly arranged. Culm leaves: sheaths 6–13 cm long, longer than internode, glabrous, acute, basal margins overlapping; outer ligule a small rim, inner ligule ovate, ciliate, membranous; blades 0.5–3 cm long, persistent, erect, linear, margin scabrous. Leafy branches 6.5–21 cm long, erect. Foliage leaves: sheath glabrous; outer ligule ca. 1 mm long, glabrous; inner ligule 0.5–3 mm long, obtuse, glabrous, abaxially scabrous; pseudopetiole 0.5–2 mm long, glabrous; blades 5–18 × 1–1.8 cm, linear, margin sclerified, thickened, scabrous, coriaceous, tessellated, apex sharp, rigid. Flowering branch complement with more than 20 leafy branches. Flowering branches 3–6 cm long, erect, rebranching, with short branches bearing 1–3 spikelets. Pedicels scabrous. Spikelets 6–8 mm long, purple-greenish, pubescent. Glumes 2, persistent, acute, 1-nerved, pubescent; lower glume 1.5–2 mm long; upper glume 2.5–3 mm long, linear. Sterile lemmas 2, aristulate, 5-nerved, appressed, distal third pubescent; lower sterile lemma 4–6 mm long, ⅔ the length of the fertile lemma, midnerve and distal third scabrous; upper sterile lemma 5–7 mm long. Fertile lemma 5–7.2 mm long, aristulate, 7-nerved, midnerve and distal third scabrous, the rest slightly pubescent. Palea 6–7.3 mm long, as long as fertile lemma, 4-nerved, nerves scabrous. Lodicules 3, 1.2–1.7 × 0.7–0.8 mm, linear, apex ciliate or glabrous. Stamens 3, anthers 4–4.5 mm long. Gynoecium fusiform, stylar branches 2. Caryopses 4–6 × 1.2–1.4 mm (Guerreiro & Rúgolo de Agrasar 2012).

Geographic distribution and habitat:—*Chusquea culeou* is widely distributed between 35ºS and 42ºS in the Andean Patagonian forests of southern Argentina. In Chile, it occurs up to 47ºS (Parodi 1945). In Argentina, it is abundant in the wet, mild climate near the Chilean border and becomes rare in the drier, colder eastern area. It is found between 700 and 1450 m above sea level, in pure stands in the open as well as beneath the dense canopy of *Nothofagus* forests.

Anatomical characters:—See Guerreiro *et al*. (2013a, 2013b).

Phenology:—Like many other bamboos (Judziewicz *et al.* 1999), *C. culeou* exhibits gregarious and synchronous flowering. In the southern hemisphere summer of 2000–2001, Andean Patagonian temperate forests of southern Argentina and Chile experienced massive flowering of this native bamboo species. The flowering event and consequent senescence extended over 200,000 ha (Giordano *et al*. 2009, Marchesini *et al*. 2009). According to Pearson *et al*. (1994), the previous documented mass flowering event of *C. culeou* took place in 1938–1939, thus establishing a life span of ca. 62 years (Guerreiro 2013).

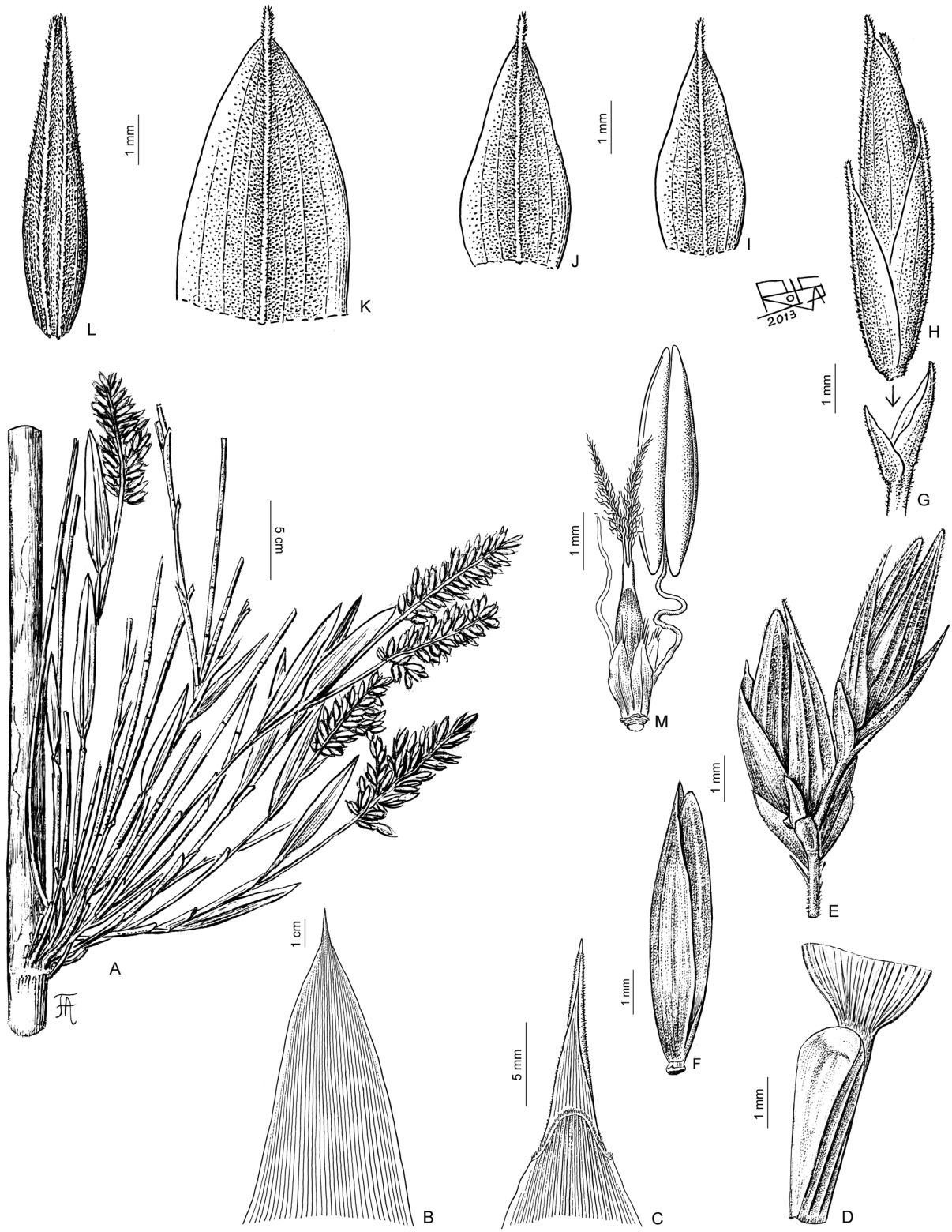

FIGURE 3. *Chusquea culeou.* A. Fragment of culm with a flowering branch complement. B. Culm leaf. C. Culm leaf blade and inner ligule. D. Foliage leaf inner ligule and pseudopetiole. E. Spikelet. F. Anthecium. G. Glumes. H. Sterile lemmas and anthecium. I. Lower sterile lemma. J. Upper sterile lemma. K. Fertile lemma. L. Palea. M. Lodicules, gynoecium and anther. A, D, E and F from *Boelcke 10918* (BAB), illustrated by Franco Antelmi, reproduced from Nicora (1978), with permission of the copyright holder, INTA; all others from *Rúgolo 2332* (SI), illustrated by Francisco Rojas.

Additional specimens examined:—ARGENTINA. Chubut: Cushamen, Esperanza lake, 1 February 1996, fl., *Johnson 632* (SI, BAB, CTES); Turbio river, 10 February 1955, fl., *Venzano s. n.* (SI, BA); Futaleufu, Futalaufquen lake, March 1940, fl., *Tortorelli s.n.* (BAA); ditto, 13 January 1941, fl., *Peréz Moreau 37661* (BAA, LIL, CTES);

ditto, 9 January 1948, fl., *Soriano 2920* (SI, BAA). Neuquén: Lácar, Lácar lake, 7 November 1982, fl., *Gentili 893* (BAB, CTES); Los Lagos, 20 December 1927, fl., *Cordini 91* (BAA, US); Correntoso lake, December 1937, fl., *Giacobbi 456* (BAB); Villa La Angostura, 23 April 2009, fl., *Rúgolo 2332* (SI); ditto, 12 September 2009, fl., *Rúgolo 2334* (SI); Minas, Epulaufquen lake, 16 January 1964, fl., *Boelcke 10918* (BAA, BAB, SI). Río Negro: Bariloche, Catedral peak, January 1978, fl., *Rubulis s.n.* (CTES); Hess lake, 17 January 1983, fl., *Cusato 2338* (BAA); Llao Llao peninsula, veg., 1 November 1990, *Pearson 1085* (SI); Puerto Blest, 4 December 1990, veg., *Pearson 1096* (SI); Old peak, January 2011, fl., *Ariza Espinar 3687* (CORD); López peak, 1030 m, 41º 5' 39''S, 71º 32' 15''W, 8 January 2012, veg., *Guerreiro 5* (SI).

CHILE. VII Región del Maule: Linares, Longavi, 17 January 1938, fl., *Castellanos 21568* (BAA, MCNS, CTES, SGO); Bellotos National Reserve, 4 January 2000, fl., *Arroyo 20131* (SGO). Talca, mountain range, 28 December 1936, fl., *Barros 555* (SI, US). VIII Región del Biobío: Concepción, 26 February 1961, fl., *Matthei 27187* (BAA). Ñuble, Atacalco, 18 December 1948, fl., *Pfister s.n.* (US); alpine grassland, 20 December 2001, fl., *Soreng 7118* (US). IX Región de La Araucanía: Cautín: Llonquimay mountain range, 9 December 1990, fl., *Roig 12975* (BAB, MERL); Villarica National Park, 26 April 1992, fl., *Finch 399* (NY). Malleco, Sierra Velluda, 3 November 1953, fl., *Ricardi 2348* (LIL). X Región de Los Lagos: Osorno: Puyehue National Park, 19 February 1992, fl., *Roig 13670* (BAB, MERL). XI Región de Aysén del General Carlos Ibañéz del Campo: Aysén, Simpson river valley, 11 January 1939, fl., *von Retzell 6213* (BAA, LIL); Buenos Aires lake, 11 February 1939, fl., *von Retzell 6258* (SI, BAA, SGO). XIV Región de Los Ríos: Valdivia, Corral, 10 February 1936, fl., *Gunckel 6763* (P); Cordillera Pelada, 5 May 1965, fl., *Eskuche 356* (BAA); ditto, 19 April 1982, fl., *Landrum 4515* (NY).

Discussion

Chusquea argentina differs from *C. culeou* by its longer spikelets and pseudopetiole, and the texture, consistency and size of the foliage leaf blades. In *C. argentina*, leaf blades are 6–13 × 0.5–1 cm, membranous, somewhat flaccid, with transverse veins hardly distinguishable. In *C. culeou*, leaf blades are 5–18 × 1–1.8 cm, coriaceous, tessellated, with transverse veins readily distinguishable. Moreover, in *C. argentina* flowering branch complements bear 10–15 branches, whereas in *C. culeou* they bear over 20 branches. They also show several differences in their reproductive structures (Table 1). The range of variation in all the above-mentioned characters in the type specimen of *C. culeou* fo. *longiramea* falls within the range of variation of *C. argentina*. Therefore, *C. culeou* fo. *longiramea* is here synonymized under *C. argentina*.

TABLE 1. Comparative morphological diagnostic characters between *Chusquea argentina* and *C. culeou.*

Character	*C. argentina*	*C. culeou*
Foliage leaf blade	6–13 × 0.5–1 cm, membranous, slightly tessellated, apex fragile	5–18 × 1–1.8 cm, coriaceous, tessellated, apex sharp
Pseudopetiole	3–5 mm long	< 2 mm long
Flowering branch complement	30–35 cm long, 10–15 branches	3–6 cm long, > 20 branches
Spikelets	8–9 mm	6–8 mm
Glumes	Obtuse, bilobate	Acute, pubescent
Sterile lemmas	1–3-nerved, mucronate	5-nerved, aristulate
Fertile lemma	Mucronate	Aristulate
Palea	2-nerved	4-nerved

Regarding anatomical characters, it is possible to distinguish between the species by the presence or absence of ribs and furrows, the shape of epidermal long cell walls, the abundance of prickle hairs and the location and shape of silica bodies on the foliage leaf blade abaxial epidermis (Table 2). As for culm characters, the two species can be distinguished by the thickness of the hypodermis, the shape of central vascular bundles and the presence or absence of silica bodies, prickle hairs and microhairs on the epidermis (Table 2).

TABLE 2. Comparative anatomical diagnostic characters between *Chusquea argentina* and *C. culeou.* Anatomical data for *C. culeou* are from Guerreiro *et al.* (2013a, 2013b).

	Character	*C. argentina*	*C. culeou*
Culm anatomy	Hypodermis	5–7 layers	4 layers
	Central vascular bundles	Elliptical	Depressed
	Silica bodies	Absent	Present
	Prickle hairs	Absent	Present
	Microhairs	Absent	Present
Foliar anatomy	Ribs and furrows	Present	Absent
	Long cell walls	Straight	Slightly wavy
	Silica bodies	Dumb-bell shaped all over the blade; rounded on midrib and leaf margin	Rounded and saddle shaped only on midrib
	Prickle hairs	Abundant	Scarce

These taxa have different flowering cycles, which is another line of evidence in support of recognizing them as different species. *Chusquea argentina* flowered massively in 2010–2011, 10 years after *C. culeou*, which flowered in 2000–2001.

We have provided evidence that morphological, anatomical and phenological characters are available to distinguish between *C. culeou* and *C. argentina*. We propose that they should be considered as distinct evolutionary lineages and therefore separate species. *Chusquea argentina* is restored as a valid species for southern Argentina and Chile, where it occurs sympatrically with *C. culeou* in the Andean Patagonian forests. Further studies involving molecular data would contribute valuable information to the delimitation of these taxa.

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