

A Revision of *Chusquea* sect. *Serpentes* (Bambuseae, Bambusoideae, Poaceae) Including Two New Species from South America

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Abstract—The Neotropical woody bamboo genus *Chusquea* consists of 193 currently described species ranging from central Mexico and the Caribbean to Chile and Argentina, primarily in montane habitats. The six previously described species of *Chusquea* subg. *Chusquea* sect. *Serpentes* are scandent in habit, with infravaginal branching, few subsidiary buds per complement, and foliage leaves that tend to be relatively large compared to those of other members of *Chusquea* s.s. A review of available material of *Chusquea* sect. *Serpentes*, found throughout montane forests from Mexico south to the central Andes in Peru, revealed at least two undescribed species. One of the new species, *Chusquea recurvata*, is native to Venezuelan montane forests and is distinguished from *Chusquea serpens* by having circular central buds, asymmetrical, acute inner foliage leaf ligules, and 6–12 foliage leaves per complement. The other new species, *Chusquea acutigluma*, has been found only in and around the Risaralda gorge in Colombia, and differs from all other known South American species of *Chusquea* sect. *Serpentes* by its broadly open panicle synflorescences. This paper includes (re-)descriptions of all known species of *Chusquea* sect. *Serpentes*, along with detailed photographs of the two newly described species, and a vegetative morphological key to the eight species belonging to the section. The morphology and foliage leaf micromorphology and anatomy of the two newly described species are compared to *C. serpens*, to which they show the greatest macromorphological similarity.

Keywords—Andes, Chusqueinae, leaf anatomy, leaf micromorphology, montane forests, Neotropical woody bamboos.

Of the Neotropical woody bamboos, the genus *Chusquea* Kunth is the most speciose, with 193 described species as of 2021 (Fadrique et al. 2019; Ruiz-Sanchez et al. 2021a, 2021b). *Chusquea* is divided into five subgenera, of which the most widespread and diverse is *C. subgenus Chusquea* (Fisher et al. 2014). Although molecular and morphological evidence support the *Chusquea* subgenera *Magnifoliae*, *Platonia*, and *Rettbergia*, the *C. subgenera Swallenochloa* and *Chusquea* and the sections within them are classified based on their morphological characteristics alone. *Chusquea* subgenus *Chusquea* is characterized by the presence of two to many subsidiary buds in a $\pm$ constellate arrangement with a triangular or circular central bud, extravaginal or infravaginal branching, and a free (not connate) lemma apex (Fisher et al. 2014; Vidal et al. 2018; Fadrique et al. 2019). The nearly 100 described species of *Chusquea* subg. *Chusquea* make up about 47% of known species of *Chusquea*, the greatest percentage of any subgenus.

Chusquea subg. *Chusquea* is represented by six sections: *C. sect. Chusquea*, *C. sect. Longifoliae* L.G.Clark, *C. sect. Longiprophyllae* L.G.Clark, *C. sect. Serpentes* L.G.Clark, *C. sect. Tenellae* L.G.Clark, and *C. sect. Verticillatae* L.G.Clark, in addition to the *C. meyeriana* Rupr. ex Döll informal group (Attigala et al. 2017). These sections are differentiated by several characters of both vegetative and fertile material, including branching pattern, number and arrangement of subsidiary buds, length of glumes relative to the spikelet, and shape of the central bud and its prophyll. Despite discussion surrounding the inclusion of several additional species of *Chusquea* in *C. sect. Serpentes* beyond those originally included in the section (Fisher et al. 2009; Ruiz-Sanchez et al. 2014, 2015; Attigala et al. 2017), a revision of the section has not taken place since its description over thirty years ago (Clark 1989).

While reviewing South American *Chusquea* specimens for ongoing floristic treatments, we recognized the need to reexamine *Chusquea* subg. *Chusquea* sect. *Serpentes*.

Species belonging to *Chusquea* sect. *Serpentes* tend to have fewer buds per node than other species of *Chusquea*, with two to 12 subequal buds in one constellate row (Clark 1989; Attigala et al. 2017). The section is also noted for having trailing, vining, or scrambling culms that are typically relatively small in diameter (≤ 5 cm), infravaginal branching, and wide foliage leaves (both absolute and relative width). Wide leaves are fairly unusual for the genus except in *C. subgenera Magnifoliae* L.G.Clark & A.E.Fisher and *Platonia* Nees, which lack aerial branching (Clark 1989; Fisher et al. 2014). Species of *C. sect. Serpentes* as originally described are found in montane forests of Mexico, Central America, and the northern and central Andes as far south as Peru (Clark 1989).

Of the five species placed in *C. sect. Serpentes* at the time the section was described, *Chusquea aspera* L.G.Clark of northern and Central Peru, *C. glauca* L.G.Clark of eastern-central Mexico, *C. latifolia* L.G.Clark of Colombia, and *C. serpens* L.G.Clark of Central and South America from Costa Rica to Ecuador are still classified in *C. sect. Serpentes*, while the southern Mexican and Honduran species *C. lanceolata* Hitchcock in Morton has been moved to *C. sect. Swallenochloa* in subg. *Swallenochloa* (McClure) L.G.Clark based on the confirmation of intravaginal branching in this species (Clark 1989; Ruiz-Sanchez et al. 2017). Two species of Mexican *Chusquea* formerly placed in *C. sect. Serpentes*, *C. enigmatica* Ruiz-Sanchez, Mejía-Saulés & L.G.Clark, and *C. gibcooperi* Ruiz-Sanchez, Mejía-Saulés, G.Cortés & L.G.Clark, have since been removed from the section and are currently considered incertae sedis within *Chusquea* subg. *Chusquea* (Ruiz-Sanchez et al.

2014, 2015; Attigala et al. 2017). *Chusquea enigmatica* and *C. gib-cooperi* display several key differences from other species in *C. sect. Serpentes*, including having extra- or intravaginal branching (often on the same culm) rather than the intravaginal branching characteristic of *C. sect. Serpentes* (Ruiz-Sanchez et al. 2014, 2015; Attigala et al. 2017). Additionally, neither species has a scandent habit, and *C. enigmatica* has foliage leaves that are narrower than is typical of species in *C. sect. Serpentes* (Ruiz-Sanchez et al. 2014, 2015). *Chusquea pohlii* L.G.Clark and *C. virgata* Hackel have recently been considered to belong to *C. sect. Serpentes* (Attigala et al. 2017; Vidal et al. 2018) based on branching pattern, subsidiary bud shape and arrangement, habit, and foliage leaf blade shape, although both have a higher subsidiary bud number than the usual two for most *C. sect. Serpentes* species. However, when the section was first described, *C. pohlii* and *C. virgata* were given uncertain placement, possibly within the section (Clark 1989).

The micromorphological and anatomical features of foliage leaves of *Chusquea* sect. *Serpentes* have not been documented in detail, and were not part of the original description of the section (Clark 1989). However, aspects of the anatomy and micromorphology of *Chusquea* foliage leaves can be useful for distinguishing between species within a given section, as previously demonstrated with members of *C. sect. Longiprophyl-lae* (Clark 1990), *C. subg. Rettbergia* (Mota et al. 2017) and *C. sect. Tenellae* (Leandro et al. 2017). Taxonomically significant features include presence or absence of stomata, macrohairs, and prickles on either or both leaf surfaces, morphology of papillae, texture of epicuticular wax, shape of subsidiary cells, and midrib structure (Clark 1990; Leandro et al. 2017; Mota et al. 2017). Micromorphology of the stomatal apparatus is often especially systematically informative (Leandro et al. 2017). When considered alongside molecular sequence data, geographic range, and morphology, foliage leaf micromorphology and anatomy can provide additional information to support the separation of species, especially when ranges overlap, differences in micromorphology are subtle, or representation of the life cycle is incomplete (Leandro et al. 2016, 2017).

When we reviewed Venezuelan collections of *Chusquea serpens*, it became clear based on ligular and branching morphology that some of these specimens represented an undescribed species. Further examination of Colombian specimens revealed another undescribed species, with broadly open paniculate synflorescences. In this paper we revise *Chusquea* sect. *Serpentes*, describe the Venezuelan and Colombian species, and provide notes on other specimens that likely represent additional undescribed species within the section. We also update existing descriptions of species that we consider to belong to this section, including features such as the morphology of the foliage leaf ligular area that are useful for distinguishing between species of *Chusquea* (Clark and Kaul 2019; Fadrique et al. 2019), but were not included in previous treatments, including Clark (1989). Foliage leaf ligular morphology is particularly important in differentiating *C. recurvata* and *C. acutigluma* from *C. serpens*, which otherwise are morphologically similar. Additionally, we present a dichotomous key to these species based on vegetative characters and distribution maps of known collections. Due to the macromorphological similarity among the two new species presented here and *C. serpens*, we examined the anatomy and

micromorphology of their foliage leaves, which provided additional characters to distinguish among the species.

MATERIALS AND METHODS

Morphological Characters—Voucher specimens from the following herbaria were examined to complete descriptions of species of *Chusquea* sect. *Serpentes*: CAS, CHAPA, COL, CR, CUVC, ECUAMZ, F, HUA, HUQ, IBUG, ISC, JAUM, K, MEDEL, MEXU, MO, NY, QCA, QCNE, SI, TULV, U, US, USJ, USM, VEN, W, and WIS (Thiers 2021). No new specimens were gathered for this study. Accession/collection numbers are provided for voucher specimens representing type material when possible; when available, a barcode number is reported following accession number and identified explicitly as a barcode.

Herbarium specimens were observed with the assistance of a Bausch & Lomb 0.7×–3 × StereoZoom dissecting microscope (Bausch & Lomb, Laval, Quebec, Canada). We followed the morphological definitions and terminology of Fadrique et al. (2019), Clark (1989), and McClure (1973), with references to Judziewicz et al. (1999), to describe the two new species. Descriptions of *C. aspera*, *C. glauca*, *C. latifolia*, and *C. serpens* were based on Clark (1989). The description of *C. pohlii* was based on Clark (1985). The description of *C. virgata* was based on Pohl (1980).

Foliage leaves were excluded from measurement if they appeared to be immature. Leaf sheath summit extensions, when present, were measured from the junction of the leaf sheath and the pseudopetiole to the distal termination of the leaf sheath summit extension where it is visible as a ridge fused to the inner leaf ligule. Synflorescences were measured from the base of the first spikelet-bearing branch or pedicel on the flowering stem to the end of the pedicel of the most distal spikelet. The peduncle was measured between the ultimate leaf node and the first spikelet-bearing branch of pedicel on the flowering stem. Proportional measurements of glumes, lemma, and palea were taken from the base of the spikelet and compared against the full spikelet length, as in Clark (1989). Pohl's solution was used for the dissection of spikelets (Pohl 1965). Means are reported in parentheses following measurement ranges when 10 or more measurements were taken across all available collections for an individual species.

Herbarium sheets were photographed in an MK Digital Direct Photo-eBox Plus using a Canon EOS 5D Mark II camera and viewed with Canon Digital Photo Professional version 4. A Nikon Digital Sight DS-Vi1 camera and Nikon Digital Sight DS-L2 camera control system were used with a Nikon SMZ745T digital stereo microscope to take images of spikelets and ligular regions.

Georeferencing and Mapping—QGIS Desktop 3.8.2 was used to construct all maps using political borders from UNIGIS Geospatial Education Resources (Belgiu 2015) and void-filled digital elevation models from the HydroSHEDS program, authored by the World Wildlife Fund and published by the US Geological Survey (World Wildlife Fund 2006, 2007). Coordinates for specimen collections were either taken from herbarium specimen labels or georeferenced from label data using Google Earth Pro (Google, Inc., Mountain View, California, US). Coordinates are placed in brackets when they were taken directly from herbarium specimen labels and converted to decimal degrees and in brackets with an asterisk when georeferenced from label data. Elevations are similarly placed in brackets with an asterisk when estimated from locality data on specimen labels.

Scanning Electron Microscopy (SEM)—Due to the macromorphological similarity among *C. serpens*, *C. recurvata*, and *C. acutigluma*, foliage leaf micromorphology of these species was comparatively described using scanning electron microscopy (SEM). Dried foliage leaf samples from the vouchers Pohl & Clark 14622 and Clark et al. 283 (*C. serpens*), and Clark et al. 543 (*C. recurvata*) were prepared and imaged following the procedures of Clark (1990); Clark et al. 540 (*C. recurvata*) and Fomnegrá et al. 5899 (*C. acutigluma*) were prepared and imaged primarily following Clark (1990), with the following modifications. To remove epicuticular wax, foliage leaf specimens were submerged in xylene twice for five to seven minutes and agitated three times throughout each treatment. Samples were rinsed with distilled water and allowed to air dry at the end of each xylene treatment. Samples were attached to cylindrical sample holders (pucks) with double-sided carbon tape and coated with a thin layer of platinum using a Cressington 208HR sputter coater. A Hitachi SU4800 FE-SEM field emission scanning electron microscope was used to visualize samples at the Roy J. Carver High Resolution Microscopy Facility at Iowa State University. Descriptions of micromorphological features mainly followed Ellis (1979). Silica bodies that Ellis (1979) considered “dumb-bell shaped” were

classified as “bilobate,” the term used in the International Code for Phyto-lith Nomenclature (ICPT 2019).

Light Microscopy (LM)—The foliar anatomy of the two new species, *C. acutigluma* (Fonnegra et al. 5899) and *C. recurvata* (Clark et al. 540), and the macromorphologically similar *C. serpens* (Clark et al. 231) were comparatively described. For *C. acutigluma* and *C. recurvata*, the middle portion of fully expanded foliage leaves was excised from dried herbarium materials, immersed in polyethylene glycol 1.500 and ethanol (1:1) solution, and embedded in an incubator at 60°C for ten days (adapted from Richter 1985). Foliage pieces were then placed in disposable base molds with embedding rings until the wax became solid. The same sampling method was employed for *C. serpens*, but samples were treated with 30% hydrofluoric acid for 72 hr, dehydrated through a graded n-ethanol series, and embedded in paraffin (Leandro et al. 2018).

Foliage leaf cross-sections were made using a Spencer 820 rotary microtome. Sections of *C. acutigluma* and *C. recurvata* were cleared in 50% sodium hypochlorite, rinsed in distilled water, stained in Epoxy Tissue Stain (Spurlock et al. 1966) or Safranblau solution (0.1% Astra blue and 1% Safranin; Kraus and Arduin 1997), and then mounted on semi-permanent slides in 50% glycerin. Samples of *Chusquea serpens* were rinsed in distilled water, dehydrated through a graded series of ethyl alcohol (25, 50, and 70%), stained with Safranin and Fast Green (Johansen 1940), and then mounted on permanent slides with Permount (Fisher, USA).

Slides were analyzed and photographed with the aid of a Nikon Eclipse 55i microscope coupled with a Nikon DS-Vi1 color camera and a Leica DM4000B microscope using the Leica Application Suite LASV4.0. The analysis and descriptions were performed in the Department of Ecology, Evolution, and Organismal Biology (EEOB) at Iowa State University, USA, and in the Department of Biodiversity at UNESP-Rio Claro, Brazil. Anatomical descriptions and terminology primarily followed Ellis (1976) and Leandro et al. (2020).

RESULTS

Morphological Characters—All species of *Chusquea* sect. *Serpentes*, including the previously described *C. aspera*, *C. glauca*, *C. latifolia*, *C. pohlii*, *C. serpens*, and *C. virgata*, as well as the two species described here, *C. acutigluma* and *C. recurvata*, display narrow culms with a scandent, vining, or scrambling habit, infravaginal branching, and foliage leaves that are at least 0.9 cm wide and with a length to width ratio of 2.5–16.

RHIZOMES AND HABIT—Rhizome morphology is only known for two representatives of this section. Pohl (1980) described *C. virgata* as having pachymorph, short-necked rhizomes, while some segments of *C. latifolia* rhizomes were recorded to be leptomorph, suggesting rhizomes that are leptomorph or amphimorph overall. No information on rhizome morphology is available for *C. acutigluma*, *C. recurvata*, *C. aspera*, *C. pohlii*, or *C. serpens*. Although sometimes erect at the base (as in *C. recurvata*), culms are scandent, climbing, and often trailing.

CULMS—Culm diameter was unavailable for *C. acutigluma* and *C. aspera*, but *C. glauca*, *C. latifolia*, *C. recurvata*, *C. serpens*, and *C. virgata* had relatively small culms with diameter no more than 2 cm, while *C. pohlii* had culms 1.3–3(–5) cm in diameter. Culms are solid and terete to slightly sulcate above the nodes or slightly laterally compressed. Internodes are 9–40 cm long and usually scabrous, sometimes with fine, appressed hairs, but glabrous in *C. virgata* and sometimes glabrous in *C. latifolia*. Pubescence may be present beneath the node. Color of internodes is usually green to green mottled with purple.

CULM LEAVES—Culm leaves are apparently persistent in all species except *C. serpens*. The sheath is fused at the base in *C. latifolia*, *C. pohlii*, and *C. virgata* (although only to 2–3 mm in *C. virgata*) but unfused at the base in all other observed species, with the base of culm leaf sheaths of *C. aspera* not seen. An outer ligule is usually absent, although occasionally a minute outer ligule is present in *C. recurvata*. The blade is

typically deciduous, triangular, and erect, without a leaf sheath summit extension, although culm leaf blades were not available for *C. aspera* and *C. acutigluma*. Culm leaf blades are moderately to distinctly cordate but narrow at the base in *C. serpens*. The girdle is usually prominent and 0.3–5.0 mm wide, but may be asymmetrically developed, as in *C. pohlii*.

BUDS AND BRANCHING—The shape of the central bud is circular in *C. recurvata*, *C. glauca*, and *C. pohlii*, but triangular in *C. acutigluma*, *C. serpens*, *C. latifolia*, and *C. virgata*. Central bud shape is unknown in *C. aspera*. In all species except *C. pohlii* and *C. virgata*, the bud complement consists of a central bud and two smaller, subequal subsidiary buds below it. The subsidiary buds of *C. pohlii* and *C. virgata* vary in number from two to nine in *C. virgata* and two to 12 in *C. pohlii*, with the subequal buds arranged in a single constellate row. Subsidiary branches are subequal to each other (in one size group). Branching is infravaginal in all species of the section, with the branches of *C. latifolia* and *C. serpens* sometimes arising from a promontory. Rebranching is common in *C. acutigluma*, *C. latifolia*, and *C. recurvata*, with *C. recurvata* exhibiting strongly recurved secondary subsidiary branches, these sometimes rebranching. Rebranching is rare in *C. serpens* and *C. glauca* and apparently absent in *C. aspera*, *C. pohlii*, and *C. virgata*. The sheath scar dips slightly below the bud complement in all species in the section, although the dip may be very slight.

FOLIAGE LEAVES—Foliage leaf sheaths are carinate and green to green mottled with purple, with the overlapping margin typically ciliate but sometimes glabrous, especially on older leaves. Leaf sheath summit extensions are present on both the underlapping and overlapping sides of the leaf sheath in all species except *C. serpens*, *C. glauca*, and *C. virgata*, in which the leaf sheath summit extension is absent from both sides of the sheath. Leaf sheath summit extensions are at least slightly longer on the underlapping compared to the overlapping sides of the leaf sheath, with the difference in size variable. Difference in size between underlapping and overlapping leaf sheath summit extensions is most pronounced in *C. pohlii*, where the underlapping leaf sheath summit extension averages about three times as long as that of the overlapping side. When asymmetrical summit extensions are present, the inner ligule is typically asymmetrical and acute to rounded in shape, although the inner ligule is occasionally truncate in *C. latifolia*. An outer ligule is always present as a short rim that may be glabrous to ciliate. Foliage leaves have a well-defined pseudopetiole that is adaxially and abaxially glabrous or sometimes scabrous, occasionally with a few scattered hairs, although *C. virgata* has stiff tan hairs around the abaxial midrib of the pseudopetiole. Foliage leaves tend to be broad, ranging between 0.9 and 8.5 cm wide. The narrowest leaves are found in *C. pohlii* and the broadest in *C. latifolia*, although there is overlap between intermediate widths of foliage leaves in these and other species of the section. The foliage leaf blade length to width ratio ranges from 2.5–10 for all species excluding *C. pohlii*, for which foliage leaf blade length to width ratios of 9–16 are typical.

SYNFLORESCENCES, SPIKELETS, AND FRUITS—Synflorescences were observed for all species in *Chusquea* sect. *Serpentes* except *C. recurvata*. In all observed species, synflorescences are borne on leafy subsidiary branches. Synflorescences are paniculate and narrow in all species except *C. glauca*, which has a more or less open synflorescence, and *C. acutigluma*, which has a broadly open synflorescence. Spikelets are typically terete or

slightly laterally compressed and straight, but are slightly falcate in *C. glauca*, *C. latifolia*, and *C. pohlii*, and falcate in *C. virgata*. Glume I is variable in shape but typically unawned and lacking a mucro, except in *C. acutigluma*. Glume II is usually rounded to mucronate or sometimes short-awned (in *C. acutigluma*), but long-awned in *C. serpens*. Glumes III and IV and lemmas are mucronate to awned in all species, except in *C. virgata*, in which glumes III and IV and the lemma are acute. Fruits were observed only in *C. acutigluma* and *C. virgata*, and appear as basic caryopses that are brown in color.

Foliage Leaf Micromorphology—Among the three species for which foliage leaf epidermal micromorphology was observed, all three (*C. serpens*, *C. acutigluma*, and *C. recurvata*) have elongated, tabular long cells with undulating anticlinal walls on both the adaxial and abaxial surfaces (Fig. 1A–F). Bulliform cells (adaxial surface) are wider than typical long cells (Fig. 1A, C, E). Trichomes in the form of bicellular microhairs are seen on the abaxial surface of *C. acutigluma* (Fig. 1B), *C. recurvata* (Fig. 1D), and *C. serpens* (not shown). Bicellular microhairs are also found on the adaxial surface of *C. acutigluma* (a single trichome in Fig. 1A) and on one specimen of *C. serpens* (Clark *et al.* 283, not shown). Prickles are seen on the abaxial surface of *C. acutigluma* (Fig. 1B), one specimen of *C. recurvata* (Clark *et al.* 540, not shown), and both specimens of *C. serpens* (not shown) as well as the adaxial surface of *C. serpens* (Fig. 1E). Macrohairs are seen only on the abaxial surface of one specimen of *C. serpens* (Fig. 1F). Silica bodies are consistently vertically elongated in both the costal and intercostal zones and are bilobate or saddle-shaped (Fig. 1A–F); ridged saddle-shaped silica bodies are seen in the costal zones of all species on the abaxial surface (Fig. 1B, D, F) and additionally on the adaxial surface of *C. serpens* (Fig. 1E). Papillae are present on the abaxial surface in all three species (Fig. 1B, D, F), although a few simple, round papillae are present on the bulliform cells of *C. serpens* (Fig. 1E). While the abaxial papillae of *C. recurvata* are typically simple and round, with only a few branching (Fig. 1D), most papillae of *C. acutigluma* (Fig. 1B) and *C. serpens* (Fig. 1F) have extensive branching from an irregularly globose, enlarged distal end. Branching papillae of *C. acutigluma* and *C. serpens* are highly crowded around the stomatal apparatuses, overarching and obscuring the stoma (Fig. 1B, F insets), while the mainly simple papillae of *C. recurvata* do not crowd around or overarch the stoma (Fig. 1D inset). Stomata are present only on the abaxial surface for *C. serpens* (Fig. 1F) and *C. acutigluma* (Fig. 1B), with a single stomatal apparatus seen on the adaxial surface of the *C. recurvata* specimen Clark *et al.* 540 (not shown) in addition to many abaxial stomatal apparatuses (Fig. 1D). Stomata on the abaxial surface are present in two to four rows in *C. serpens*, three to four rows in *C. acutigluma*, and two to three rows in *C. recurvata*.

CHUSQUEA ACUTIGLUMA ADAXIAL SURFACE—**Long cells** sometimes shorter in costal than intercostal zone. **Bulliform cells** typically at least three times as long as wide. **Silica cells** alternating with long cells, more frequent in the costal than the intercostal zone; rarely present as basal cells of bicellular microhairs. **Silica bodies** vertically elongated in both zones; saddle-shaped to bilobate with a wide central portion in costal zones, typically single but occasionally paired; bilobate with a wide central portion or saddle-shaped in intercostal zones. **Papillae** absent. **Prickles** absent. **Microhairs** rare in the intercostal zone; basal cell much longer than the distal cell; basal cell much longer than wide, parallel sided; distal

cell with length equal to width, broadly rounded at the apex. **Macrohairs** absent. **Stomatal apparatuses** absent.

CHUSQUEA ACUTIGLUMA ABAXIAL SURFACE—**Long cells** elongated in the intercostal zone, typically shorter in the costal zone and often equidimensional or elongated vertically. **Silica cells** alternating with long cells in the costal zone, infrequent and scattered in the intercostal zone between long cells; occasionally present as basal cells of bicellular microhairs in costal and edges of intercostal zones. **Silica bodies** vertically elongated in both zones; ridged saddle to occasionally saddle-shaped in costal zone; in one to rarely two rows in costal zones, often tightly spaced; saddle-shaped to bilobate in intercostal zones. **Papillae** usually distally enlarged, with 2–10 short branches arising from an irregularly globose distal end, often branching again, sometimes simple and rounded, especially on long cells of the intercostal zone; in one to two horizontal rows on long cells in the costal zone and interstomatal band of intercostal zone; common and crowded in stomatal bands of intercostal zone, overarching and obscuring the stoma. **Prickles** rare in intercostal zones; barbs long, pointing both directions. **Microhairs** frequent, located in intercostal zones; basal and distal cells approximately the same length; basal cell much longer than wide, parallel sided and tapering to a constricted base; distal cell slightly longer than wide, broadly rounded at apex to very slightly tapered. **Macrohairs** absent. **Stomatal apparatuses** in three to four rows on both sides of a costal zone; shape of the subsidiary cells obscured by abundant papillae.

CHUSQUEA RECURVATA ADAXIAL SURFACE—**Long cells** typically elongated in costal and intercostal zones but shorter between silica cells in costal zones. **Bulliform cells** usually at least five times as long as wide. **Silica cells** alternating with long cells in costal and intercostal zones. **Silica bodies** vertically elongated in both zones; bilobate to saddle-shaped in costal and intercostal zones, between most long cells in costal zones and frequent but scattered in intercostal zones. **Papillae** absent. **Prickles** absent. **Microhairs** absent. **Macrohairs** absent. **Stomatal apparatuses** rare; subsidiary cells low triangular, lacking papillae.

CHUSQUEA RECURVATA ABAXIAL SURFACE—**Long cells** typically elongated in costal and intercostal zones but shorter between silica cells in the costal zone. **Silica cells** alternating with long cells in the costal zone, infrequent in the intercostal zone; occasionally present as basal cells of bicellular microhairs in costal and edges of intercostal zones. **Silica bodies** vertically elongated in both zones; ridged saddle to saddle-shaped in the costal zone; in one to rarely two rows in costal zones, often tightly spaced; bilobate in intercostal zones, scattered. **Papillae** simple and rounded, rarely branched; in one to occasionally two horizontal rows on long cells in the costal zone; in one to two horizontal rows on long cells in the intercostal zone. **Prickles** absent to frequent in costal and intercostal zones; barbs long, pointing both directions. **Microhairs** rare in costal and intercostal zones; basal cell slightly shorter than distal cell; basal and distal cells much longer than they are wide; basal cell inverted cone-shaped; distal cell slightly tapering to a rounded apex. **Macrohairs** absent. **Stomatal apparatuses** in two to three rows, subsidiary cells low domed, two papillae per subsidiary cell.

CHUSQUEA SERPENS ADAXIAL SURFACE—**Long cells** elongated in the intercostal zone, shorter to nearly equidimensional between silica cells in the costal zone. **Bulliform cells** at least twice as long as wide. **Silica cells** more frequent in costal

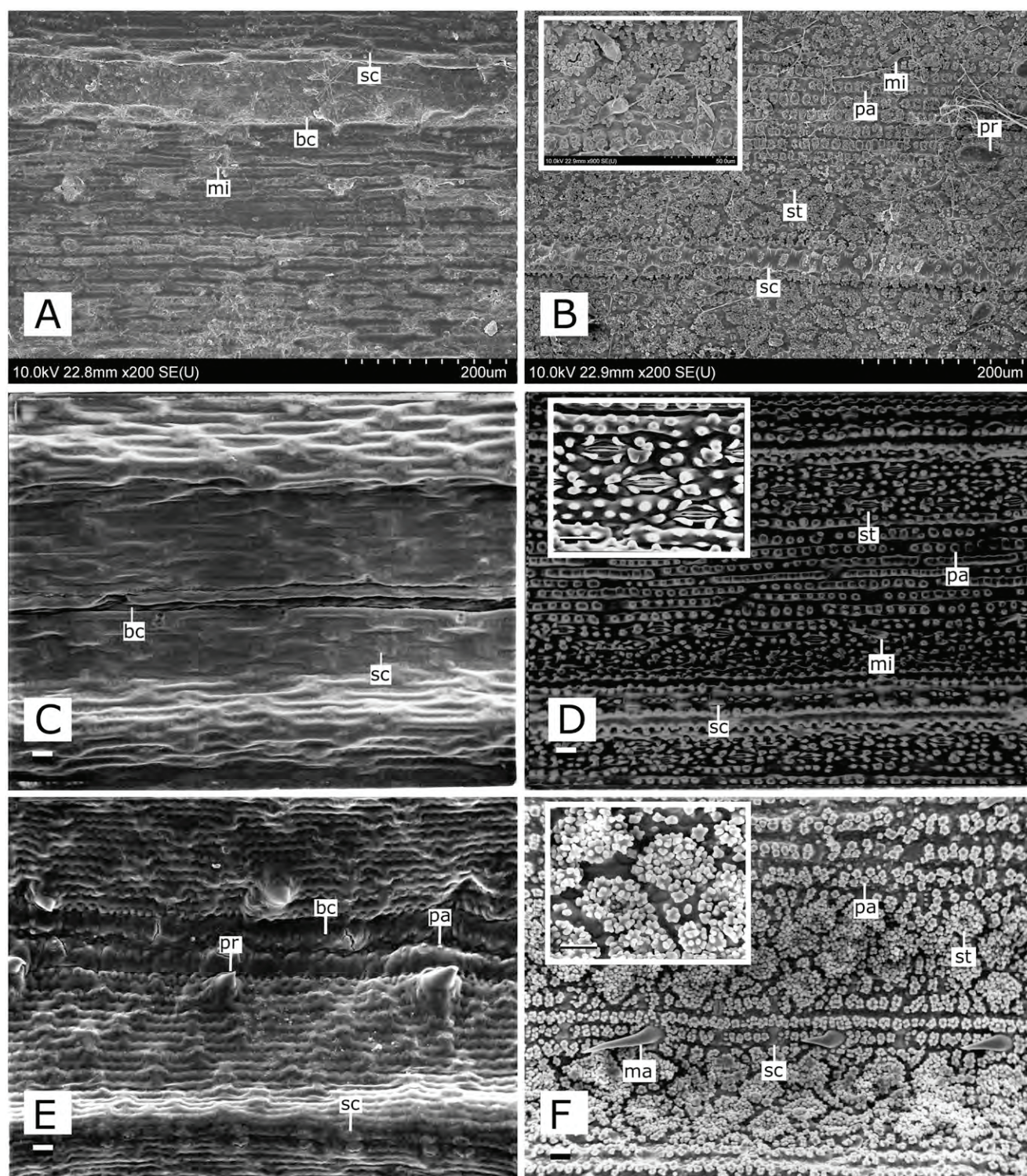


FIG. 1. Micromorphology of foliage leaves from SEM of *Chusquea* sect. *Serpentes*. Adaxial surface (A, C, E), abaxial surface (B, D, F). A–B. *C. acutigluma* (Fomnegera et al. 5899). C–D. *C. recurvata* (Clark et al. 543). E–F. *C. serpens* (Pohl & Clark 14622). Abbreviations: bc = bulliform cell; ma = macrohair; mi = bicellular microhair; pa = papilla; pr = prickle; sc = silica cell; st = stomatal apparatus. Scale bars: 25 μ m (A, B, C, D); 200 μ m (E, F); 25 μ m (B inset, D inset); 50 μ m (F inset).

than intercostal zones; occasionally present as basal cells of bicellular microhairs. **Silica bodies** vertically elongated in both zones; bilobate with wide central portion or saddle-shaped in costal zones, sometimes ridged; when ridged, often in regularly spaced rows; bilobate in intercostal zones, scattered. **Papillae** mostly absent; a few simple, circular papillae

present on < 50% of bulliform cells, irregularly arranged. **Prickles** infrequent to frequent in one to three rows in costal zones, a few present in intercostal zones; barbs long, all pointing the same direction. **Microhairs** occasional at edges of intercostal zones; basal cells slightly shorter than distal cells; basal and distal cells much longer than they are wide; basal

cell parallel sided with the point of attachment constricted; distal cell slightly tapering to a rounded apex. **Macrohairs** absent. **Stomatal apparatuses** absent.

CHUSQUEA SERPENS ABAXIAL SURFACE—**Long cells** typically shorter in costal than intercostal zones. **Silica cells** alternating with long cells in costal zones, infrequent in intercostal zones between long cells; occasionally present as basal cells of bicellular microhairs in costal zones. **Silica bodies** vertically elongated in both zones; ridged saddle to saddle-shaped in costal zones; in one row in costal zone; saddle-shaped in intercostal zones, occasionally bilobate. **Papillae** usually distally enlarged, with 2–18 short branches arising from an irregularly globose distal end, sometimes branching again, occasionally simple and rounded; in one or two horizontal rows or occasionally absent on long cells in costal zones and interstomatal band in intercostal zones; common and crowded in stomatal band of intercostal zones, especially around stomatal apparatuses, overarched and obscuring the stomata. **Prickles** rare to frequent; in one to three rows in costal zones, absent to frequent in intercostal zones; barbs long, pointing the same direction or both directions. **Microhairs** rare to frequent in costal zones, absent to frequent in intercostal zones; basal cells approximately equal in length to slightly longer than distal cells; basal and distal cells much longer than they are wide; basal cell parallel sided with the point of attachment slightly constricted; distal cell slightly tapering to a rounded apex or broadly rounded. **Macrohairs** absent to rare in costal zones, absent from intercostal zones; unicellular, similar to prickles but elongated up to three times the size of the hair base, accompanied by many small cells at base of hair. **Stomatal apparatuses** in two to four rows between costal zones; shape of the subsidiary cells obscured by abundant papillae.

Foliage Leaf Anatomy—The general foliage leaf anatomy of *C. acutigluma*, *C. recurvata*, and *C. serpens* is described and illustrated (Fig. 1A–M), highlighting relevant differences. The outline of the foliage leaf blades in cross-section is gently undulated in *C. acutigluma* (Fig. 2A, C) and *C. recurvata* (Fig. 2B, D), whereas *C. serpens* (Fig. 2H, I) displays corrugated foliage blades (i.e. waves rounded). The epidermis exhibits one layer of cells with thickened periclinal cell walls (Fig. 2A–M). Cells comprising the epidermis are about the same size on both surfaces, except for the fan-shaped arrays of three to six adaxial bulliform cells (Fig. 2A–D, H, I). Papillae are readily distinguishable on the abaxial surface of all species examined (Fig. 2A–E, G, I). As seen using SEM, while *C. acutigluma* (Fig. 1A, C) and *C. serpens* display branched papillae (Fig. 1I), *C. recurvata* (Fig. 1B, D) has simple papillae. Stomatal apparatuses with a large substomatal chamber occur in *C. acutigluma* (Fig. 2A, C, E—black circle) and *C. recurvata* (Fig. 2G—black circle). In contrast, the stomatal apparatus of *C. serpens* has a smaller substomatal chamber (Fig. 2I—black circle).

The non-radiate mesophyll consists of strongly invaginated arm cells, cavities, and rosette cells (Fig. 2A–I). Three layers of adaxial arm cells occur in *C. acutigluma* (Fig. 2A, C, E) and *C. recurvata* (Fig. 2B, D, F, G), whereas *C. serpens* exhibits two layers (Fig. 2H inset, I). Adaxial arm cells display deep invaginations (i.e. lobes) from the adaxial and abaxial surfaces (Fig. 2F, H inset). While the first layer of adaxial arm cells (i.e. adjacent to the adaxial epidermis) is vertically elongated, the remaining layers are mostly horizontally elongated (Fig. 2A–G, H inset). Similarly, abaxial arm cells are horizontally elongated, comprising two layers in *C. acutigluma* (Fig. 2A, C, E) and

C. recurvata (Fig. 2B, D, G), and only one layer in *C. serpens* (Fig. 2H, I). Cavities occur in the middle portion of the mesophyll, adjacent to the vascular bundles and surrounded by arm cells, exhibiting different shapes and sizes throughout the mesophyll (Fig. 2A–E, G–I). Remains of cell walls of collapsed fusoid cells are visible in many cavities (Fig. 2A–D, G, H). Horizontally elongated rosette cells occur between cavities and usually comprise a set of two cells in *C. serpens* (Fig. 2H), two to three cells in *C. recurvata* (Fig. 2B, D), and three to four cells in *C. acutigluma* (Fig. 2A, C). While rosette cells are weakly lobed in *C. serpens* (Fig. 2H), moderate lobes occur in *C. acutigluma* (Fig. 2A, C) and *C. recurvata* (Fig. 2B, D).

The vascular system is composed of first- and second-order collateral vascular bundles each surrounded by a double sheath consisting of an outer parenchyma sheath and inner mestome sheath (Fig. 2A–E, G–M). First-order vascular bundles display distinguishable metaxylem and phloem (Fig. 2B–D, H). In contrast, the second-order vascular bundles exhibit small metaxylem vessels and a relatively small patch of phloem (Fig. 2B, E, G, H, I). Girders occur in both types of vascular bundles (Fig. 2A–E, G–I). However, the second-order vascular bundles of *C. acutigluma* often exhibit girders composed of one file of sclerenchyma cells (Fig. 2E), whereas two to four files occur in *C. recurvata* (Fig. 2B, G). The arrangement of these sclerenchyma files is nearly equidimensional in both species (Fig. 2A–E, G). Conversely, *C. serpens* displays second-order vascular bundles with V-shaped girders (i.e. narrowing towards the vascular bundle), composed of several sclerenchyma files (Fig. 2I). A patch of sclerenchyma cells occurs below the first-order vascular bundles, interrupting their parenchyma sheath (Fig. 2B–D, H). These cells also interrupt the parenchyma sheath of second-order vascular bundles in *C. serpens* (Fig. 2I), whereas *C. acutigluma* (Fig. 2E) and *C. recurvata* (Fig. 2G) display intact parenchyma sheaths. The abaxially projecting midrib is complex, and one large abaxial vascular bundle occurs in all three species examined (Fig. 2J–L). Adaxially, *C. acutigluma* (Fig. 2J) and *C. recurvata* (Fig. 2K) have two vascular bundles, whereas three adaxial vascular bundles occur in *C. serpens* (Fig. 2L). While all vascular bundles (i.e. the two adaxial and the sole abaxial) share the same bundle sheath in the midrib of *C. acutigluma* (Fig. 2J) and *C. recurvata* (Fig. 2K), only the three adaxial ones share the same bundle sheath in *C. serpens* (Fig. 2L).

The foliar margins are acute in all studied species, and internally composed of sclerenchyma cells (e.g. Fig. 2M).

Notes on Foliage Leaf Anatomy and Micromorphology—*Chusquea acutigluma* can be distinguished from *C. recurvata* by the presence of branched papillae that crowd around and overarch the stoma and an often single file of sclerenchyma cells comprising the girders associated with second-order vascular bundles (Table 1). Conversely, *C. recurvata* can be distinguished from *C. acutigluma* by its simple papillae that do not crowd around or overarch the stomata and several sclerenchyma files comprising equidimensional girders associated with second-order vascular bundles (Table 1). The equidimensional girders associated with second-order vascular bundles, three layers of adaxial arm cells, and complex midrib composed of two adaxial vascular bundles in *C. acutigluma* and *C. recurvata* distinguish these new species from *C. serpens*, which in turn displays V-shaped girders associated with second-order vascular bundles, two layers of adaxial arm cells, and a complex midrib with three adaxial vascular bundles (Table 1). Additionally, the two new species differ

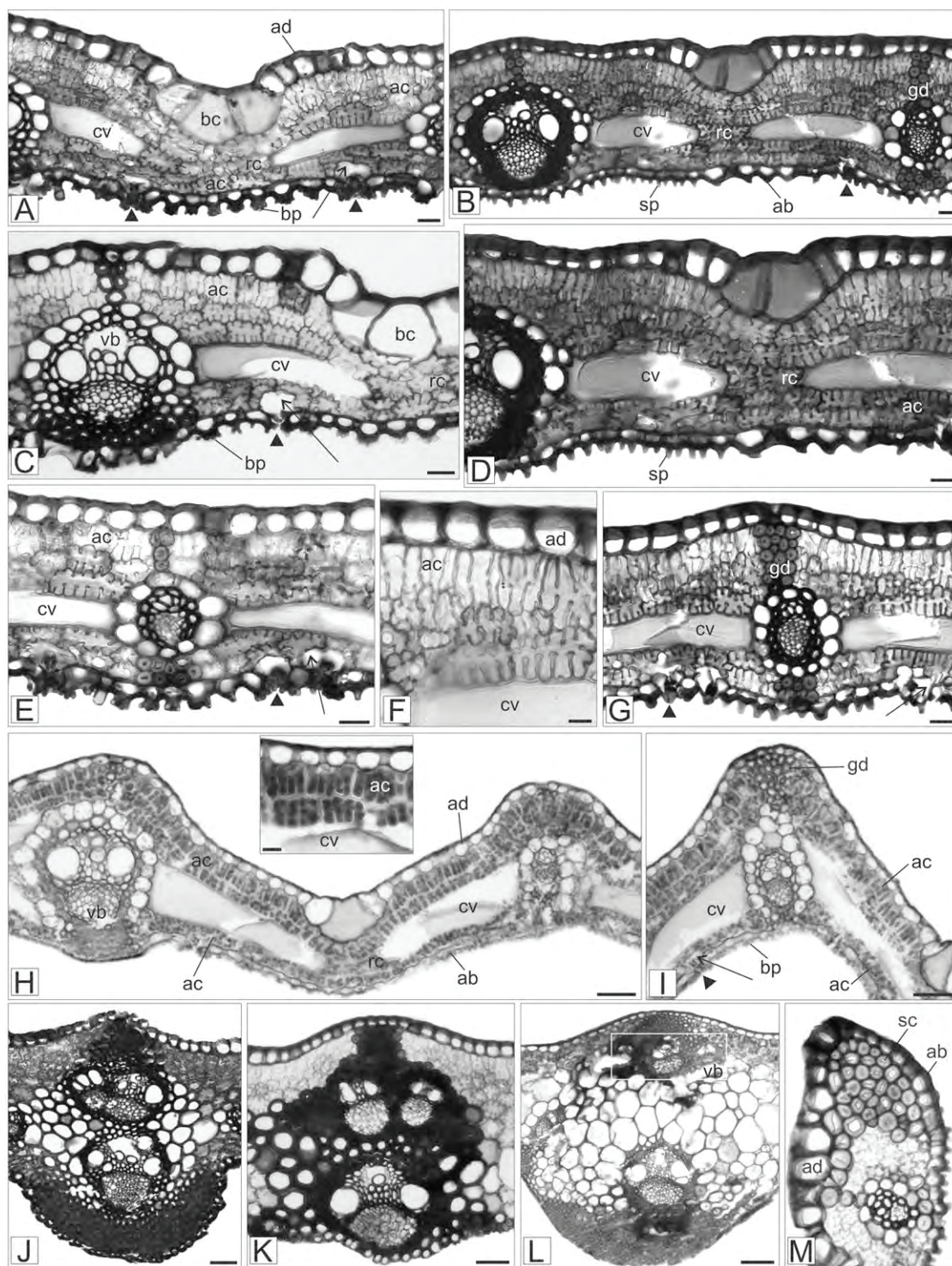


FIG. 2. Cross-sections of foliage leaf blades. *Chusquea acutigluma* (Fonnegra et al. 5899) (A, C, E, J), *C. recurvata* (Clark et al. 540) (B, D, F, G, K, M), and *C. serpents* (Clark et al. 231) (H, I, L). A–B. General view of the mesophyll showing anatomical features commonly found in Bambusoideae, such as arm cells, cavities with remains of cell walls of fusoid cells, rosette cells, and first- and second-order vascular bundles. C–D. Mesophyll comprising three layers of adaxial arm cells and two layers of abaxial arm cells, cavities, and rosette cells. E. Detail of a second-order vascular bundle showing nearly equidimensional girders. F. Detail of arm cells showing deep lobes from the adaxial and abaxial surfaces. G. Detail of a second-order vascular bundle showing nearly equidimensional girders. H. General view of the mesophyll showing arm cells (inset: two layers of adaxial arm cells), cavities, rosette cells, and first- and second-order vascular bundles. I. Detail of a second-order vascular bundle showing V-shaped girders. J–K. Complex midrib comprising one major abaxial vascular bundle and two adaxial vascular bundles, all sharing the same bundle sheath. L. Complex midrib comprising one major abaxial vascular bundle. Three adaxial vascular bundles share the same bundle sheath. M. Acute foliage leaf margin internally composed of sclerenchyma cells. ab = abaxial epidermis; ac = arm cells; ad = adaxial epidermis; bc = bulliform cell; bp = branched papilla; cv = cavity; gd = girder; rc = rosette cell; sc = sclerenchyma; sp = simple papilla; vb = vascular bundle. Long black arrow = substomatal chamber; Arrowhead = stomatal apparatus. Scale bars: 10 μ m (C, F, H, I, K, L, M); 20 μ m (A, B, D, E, G); 40 μ m (J).

from *C. serpens* by having two layers of abaxial arm cells in the mesophyll and having all vascular bundles sharing the same bundle sheath in the midrib, as well as lacking adaxial prickles and ridged saddle-shaped silica bodies (Table 1).

TAXONOMIC TREATMENT

CHUSQUEA SECT. SERPENTES L.G.Clark, Syst. Bot. Monogr. 27: 91. 1989. TYPE: *Chusquea serpens* L.G.Clark.

Culms vining, trailing, or clambering and hanging, up to 40 m long in *C. latifolia*. **Internodes** 9–40 cm long, solid, mostly terete, usually scabrid to scabrous, sometimes glabrous, not waxy. **Culm leaves** usually persistent, often abaxially scabrous or asperous; sheaths more or less rectangular to triangular; outer ligule typically absent; blades erect, usually deciduous, variable in size relative to sheaths, non-pseudopetiolate and more or less similar to the sheath in color; girdle 0.3–5 cm wide, usually well developed. **Nodes** at mid-culm with one circular or triangular central bud subtended by 2(–12) smaller, subequal subsidiary buds; sheath scar dipping slightly below bud complement; root thorns absent; supranodal ridge evident, usually not prominent. **Branching** infravaginal, with or without a promontory at the base; central bud developing or not; subsidiary branches 0.9–5.7 mm in diameter. **Foliage leaf** blades 7.5–36 cm long, 0.9–8.5 cm wide, L: W = 2.5–16, abaxially tessellate or not, lacking an abaxial basal tuft of hairs, green, flat in cross section. **Synflorescences** 4.7–60 cm long, narrowly or sometimes openly paniculate. **Spikelets** 6.8–15.7 mm long, terete or slightly laterally compressed; glumes variable, often at least 1/10 the spikelet length, although smaller in *C. glauca*, *C. pohlii*, and *C. virgata*; glume II often 1/4(–1/2) the spikelet length, but much smaller in *C. glauca*, *C. pohlii*, and *C. virgata*; glumes III and IV unequal, mucronate to awned except acute in *C. virgata*; glume III 1/2(–2/3) the spikelet length (1/3–2/5 in *C. virgata*); glume IV at least 5/8 the spikelet length (ca. 2/5 in *C. virgata*).

Chusquea acutigluma L.G.Clark & McMurchie, sp. nov. TYPE: COLOMBIA. Antioquia: Mpio. de San Luís, rivera de la quebrada la Risaralda, [6.02°, –75.00°]*, 1300–1500 m, 12 November 1995 (fl), R.Fonnegra y curso tax. plant. vas. sem 2/95 5899 (holotype, HUA; isotypes, ISC!, MO! [04848468, barcode MO-1308970]).

Chusquea acutigluma differs from all other known species of *Chusquea* sect. *Serpentes* by the following combination of characters: Foliage leaf inner ligule 1.9–6.7 ($\bar{x}$ = 3.6) mm long, glabrous, asymmetrical, longer side often tapering to an acute tip, often splitting with age; synflorescence broadly open, paniculate, primary branches diverging 45–120° from the rachis; spikelets 8.3–10.0 ($\bar{x}$ = 9.0) mm long; glume I 2.5–4.3 ($\bar{x}$ = 3.1) mm long, 1/4–2/5 the length of the spikelet, apically acute, mucronate to short-awned, 3-nerved; glume II apically acute, mucronate to rarely short-awned; and lemma 7.5–8.8(–9.3) ($\bar{x}$ = 8.3) mm long.

Rhizomes unknown. **Culms** scandent. **Internodes** 10–15.5 cm long on flowering culms, terete to slightly sulcate, solid, irregularly scabrous to having fine appressed, scattered hairs, green to greenish-tan. **Culm leaves** observed from partial sheaths, the sheaths abaxially scabrous to pubescent with fine hairs, adaxially glabrous, the margins not fused, ciliate; blades not seen; girdle 2.3 mm wide in the single partial example observed, sparsely pubescent, brown. **Nodes** slightly swollen with triangular central bud subtended by two subsidiary buds, adventitious roots often present; supranodal ridge conspicuous. **Branching** with central bud developing tardily; subsidiary buds initially two per node, rebranching almost immediately when rebranching; branches (6.5–)20.5–62.7 ($\bar{x}$ = 39.5) cm when flowering, including synflorescence, 1.1–3.4 mm diam. **Foliage leaves** 3–4 per complement on flowering branches, excluding flag leaves; foliage leaf sheaths green to greenish-tan mottled with brown, carinate, glabrous to scabrous or with fine appressed pubescence near the summit and along the keel, the overlapping margin ciliate, becoming glabrous with age; sheath summit extension 0.4–2.6 ($\bar{x}$ = 1.3) mm on the overlapping side, 2.6–5.3 ($\bar{x}$ = 3.5) mm long on the underlapping side, glabrous, margins glabrous to ciliate, fused to inner ligule; outer ligule 0.3–0.9 ($\bar{x}$ = 0.5) mm long, glabrous, truncate; inner ligule 1.9–6.7 ($\bar{x}$ = 3.6) mm long, glabrous, asymmetrical, longer side often tapering to an acute tip, often splitting with age; pseudopetiole (2.5–)4.0–6.4 ($\bar{x}$ = 4.7) mm long, distinct, adaxially scabrous to glabrous, abaxially glabrous; blades (8.9–)12.0–17.5 ($\bar{x}$ = 14.3) cm long, 1.7–3.0 ($\bar{x}$ = 2.2) cm wide, L: W = 4.8–7.0 ($\bar{x}$ = 5.8), linear-lanceolate to lanceolate, not tessellate, adaxially glabrous to slightly scabrous, abaxially nearly glabrous to scabrous, to pilose, the base rounded, occasionally somewhat tapering, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex tapering to a short bristle-like tip. **Synflorescences** (4.7–)10.0–32.6 ($\bar{x}$ = 19.5) cm

TABLE 1. Micromorphological and anatomical comparison of *Chusquea acutigluma*, *C. recurvata*, and *C. serpens* foliage leaves.

Character	<i>C. acutigluma</i>	<i>C. recurvata</i>	<i>C. serpens</i>
Adaxial costal zone ridged saddle-shaped silica bodies	Absent	Absent	Present
Abaxial papillae typical shape	Branching	Simple	Branching
Papillar distribution in stomatal band	Crowded, overarching stoma	In 1–2 rows, not overarching stoma	Crowded, overarching stoma
Stomatal rows adjacent to costae	3–4	2–3	2–4
Layers of adaxial arm cells in mesophyll	3	3	2
Layers of abaxial arm cells in mesophyll	2	2	1
Girders associated with second-order vascular bundles	Equidimensional; often only one file of sclerenchyma cells	Equidimensional; several files of sclerenchyma cells	V-shaped; several files of sclerenchyma cells
Structure of the complex midrib	3 vascular bundles, 1 major abaxial and 2 opposing adaxially; all sharing a bundle sheath	3 vascular bundles, 1 major abaxial and 2 opposing adaxially; all sharing a bundle sheath	4 vascular bundles, 1 major abaxial and 3 opposing adaxially; only the 3 adaxial sharing a bundle sheath

long, 4–10.5 ($\bar{x}$ = 6.9) cm wide, broadly open, paniculate, peduncle exerted or not, when exerted, up to 14.1 cm visible beyond subtending sheath; peduncle (1.1–)5–20.5 ($\bar{x}$ = 11.1) cm long, adaxially grooved, abaxially grooved to nearly flat, glabrous, sometimes becoming lightly pubescent toward the rachis; rachis usually grooved on both sides, occasionally nearly flat on one side, pubescent with short, straight hairs; primary branches more or less quadrangular in cross section, grooved on sides facing towards and away from rachis, diverging at an angle of 45–120° from the rachis, (0.6–)1.5–6.5 ($\bar{x}$ = 3.7) cm long near the base, becoming shorter towards the apex of rachis until reduced to pedicels; pulvinus present at the bases of branches and pedicels, glabrous; secondary branches often present, short, to about 1 cm, diverging at an angle of more or less 90° from the primary branches; pedicels 0.7–2.1 ($\bar{x}$ = 1.3) mm near the base of branches and 3.0–4.7(–6.8) ($\bar{x}$ = 4.3) mm at the tips of branches, quadrangular, grooved, pubescent, diverging at an angle of 90° or slightly greater from the branches or rachis. **Spikelets** 8.3–10.0 ($\bar{x}$ = 9.0) mm long, 2.0–2.6 ($\bar{x}$ = 2.3) mm wide, slightly laterally compressed, straight, glabrous, shiny; glumes I and II carinate, glabrous, apex acute; glume I 2.5–4.3 ($\bar{x}$ = 3.1) mm long, 1/4–2/5 the spikelet length, mucronate to short-awned, mucro or awn (0.1–)0.4–0.8 mm, 3-nerved; glume II 3.0–5.0 ($\bar{x}$ = 4.0) mm long, 2/5–1/2 the spikelet length, mucronate to rarely short-awned, mucro or awn 0.3–1.0 mm, 5- or 7-nerved; glumes III and IV keeled near the apex, glabrous with apically ciliate margins, apex acute to obtuse; glume III 3.8–5.6 ($\bar{x}$ = 4.4) mm long, 1/2–2/3 the spikelet length, mucronate, mucro 0.2–0.4 mm long, (5-) 7- or 9-nerved; glume IV (5.4–)6.0–7.6 ($\bar{x}$ = 6.8) mm long, (2/3–)3/4(–4/5) the spikelet length, mucronate, mucro 0.1–0.4 mm long, 7- or 9-nerved, ciliate to nearly glabrous at the apex; lemma 7.5–8.8(–9.3) ($\bar{x}$ = 8.3) mm long, keeled near the apex, apex mucronate, mostly glabrous, shiny, with margins slightly ciliate towards the apex, 7-, 9-, or 11-nerved; palea 7.0–8.6(–9.2) ($\bar{x}$ = 7.8) mm long, weakly 2-keeled and sulcate near the apex, apex biapiculate, 4-nerved, ciliate to nearly glabrous at the apex. **Lodicules** 3, lanceolate, apex acute, ciliate, anterior pair 2.4–3.0 mm long, the posterior one 2.5–2.9 mm long. **Anthems** 4.5–5.0 mm long, yellow-greenish. **Caryopsis** 5.4–6.2 mm long, brown to reddish brown, embryo ca. 0.8 mm long, hilum linear, style bases persistent. Figures 3, 4.

Distribution and Habitat—San Luís Municipality, Antioquia, Colombia; Risaralda gorge and Ecoparque el Castellón, a forested natural reserve through which runs much of the Risaralda gorge; 1300–1500 m.

Phenology—Three flowering collections from two collecting expeditions in San Luís in November of 1995 indicate a probable gregarious blooming event that year.

Etymology—This species is named for the unusually acute lower glumes (glumes I and II) of the spikelets in comparison to the lower glumes of other species of *Chusquea* sect. *Serpentes*.

Informal Conservation Assessment—*Chusquea acutigluma* has only been collected within the San Luís Municipality in Antioquia, Colombia. Collections were made in the Risaralda gorge and at an unspecified location in the Ecoparque el Castellón reserve. As much of the Risaralda gorge is contained within Ecoparque el Castellón, it is likely that these collections were made in close geographic proximity to each other; for the purposes of determining threat category, collections were considered to be made at a single protected location. Although there are too few collections to estimate extent of occurrence (EOO), area of occupancy (AOO) is estimated

to be 4–8 km². Abundance of this species in these locations is unknown, but a gregarious bloom in 1995 is likely, possibly resulting in the death of most plants in the stand, with recovery in this location potentially dependent on success of seeds. According to the results of the AOO analysis and suspected extreme fluctuation in number of mature individuals associated with likely gregarious monocarpy, we hypothesize that if a formal conservation assessment were performed, this species would be considered Critically Endangered (CR) under criteria B2ac(iv) (IUCN 2019).

Due to the great similarity between vegetative specimens of *C. acutigluma* and *C. serpents*, which is also found in montane habitats in Colombia, it is possible that there are additional specimens of *C. acutigluma* in herbaria that have yet to be correctly identified.

Notes—*Chusquea acutigluma* is readily distinguished from all other known South American species in *Chusquea* sect. *Serpentes* when fertile by having broadly open paniculate synflorescences. Glumes I and II are markedly different in *C. acutigluma* than *C. serpents*, with glume I of *C. acutigluma* 3-nerved and averaging about twice as large in as those of *C. serpents*, and glume II in *C. acutigluma* lacking a long awn (Table 2). Glumes I and II of *C. acutigluma* are also more narrowly acute than those of *C. serpents*. Vegetatively, this species resembles *C. serpents* and *C. recurvata*, but differs from *C. serpents* in having asymmetrical, acute foliage leaf inner ligules that are fused to the leaf sheath summit extensions and more frequent rebranching. *Chusquea acutigluma* can be distinguished from *C. recurvata* by its triangular central buds, lack of secondary subsidiary rebranching, with branches not recurved, and its complement of fewer, sometimes pilose foliage leaves (Table 2).

Additional Specimens Examined—Colombia. —ANTIOQUIA: Mpio. de San Luís, rivera de la quebrada la Risaralda, [6.02°, –75.00°]*, 1300–1500 m, 12 November 1995 (fl), *R.Fonnegra y curso tax. plant. vas. sem 2/95 5847* (HUA, ISC, MO). Mpio. de San Luís, Ecoparque el Castellón, [6.00°, –75.03°]*, 1300–1500 m, 9 November 1995 (fl), *R.Fonnegra y curso tax. plant. vas. sem 2/95 5705* (HUA, ISC, MO).

Chusquea recurvata L.G.Clark, McMurchie & B.J.Peterson, sp. nov. TYPE: VENEZUELA. Táchira: via Pregonero-San Cristobál, about 6 km above the dam of Presa La Honda, [8.1°, –71.65°], 1360 m, 16 June 1989, L.G. Clark, J. Gaviña & G. Adamo 543 (holotype, VEN; isotypes, ISC! [411626; 411627; 411628], MO [4254400, barcode MO-1144078; 4254401, barcode MO-1144079], US [3251278, barcode 00424010; 3251277, barcode 00424011; 3251276, barcode 00424012]).

Chusquea recurvata differs from all other known species of *Chusquea* sect. *Serpentes* by the following combination of characters: Culm length of 8–10 m; culm leaf sheaths 9.9–25.4 cm long, persistent; culm leaf sheath:blade ratio 3.2–13.7; central bud circular in outline subtended by two conical subsidiary buds; two initial subsidiary branches usually rebranching almost immediately to each produce a recurved secondary subsidiary branch, these often branching again; foliage leaves 6–12 per complement; foliage leaf inner ligule acute, rarely rounded, asymmetrical 2.6–8.5 ($\bar{x}$ = 5.6) mm long; foliage leaf base rounded, sometimes obliquely so.

Rhizomes unknown. **Culms** 0.6–1.0 cm diam, 8–10 m long, erect at base and thereafter scandent. **Internodes** 30 to 40 cm long, terete, solid, scabrous, pubescent just below the node, more or less glabrous just above the node, green mottled with small purple spots. **Culm leaves** 12.6–27 cm long, persistent,



FIG. 3. *Chusquea acutigluma*, Fonnegra et al. 5899 (MO).

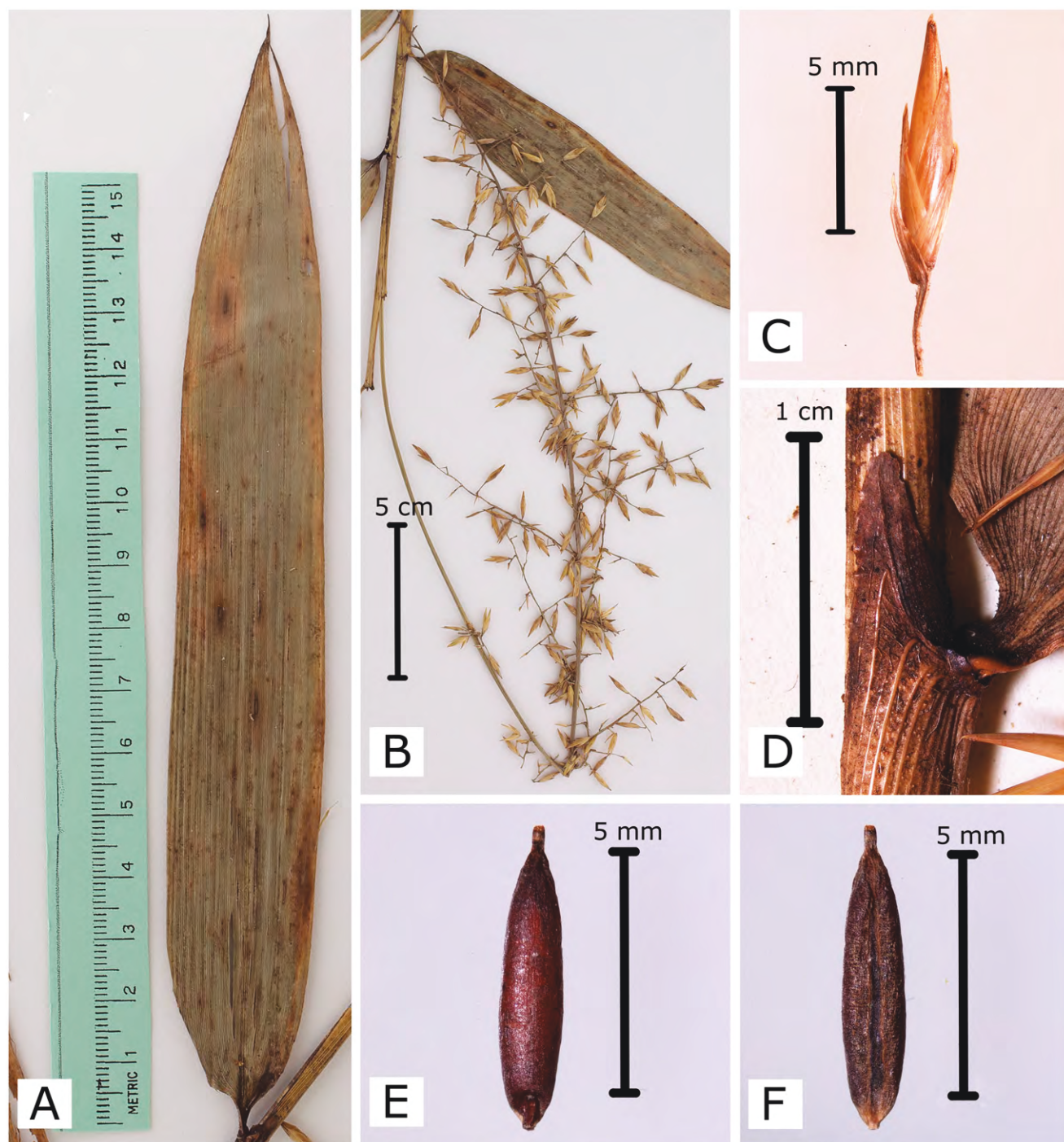


FIG. 4. *Chusquea acutigluma*. A. Foliage leaf, adaxial surface, B. Synflorescence displaying broadly open, paniculate structure, C. Spikelet. D. Ligular region of foliage leaf, showing leaf sheath summit extension and fused inner ligule. E. Caryopsis, showing the embryo. F. Caryopsis, showing the hilum. A–C are based on Fonnegra et al. 5899 (ISC), D on Fonnegra et al. 5899 (MO), and E–F on Fonnegra et al. 5847 (MO).

extending from two-thirds of the way up the internode to past the next node, juncture of sheath and blade highly visible, more or less concave; sheaths 9.9–25.4 ($\bar{x}$ = 16.8) cm long, 3.2–13.7 times as long as the blade, tightly wrapped around the culm, retrorsely scabrous, sometimes with sparse hairs, more or less basally hispid when young, the overlapping margin ciliate, not fused; sheath summit extensions absent; inner ligule 0.7–1.9 ($\bar{x}$ = 1.4) a short, glabrous to ciliate rim; outer ligule lacking to ca. 0.5 mm when present; blades 1.7–6.2 ($\bar{x}$ = 3.5) cm long, sometimes deciduous before the

sheath separates from the culm, narrowly triangular, more or less reflexed, glabrous, the margins entire, the apex acuminate and tapering to bristle-like tip; girdle 0.7–2.8 mm wide, more or less prominent, densely pubescent, disintegrating before the rest of the culm leaf. **Nodes** at mid-culm slightly swollen, with one circular central bud subtended by two conical buds essentially in contact with the nodal line; supranodal ridge conspicuous. **Branching** with central bud often developing tardily at basal nodes, sometimes at higher nodes; subsidiary branches initially two per node, usually rebranching

TABLE 2. Macromorphological comparison of *Chusquea acutigluma*, *C. recurvata*, and *C. serpens*.

Character	<i>C. acutigluma</i>	<i>C. recurvata</i>	<i>C. serpens</i>
Culm leaf persistence	Unknown	Persistent	Deciduous
Culm leaf sheath length (cm)	Unknown	9.9–25.4 ($\bar{x}$ = 16.8)	6.5–11.5 ($\bar{x}$ = 9.1)
Culm leaf sheath:blade ratio	Unknown	3.2–13.7	(1–)1.5(–2) ($\bar{x}$ = 1.6)
Central bud shape	Triangular	Circular	Triangular
Subsidiary branch rebranching frequency	Rebranching common	Rebranching common	Rebranching rare
Foliage leaf number per complement	3–4	6–12	3–7(–16)
Foliage leaf inner ligule length (mm)	1.9–6.7 ($\bar{x}$ = 3.6)	2.6–8.5 ($\bar{x}$ = 5.6)	1.0–1.9(–2.5) ($\bar{x}$ = 1.7)
Foliage leaf inner ligule shape	Asymmetrical, acute	Asymmetrical, acute to rarely rounded	Symmetrical, truncate
Synflorescence shape	Broadly paniculate	Unknown	Narrowly paniculate
Spikelet length (mm)	8.3–10.0 ($\bar{x}$ = 9.0)	Unknown	11.3–14.6 ($\bar{x}$ = 12.7)
Glume I length (mm)	2.5–4.3 ($\bar{x}$ = 3.1)	Unknown	1.2–2.5 ($\bar{x}$ = 2.0)
Glume I number of nerves	3	Unknown	1
Glume II apex	Mucronate to short-awned	Unknown	Long-awned

almost immediately to each produce a recurved secondary subsidiary branch, these often branching again, mature branch complement with 2–10 subsidiary branches; subsidiary branches 9.5–38 cm long, 1.3–5.7 ($\bar{x}$ = 3.1) mm diam. **Foliage leaves** 6–12 per complement; sheaths carinate, glabrous, sometimes with sparse hairs, the overlapping margin ciliate when young to nearly glabrous when older; sheath summit extension 1.2–3.2 ($\bar{x}$ = 2.1) mm on the overlapping side, (2.5–)3.2–7.1 ($\bar{x}$ = 4.8) mm long on the underlapping side, glabrous, margins ciliate to glabrous, fused to inner ligule; outer ligule (0.4–)0.8–2.4 ($\bar{x}$ = 1.4) mm long, truncate; inner ligule 2.6–8.5 ($\bar{x}$ = 5.6) mm long, asymmetrical, acute to rarely rounded at the tip; pseudopetiole distinct, 2.0–5.8 ($\bar{x}$ = 4.6) mm long, adaxially and abaxially glabrous; blades 9.1–22.0 ($\bar{x}$ = 17.2) cm long, 1.4–3.3 ($\bar{x}$ = 2.4) cm wide, L: W = 5.1–9.4 ($\bar{x}$ = 6.9), linear-lanceolate to lanceolate, adaxially glabrous, not tessellate, abaxially mostly glabrous with sparse hairs near base, not tessellate to very weakly so, the base rounded, sometimes obliquely so with relation to the pseudopetiole, not truncate, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex tapering into a long bristle-like tip. **Synflorescences** unknown. Figures 5, 6.

Distribution and Habitat—Táchira and Mérida, Venezuela; disturbed montane forests, including along a roadside, and in primary forest over sandstone substrate; 1150–2072 m.

Phenology—Because there are no known flowering specimens belonging to this species, nothing can be inferred about its phenology.

Etymology—This species is named for the recurved secondary subsidiary branches that help to distinguish it from *C. serpens*.

Informal Conservation Assessment—*Chusquea recurvata* has been collected in four different locations in the states of Táchira and Mérida, Venezuela. Extent of occurrence (EOO) was calculated to be 369 km² and area of occupancy (AOO) 16 km² based on estimates of collection locations. Collections were made in or near the boundaries of Chorro el Indio and El Tamá National Parks, with the majority of the EOO within these protected areas. *Chusquea recurvata* has been found in both disturbed and primary forests, but appears restricted to montane forests at elevations of at least 1150 m. Although large clumps described as “ill-defined” and consisting of many scattered individuals were recorded in one location in Táchira (Clark *et al.* 543), only occasional individuals were recorded at a collection location in Mérida (Steyermark 56392), despite being described as a “common type.” The specimen label of Clark *et al.* 540 indicates that another population of *C.*

recurvata was found at [8.1°, –71.65°], 1900 m, along the same road as Clark *et al.* 540, but no voucher was taken for this population, precluding verification. As *C. recurvata* is vegetatively similar to *C. serpens*, some collections in montane regions of Venezuela previously identified as *C. serpens* may actually represent *C. recurvata*.

According to the results of the EOO and AOO analysis, limited number of locations in which this species has been collected, and likely extreme fluctuation in number of mature individuals due to gregarious monocarpy, which is common in *Chusquea*, we hypothesize that if a formal conservation assessment were performed, this species would be considered Endangered (EN) under criteria B2ac(iv,v) (IUCN 2019).

Notes—Specimens of *C. recurvata* are visually similar to those of *C. serpens*, though *C. recurvata* is more prone to rebranching, often with recurved secondary subsidiary branches. The longer, acute inner ligule of the foliage leaves that are fused to the leaf sheath summit extensions, typically greater number of foliage leaves per complement, circular central bud, and persistent culm leaf sheaths also readily help to distinguish this species from the more widely distributed *C. serpens*, which can be found in similar habitats (Table 2). The micromorphology of the abaxial surfaces of the foliage leaves of *C. recurvata* is strikingly different from that of *C. serpens* as well. Most notably, the abaxial surface of *C. recurvata* foliage leaves has mainly simple, round papillae typically distributed in one or two rows on long cells throughout the leaf, while that of *C. serpens* has distally enlarged, highly branched papillae distributed in one or two rows in the costal zone, and crowded around and overarching the stomata in the intercostal zone.

Additional Specimens Examined—Venezuela. —TÁCHIRA: Cerro Las Minas, bordering Quebrada Las Minas, 18–20 km SE of Santa Ana, [7.6°, –72.216°], 1150–1250 m, 29 July 1979, Steyermark & Liesner 119014 (ISC, VEN, US). —MÉRIDA: Dto. Rivas Dávila, via Mesa de Quintero-Pregonero, Río Capurí, [8.0979°, –71.6222°], 1470 m, 15 June 1989, Clark *et al.* 540 (ISC, MO, VEN, US); rich dam forest along northwest and west-facing slopes of Quebrada de Montaña en la montaña de Los Torritos, tributary to Río Canaguá, above finca “La Montaña,” 2 leagues SW of Canaguá, [8.09°, –71.51°]*, [1920–2072 m], 8 May 1944, Steyermark 56392 (F, US, VEN).

CHUSQUEA ASPERA L.G.Clark, Iowa State J. Res. 61: 112. 1986.

TYPE: PERU. Huánuco: Leoncio Prado, Dist. Hermilio Valdizán, la cumbre de la Divisoria, [–9.09°, –76.85°]*, 1600 m, 20 May 1978 (fl), Schunke V. 10178 (holotype: US [2889197, barcode 00074279; 2889198, barcode 00074280; barcode 00381672]; isotypes: F [1958041, barcode V0040681F], ISC! [447629, barcode ISC-v-0000947; 447630,



FIG. 5. *Chusquea recurvata*, Clark et al. 543 (ISC).

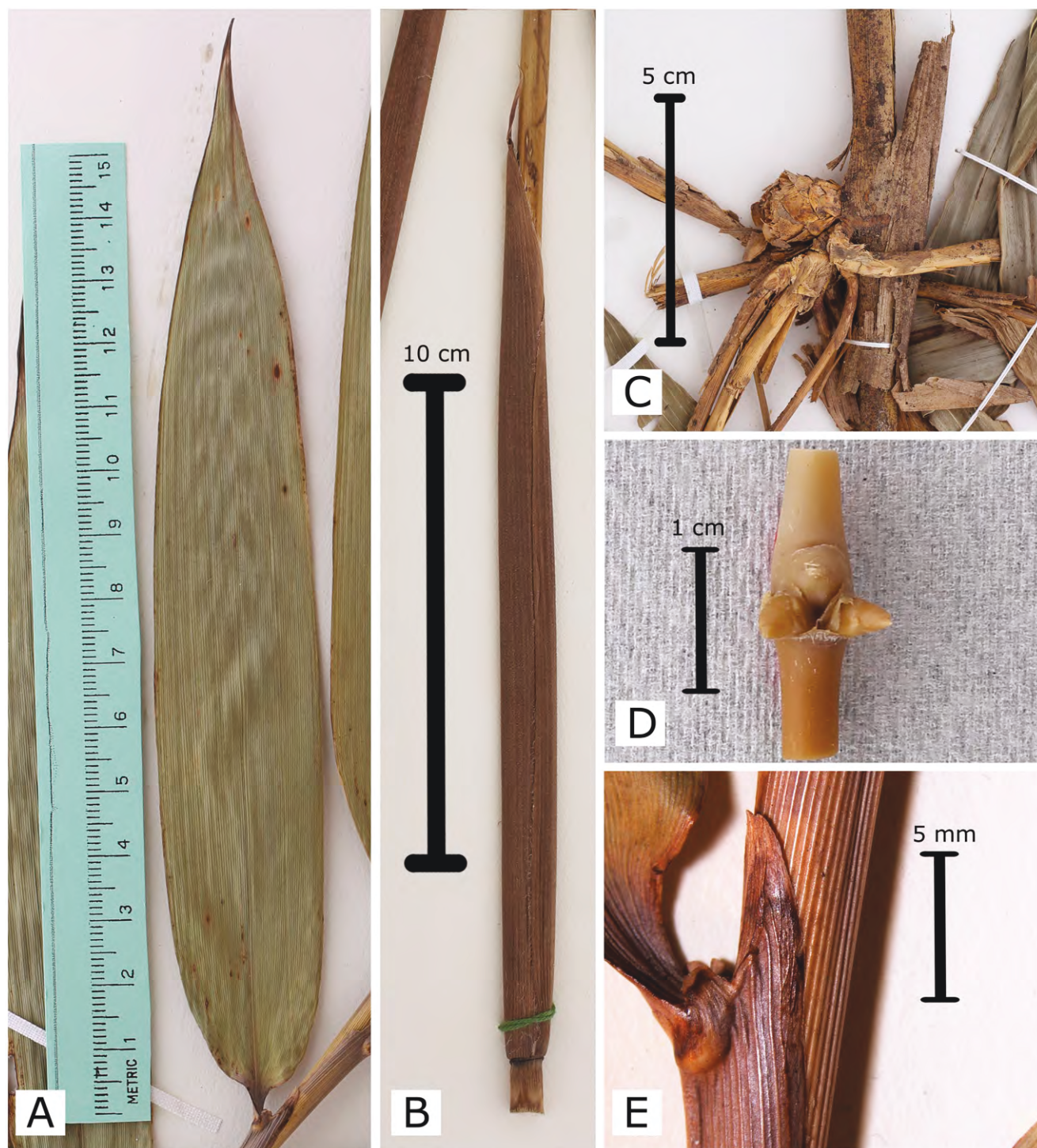


FIG. 6. *Chusquea recurvata*. A. Foliage leaf, adaxial surface. B. Culm leaf wrapped around culm, abaxial surface visible. C. Branch complement showing recurved subsidiary branches. D. Bud complement showing circular central bud above two subsidiary buds. E. Foliage leaf ligular region showing leaf sheath summit extension and fused inner leaf ligule. A–B are based on Clark *et al.* 543 (ISC), C on Steyermark & Liesner 119014 (ISC), and D on the spirit-preserved component of Clark *et al.* 540 (ISC).

barcode ISC-v-0000948], K [barcode K000433279], MO [3272604, barcode MO-128807], SI [si 61662; si 61663], U [407600B, barcode U 1037269], USM [162627], VEN [407501, barcode 407501]).

Rhizomes unknown. **Culms** 10–15 m long, diameter unknown, vining, clambering. **Internodes** terete, scabrous,

green mottled with purple, length unknown. **Culm leaves** abaxially asperous (complete leaves not seen); girdle 4–5 mm wide, glabrous. **Nodes** with supranodal ridge conspicuous; buds not seen. **Branching** probably initially infravaginal, with the first developing subsidiary branches breaking through the girdle and the central branch later rupturing the sheath base; subsidiary branches 4–10, 57–74 cm long when

flowering, including synflorescence, 3.3–4.6 diam, surrounding single central branch, apparently not rebranching. **Foliage leaves** 6–7 per complement; foliage leaf sheaths green, carinate, mostly glabrous with a few sparse hairs, the overlapping margin ciliate; sheath summit extension 1.0–2.0 ($\bar{x}$ = 1.4) mm on the overlapping side, 2.2–5.8 mm on the underlapping side, margins often ciliate, sometimes glabrous, fused to inner ligule; outer ligule 1.5–2.5 mm long, glabrous, truncate, erect; inner ligule 2.5–7 mm long, glabrous, somewhat asymmetrical, rounded; pseudopetiole 1.5–6 mm long, distinct, adaxially and abaxially glabrous; blades 13.5–23.5 cm long, 2–3.2 cm wide, L: W = 6–8.3, linear-lanceolate to lanceolate, adaxially and abaxially glabrous, weakly tessellate, the base attenuate to rounded-attenuate, often slightly asymmetrical, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex setose. **Synflorescences** 13–38 cm long, 1.5–5 cm wide, more or less narrowly paniculate, just exserted from subtending sheath; peduncle 4.5–7.5 cm, rounded on one side, slightly grooved on the other, glabrous; rachis slightly sinuate, flattened, one side rounded, the other ridged, glabrous, the angles scabrous; branches ascending but not strongly appressed, arising from the ridged side of the rachis only, slender, flexible, the lower ones ca. 5–15 cm long, those near the apex ca. 0.7–1.5 cm long, angular, scabrous; pulvinus not visible; pedicels 2–5 mm long, angular, scabrous. **Spikelets** 11–15.7 mm long, 1.5–3.0 mm wide, terete to slightly laterally compressed, straight, scabrous; glume I 0.9–2 mm long, ca. 1/10 the spikelet length, abaxially scabrid, apically broadly acute to rounded, ciliate, 1-nerved or nerves absent; glume II 1.3–4 mm long, 1/8–1/4 the spikelet length, abaxially scabrous, marginally ciliate toward apex, mucronate, mucro 0.3–0.5 mm, 3–5-nerved; glumes III and IV mucronate, abaxially scabrous, marginally ciliate toward apex, carinate toward apex; glume III 5.5–6.4 mm long, ca. 1/2 the spikelet length, mucro ca. 0.5 mm long, 5-, 7-, or 9-nerved; glume IV 7.7–11.6 mm long, ca. 3/4 the spikelet length, mucronate, mucro ca. 0.6 mm long, 7-, 9-, or 11-nerved; lemma 10.2–13.6 mm long, mucronate, mucro 0.4–0.7 mm, abaxially scabrous, marginally ciliate toward apex, 9–11-, or 13-nerved; palea 10–12.4 mm long, sulcate for the full length, acute, abaxially scabrous, 4-, 6-, or 8-nerved. **Lodicules** 3, apex ciliate, anterior pair ca. 2.0 mm long, the posterior one ca. 1.5 mm long. **Anthers** 6–8 mm long, brown. **Caryopsis** unknown. Figures 7, 8.

Distribution and Habitat—Central to northwestern Peru; montane forests; 1450–3180 m.

Phenology—Flowering specimens were observed in Cajamarca in 1957 (*Sagastegui* 2521) and 2003 (*Baldeón* 5181) and in Huánuco from 1978 to 1980 (*Plowman & Schunke* V. 10178 and 7392, *Davidson* 9321, and *Gentry et al.* 29577), indicating a flowering cycle of approximately 21–25 yr. However, it remains unknown whether flowering specimens of *C. aspera* represent gregarious blooms.

Additional Specimens Examined—**Peru.** —AMAZONAS: trail ca. 12–18 km E of La Peca in Serranía de Bagua, [–5.64°, –78.33°]*, [1800–1950 m], 14 June 1978, *Gentry et al.* 22931 (ISC, MO, US); —CAJAMARCA: Prov. Contumaza, Dist. Guzmango, Herilla, [–7.40°, –78.9°]*, [1800–2000 m]*, 5 August 1957 (fl), *Sagastegui* 2521 (NY); Provincia: San Ignacio, Distrito: Tabaconas, Localidad: Santuario Nac. Tabaconas-Namballe, Lagunas Coyona (Arrebiatadas). Bajando de las lagunas hacia la Quebrada Chichilapa, [–5.24°, –79.30°]*, 3150–3180 m, 10 April 2003 (fl), *Baldeón* 5181 (USM). —HUÁNUCO: Prov. Leoncio Prado, La Divisoria, Cord. Azul near border with Ucayali, [–9.08°, –75.80°], 1620–1760 m, 10 August 1980 (fl), *Gentry et al.* 29577 (MO, US, USM); Prov. Leoncio Prado, Dto. Hermilio Valdizán, La Divisoria, road from Pumahuasi to la Cumbre, [–9.10°, –75.80°]*,

[1600–1900 m]*, 26 June 1978 (fl), *Plowman & Schunke* V. 7392 (MO, US); Cordillera Azul, 38.2 km E of Tingo María on the highway to Pucallpa, [–9.16°, –75.80°]*, [1450–1650 m]*, 1979 (fl), *Davidson* 9321 (US).

CHUSQUEA GLAUCA L.G. Clark, Syst. Bot. Monogr. 27: 95, fig (1989). TYPE: MEXICO. Veracruz: Mpio. Xico, trail from El Rosario to Xico, 3 km past Buena Vista, [19.44°, –96.99°], 1900 m, 21 January 1989, *Clark et al.* 459 (holotype: MEXU! [481817, barcode MEXU 00481817]; isotypes: ISC! [406162, barcode ISC-v-0000967], MO [3648264, barcode MO-1936318], US [3129504, barcode 00170136]).

Rhizomes unknown. **Culms** 0.5–1 cm diam, 5–6 m long, vining, scrambling, and hanging from vegetation. **Internodes** 9–12 cm long, terete, solid, scabrid, green to green mottled with purple, a glaucous white band ca. 0.5 cm wide usually present on younger culms just below the nodal line. **Culm leaves** 5.9–13.3 cm long, persistent, juncture of sheath and blade a horizontal line; sheaths 4.2–8.7 cm long, 2–4.5 times as long as the blade, triangular, persistent, not fused, glabrous; sheath summit extensions absent; inner ligule ca. 0.5 mm long, ciliate; outer ligule absent; blades 1.1–4.8 cm long, narrowly triangular, erect, deciduous, adaxially glabrous, abaxially scabrid, apex apiculate; girdle 1.5–2.8 mm wide, glabrous to pubescent. **Nodes** at mid-culm with the circular central bud subtended by 2 subequal subsidiary buds; supranodal ridge conspicuous. **Branching** with central branch sometimes developing, exserted more or less horizontally; subsidiary branches leafy, 17–45 cm long, 1.5–4.0 mm diam, rarely rebranching. **Foliage leaves** 5–8(–13) per complement; sheaths carinate, glabrous, margins glabrous, apex truncate, ciliate; sheath summit extension absent; outer ligule 1–2 mm long, truncate, glabrous to ciliate; inner ligule 1–3 mm long, truncate to rounded, abaxially pubescent; pseudopetiole 4–7 mm long, distinct, adaxially scabrid, abaxially glabrous to scabrid; blades 14.4–29 cm long, 2.1–4 cm wide, L: W = 5.5–10, lanceolate, adaxially glabrous, abaxially scabrid to pilose, glaucous, not tessellate, the base rounded to rounded attenuate, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex acuminate. **Synflorescences** 14–18 cm long, more or less open, paniculate, not fully exserted; rachis angular, pubescent; branches spreading, the lower ones to 11 cm long, angular, pubescent; pulvinus present at base of branches but not prominent. **Spikelets** 7.2–7.5 mm long, slightly falcate; glumes I and II scalelike, pubescent, nerves absent; glume I ca. 0.4 mm long, ca. 5/100 the spikelet length; glume II ca. 0.5 mm long, 1/14–1/10 the spikelet length; glumes III and IV apiculate; glume III ca. 3 mm long, 2/5–1/2 the spikelet length, 1-nerved; glume IV ca. 3.6 mm long, ca. 5/8 the spikelet length, 5-nerved; lemma ca. 6.7 mm long, apiculate, 7-nerved; palea ca. 4.5 mm long, apiculate, 2-nerved. **Lodicules** unknown. **Anthers** unknown. **Caryopsis** unknown. Figures 9, 10.

Distribution and Habitat—Eastern-central Mexico; mixed pine-oak cloud forest and secondary vegetation along roadsides, sometimes near waterfalls; 1700–2200(–2500) m.

Phenology—As we observed only one flowering specimen of *C. glauca* (*Ventura* A. 907, collected in 1970), we could not determine anything about the phenology of this species.

Additional Specimens Examined—**Mexico.** —HIDALGO: Mpio. Tenango de Doria, camino entre Metepec y Tenango de Doria, 18 km al NNE de Metepec, [20.3°, –98.24°]*, 2200 m, 31 October 1997, *Koch* 77317 (CHAPA, ISC, US). —VERACRUZ: Mpio. Acajete, Cascada de Plan de Sedeño, [19.57°, –96.98°]*, [1700–1750 m]*, *Cházaro & Hernández* de Cházaro 5077 (CHAPA, IBUG); Mpio. Acajete, cerca de una cascada, en la carretera Plan de Sedeño a



FIG. 7. *Chusquea aspera*, Schunke V. 10178 (ISC).

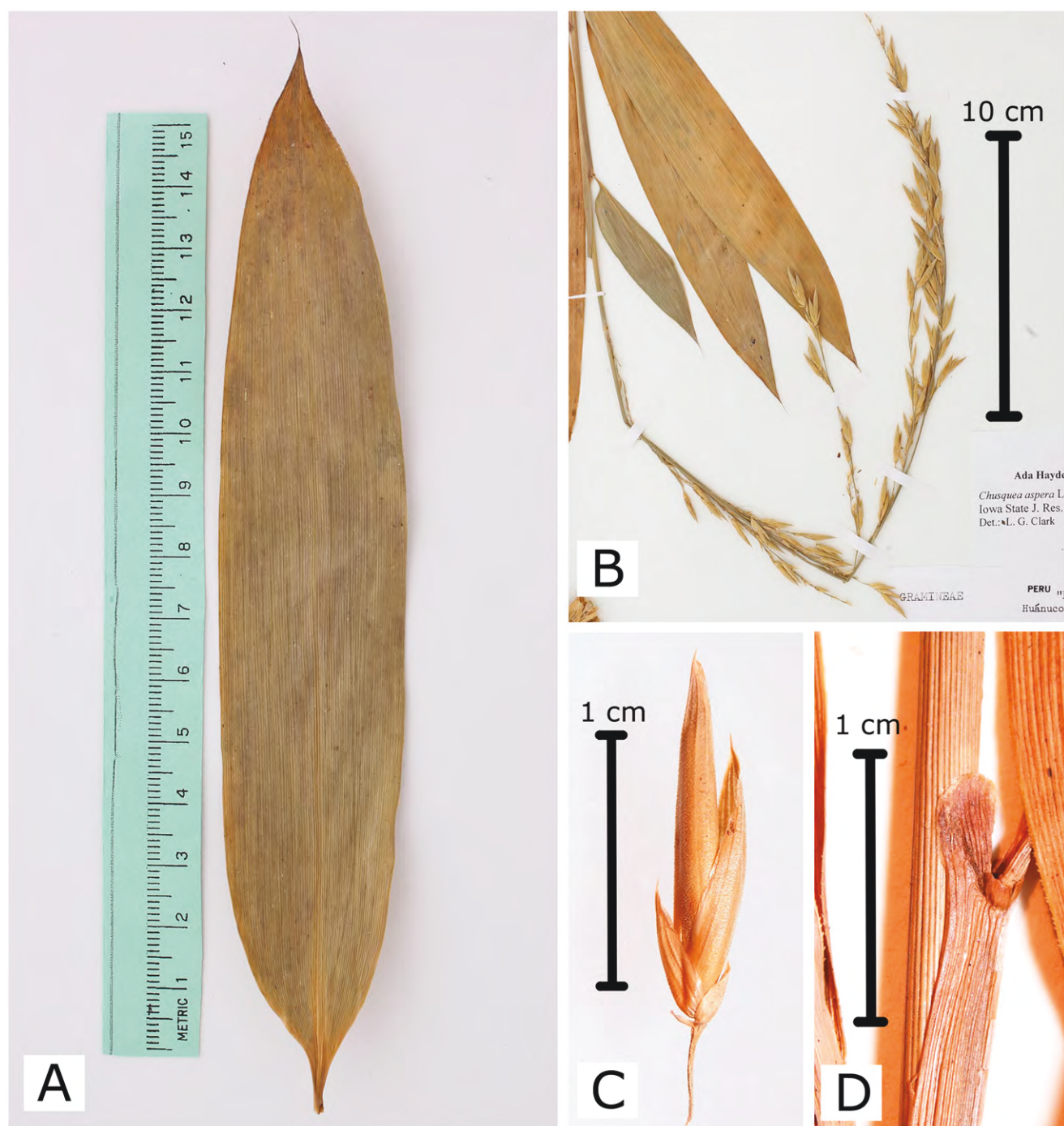


FIG. 8. *Chusquea aspera*. A. Foliage leaf, adaxial surface. B. Synflorescence. C. Spikelet. D. Foliage leaf ligular region showing leaf sheath summit extension and fused inner leaf ligule. A–D are based on *Schunke V. 10178* (ISC).

San Andrés Tlanehuayocan, [19.57°, –96.98°]*, [1700–1750 m]*, *Cházaro & Leach* 3419 (MEXU, WIS); Mpio. Coatepec, entre Loma Alta y Mesa de Los Laureles, [19.51°, –97.05°]*, 2500 m, February 1983, *Cházaro & Robles* 2692 (ISC, WIS); Mpio. Acajete, Río Plan de Sedeño, waterfall by paved road from Plan de Sedeño to Masatepec, [19.5667°, –97.0028°], 1800 m, 23 January 1989, *Clark et al.* 461 (ISC, MEXU, MO, US); Mpio. Acajete, Plan de Sedeño, [19.57°, –97.00°]*, [1800–1850 m]*, *Cortés R.* 81 (US); Mpio. Jalacingo, Atzaleno, [19.79°, –97.25°]*, [1700]*, 13 Apr 1970 (fl), *Ventura A.* 907 (US); Mpio. Xico, road Tonalaco to Oxtlapa to Xico, 2 km below La Garita, 1 km above Oxtlapa, 18 km above Xico, [19.4278°, –97.0917°], 2030 m, 20 September 1994, *Clark et al.* 1310 (CAS, ISC, MEXU, MO, US).

CHUSQUEA LATIFOLIA L.G.Clark, Ann. Missouri Bot. Gard. 72: 868, fig (1985). TYPE: COLOMBIA. Tolima: El Libano a Murillo

(Km 11 al 22 de la carretera), subpáramo en el Alto de Peñones, [4.88°, –75.13°]*, 2200–2950 m, 20 July 1947 (fl), *García-Barriga* 12259 (holotype: US [1937305, barcode 00074310]; isotypes: COL! [59070, barcode COL000006350]).

Rhizomes with some segments leptomorph (overall rhizomes may be leptomorph or amphi-morph). **Culms** 1–2 cm diam, 3–40 m long, vining, scandent, often trailing for part of their length. **Internodes** 25–39 cm long, terete to slightly compressed laterally, solid, glabrous to scabrous or pubescent just below the nodes, green. **Culm leaves** 17.8–30 cm long, persistent, triangular in shape, pubescent at slightly concave



FIG. 9. *Chusquea glauca*, Clark et al. 459 (ISC).

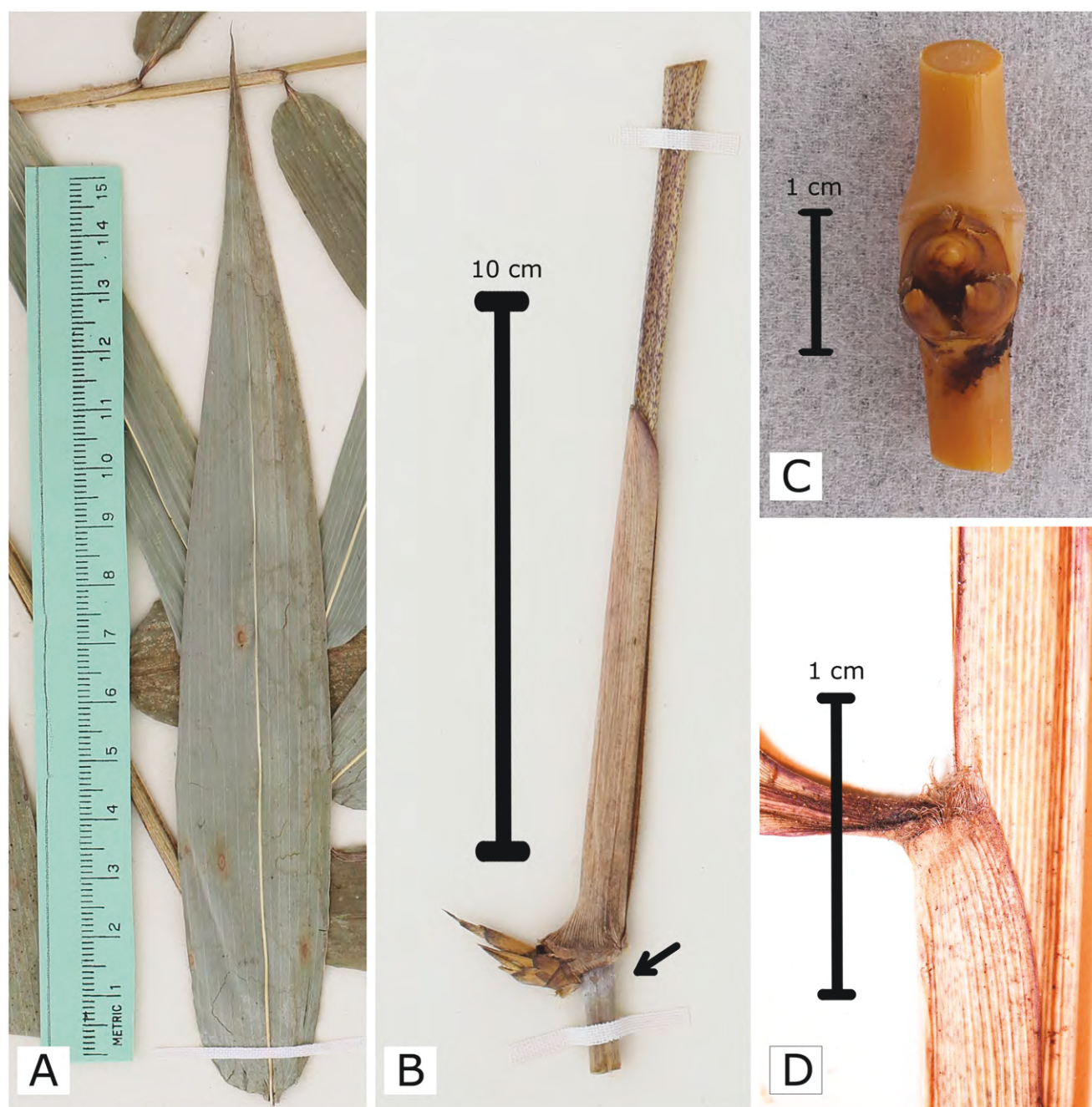


FIG. 10. *Chusquea glauca*. A. Foliage leaf, abaxial surface. B. Culm leaf and immature branch complement displaying infravaginal branching; culm leaf wrapped around culm, abaxial surface visible, blade missing, with arrow indicating glaucous white band beneath nodal line. C. Bud complement showing circular central bud above two subsidiary buds. D. Foliage leaf ligular region. A is based on Clark *et al.* 461 (ISC), B on Clark *et al.* 1310 (ISC), and C–D on Clark *et al.* 459 (ISC), with C representing the spirit-preserved component of the collection.

to nearly horizontal juncture of sheath and blade, chartaceous; sheaths 15–26.5 cm long, at least 9 times as long as the blade, triangular, scabrous or sometimes pubescent, the margins ciliate, fused to 2.5 cm above the base; sheath summit extensions absent; inner ligule 0.4–0.6 mm long, a short, ciliate rim; outer ligule absent; blades 1–3.5 cm long, deciduous, triangular, adaxially pubescent, abaxially scabrous or sometimes glabrous, the margins ciliate, the apex acuminate; girdle (0.3–)1.0–1.5 cm wide, usually well-developed, pubescent, forming a flap through which the branches emerge, often disintegrating before the rest of the culm leaf. **Nodes** slightly

swollen with the triangular central bud subtended by two subequal subsidiary buds, adventitious roots sometimes present; nodal line nearly horizontal, dipping only slightly below bud complement. **Branching** sometimes arising from a promontory, with central bud sometimes developing into a robust branch more or less equal in size to the main culm and rebranching; subsidiary buds developing into leafy branches 17–66(–103) cm long, 2.8–5.5 ($\bar{x}$ = 4) mm diam, rebranching extensively from their lower nodes. **Foliage leaves** 5–9 per complement; foliage leaf sheaths green, carinate, glabrous to scabrous, the margins ciliate, sometimes becoming nearly

glabrous with age; sheath summit extensions 1.2–3.2 ($\bar{x}$ = 2.0) mm on the overlapping side, 2.0–8.6 ($\bar{x}$ = 4.4) mm on the underlapping side, pubescent to glabrous, margins glabrous to ciliate, fused to the inner ligule; outer ligule 0.5–2 mm long, conspicuous, stiff; inner ligule (1–)2–15 mm long, usually conspicuous, rounded to truncate, usually abaxially pubescent at least on the lower half, chartaceous; pseudopetiole 3–9 mm long, distinct, adaxially scabrid, abaxially glabrous; blades 13–32 cm long, 3–8.5 cm wide, L: W = 2.5–6, lanceolate to ovate, adaxially glabrous, not tessellate, abaxially glabrous to slightly scabrous, weakly tessellate, the base rounded to rounded-truncate, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex acuminate. **Synflorescences** 19.5–54.5 cm long, 1.5–2.5 cm wide, narrowly paniculate, the base enclosed by the subtending leaf at maturity or peduncle exerted for up to 9.5 cm; peduncle (6.0–)11.5–24.5 cm long, grooved on both sides to grooved on one side and rounded on the other, glabrous; rachis glabrous, one side flat and slightly ridged, the other rounded; branches glabrous, appressed, second, arising only from the flat, slightly ridged side of the rachis, angular, 3–9 cm long at the base of the rachis, becoming progressively shorter toward the apex, the spikelets eventually arising directly from the rachis; pulvinus not visible; pedicels (1–)2.5–5 mm long, rounded to angular, often at least slightly sinuate. **Spikelets** 8.2–12 mm long, 1.8–2.5 mm wide, terete, slightly falcate, glabrous; glume I 0.5–1.3 mm long, ca. 1/10 the spikelet length, rounded, nerves absent; glume II 2.4–2.5 mm long, ca. 1/4 the spikelet length, mucronate to short-awned, the mucro or awn 0.2–0.7 mm long, 3- or 5-nerved; glume III 3.2–4.2 mm long, ca. 1/2 the spikelet length, short-awned, awns 0.5–1.2 mm, 7- or 9-nerved; glume IV 4.4–6.4 mm long, ca. 5/8 the spikelet length, mucronate to short-awned, the mucros or awns 0.4–0.7 mm long, 7-nerved; lemma 8–10.6 mm long, shiny, keeled near apex, mucronate to short-awned, the mucros or awns 0.2–0.7 mm long, 9- or 11-nerved; palea 8.3–9.6 mm long, sulcate, apex acute but not apiculate, 6- or 8-nerved. **Lodicules** 3, apex ciliate, anterior pair 2.5–2.7 mm long, swollen at base, the posterior one 1.6 mm long. **Anthers** 4.5–5.2 mm long, yellow-tan to brown. **Caryopsis** unknown. Figure 11.

Distribution and Habitat—Colombia; cloud forests; 1280–2350 m. Although the holotype specimen was reported as 2200–2950 m on the label, the elevation appears to be part of a pre-printed description for the entire expedition. Given the typical elevational range of *C. latifolia*, it is likely that this specimen was found at the lower end of this range.

Phenology—Flowering was recorded in 1944 in Valle del Cauca (*Cuatrecasas* 18767) and 1947 in Tolima (*García-Barriga* 12259), and in 1987–1989 in Antioquia, Chocó, and Risaralda (*Brant & Martínez* 1431, *MacDougal et al.* 3713, *Sánchez et al.* 1717, *Zarucchi et al.* 7160, *Wood* 5357, *Rangel et al.* 5712 & 5799). Flowering was also recorded in 1983 in Cundinamarca (*Wood* 4132), and 1980 in Risaralda (*Idrobo & Cleef* 9784). Gregarious flowering with regrowth from seed was observed in June 2015 in Quindío near the border with Risaralda (*Londoño & Dransfield* 2000), and was likely related to the flowering events in 1987–1989, indicating a gregarious flowering cycle of about 26–28 yr, possibly preceded by sporadic flowering.

Notes—According to the labels of *Cogollo et al.* 2692, *Kilmkiewicz* 152, and *Londoño & Dransfield* 2000, this species is used as a fiber for basket-making. The label of *Cogollo et al.* 2692 also notes that a common name for the species is “chusco.”

Additional Specimens Examined—**Colombia**. —ANTIOQUIA: P.N. Natural “Las Orquídeas”, Sector Calles, margen derecho del río Calles, 1310–1365 m, [6.5833°, –76.8333°], 27 March 1988, *Cogollo et al.* 2692 (COL, JAUM, MO); Urrao Municipio, Parque Nacional Natural Las Orquídeas. Vereda Calles. Alto de Palmitas, ca. 1 km de la Cabaña de Calles del Inderena, [6.5333°, –76.3167°], 1700–1750 m, 4 December 1993, *Pipoly et al.* 17464 (ISC, MO); en selvas densas y húmedas en las montañas al oeste de Sonsón, [7.12°, –75.35°]*, [1530 m]*, *Johnson & Barkley* 18C822 (COL); Mpio. Frontino, road to Murri, 22.7 km W of Nutibara, [6.75°, –76.4167°], 1300 m, 20 October 1987 (fl), *Brant & Martínez* 1431 (COL, HUA, ISC, MEDEL, MO, US); Mpio. Frontino, road between Nutibara and La Blanquita, region of Murri, ca. 9 km below and west of high point on road, or 20 km from Nutibara, [6.7°, –76.4°], 1280–1380 m, 7 February 1989 (fl), *MacDougal et al.* 3713 (HUA, ISC, MO, US); Mpio. Frontino, corr. Nutibara, cuenca alta del Río Cuevas, [6.79°, –76.23°]*, 1300 m, 20 October 1987 (fl), *Sánchez et al.* 1717 (HUA); Mpio. Frontino, km 22.6 of road Nutibara – La Blanquita, region of Murri, [6.7°, –76.4167°], 1370 m, 5 November 1988 (fl), *Zarucchi et al.* 7160 (HUA, ISC, MO, US); Between Yarumal & Las Ventanas, [7.02°, –75.45°]*, 2200 m, 23 March 1986, *Wood* 5357 (ISC). —CHOCÓ: de Atrato, carretera alterna El Siete-Guaduas, Km 4.1, [5.83°, –76.42°]*, 1700 m, 23 March 1987 (fl), *Londoño & Quintero* 263 (ISC, MO, US). —CUNDINAMARCA: Santandercito, by the Tequendama-Mesitas road, [4.59°, –74.34°]*, [1600 m]*, 10 December 1983 (fl), *Wood* 4132 (K, US). —RISARALDA: Mpio. Santa Rosa, camino de herradura entre Termales y el Páramo de Santa Rosa, declive al lado izquierdo de la quebrada El Contiojo, [4.84°, –75.54°]*, 2350 m, 20 July 1980 (fl), *Idrobo & Cleef* 9784 (COL); El Cedral, rocha a El Silento, 20 km de Pereira, [5.0333°, –75.7039°], 2140 m, 15 October 1989 (fl), *Rangel et al.* 5712 (COL, MO) & 5799 (COL). RISARALDA-QUINDIO: Río Barbas, [4.71°, –75.68°]*, [1575 m]*, 16 January 1950, *McClure* 21748 (ISC, US); Mpio. Filandia, autopista del Café, margen izquierda vía Armenia-Pereira, en inmediaciones del Peaje de Circasia, [4.698°, –75.607°], [2030 m]*, 24 June 2015 (fl), *Londoño & Dransfield* 2000 (COL, HUQ). —VALLE DEL CAUCA: old Cali-Buenaventura road, 17 km NW from Cali, Villa-Monica-El Rancho de Yo, [3.55°, –76.61°]*, [1500 m]*, 23 August 1981, *Calderón* 2997 (COL, ISC, MO, US); Cordillera Occidental, vertiente oriental, hoya del Río Cali, vertiente derecha confluencia del Río Pichindécito con el Pichindé, [3.46°, –76.60°]*, [1350–1400 m]*, 7 November 1944 (fl), *Cuatrecasas* 18767 (US); Cordillera Occidental, vertiente oriental, hoya del Río Cali, Río Pichindé, en Los Carpatos, [3.46°, –76.60°]*, [1350–1400 m]*, *Cuatrecasas* 21629 (US); Finca Zingara, Corregimiento La Dividera, crest of Cordillera Occidental W of Cali, 6 km N of Cali-Buenaventura Hwy, [3.5333°, –76.5833°], 1960 m, 13 December 1985, *Gentry et al.* 53215 (CUVC, MO); Finca Zingara, correg. La Divisora, crest of the Cordillera Occidental 6 km N of Cali – Buenaventura highway, W of Cali, 1960 m, [3.5333°, –76.5833°], 24 March 1986, *Gentry et al.* 53531 (CUVC, MO); El Silencio, Hacienda Himalaya, Cord. Occidental W of Yumbo, 1860 m, [3.6333°, –76.55°], 2 February 1989, *Gentry et al.* 65394 (CUVC, MO); San Antonio, west of Cali, near a summit of Cordillera Occidental, [3.42°, –76.60°]*, [1800 m]*, 26 February 1939, *Killip & García* 33904 (US); Mpio. La Cumbre, Vereda La Sofía, Corr. Bitaco, Cerro de Yumbillo, Cord. Occidental, vertiente occidental, [3.61°, –76.57°]*, 1900 m, 28 October 1988, *Kilmkiewicz* 152 (CUVC); Mpio. Yumbo, Correg. Dapa, aprox. 10 km de la Iglesia por la vía a la carretera al mar, finca Debusale, [3.56°, –76.56°]*, [1800 m], 23 November 1987, *Londoño* 42 (CUVC); Mpio. Yumbo, correg. Dapa, finca Debusale, [3.56°, –76.56°]*, 1800 m, 28 October 1990, *Londoño & Kobayashi* 523 (CUVC); along Cali-Buenaventura highway on eastern slope of Cordillera Occidental, [3.53°, –76.61°]*, c. 2000 m, 15 September 1943, *McClure* 21234 (ISC, MO, US); Mpio. Cali, 6 km above the church in Dapa, on the Dapa-Buenaventura road, NW of Cali, [3.5167°, –76.6°], 2010 m, 14 February 1988, *Clark & Londoño* 417 (COL, ISC, MO, US); Mpio. Tuluá, about 1.6 km above the Escuela Simón Bolívar, Venus-Monteloro road, canyon of the Río Morales, [4.0°, –76.0833°], 1510 m, 16 March 1988, *Clark & Londoño* 442 (ISC, MO, US).

CHUSQUEA POHLII L.G.Clark, Ann. Missouri Bot. Gard. 72: 867, fig (1985). TYPE: COSTA RICA. San José: along the Interamerican Hwy. between km 44–45, closer to km 45, [9.71°, –83.95°]*, 2190 m, 27 February 1982, *Clark & Clark* 275 (holotype: ISC! [366919, barcode ISC-v-0000990; 366920, barcode ISC-v-0000989; 366921, barcode ISC-v-0000988; 366922, barcode ISC-v-0000987]; isotypes: CR [114067, barcode CR114067], K [barcode K000433239; barcode K000433240], MO [3304846, barcode MO-115998; 3304845, barcode MO-115999], NY [barcode 380451; barcode

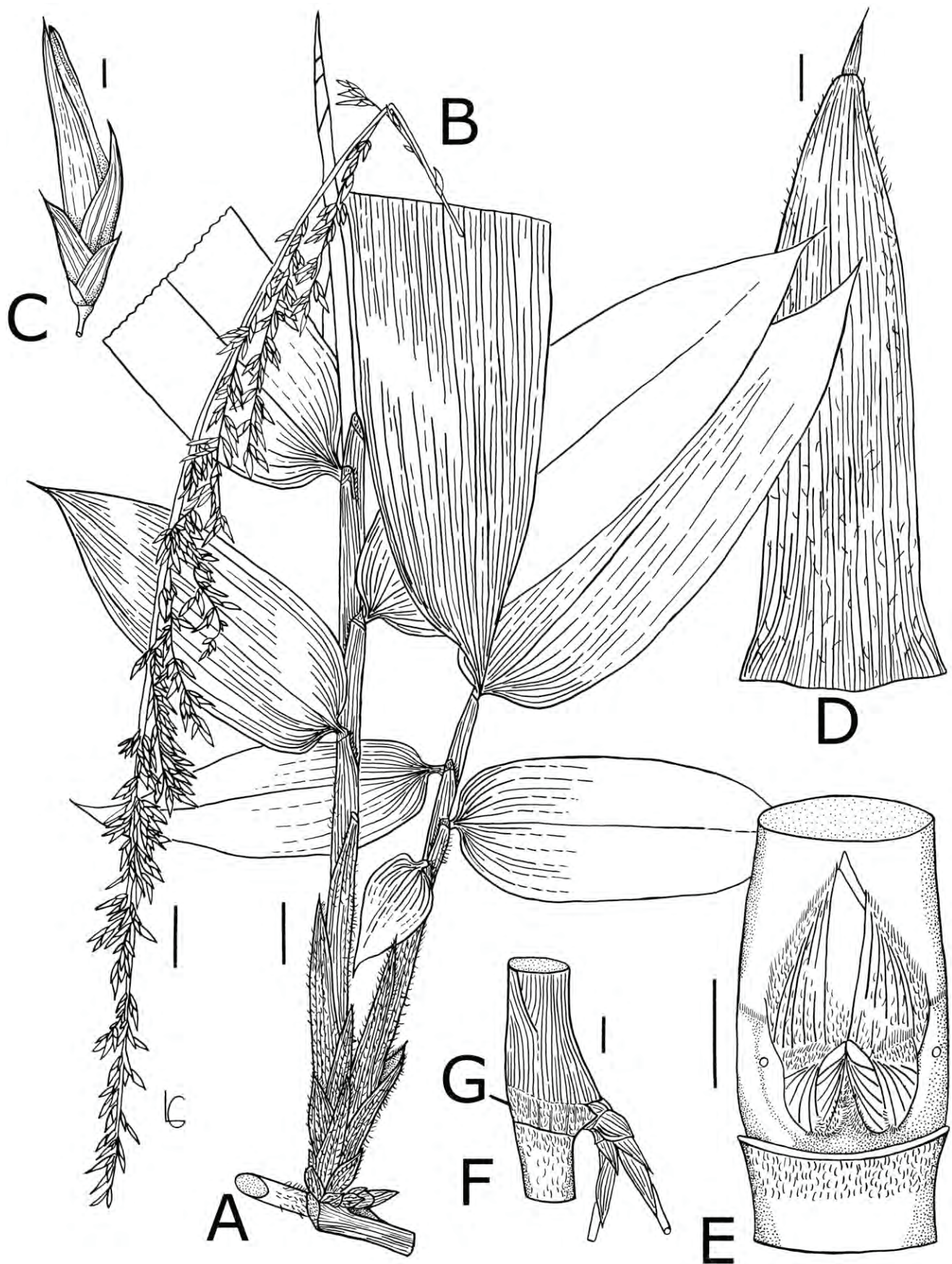


FIG. 11. *Chusquea latifolia*. A. Leafy branch complement. B. Synflorescence. C. Spikelet. D. Culm leaf. E. Bud complement. F. Node with branches emerging infravaginally (base of sheath with fused margins). G. Girdle. A is based on Killip & García 33904, B–C on García-Barriga 12259, D–E on Calderón 2997, and F–G on McClure 21748. Scale bars: 2 cm (A, B, D), 1 mm (C), 1 cm (E, F). Adapted from Fig. 3 of Clark 1985.

380452], US [2960369, barcode 00009710; 2960370, barcode 00009711; 2960371, barcode 00009712; barcode 00382307]).

Rhizomes unknown. **Culms** 1.5–3(–5) cm diam, 2–30 m long, scandent, arching. **Internodes** 22–26 cm long, terete, often shallowly sulcate above the central bud on more mature culms, solid, scabrous-hispid below node, becoming scabrous to glabrous farther from node, green to green mottled with purple. **Culm leaves** 21–47.6 cm long, persistent, usually extending past the next node, chartaceous to cartilaginous, juncture of sheath and blade nearly horizontal, very slightly concave; sheaths 18.5–39.2 cm long, 5.4–10.5 cm wide at base, usually 5.5–7.5 times, occasionally only 3–4 times, as long as the blade, triangular, abaxially hispid but hairs deciduous with age so the sheath often seems scabrous only, adaxially shiny and sparsely hispid toward the apex or sometimes the whole upper half hispid, the margins glabrous, the base often densely pubescent, fused for ca. 2.3 cm above the base; sheath summit extensions lacking; inner ligule 1–2 mm long, a short, stiff rim; outer ligule absent; blades 2.5–8.4 cm long, persistent, triangular, abaxially scabrous, adaxially glabrous and shiny, the margins glabrous, the apex acuminate; girdle asymmetrically developed, 0.3–3.4 mm at widest point, pubescent, prominent only in the region of the bud complement where the sheath scar dips markedly forming a flap through which the lowermost subsidiary branches emerge. **Nodes** at mid-culm only slightly swollen, with one circular central bud subtended by (2–)4–9(–12) smaller subequal subsidiary buds, adventitious roots sometimes present; supranodal ridge conspicuous. **Branching** with central bud rarely developing but sometimes rebranching when developed; lowermost subsidiary buds developing first and emerging through the girdle, the upper ones developing shortly thereafter and emerging through the sheath, forming leafy branches 24–39 cm long, 1.0–3.8 ($\bar{x}$ = 2.5) mm diam, which do not rebranch. **Foliage leaves** 4–6 per complement; foliage leaf sheaths green to greenish-tan mottled, carinate, hispid but often glabrous just below the pseudopetiole and toward the margins, the overlapping margin ciliate; sheath summit extension (0.4–)2.0–8.6 ($\bar{x}$ = 3.4) mm on the overlapping side, (4.0–)8.8–19.2 ($\bar{x}$ = 11.3) mm on the underlapping side; outer ligule 0.5–2 mm long, forming a conspicuous, stiff rim; inner ligule (7–)11–30 mm long, elongate, asymmetrical; pseudopetiole ca. 2.5 mm long, more or less distinct, adaxially scabrid, occasionally with few sparse hairs, abaxially glabrous; blades 14–25.6 cm long, 0.9–2.3 cm wide, L: W = 9–16, linear-lanceolate, adaxially scabrid, not tessellate, abaxially glabrous and weakly tessellate, the base attenuate-rounded the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex acuminate. **Synflorescences** 10.5–27.5(–45) cm long, 0.5–1.5 cm wide, narrowly paniculate, usually not exerted at maturity, when exerted, up to 4 cm of peduncle visible beyond subtending sheath; peduncle 4.5–9 cm long, grooved on both sides to nearly flat on one side and grooved on the other, glabrous; rachis puberulent, one side slightly rounded, the other ridged; branches appressed, arising only from the ridged side of the rachis, angular, 5–6 cm long at the base of the rachis, puberulent; pulvinus not visible; pedicels 1–4 mm long, angular, grooved, pubescent. **Spikelets** 6.8–9 mm long, 1.5–1.8 mm wide, terete, lanceolate, slightly falcate; glumes I and II scale-like; glume I 0.5–0.6 mm long, less than 1/10 the spikelet length, glabrous, nerves lacking; glume II 0.8–1 mm long, ca. 1/10 the spikelet length, apically obtuse, abaxially pubescent, nerves lacking;

glumes III and IV mucronate to short awned, abaxially pubescent on the upper half, adaxially pubescent just below apex, marginally ciliate toward apex, 5-nerved; glume III 3.1–4.5 mm long, 1/2–3/5 the spikelet length, triangular, the mucro or awn 0.3–0.6 mm long; glume IV 4.1–5.5 mm long, 5/8–3/4 the spikelet length, lanceolate, the mucro or awn (0.4–)0.6–0.7 mm; lemma 6.6–7.6 mm long, lanceolate, apiculate, abaxially scabrous-pubescent on the upper half, adaxially pubescent just below apex, marginally ciliate toward apex, 7-nerved; palea 6.4–7.7 mm long, lanceolate, 2-keeled, sulcate only toward the apex, apiculate, abaxially scabrous-pubescent between the keels, otherwise scabrid toward apex, 4-nerved. **Lodicules** 1.5–1.9 mm long, the posterior lodicule narrower than the anterior pair, all ciliolate on the upper margins. **Anthers** 3.3–4.5 mm long, greenish-yellow to tan. **Caryopsis** unknown. Figure 12.

Distribution and Habitat—Costa Rica and Panama; cloud forests, often in disturbed areas; 1100–2300 m. One collection from 1964 (*Booth 161*) was recorded at 2600 m, but this estimate is likely inaccurate. A collection from Limón, Costa Rica (*Davidse et al. 28722*) was recorded at 2300–2400 m, while a collection from Heredia, Costa Rica, was recorded at 2100–2380 m; examination of collection locations using satellite imagery indicate that these collections were likely made at the lower end of these elevational ranges.

Phenology—Flowering specimens in Cartago and Guanacaste, Costa Rica in 1976 (*Croat 36232*) and 1995 (*Aguilar et al. 4406*, and *Haber & Zuchowski 11864*) indicate a possible flowering cycle of 19 yr. A flowering specimen was also collected in San José, Costa Rica, in 1990 (*Pohl 15737*). Flowering specimens were collected between 1985 and 1988 in the Chiriquí and Bocas del Toro border area of Panama (*McPherson 6796, 8084*, and *8384* and *Thompson 4943*), though it is unknown whether flowering was gregarious or sporadic.

Additional Specimens Examined—**COSTA RICA**. —ALAJUELA: Cantón de San Ramón, R. B. Monteverde, Cordillera de Tilarán, Valle del Río Peñas Blancas, [10.3208°, –84.775°], 1600 m, 22 July 1993, *Bello 5164* (CR, ISC, MO, US) [pathological specimen]; Km 15–16, N of San Ramón, [10.33°, –84.40°]*, 1030 m, 30 July 1982, *Pohl & Clark 14115* (CR, ISC, MO, US); 3.5 km N. of La Paz, [10.23°, –84.17°]*, 1160 m, 15 December 1984, *Pohl & Clark 14579* (CR, ISC, MO, US). **CARTAGO**: Tapantí Hydroelectric Reserve trail along Río Dos Amigos, [9.69°, –83.79°], 1600–1700 m, 23 June 1976 (fl), *Croat 36232* (MO, US); Reserva de Tapantí, [9.7811°, –83.8122°], 1300–1800 m, November 1982, *Gómez 18866* (CR, ISC, MO, 7US); Alto Patillos, NE of Tapantí, along road to Turrialba, [9.75°, –83.67°]*, 1500–1600 m, 20 August 1982, *Pohl 14139* (CR, ISC, MO); Side canyon, Río Grande de Orosi, s. of Tapantí, near tunnel portal, [9.77°, –83.80°]*, 1500 m, 9 June 1973, *Pohl & Selva 12886* (CR, ISC, MO, US); Ca. 8 km S of Cartago by air. Finca El Chaparral. 4.5 km S of bridge on Agua Caliente at Lourdes, [9.8167°, –83.9167°], 1500 m, 21 April 1983, *Liesner & Judziewicz 14607* (CR, ISC, MO, US); Near a quebrada by a small bridge just above Santa Cruz [9.8833°, –83.7417°], 1500 m, 28 May 1989, *Clark et al. 493* (CR, ISC, MO, US); Cantón de Paraiso, Valle del Reventazón, Oroz, Mirador Ecológico Monte Sky, Entre los Ríos Lajas y Blanco, [9.7444°, –83.8333°], 1700–2000 m, 24 September 1995 (fl), *Aguilar et al. 4406* (CR, ISC, MO, US). —**GUANACASTE**: Cantón de Abangares, Cordillera de Tilarán. Reserva Santa Elena. Sendero Youth Challenge, 4 km N of Santa Elena Village, [10.3667°, –84.7833°], 1700 m, 2 January 1995 (fl), *Haber & Zuchowski 11864* (CR, ISC, MO, US). —**HEREDIA**: Volcano Barva, wet submontane forest, at end of road, [10.14°, –84.11°]*, 2600 m, 14 August 1964, *Booth 161* (US); North end of Cerros Las Marías, N slope of Volcán Barva, [10.175°, –84.1083°], 2100–2380 m, 19 April 1986, *Grayum 7267* (ISC, MO) [pathological specimen]; Forest along ridge between Río Sardinal and headwaters of Quebrada Arrayanes, N slope of Volcán Barva, [10.2°, –84.1167°], 1850–2000 m, 20 April 1986, *Grayum 7304* (CR, ISC, MO); Route 9, S of the Vara Blanca intersection, between Km 28 & 29, [10.16°, –84.12°]*, 1930 m, February 28, 1982, *Clark & Clark 277* (CR, ISC, MO, US); 0.5 km E. of Vara Blanca intersection, [10.18°, –84.15°]*, 2000 m, 23 June 1982, *Pohl 14074* (CR, ISC, MO, US); Alto del Roble, near Río Las Vueltas, [10.09°, –84.07°]*, 2000 m, 8 December 1974, *Pohl & Lucas 12998*

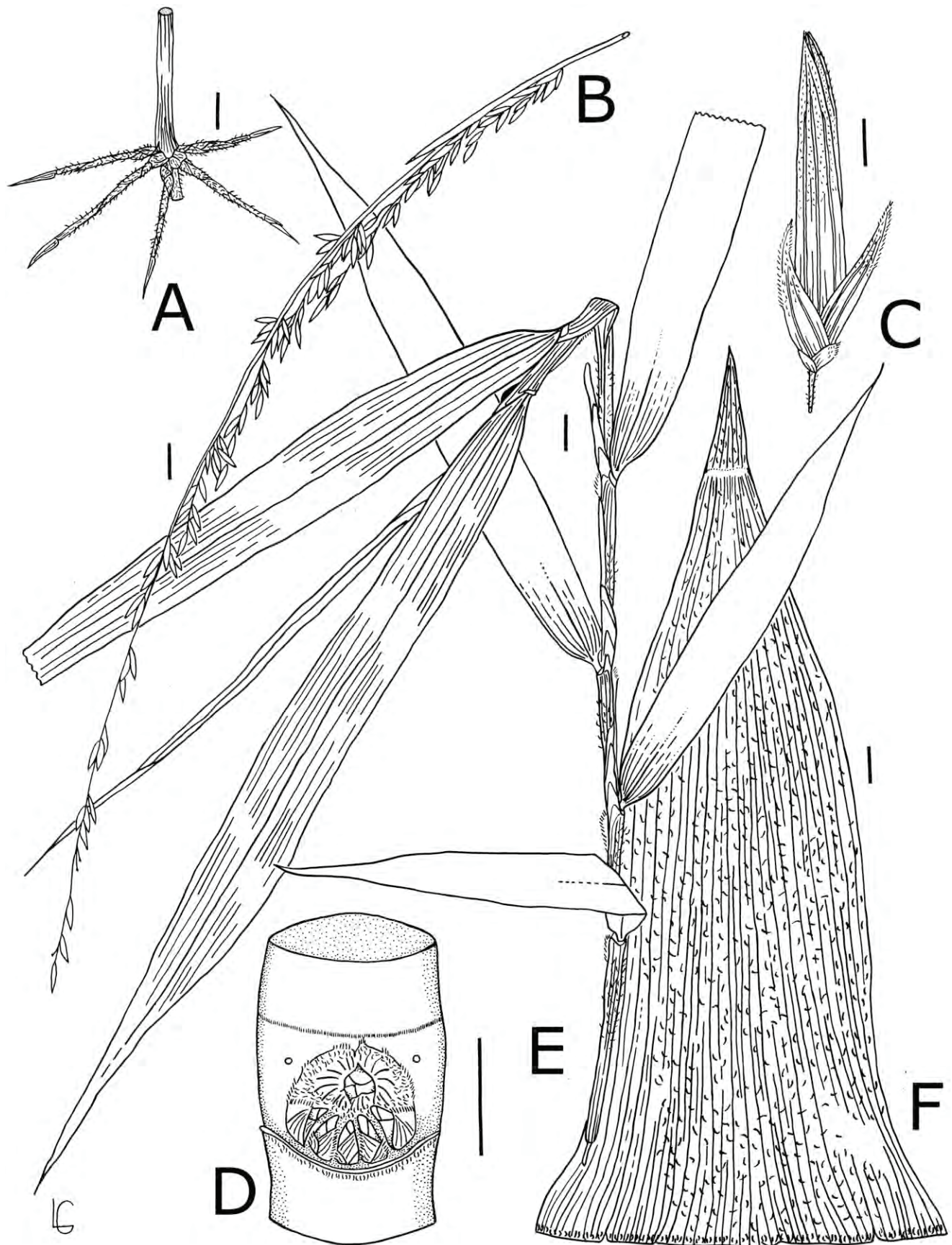


FIG. 12. *Chusquea pohlii*. A. Node with branches emerging infravaginally. B. Synflorescence. C. Spikelet. D. Bud complement. E. Leafy branch. F. Culm leaf. A and D–F are based on Clark & Clark 275, and B–C on Croat 36232. Scale bars: 1 cm (A, B, D, E, F), 1 mm (C). Adapted from Fig. 2 of Clark 1985.

(ISC, US); Alto del Roble, Río Las Vueltas, ca. 10 km NNE of Heredia, [10.90°, -84.07°]*, 2000 m, 8 December 1978, *Pohl & Gabel 13675* (ISC) & 13676 (ISC, US); Alto del Roble, along Río Vueltas (upper Río Patria), [10.90°, -84.07°]*, 2000 m, 4 March 1982, *Clark et al. 281* (CR, ISC, MO, US); Alto del Roble: along Río Las Vueltas at bridge, [10.15°, -84.08°]*, 2000 m, 8 January 1988, *Pohl 15653* (CR, ISC); Hda. Cayuga. Shaded banks above river, [9.89°, -84.16°]*, 1550 m, 1 January 1985, *Pohl & Clark 14606* (ISC); Parque Nal. Braulio Carrillo Sendero del Transecto, [10.1828°, -84.1067°], 2000 m, 15 August 1992, *Boyle 1017* (CR, ISC). —LIMÓN: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, along the Río Tercebi, 0.5–1.5 airline km W of the Costa Rican-Panamanian border, [9.1333°, -82.95°], 2300–2400 m, 9 September 1984, *Davidse et al. 28722* (CR, ISC, MO). —PUNTARENAS: Cerro Amigos, Monteverde; tricorner of Provs. of Puntarenas, Alajuela, and Monteverde, [10.31°, -84.80°]*, 1840 m, 12 April 1983, *Judziwicz 4629* (ISC, MO, US, WIS); Monteverde, along forest road in forest preserve, [10.31°, -84.08°]*, 1500 m, 2 June 1976, *Pohl & Pinette 13246* (CR, F, ISC, MO, US); Monteverde: Along horse trail through Biological Reserve, [10.31°, -84.81°]*, ca. 1700 m, 10 March 1990, *Pohl 15734* (CR, ISC, MO); Reserva Biológica Monteverde Road to divide, swamp on continental divide (Sendero Pantanos), and Sendero Chomogo [10.3°, -84.7833°], 1500–1600 m, 16 July 1990, *Haber & Zuchowski 10027* (CR, ISC, MO, US). —SAN JOSÉ: Cascajal, Brow of hill above Bajo de la Maquina, [9.92°, -84.07°]*, 1650 m, 18 February 1990, *Pohl 15712* (CR, ISC, MO); along road N of Cascajal, N of Río Cascajal, [9.92°, -84.07°]*, 1600 m, 22 July 1982, *Pohl 14101* (CR, ISC, MO, US); along CIA, km. 48, [9.73°, -84.09°]*, 1500 m, 17 June 1982, *Pohl 14067* (CR, ISC, US); Parque Nacional Braulio Carrillo, S boundary, 2 km S of Bajo de Hondura, [10.05°, -83.99°]*, 1400 m, 26 July 1982, *Pohl & Clark 14104* (CR, ISC, MO, US); Parque Nacional Braulio Carrillo s. of Bajo de Hondura, [10.07°, -83.98°]*, [1150–1200 m]*, 13 March 1990 (fl), *Pohl 15737* (CR, ISC, MO, US); New road to Guapiles, 2 km s. of tunnel, [10.14°, -83.99°]*, [1100 m]*, 13 February 1989, *Pohl 15691* (CR, ISC). **Panama.** —Bocas del Toro: On gravel road branching N from main Fortuna Dam-Chiriquí Grande road, 1.1 miles from junction, [8.75°, -82.25°], c. 1200 m, 11 March 1985 (fl) *McPherson 6796* (ISC, MO); N of Fortuna Dam on road to Chiriquí Grande, [8.75°, -82.25°], c. 1150 m, 18 January 1986 (fl), *McPherson 8084* (ISC, MO). —CHIRIQUÍ/Bocas del Toro: ca. 5 km N of Fortuna Dam, trail along Continental Divide, [8.75°, -82.25°], 1200–1300 m, 25 April 1988 (fl), *Thompson 4943* (ISC, MO). —CHIRIQUÍ: Distrito Bugaba, Cerro Punta, from STRI house to mountain across the river, [8.8667°, -82.55°], 2200 m, 24 January 1985, *Van der Werff & Herrera 6345* (ISC); Fortuna Dam region, [8.75°, -82.25°], c. 1100 m, 10 February 1986 (fl), *McPherson 8384* (ISC, MO, US) & 8392 (ISC, MO, US).

CHUSQUEA SERPENS L.G.Clark, Ann. Missouri Bot. Gard. 72: 867, fig (1985). TYPE: COSTA RICA. Alajuela: edge of Valley of Río Cariblanco, Cariblanco, [10.26°, -84.18°]*, 839 m, 26 August 1968 (fl), *Pohl & Davidse 11023* (holotype: ISC! [278246, barcode ISC-v-0000996; 278247, barcode ISC-v-0000995]; isotypes: K [barcode K000433242], MO [2927977, barcode MO-356322; 3181343, barcode MO-356323], US [2835729, barcode 00074596; barcode 00381556]).

Rhizomes unknown. **Culms** 0.5–1 cm diam, 2–20 m long, scandent or vining, often trailing for part of their length. **Internodes** 17–35 cm long, terete but often shallowly sulcate above the primary bud, solid, retrorsely scabrous for most of their length, glabrous just above the node, green to green mottled with purple. **Culm leaves** 10.0–20.1 ($\bar{x}$ = 15.3) cm long, deciduous, chartaceous, juncture of sheath and blade horizontal; sheaths 6.5–11.5 ($\bar{x}$ = 9.1) cm long, (1–)1.5(–2) ($\bar{x}$ = 1.6) times as long as the blades, abaxially glabrous to verrucose with sometimes numerous rigid hairs, adaxially glabrous, the overlapping margins densely ciliate, nearly glabrous on the internal side, not fused at the base; sheath summit extensions lacking; inner ligule 0.5–0.8 mm long, forming a short, ciliate rim; outer ligule absent; blades 3.0–8.4 ($\bar{x}$ = 6.1) cm long, moderately to distinctly cordate, narrow at the base, abaxially glabrous except at the base, where glabrous to densely pubescent, adaxially glabrous, the margins glabrous to ciliate, the apex setose; girdle 2.0–5.0 mm wide, densely pubescent, more

or less prominent, forming a flap through which the branches emerge, disintegrating before the rest of the culm leaf. **Nodes** at mid-culm slightly swollen, with one triangular central bud subtended by 2 smaller subequal subsidiary buds, adventitious roots sometimes present, especially at nodes trailing on ground; supranodal ridge conspicuous. **Branching** sometimes arising from a promontory, with central bud often developing into a robust branch more or less equal in size to the main culm, this branch rebranching extensively, forming a long clambering network; subsidiary branches developing into leafy branches 15–35 cm long, (1.6–)2.7–5.5 ($\bar{x}$ = 3.4) mm diam, rarely rebranching. **Foliage leaves** 3–7(–16) per complement; foliage leaf sheaths green, carinate, glabrous to scabrous, sometimes pubescent farther from blade, the overlapping margin ciliate; sheath summit extension absent; outer ligule 0.5–1.6 (–2.5) ($\bar{x}$ = 1.2) mm long, conspicuous, stiff; inner ligule 1.0–1.9(–2.5) ($\bar{x}$ = 1.7) mm long, symmetrical, truncate, chartaceous; pseudopetiole 3–12 ($\bar{x}$ = 7.5) mm long, distinct, adaxially glabrous, abaxially glabrous to having sparse hairs; blades 11.5–35.8 ($\bar{x}$ = 22.7) cm long, 1.8–5.0 ($\bar{x}$ = 3.3) cm wide, L: W = 5.1–9.1 ($\bar{x}$ = 6.9), linear-lanceolate, adaxially glabrous, not tessellate, abaxially mostly glabrous and pilose only near the apex to entirely pilose, not tessellate to weakly so, the base rounded-truncate; midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex tapering, setose. **Synflorescences** 33–50(–63.4) cm long, ca. 1.0 cm wide, narrowly paniculate, exerted 4.8–7.8 cm at maturity; peduncle 5.0–12.5 cm long, one side flat to slightly grooved, the other rounded, glabrous; rachis glabrous or pilose, one side flat and slightly ridged, the other rounded; branches appressed, second, arising only from the flat, slightly ridged side of the rachis, angular, 5–9 cm long at the base of the rachis, becoming progressively shorter toward the apex, the spikelets eventually arising directly from the rachis; pulvinus generally not visible, occasionally seen as slight swelling at base of pedicel; pedicels 1–5(–7) mm long, angular, glabrous to pilose. **Spikelets** 11.3–14.6 ($\bar{x}$ = 12.7) mm long, 1.2–2.2 mm wide, terete, straight, glabrous; glume I 1.2–2.5 ($\bar{x}$ = 2.0) mm long, 1/10 or slightly more the spikelet length, broadly acute, 1-nerved; glume II 3.5–7 ($\bar{x}$ = 4.9) mm long, 1/3–1/2 the spikelet length, awned, the awns 1.5–3.0 mm, 1- or 3-nerved; glumes III and IV awned; glume III 5.4–8.6 ($\bar{x}$ = 7.6) mm long, ca. 2/3 the spikelet length, the awn 2.0–3.5 mm long, (5–)7(–9)-nerved; glume IV 7.7–9.9 ($\bar{x}$ = 8.5) mm long, 3/4 or slightly more the spikelet length, keeled, the awn 0.9–3.0 mm, (4–), 7-, 9-, or 11-nerved; lemma 10.6–13.2 ($\bar{x}$ = 11.5) mm long, boat-shaped, shiny, short-awned, the awn 0.8–2.0 mm long, usually obscurely 7–18 nerved; palea 10.1–11.5 ($\bar{x}$ = 10.8) mm long, sulcate, shiny, apiculate, marginally ciliate toward the apex, 2–4(–8)-nerved. **Lodicules** unknown. **Anthers** 4.4–7.5 mm long, greenish-yellow to cream. **Caryopsis** unknown. Figure 13.

Distribution and Habitat—Costa Rica to Venezuela, Colombia, and Ecuador; cloud forests; (400–)800–1650 m. *Chusquea serpens* is the most widespread species in *C. sect. Serpentes*, and the only species in the section occurring in both Central and South America.

Phenology—A gregarious blooming episode was recorded in 1968 in Costa Rica (*Pohl & Davidse 11023, 11033, 11176*, and 11267, *Pohl & Pinette 13224*) followed by regeneration of the population, with no known fertile collections since. A gregarious blooming was also recorded in 1940–1942 in Colombia, at which time a flowering specimen was also collected from Venezuela. Although another flowering specimen was

collected from Venezuela in 1978, it is unclear whether this specimen was taken from a gregarious blooming event. If widespread blooming did occur in 1978, a 36–38 yr cycle could be hypothesized for the South American populations of *C. serpentes*.

Additional Specimens Examined—Colombia. —ANTIOQUIA: P.N. Natural “Las Orquídeas”, Sector Calles, margen derecho del río Calles, 1420 m, [6.5333°, –76.3167°], 25 March 1988, *Cogollo et al.* 2610 (JAUM, MO); Zona limitrofe del Parque Nacional Natural de Las Orquídeas. Vereda Calles. Margen izquierda del Río Calles, [6.5333°, –76.3167°], 1450–1500 m, 30 November 1993, *Pipoly et al.* 17396 (ISC, MO, US); Mpio. Urao, carretera a La Encarnación, [7.42°, –75.5°]*, 1570 m, 10 September 1986, *Pohl & Betancur* 15483 (HUA, ISC, MO, US); Municipio Jardín: Vereda Las Manguitas, 18 km oeste de Jardín, [5.58°, –76.14°]*, 1500 m, 19 September 1986, *Pohl & Betancur* 15570 (HUA, ISC, MO). —CAQUETA: Cordillera Oriental, vertiente oriental, Sucre, [1.79°, –75.66°]*, [1300–1400 m]*, 4 April 1940 (fl), *Cuatrecasas* 9068 (COL, F, US); San Antonio de Atenas La Esperanza Alto Río Ortega, Florencia, [1.66°, –75.55°]*, 1040 m, 7 March 1991, *Barbosa & Kobayashi* 6895 (ISC). —HUILA: Río Ambicá, near Quebrada San Pedro, 18 km SE of Colombia, [3.28°, –74.69°]*, [1300–1350 m]*, 24 December 1942 (fl), *Fosberg & Holdridge* 19568 (US). META: Las Lagartijas, plateau between Río Papamene and Río Duda, Colombia-Urube trail, 8–9 km SW of Uribe, [3.16°, –74.38°]*, [550 m]*, 22 December 1942 (fl), *Fosberg* 19504 (US). —VALLE DEL CAUCA: Mun. Dagua, old road between Cali and Buenaventura, 4.2 km SW of Queral, [3.5°, –76.7333°], 1380 m, 30 June 1994, *Clark & Londoño* 1253 (COL, ISC, TULV, US); Km 51 carretera vieja Cali–Buenaventura, [3.78°, –76.74°]*, 400 m, 14 February 1987, *Londoño & Quintero* 175 (TULV). COSTA RICA. —ALAJUELA: Cariblanco, across bridge N or village, along Río Cariblanco, [10.42°, –84.41°]*, 800 m, 6 March 1982, *Clark et al.* 283 (CR, ISC, MO, US); Cataratas de San Ramón, [10.12°, –84.53°]*, [1000–1100 m]*, 5 October, 1976, *Ocampo* 1326 (CR, ISC, US); edge of valley of Río Cariblanco, Cariblanco, [10.26°, –84.18°]*, 830 m, 4 September 1968 (fl), *Pohl & Davidge* 11033 (ISC, US), 29 September 1968 (fl), *Pohl & Davidge* 11176 (ISC), 17 October 1968 (fl), *Pohl & Davidge* 11267 (ISC), 15 June 1976, *Pohl & Pinette* 13224 (ISC, MO), 5 February 1989, *Pohl* 15687 (CR, ISC, MO). —CARTAGO: 10 km S of Cartago by air, along confluence of Río Empalme and Río Estrella, 1 km S of Palo Verde by road, [9.7667°, –83.95°], 1450 m, 21 April 1983, *Liesner & Judziwicz* 14538 (CR, ISC, MO); Tausito, above Tapanti on road to Turrialba, [9.78°, –83.77°]*, 1800–2000 m, 23 April 1990, *Pohl* 15769 (CR, ISC, MO). —HEREDIA: Primary forest between Río Peje and Río Sardinálito, Atlantic slope of Volcán Barva, [10.2917°, –84.075°], 700–750 m, 5 April 1986, *Grayum & Jermy* 6777 (CR, ISC, MO). —SAN JOSÉ: Tinamastes, 13 km SW of San Isidro del General on road to Dominical, [9.30°, –83.77°]*, 1050 m, 1 November 1982, *Pohl* 14187 (CR, ISC, MO, US); 3 km by road NE of Tinamastes, [9.30°, –83.77°]*, 1020 m, 11 January 1985, *Pohl & Clark* 14622 (CR, ISC, MO, US); Tinamastes, 13 km W. of San Isidro del General, road to Dominical, [9.30°, –83.77°]*, 920 m, 27 March 1990, *Pohl* 15742 (CR, ISC, MO, US). ECUADOR. —MORONA SANTIAGO: Cordillera del Cóndor, Cuangos, 20 km east of Guilaquiza, near disputed Peru-Ecuador border, [–3.4833°, –78.2333°], 1510 m, 18 July 1993, *Gentry* 80045 (MO, QCNE); Cantón Morona, Parroquia Sinaí, Sector Sinaí, por la salida al Cementerio, [–2.1017°, –78.0575°], 1247 m, 17 November 2020, *Londoño* 2049 (ECUAMZ). NAPO: 5 km E of the town of Reventador on the road to Lumbagui, [–0.25°, –77.6667°], 1330 m, *Young* 101 (QCA, MO, US). PANAMA. —Bocas del Toro: Between Buenavista coffee finca and Cerro Pilón, on Chiriquí trail, cloud forest, [8.8°, –82.1833°], 17 April 1968 (fl), *Kirkbride & Duke* 692 (MO). —CHIRIQUÍ: vicinity of Gulaca, ca. 8.5 mi from Planes de Hornito, La Fortuna on road to damsite, [8.70°, –82.23°]*, ca. 1340 m, 10 July 1980, *Antonio* 5089 (ISC, MO, US). PANAMA/Colombia. —DARIÉN/CHOCÓ: Alto de Nique, southernmost peak of Cerro Pirre massif, [7.73°, –77.74°]*, 1300–1520 m, 19 April 1980, *Gentry et al.* 28692 (ISC, MO, US). VENEZUELA. —LARA: Dttto. Morán, road between Guarico and Villa Nueva, going toward Villa Nueva a little past hill, [9.59°, –69.77°]*, 1640 m, October 1978 (fl), *Burandt* V0457 (ISC, MO); Parque Nacional Yacambú, about 6–10 km from main entrance, at a picnic area, [9.70°, –69.59°]*, 1350–1400 m, 14 January 1982, *Clark et al.* 231 (ISC, MO, US); Guárico: On the road to Villa Nuevita, 8 km from Guárico, [9.70°, –69.59°]*, 1520–1550 m, 15 January 1982, *Clark et al.* 232 (ISC, MO, US); Guárico, San Isidro, [8.00°, –66.17°]*, [1600 m], 12 September 1942 (fl), *Tamayo* 2476 (VEN).

CHUSQUEA VIRGATA Hack., Oesterr. Bot. Z. 53: 156 (1903). TYPE: COSTA RICA. San José: San Marcos de Tarrazú, [9.66°, –84.01°]*, 1350 m, March 1893 (fl), *Tonduz (Pittier)* 7730 (holotype: W [12134, barcode W19160012134]; isotypes:

CR [7730, barcode CR7730], ISC! [280938, barcode ISC-v-0001010], US [1021540, barcode 00074243; 471816, barcode 00074244; 2874670, barcode 00133422]).

Rhizomes pachymorph, short-necked. **Culms** 4–8(–15) m long, 0.7–2 cm diam, weak, scrambling into brush and trees, the tips arched or drooping. **Internodes** 9–21 cm long, terete, solid, glabrous, green to green marbled with purple. **Culm leaves** 10.5–15.3 cm long, persistent, chartaceous, juncture of sheath and blade concave, often obscure from abaxial side, rounded or angular; sheaths 9.5–12.3 cm long, abaxially glabrous, purplish when fresh, brown in older specimens, strongly and closely ridged, not tessellate, adaxially glabrous, weakly tessellate, the margins glabrous, fused to only 2–3 mm above the base; sheath summit extensions absent; inner ligule ca. 1–1.5 mm long, an erose membrane, glabrous with the margin ciliate; outer ligule absent; blades 1.0–4.4 cm long, persistent, triangular, abaxially glabrous, adaxially glabrous to scabrous, the margins glabrous, the apex acuminate to acute; girdle 1.6–3.0 mm, prominent, glabrous, dipping slightly beneath branches. **Nodes** swollen, at mid-culm with one broadly triangular central bud subtended by 2–9 smaller subequal subsidiary buds; supranodal ridge evident. **Branching** with central bud sometimes not developing and when developing, only slightly larger than the minor branches, subtended by a row of flattened subsidiary buds; subsidiary branches few, usually ca. 5 per node, (12–)19–50 cm long, 0.9–3.5 ($\bar{x}$ =1.9) mm diam, with a few leaves borne towards their tips, not rebranching. **Foliage leaves** 3–6 per complement; foliage leaf sheaths green, carinate, though sometimes weakly so, glabrous, the overlapping margin finely ciliate to glabrous; sheath summit extension absent; outer ligule ca. 0.5 mm long, a conspicuous rim, slightly reflexed, glabrous to sometimes ciliate; inner ligule ca. 1 mm long, truncate, membranous; pseudopetiole 1–3 mm long, distinct, flattened, adaxially glabrous, abaxially glabrous near margins, with stiff tan hairs surrounding midrib; blades 7.5–17 cm long, 1.6–3.3 cm wide, L: W = 3.2–5.2, ovate to lanceolate, adaxially glabrous, not tessellate, abaxially glabrous except for a line of short, stiff, tan hairs on each side of the midrib just above base of blade, not tessellate to very weakly tessellate, the base rounded, often asymmetrically so, sometimes attenuate-rounded, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex abruptly acuminate. **Synflorescences** (5.2–)10.5–16.5 cm long, 1–1.5 cm wide, narrowly paniculate, usually not exerted at maturity, sometimes exerted up to ca. 1 cm; peduncle (2.7–)4.0–12.8 cm long, rounded, slightly grooved on one side, glabrous; rachis glabrous, grooved on one side, flat on the other; branches slender, appressed, ca. 3 cm long at the base of the rachis, glabrous; pulvinus not visible; pedicels (1.6–)5.0–8.0 mm long, variable in length even on the same specimen, slender, erect, rounded to slightly flattened, often sinuate, glabrous, with spikelets set at an angle of ca. 30° to the pedicel. **Spikelets** 6.8–10.2 mm long, 1.0–1.8 mm wide, terete, linear, falcate; glumes I and II reduced, semicircular, nerveless, their margins overlapping, glabrous; glume I 0.2–0.3 mm long, ca. 3/100 the spikelet length; glume II 0.3–0.5 mm long, less than 1/20 the spikelet length; glumes III and IV with tips diverging from lemma, glabrous, 1- or faintly 2–3-nerved; glume III 2.5–3.4 mm long, 1/3–2/5 the spikelet length, acute; glume IV 3.4–4.2 mm long, ca. 2/5 the spikelet length, acuminate, keeled near apex; lemma 6.5–10.0 mm long, linear, subcylindrical, arcuate, acute, its margins covering the palea, glabrous, 7-nerved, nerves faint; palea essentially equal in length to lemma, rounded to the keels,

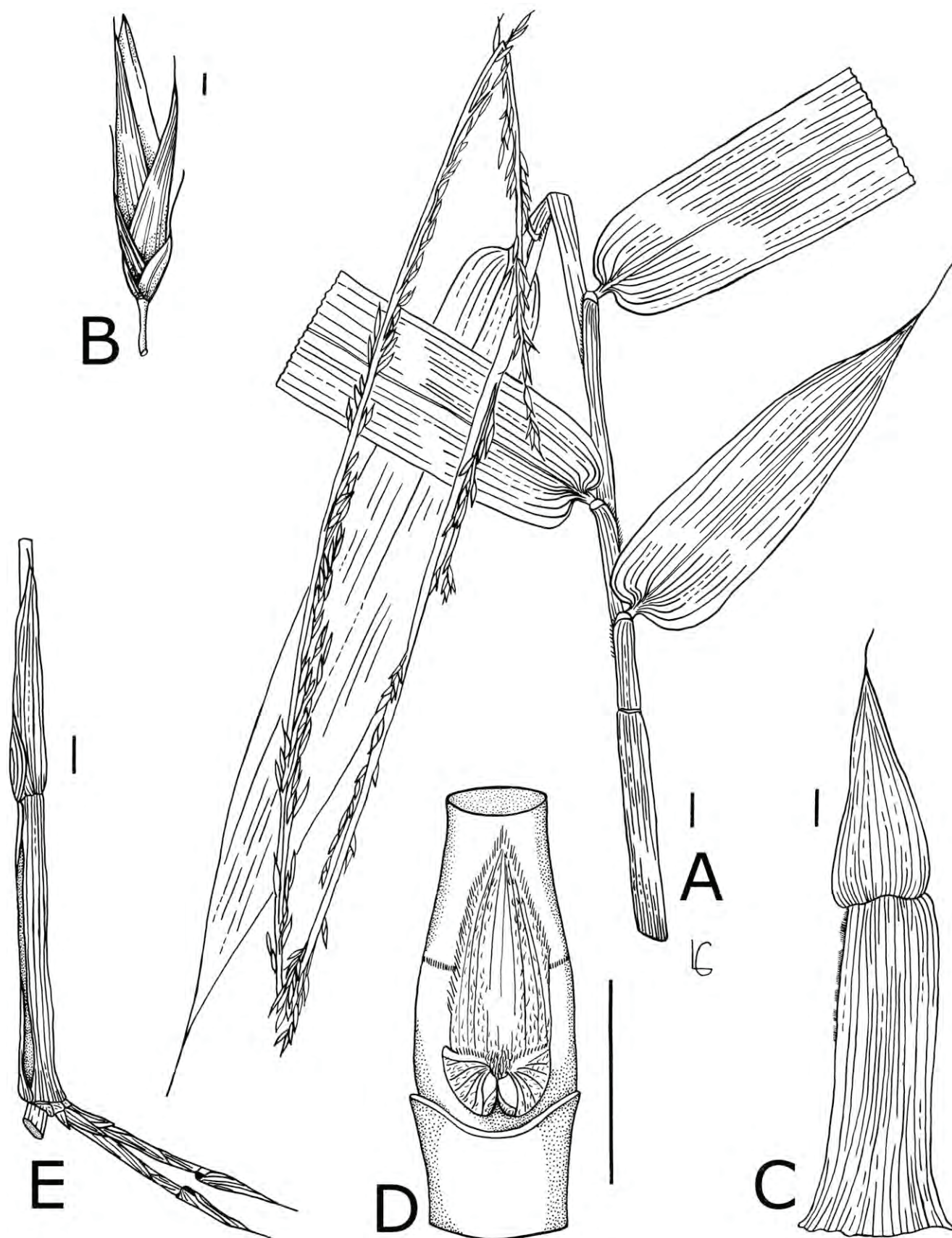


FIG. 13. *Chusquea serpens*. A. Flowering branch. B. Spikelet. C. Culm leaf. D. Bud complement. E. Node with branches emerging infravaginally. A is based on Pohl & Davidse 11023, B on Pohl & Davidse 11176, C on Young 101, and D-E on Clark 283. Scale bars: 1 cm (A, C, D, E), 1 mm (B). Adapted from Fig. 4 of Clark 1985.

a deep groove between the keels, 4-nerved. **Lodicules** flat, vasculated, broadly spatulate, the tips densely ciliate with long hairs. **Anthers** 3.8–5.5 mm long, yellow. **Caryopsis** 5.0–7.0 mm long, brown to reddish brown, embryo 0.5–0.9 mm long, hilum linear, style bases persistent. Figures 14, 15.

Distribution and Habitat—Costa Rica and Panama near the Costa Rica border; along streams, ravines, and roadsides, usually in montane forests; 1300–2000 m.

Phenology—A large colony in Heredia and San José provinces, Costa Rica, exhibited continuous gregarious flowering from January 1988 to at least April 1989 (Pohl 15662 and 15672), with the colony fruiting and dying by February 1990 (Pohl 15706 and 15728, Grayum et al. 9703). Other recorded blooms in La Peña de Zarcero, Tapesco, and Río Segunda, Barba, all in southern Alajuela province, in 1938, 1940, and 1941, respectively, as well as Tapesco, Alajuela and Frailes, San José in 1965 (Pohl 1980), indicate a possible cycle of about 23–27 yr.

Additional Specimens Examined—**COSTA RICA**.—ALAJUELA: La Peña de Zarcero, Canton Alfaro Ruiz, [10.15°, –84.39°]*, 1525 m, 21 July 1938 (fl), Smith NY993 (ISC).—CARTAGO: 3 km N.E. of Pacayas; road crossing of Río Birris, [9.92°, –83.79°]*, 1600 m, 4 June 1976, Pohl & Pinette 13304 (CR, ISC, MO, US); n. side of Río Navarro, [9.81°, –83.97°]*, ca. 1300 m, 9 July 1982, Pohl 14090 (CR, ISC, MO).—HEREDIA: 2.5 km by road n. of San José de la Montaña, at stream crossing, [10.07°, –84.11°]*, [1650–1700 m]*, 7 December 1978, Pohl & Gabel 13670 (CR, ISC, MO, US); Road crossing of Río Porros, 2.7 km n. of San José de la Montaña, [10.11°, –84.11°]*, 1670 m, 29 July 1982, Pohl & Clark 14111 (CR, ISC); 2.8 km by road above (north of) San José de la Montaña church. East of road at new bridge, [10.07°, –84.11°]*, 1650 m, 18 January 1988 (fl), Pohl 15662 (CR, ISC, MO, US); 2.8 km n. of San José de la Montaña, [10.07°, –84.11°]*, 1650 m, 24 January 1989 (fl), Pohl 15672 (CR, ISC, MO, US). PUNTARENAS: La Amistad National Park, at campground n. of La Tigra, [8.95°, –82.7833°], 1430 m, 14 July 1982, Pohl 14093 (CR, ISC, MO, US); Cordillera de Talamanca, area between headwaters of Río Bella Vista and Sitio Cotón, [9.51°, –83.65°]*, 1600–1800 m, 25 August 1983, Davidse et al. 24052 (CR, ISC, MO, US); Foothills of the Cordillera de Talamanca, lower montane forest directly N of Las Alturas, [8.95°, –82.8333°], 1400–1500 m, 28 August 1983, Davidse 24168 (CR, ISC, MO); Cantón de Coto Brus Cotocito, [8.9333°, –82.775°], 1500 m, 15 April 1989 (fl), Chacón 2458 (CR, ISC, MO). SAN JOSÉ: 2.7 km n. of San José de la Montaña, at a bridge, [10.08°, –84.11°]*, [1650–1700 m]*, 9 February 1990 (fl), Pohl 15706 (CR, MO, ISC); Cantón de Dota: Along Río Pedregoso, ca. 1–2 km (by road) SE of Copey, [9.6417°, –83.9167°], 1940 m, 27 February 1990 (fl), Grayum et al. 9703 (CR, ISC, MO); ca. 2 km S.E. of Copey, along Río Pedregoso, [9.64°, –83.92°]*, 2000 m, 5 March 1990 (fl), Pohl 15728 (CR, ISC, MO, US). **PANAMA**.—CHIRIQUÍ: Río Piedras Candela, 4 miles along logging road into forest, [8.9031°, –82.7108°], 1800–2000 m, 1 May 1973, McAlpin 2202 (MO).

Chusquea sect. Serpentes incertae sedis—These collections clearly represent *C. sect. Serpentes* but are not referable to any described species; some almost certainly represent currently undescribed species.

1) Colombia: Dept. Antioquia: Mun. San Luis: 12.4 km de la entrada a San Luis hacia Medellín, Cordillera Central, ladera Oriental, Autopista Medellín-Bogotá, bosque 500 mts. mas adentro, bmh-T, [5.9957°, –74.9957°], 800 m, 15 September 1988 (fl), Betancur et al. 608 (COL, F, HUA, ISC). The pubescence of the foliage leaf sheaths is similar to that of *C. pohlii*, but the foliage leaf inner ligules are only ca. 1 mm long. Unlike *C. pohlii*, the foliage leaf bases are truncate to rounded, and the abaxial midrib of the foliage leaf is pubescent. A single example of a culm leaf sheath was only 11.55 cm long. Spikelets are similar in shape to, but longer than, those of *C. pohlii*, at 10.8–13.4 ($\bar{x}$ = 12.3) mm long (vs. 6.8–9 mm long).

2) Colombia: Dept. Putumayo: Mun. San Francisco de Sibundoy, por la trocha que conduce a la planada de Minchoy, a 150 m del puente que cruza el río Minchoy, a orilla de un tributario, [1.1167°, –76.8°], 2100 m, 7 March 1987, Londoño & Lozano 228 (COL, ISC, TULV). The appearance of the branching pattern is similar to *C. serpens* but with more extensive rebranching of subsidiary branches, which often curve around the culm. Foliage and culm leaf sheaths are pubescent, unlike those of *C. serpens*. Foliage leaves also often have a greater length to width ratio than those of *C. serpens*, with L: W 6.7–12 compared to the 5–9 length to width ratio found in *C. serpens*.

3) Colombia: Dept. Chocó: Mun. San José de Palmar, vereda “La Badea”, [4.90°, –76.24°]*, 920m, 24 January 1983 (fl), Franco et al. 1823 (COL). This specimen is similar to *C. serpens* but shrublike rather than scrambling, with spikelets that are more strongly falcate, and glumes II, III, and IV with short awns ca. 0.5 mm long.

4) Colombia: Dept. Huila: Hills above ranch house, Finca Balsillas, Upper Río Balsillas, 40 km E.S.E. of Neiva, [2.8833°, –74.95°], 1700 m, 7 December 1942, Fosberg 19280 (US); Cordillera Oriental, vertiente occidental, abajo de Gabinete en la hondonada del Abra de San Andrés, bosques, 1900–2100 m, 24 March 1940, Cuatrecasas 8652 (COL, ISC). Foliage leaves are similar to those of *C. serpens*, but branching, at least on floral stems, is more extensive. Spikelets are 8.2–9.7 mm long when mature, with glume I 1–1.5 mm long, glume II 2.5–2.8 mm long, scabrous and mucronate, glume III about 4.5 mm long, scabrous, mucronate, and very finely ciliate at apex, and glume IV 7.0–8.2 mm long, finely ciliate at the apex with fine interior pubescence.

KEY TO THE SPECIES OF CHUSQUEA SECT. SERPENTES BASED ON VEGETATIVE CHARACTERS

1. Foliage leaf inner ligules acute to rarely rounded at the tip. 2
2. Culm leaf margins fused for 2.3 cm above base; subsidiary buds (2–)4–9(–12) per node; subsidiary branches not rebranching; Costa Rica and Panama. *C. pohlii*
2. Culm leaf margins not fused; subsidiary buds 2 per node; subsidiary branches often rebranching; Colombia or Venezuela. 3
3. Foliage leaves 3–4 per complement; foliage leaf inner ligules acute, 1.9–6.7 mm long; central bud triangular; Colombia. *C. acutigluma*
3. Foliage leaves 6–12 per complement; foliage leaf inner ligules acute to rarely rounded, 2.2–8.5 mm long; central bud circular; Venezuela. *C. recurvata*
1. Foliage leaf inner ligules truncate to rounded, never acute. 4
4. Internodes scabrid, with a glaucous white band ca. 0.5 cm wide usually present on younger culms just below the nodal line; eastern-central Mexico. *C. glauca*
4. Internodes glabrous to scabrous or hirsute, lacking a glaucous white band on younger culms below the nodal line; Central or South America. 5
5. Subsidiary buds 2–9 per node; internodes glabrous; subsidiary branch diameter 0.9–3.5 mm; foliage leaf blades 7.5–17 cm long, pseudopetiole with stiff tan hairs surrounding midrib abaxially, glabrous at margins. *C. virgata*
5. Subsidiary buds always 2 per node; internodes usually scabrous for at least part of length, sometimes glabrous; subsidiary branch diameter (1.6–)2.7–5.5 mm; foliage leaf blades 11.5–36 cm long, pseudopetiole abaxially glabrous, occasionally with sparse hairs. 6



FIG. 14. *Chusquea virgata*, Pohl 15672 (ISC).

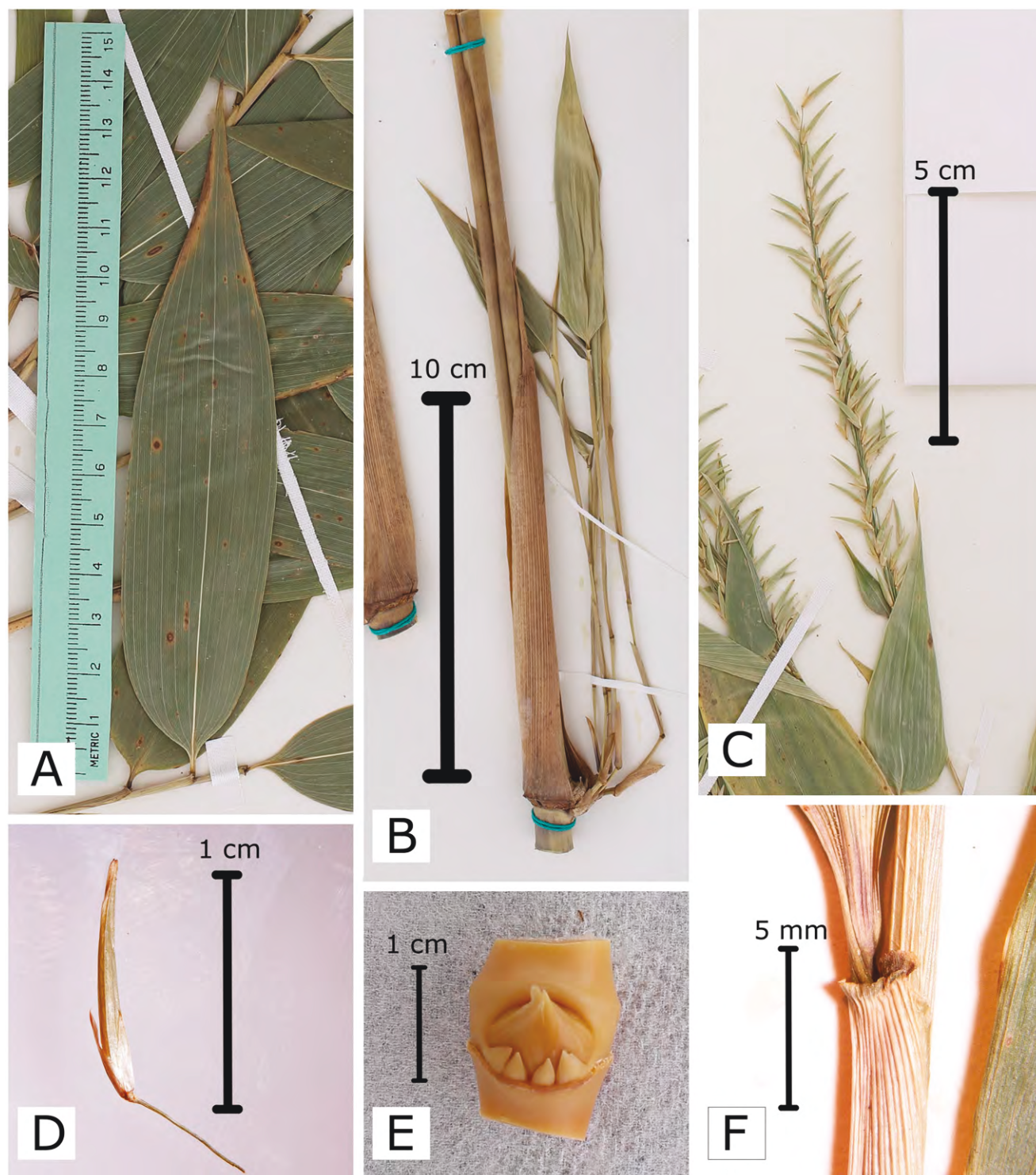


FIG. 15. *Chusquea virgata*. A. Foliage leaf, abaxial surface. B. Culm leaf and immature branch complement displaying infravaginal branching; culm leaf wrapped around culm, abaxial surface visible. C. Synflorescence. D. Spikelet. E. Bud complement showing broadly triangular central bud above four subsidiary buds. F. Foliage leaf ligular region. A is based on *Pohl 14093* (ISC), B and E on *Pohl & Clark 14111* (ISC), with E representing the spirit-preserved component of the collection, C and D on *Pohl 15672* (ISC), and F on *Pohl & Gabel 13670* (ISC).

6. Foliage leaf blades 3–8.5 cm wide, L: W = 2.5–6; culms rebranching extensively from the lower nodes. *C. latifolia*
6. Foliage leaf blades 1.8–5 cm wide, L: W = 5–9; culms rarely or apparently not rebranching. 7
7. Culm leaf sheaths abaxially asperous; foliage leaf inner ligules 2.5–7 mm long; Peru. *C. aspera*
7. Culm leaf sheaths glabrous to verrucose, sometimes with numerous rigid hairs; foliage leaf inner ligules 1–2(–2.5) mm long; Central and South American cloud forests from Costa Rica to the southern border of Ecuador. *C. serpens*

DISCUSSION

Criteria for Circumscription of *Chusquea* sect. *Serpentes*—The most notable features of *Chusquea* sect. *Serpentes*, as described in Clark (1989), include a vining or trailing habit, wide foliage leaves, infravaginal branching, and generally two subsidiary buds per node. All species that we included in the section have these features; although *C. pohlii* and *C. virgata* sometimes have more than two subsidiary buds per node, they have fewer subsidiary buds per node than most other species in *Chusquea* subg. *Chusquea* and differ from species belonging to other sections in that their subsidiary buds are arranged in a single constellate row (Attigala et al. 2017). Reproductive features that Clark (1989) described as common to the section included glumes at least 1/10 the length of the spikelet and usually narrow, often long synflorescences compared to most other species in *C.* subg. *Chusquea* (Clark 1989; Attigala et al. 2017). However, these reproductive characteristics are not unique to *C.* sect. *Serpentes* (Clark and Mason 2019; Ruiz-Sanchez et al. 2021a), nor are they present in all of the species that we placed in *C.* sect. *Serpentes*. Long synflorescences are found in all species in *C.* sect. *Serpentes*, although shorter synflorescences may be found on the same specimens of some species, including *C. acutigluma*. Glumes were usually at least 1/10 the spikelet length, but less than 1/10 the spikelet length in *C. glauca*, *C. pohlii*, and *C. virgata*. Due to the variability seen in reproductive characters in this section, as well as the difficulty in obtaining flowering specimens, we placed greater importance on the vegetative characters of the species examined in this study to determine whether they belonged to *C.* sect. *Serpentes*.

Although *C. pohlii* and *C. virgata* share the vining or trailing habit and wide foliage leaves typical of *C.* sect. *Serpentes* and often have two subsidiary buds per node, they also can have greater numbers of subsidiary buds in a single constellate row, up to nine in *C. virgata* and 12 in *C. pohlii*. The placement of relatively few subsidiary buds in a single constellate row subtending the central bud appears characteristic of *C.* sect. *Serpentes*; other sections of *Chusquea* tend to have subsidiary buds in two or more rows or differing arrangements (Attigala et al. 2017; Fadrique et al. 2019). Other sections of *Chusquea* subg. *Chusquea*, though occasionally having as few as five subsidiary buds, usually have far more, with all other sections containing species that can have at least 30 subsidiary buds, and some having as many as 100 or more (Attigala et al. 2017). The glumes of *C. virgata* also tend to be smaller with relation to the spikelet than those of the rest of the section, though the first glumes of *C. glauca*, firmly placed within *C.* sect. *Serpentes* based on its habit and wide foliage leaves, are only slightly larger. Ultimately, the habit, size of the foliage leaves, infravaginal branching, and relatively few subsidiary buds in a single row, as well as the montane forest habitat of all these species support their placement in *C.* sect. *Serpentes*. Furthermore, the continued placement of *C. gibcooperi* and *C. enigmatica* as incertae sedis within *Chusquea* subg. *Chusquea* is also supported by the criteria used here, as neither species displays a scandent habit and both have extra- and intravaginal branching (Ruiz-Sanchez et al. 2014, 2015). *Chusquea glauca* remains the only described species of *C.* sect. *Serpentes* in Mexico (Fig. 16). The decision to retain *C. virgata* and *C. pohlii* in *C.* sect. *Serpentes* results in three known species of *C.* sect. *Serpentes* in Central America (Fig. 17). With the addition of *C. acutigluma* and *C. recurvata* to the section,

C. sect. *Serpentes* contains five species in South America (Fig. 18), including the widely-distributed *C. serpens*, which is also found in Central America. In the past, low variation in plastid DNA has resulted in the failure to resolve species relationships within the *Euchusquea* clade to which *C.* sect. *Serpentes* belongs (Fisher et al. 2014). However, molecular techniques based on genome-wide analysis of nuclear DNA have facilitated the resolution of other complex bamboo phylogenies (Wang et al. 2017), and could provide another way to test the classification of species in *C.* sect. *Serpentes*.

Recognition of New Species—Identifying undescribed species of *Chusquea* within a given section is complicated by the rarity with which these species flower. Previously described species of *Chusquea* sect. *Serpentes* have been documented flowering at possible cycles of between 19 and 38 yr, with *C. latifolia*, *C. serpens*, and *C. virgata* appearing to have gregarious flowering (Clark 1989). Specimens of *C. acutigluma* were found in flower, allowing for direct comparison with flowering *C. serpens*, to which *C. acutigluma* is vegetatively very similar. However, no flowering specimens of *C. recurvata* have been located, requiring the use of vegetative characters to distinguish this species from the similar *C. serpens*, the name with which these specimens were originally associated. As foliage leaves are present on all the vegetative specimens that we observed, morphology of foliage leaves, including the shape and size of leaf sheath ligular regions, was particularly useful for differentiating among species. Morphology of the inner leaf ligule and leaf sheath summit extension has been found to be a taxonomically significant character in other species of the genus, and does not appear to show great variability within a species (Clark and Kaul 2019; Clark and Mason 2019; Fadrique et al. 2019). Other vegetative parts of the plant that can be taxonomically significant, such as bud and branch complements and culm leaves, are frequently absent from vegetative collections, including several of the *C. recurvata* and *C. acutigluma* specimens that we examined. Due to the incomplete nature of many *Chusquea* collections, observation of multiple characters, both macro- and micromorphological as well as anatomical, was necessary for the identification of previously undescribed species of *C.* sect. *Serpentes*.

COMPARISON OF LEAF MICROMORPHOLOGY AND ANATOMY AND POTENTIAL USE IN SYSTEMATICS—Leaf micromorphology can aid in distinguishing between different species of *Chusquea* even when the macromorphological features of these species are fairly similar (Clark 1986, 1990; Leandro et al. 2017). In particular, the presence and morphology of papillae found on the surface of foliage leaves can vary even between closely related species (Leandro et al. 2016, 2017). Despite some strong similarities, there are consistent differences in the foliar micromorphology of *C. serpens*, *C. acutigluma*, and *C. recurvata* that support the recognition of *C. acutigluma* and *C. recurvata* as separate species.

The differences seen in the structure and shape of papillae on the abaxial surface of *C. recurvata* foliage leaves and those of *C. acutigluma* and *C. serpens* provided the clearest micromorphological evidence for *C. recurvata* as a separate species. Shape and placement of silica bodies, stomatal apparatuses, and prickles also differed among species. Although seen on only one of the specimens of *C. serpens*, there were clear differences in the shape of bicellular microhairs on the adaxial surface of *C. serpens* and *C. acutigluma*. Despite typically being few in number, the presence and structure of bicellular microhairs can be taxonomically significant even when only a

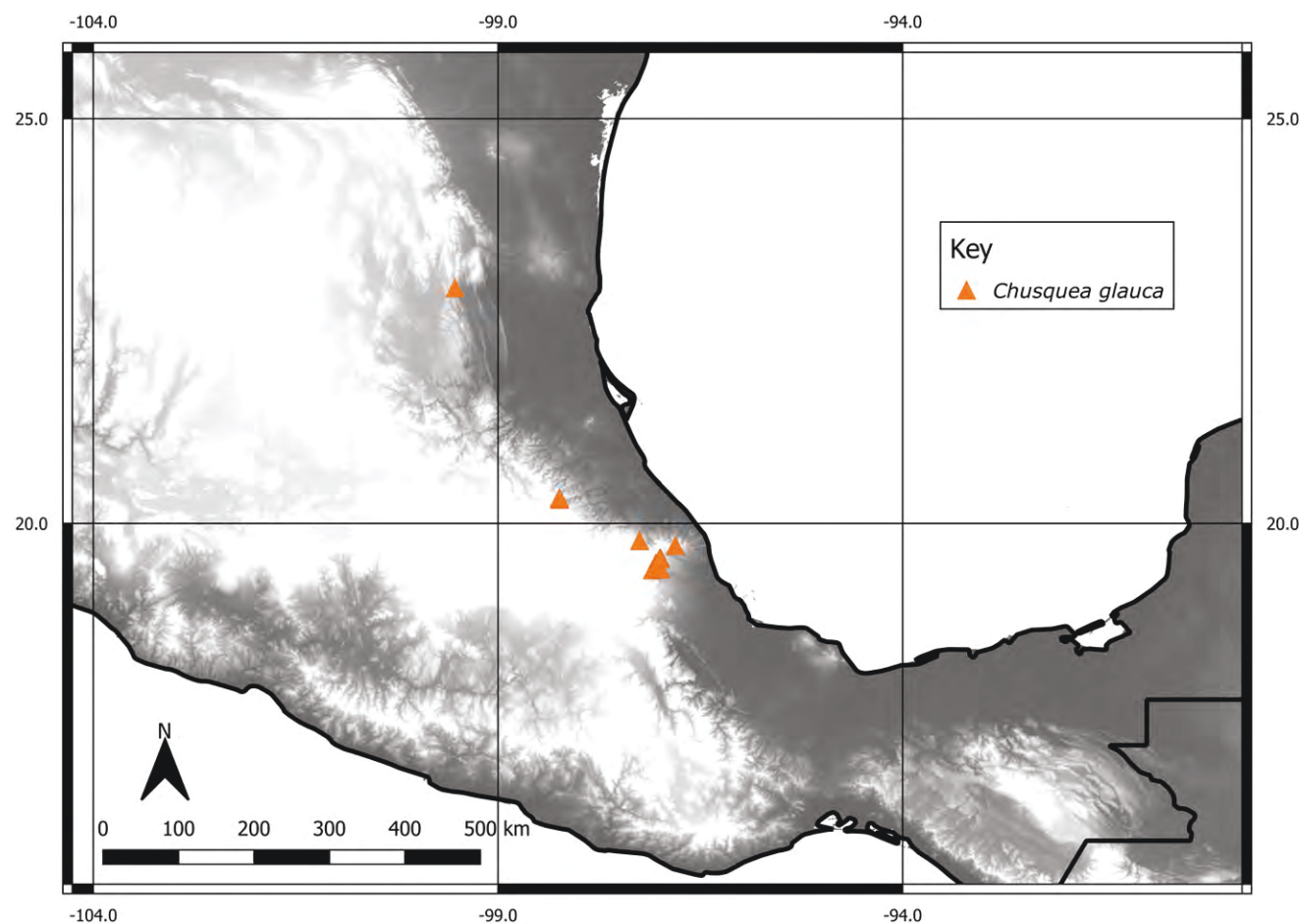


FIG. 16. Distribution of the species of *Chusquea* sect. *Serpentes* in Mexico.

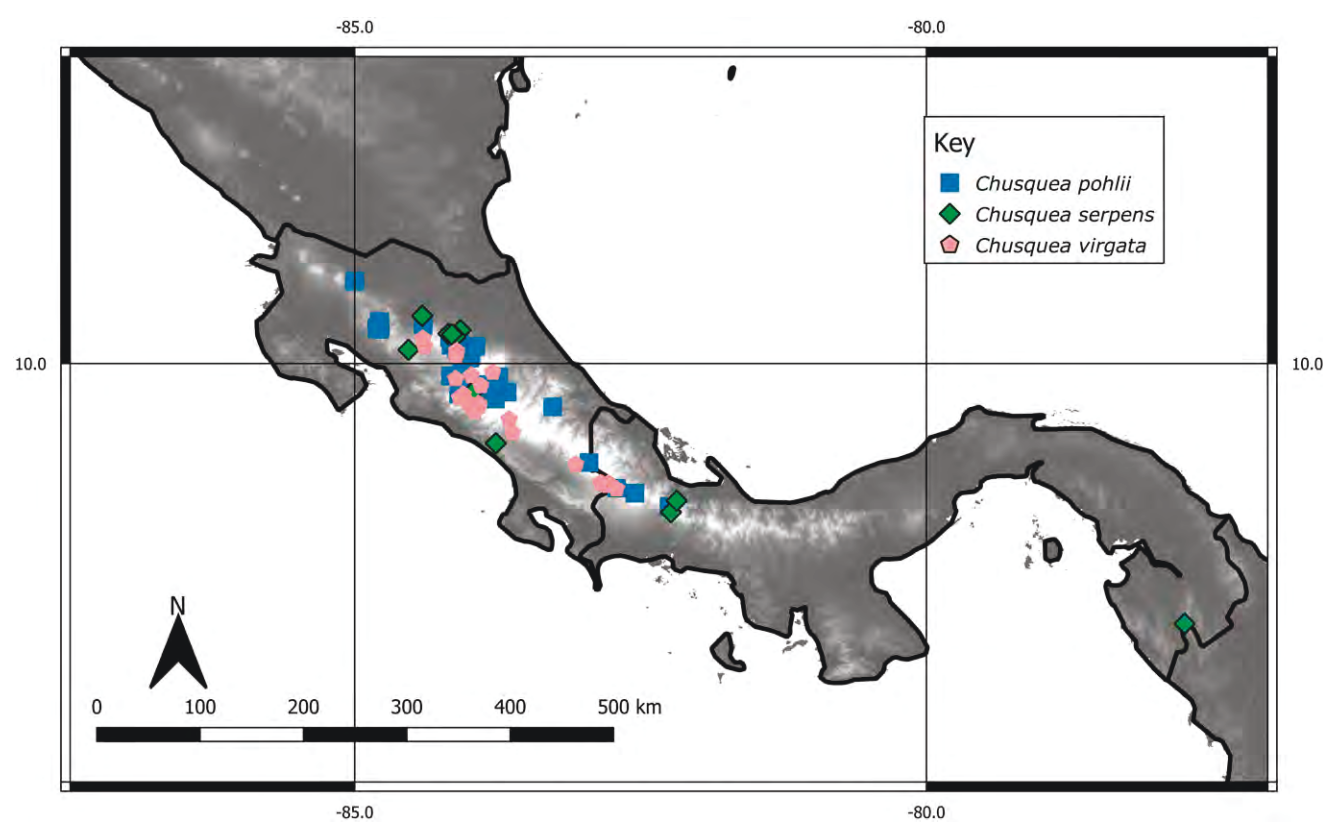


FIG. 17. Distribution of the species of *Chusquea* sect. *Serpentes* in Central America.

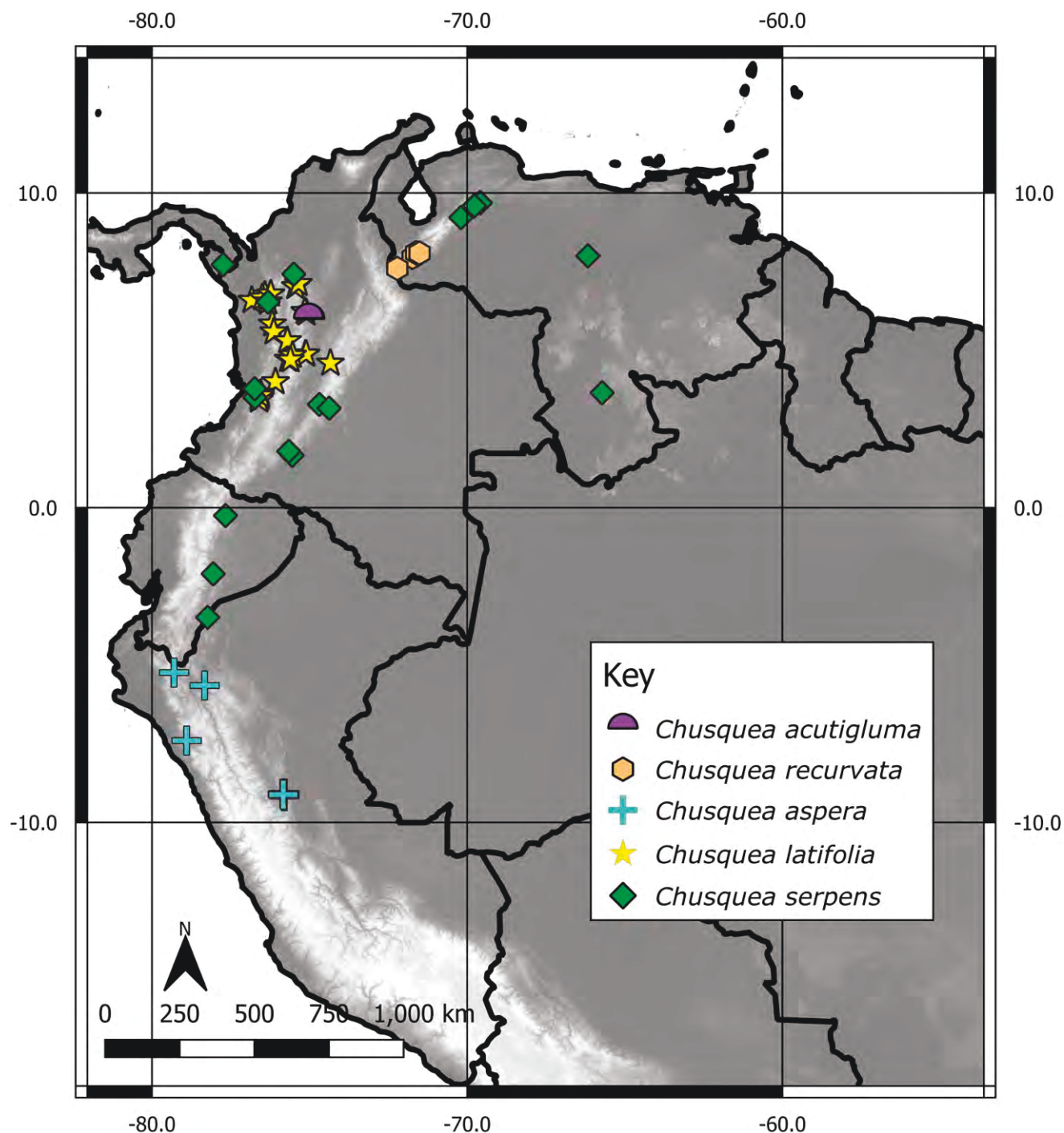


FIG. 18. Distribution of the species of *Chusquea* sect. *Serpentes* in South America.

single such hair is observed, as on the adaxial surface of *C. acutigluma* (Ellis 1979). Presence of macrohairs that are similar in appearance to prickles, such as those sometimes seen on the abaxial surface of *C. serpens*, may also be useful for distinguishing between species (Ellis 1979). On specimens where identification is uncertain, especially if important vegetative structures such as buds and foliage leaf ligular structures are missing or damaged, use of foliage leaf micromorphology can provide an additional means of identification. While homoplasy in papilla distribution and morphology has been reported in temperate woody bamboos (Zhang et al. 2014),

some patterns in foliage leaf micromorphology could be useful for determining placement of a species at the section level within a genus. Unlike members of *Chusquea* sect. *Tenellae*, the species that we observed in *C. sect. Serpentes* had vertically-oriented silica bodies throughout the leaf and lacked horizontally-oriented bilobate silica bodies in the costal zones (Attigala et al. 2017; Leandro et al. 2017). Although micromorphological analyses require destructive sampling, the amount of leaf required to conduct these analyses is typically small.

Anatomically, the two new species, *Chusquea acutigluma* and *C. recurvata*, plus *C. serpens* display features as seen in

cross-section commonly found in Bambusoideae in that they share a single-layered epidermis bearing papillae; fan-shaped arrays of adaxial bulliform cells; non-radiate mesophyll (C_3 plants) comprised of strongly invaginated arm cells, cavities formed by the collapse of fusoid cells, and rosette cells; collateral vascular bundles with a double sheath and opposing sclerenchyma cells (Metcalf 1960; Ellis 1987; Judziewicz et al. 1999; Leandro et al. 2020). The studied species also share a complex midrib, which is found in virtually all *Chusquea* species and has been useful to recognize this genus anatomically within the Neotropical woody bamboos (BPG 2012; Clark et al. 2015; Leandro et al. 2020).

While papillae are characteristic of bamboo leaves (Judziewicz et al. 1999), these epidermal outgrowths have been mostly described in surface view. However, in this study, the morphology of papillae as seen in leaf-blade cross-sections (i.e. longitudinal section of the papillae) is useful for recognizing and distinguishing the studied species. Similarly, the morphology of girders and the number of abaxial arm cells in the mesophyll also prove relevant to differentiate among *C. acutigluma*, *C. recurvata*, and *C. serpens*. We thus recommend the incorporation of detailed descriptions of these features in bamboo anatomical studies.

Differences in the number of layers of adaxial arm cells in the mesophyll and adaxial vascular bundles in the midrib have proven taxonomically informative for *Chusquea* at the species level (e.g. da Mota 2013; Leandro et al. 2017). These features, along with characteristics associated with the bundle sheath in the midrib (e.g. shared or not), are also helpful to distinguish among the species studied herein. This result supports the use of these features for taxonomic purposes.

Potentially Undescribed Species of *Chusquea* sect. *Serpentes*—More species of *Chusquea* sect. *Serpentes* are likely to be described in the future. The ranges of species of *C. sect. Serpentes* appear to be restricted to only one or two countries, except for *C. serpens* (Clark 1985, 1989), raising the possibility that some species with limited range or abundance have not been collected or identified from existing collections. Members of the section can also be more difficult to spot and collect in the wild than species of other sections of *Chusquea* due to their climbing habit (Clark 1989). However, it is likely that more species have already been collected but have not yet been identified due to similarity to described species. An additional five specimens that we examined appear to belong to *C. sect. Serpentes*, but due to lack of material, are currently incertae sedis. Further examination of herbarium material and collection of wild specimens is likely necessary to clarify the status of these specimens, and could reveal more species that are still undescribed.

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AUTHOR CONTRIBUTIONS

Collections and field observations of *C. glauca*, *C. latifolia*, *C. pohlii*, *C. recurvata*, *C. serpens*, and *C. virgata* were made by LGC, with observations of herbarium specimens made by LGC, BJP, and EKM. XL made additional field observations and collections of *C. serpens* and *C. latifolia*. The description of *C. recurvata* was begun by BJP and completed by EKM. EKM used herbarium specimens to describe *C. acutigluma*. Existing descriptions of *Chusquea* sect. *Serpentes* were updated by EKM. XL contributed to descriptions of *C. recurvata*, *C. acutigluma*, and previously described species of *Chusquea* sect. *Serpentes*. TDL produced, photographed, and described all foliage leaf cross sections. Foliage leaf SEM images were made by LGC and EKM, and described by EKM. Maps of all *C. sect. Serpentes* specimen collection locations and conservation assessments for *C. recurvata* and *C. acutigluma* were completed by EKM. The manuscript was reviewed by LGC, XL, TDL, and BJP. EKM took all photos of herbarium specimens and prepared photographic plates for *C. acutigluma*, *C. recurvata*, *C. aspera*, *C. glauca*, and *C. virgata*. Line drawings of *C. latifolia*, *C. pohlii*, and *C. serpens* were prepared by LGC, with modifications by EKM.

LITERATURE CITED

- Attigala, L., A. F. Fuentes, and L. G. Clark. 2017. *Chusquea* sect. *Tenellae* (Bambuseae, Bambusoideae, Poaceae), a taxonomic revision of a new section from South America. *Phytotaxa* 324: 239–265.
- BPG. 2012. Bamboo Phylogeny Group. An updated tribal and subtribal classification of the bamboos (Poaceae: Bambusoideae). *Bamboo Science & Culture: The Journal of the American Bamboo Society* 24: 1–10.
- Belgiu, M. 2015. Countries WGS84. https://hub.arcgis.com/datasets/a21fdb46d23e4ef896f31475217cbb08_1 (last accessed January 2021).
- Clark, L. G. 1985. Three new species of *Chusquea* (Gramineae: Bambusoideae). *Annals of the Missouri Botanical Garden* 72: 864–873.
- Clark, L. G. 1986. *Systematics of Chusquea section Chusquea, section Swallenochloa, section Verticillatae, and section Serpentes* (Poaceae: Bambusoideae). Ph.D. dissertation. Ames, Iowa: Iowa State University.
- Clark, L. G. 1989. Systematics of *Chusquea* section *Swallenochloa*, section *Verticillatae*, section *Serpentes*, and section *Longifoliae* (Poaceae: Bambusoideae). *Systematic Botany Monographs* 27: 1–127.
- Clark, L. G. 1990. *Chusquea* sect. *Longiprophylloae* (Poaceae: Bambusoideae): A new Andean section and new species. *Systematic Botany* 15: 617–634.
- Clark, L. G. and A. D. Kaul. 2019. *Chusquea montisylvicola* (Poaceae: Bambusoideae), a new species endemic to the Andes of southern Ecuador. *Journal of the American Bamboo Society* 30: 6–11.
- Clark, L. G. and J. J. Mason. 2019. Redescription of *Chusquea perligulata* (Poaceae: Bambusoideae: Bambuseae: Chusqueinae) and description of a similar but new species of *Chusquea* from Ecuador. *Phytotaxa* 400: 227–236.
- Clark, L. G., X. Londoño, and E. Ruiz-Sanchez. 2015. Bamboo taxonomy and habitat. Pp. 1–30 in *Bamboo: The Plant and its Uses*, Tropical Forestry Series, vol. 10, eds. W. Liese and M. Köhl. Cham: Springer International Publishing.
- Ellis, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf-blade as viewed in transverse section. *Bothalia* 12: 65–109.
- Ellis, R. P. 1979. A procedure for standardizing comparative leaf anatomy in Poaceae. II. The epidermis as seen in surface view. *Bothalia* 12: 641–671.
- Ellis, R. P. 1987. A review of comparative leaf blade anatomy in the systematics of the Poaceae: the past twenty-five years. Pp. 3–10 in *Grass Systematics and Evolution*, eds. T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth. Washington: Smithsonian Institution Press.
- Fadrique, B., E. M. Pianissola, K. J. Feeley, and L. G. Clark. 2019. A preliminary revision of *Chusquea* sect. *Swallenochloa* (Bambuseae, Bambusoideae, Poaceae) in Peru including the description of two new species and the resurrection of two other species. *Phytotaxa* 418: 171–194.
- Fisher, A. E., J. K. Triplett, C.-S. Ho, A. D. Schiller, K. A. Oltrogge, E. S. Schroder, S. A. Kelchner, and L. G. Clark. 2009. Paraphyly in the bamboo subtribe Chusqueinae (Poaceae: Bambusoideae) and a

- revised infrageneric classification for *Chusquea*. *Systematic Botany* 34: 673–683.
- Fisher, A. E., L. G. Clark, and S. A. Kelchner. 2014. Molecular phylogeny estimation of the bamboo genus *Chusquea* (Poaceae: Bambusoideae: Bambuseae) and description of two new subgenera. *Systematic Botany* 39: 829–844.
- ICPT. 2019. International Committee for Phytolith Taxonomy. International Code for Phytolith Nomenclature (ICPN) 2.0. *Annals of Botany* 124: 189–199.
- IUCN. 2019. International Union for Conservation of Nature. Guidelines for using the IUCN Red List categories and criteria. Version 14. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (last accessed June 2021).
- Johansen, D. 1940. *Plant Microtechnique*. New York: McGraw-Hill.
- Judziwicz, E. J., L. G. Clark, X. Londoño, and M. J. Stern. 1999. *American Bamboos*. Washington, D.C.: Smithsonian Institution Press.
- Kraus, J. E. and M. Arduin. 1997. *Manual Básico de Métodos em Morfologia Vegetal*. Rio de Janeiro: Editora da Universidade Rural.
- Leandro, T. D., R. T. Shirasuna, T. S. Filgueiras, and V. L. Scatena. 2016. The utility of Bambusoideae (Poaceae, Poales) leaf blade anatomy for identification and systematics. *Brazilian Journal of Biology* 76: 708–717.
- Leandro, T. D., V. L. Scatena, and L. G. Clark. 2017. The contribution of foliar micromorphology and anatomy to the circumscription of species within the *Chusquea ramosissima* informal group (Poaceae, Bambusoideae, Bambuseae). *Plant Systematics and Evolution* 303: 745–756.
- Leandro, T. D., T. M. Rodrigues, L. G. Clark, and V. L. Scatena. 2018. Fusoid cells in the grass family Poaceae (Poales): A developmental study reveals homologies and suggests new insights into their functional role in young leaves. *Annals of Botany* 122: 833–848.
- Leandro, T. D., V. L. Scatena, and L. G. Clark. 2020. Comparative leaf blade anatomy and micromorphology in the systematics and phylogeny of Bambusoideae (Poaceae: Poales). *Botanical Journal of the Linnean Society* 192: 165–183.
- Metcalfe, C. R. 1960. *Anatomy of the Monocotyledons I: Gramineae*. Oxford: Clarendon Press.
- McClure, F. A. 1973. Genera of bamboos native to the New World (Gramineae: Bambusoideae). *Smithsonian Contributions to Botany* 9: 1–148.
- da Mota, A. C. 2013. *Sistemática de Chusquea subgênero Rettbergia (Bambusoideae, Poaceae)*. Ph.D. dissertation. Feira de Santana: Universidade Estadual de Feira de Santana.
- Mota, A. C., R. P. Oliveira, J. G. Carvalho-Sobrinho, K. V. A. Vidal, and L. G. Clark. 2017. *Chusquea kleinii*, a new bamboo from the Atlantic forests of Brazil segregated from *C. capituliflora* (Poaceae: Bambusoideae). *Phytotaxa* 313: 166–174.
- Pohl, R. W. 1965. Dissecting equipment and materials for the study of minute plant structures. *Rhodora* 67: 95–96.
- Pohl, R. W. 1980. Gramineae. Pp. 140–141 in *Flora Costaricensis*, vol. 4, ed. W. Burger. Chicago: Fieldiana Botany.
- Richter, H. G. 1985. Wood and bark anatomy of Lauraceae. II. *Licaria* Aublet. *IAWA Bulletin* 6: 187–199.
- Ruiz-Sanchez, E., T. Mejía-Saulés, and L. G. Clark. 2014. A new endangered species of *Chusquea* (Poaceae: Bambusoideae) from the Acatlán volcano in central Veracruz, Mexico, and keys to the Mexican *Chusquea* species. *Phytotaxa* 163: 16–26.
- Ruiz-Sanchez, E., T. Mejía-Saulés, G. Cortés, and L. G. Clark. 2015. *Chusquea gibcooperi* (Poaceae: Bambusoideae: Bambuseae: Chusqueinae), a new species endemic to Mexico. *Brittonia* 67: 227–232.
- Ruiz-Sanchez, E., A. Castro-Castro, and L. G. Clark. 2017. *Chusquea septentrionalis* sp. nov. (Poaceae: Bambusoideae) from the Madrean region in Durango, Mexico. *Nordic Journal of Botany* 35: 546–551.
- Ruiz-Sanchez, E., R. Romero-Guzman, A. Fores-Argüelles, J. P. Ortiz-Brunel, and L. G. Clark. 2021a. *Chusquea contrerasii* and *C. guzmanii* (Poaceae, Bambusoideae, Bambuseae, Chusqueinae), two new endemic species from Jalisco, Mexico. *Phytotaxa* 497: 285–297.
- Ruiz-Sanchez, E., C. D. Tyrrell, X. Londoño, R. P. Oliveira, and L. G. Clark. 2021b. Diversity, distribution, and classification of Neotropical woody bamboos (Poaceae: Bambusoideae) in the 21st Century. *Botanical Sciences* 99: 198–228.
- Spurlock, B. O., M. S. Skinner, and A. A. Kattine. 1966. A simple rapid method for staining epoxy-embedded specimens for light microscopy with the polychromatic stain paragon-1301. *American Journal of Clinical Pathology* 46: 252–258.
- Thiers, B. 2021. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/> (last accessed May 2021).
- Vidal, K. V. A., C. A. D. Welker, I. L. C. Oliveira, A. C. Mota, R. P. Oliveira, and L. G. Clark. 2018. A new species of *Chusquea* subg. *Chusquea* (Poaceae—Bambusoideae—Bambuseae) from Minas Gerais, Brazil: morphological evidence and phylogenetic placement within the *Euchusquea* clade. *Phytotaxa* 365: 73–88.
- Wang, X. Q., X. Y. Ye, L. Zhao, D. Z. Li, Z. H. Guo, and H. F. Zhuang. 2017. Genome-wide RAD sequencing data provide unprecedented resolution of the phylogeny of temperate bamboos (Poaceae: Bambusoideae). *Scientific Reports* 7: 11546.
- World Wildlife Fund. 2006. South America: Void-filled digital elevation model, 15s resolution, 2006 in EarthWorks. <https://earthworks.stanford.edu/catalog/stanford-rm470dn6126> (last accessed January 2021).
- World Wildlife Fund. 2007. Central America: Void-filled digital elevation model, 15s resolution, 2007 in EarthWorks. <https://earthworks.stanford.edu/catalog/stanford-jf534gx6067> (last accessed January 2021).
- Zhang, Y.-X., C.-X. Zeng, and D.-Z. Li. 2014. Scanning electron microscopy of the leaf epidermis in Arundinarieae (Poaceae: Bambusoideae): Evolutionary implications of selected micromorphological features. *Botanical Journal of the Linnean Society* 176: 46–65.