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Research Article

Taxonomic revision of *Muhlenbergia* (Poaceae, Chloridoideae, Cynodonteae, Muhlenbergiinae) in Central America: phylogeny and classification

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Abstract

A taxonomic treatment of 38 species of *Muhlenbergia*, a phylogeny based on analysis of six DNA sequence markers, and classification of *Muhlenbergia* for Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; and Campeche, Chiapas, Quintana Roo, Tabasco, and Yucatán, México) is given. With the support from a molecular phylogeny we describe *Muhlenbergia* subg. *Ramulosae* **subgen. nov.** In our treatment we place *M. gigantea* (younger name) as a synonym of *M. mutica*. Lectotypes are designated for the names *Agrostis microsperma* Lag., *Epicampes gigantea* E. Fourn., *Lamarckia tenella* DC., *Muhlenbergia adspersa* Trin., *M. diversiglumis* Trin., *M. exilis* E. Fourn., *M. flabellata* Mez, *M. setarioides* E. Fourn., *Pereilema ciliatum* E. Fourn., *P. crinitum* var. *cirratum* E. Fourn., *Podosemum ciliatum* Kunth, *P. tenuissimum* J. Presl, and *Schellingia tenera* Steud.

Resumen

Brindamos un tratamiento taxonómico para 38 especies de *Muhlenbergia*, una filogenia basada en el análisis de seis marcadores de secuencia de ADN y la clasificación de *Muhlenbergia* para América Central (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; y Campeche, Chiapas, Quintana Roo, Tabasco y Yucatán, México). Con el apoyo de una filogenia molecular describimos *Muhlenbergia* subg. *Ramulosae* **subgen. nov.** En nuestro tratamiento colocamos a *M. gigantea* (nombre más joven) como sinónimo de *M. mutica*. Se designan lectotipos para los nombres *Agrostis microsperma* Lag., *Epicampes gigantea* E. Fourn., *Lamarckia tenella* DC., *Muhlenbergia adspersa Trin.*, *M. diversiglumis* Trin., *M. exilis* E. Fourn., *M. flabellata* Mez, *M. setarioides* E. Fourn., *Pereilema ciliatum* E. Fourn., *P. crinitum* var. *cirratum* E. Fourn., *Podosemum ciliatum* Kunth, *P. tenuissimum* J. Presl y *Schellingia tenera* Steud.

Key words: Central America, classification, ITS, lectotypification, *Muhlenbergia*, phylogeny, plastid DNA sequences, Poaceae, systematics, taxonomy

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Introduction

With the incorporation of molecular DNA studies, the classification of the grass family has improved, and we now recognize 12 subfamilies, seven supertribes, 54 tribes, five super subtribes, and 109 subtribes (Soreng et al. 2022). Many satellite genera have been subsumed within larger genera and new genera have been described to recognize monophyletic clades. Sequence-derived phylogenies are extremely useful for elucidating synapomorphies, and these are used to circumscribe a clade or lineage of closely related species.

The subtribe Muhlenbergiinae Pilg. (Cynodonteae Dumort.) is a diverse assemblage of 183 species represented by a single, monophyletic genus, *Muhlenbergia* Schreb. (Peterson et al. 2010a, b, 2016, 2018, 2021; Soreng et al. 2017, 2015, 2022). Species within *Muhlenbergia* are morphologically highly variable and are characterized in having membranous ligules (rarely a line of hairs); paniculate inflorescences that are rebranched or composed only of primary branches; spikelets that are usually solitary but sometimes in pairs or triads, with cleistogenes (self-pollinated flowers that do not open at maturity) occasionally present in the leaf sheaths; one floret (rarely more) per spikelet that is perfect, staminate, or sterile; glumes that are awned or unawned; lemmas 3-veined, awned or unawned; and a base chromosome number of x = 8–10 (Peterson et al. 1995, 1997, 2007a, b; Peterson 2000, 2003). Two subtypes of C_4 photosynthesis based on nicotinamide adenine dinucleotide cofactor malic enzyme (NAD-ME) and phosphoenolpyruvate carboxykinase (PCK) have been identified anatomically in *Muhlenbergia*, with a few species verified by biochemical assay (Gutierrez et al. 1974; Brown 1977; Hattersley and Watson 1992).

Based on analysis of seven molecular markers (nuclear ITS and plastid *ndhA* intron, *ndhF*, *rps16-trnK*, *rps16* intron, *rps3*, and *rpl32-trnL* DNA sequences), Peterson et al. (2010b) provided a phylogeny and classification for 124 species (68%) of the Muhlenbergiinae. They recognized five subgenera within *Muhlenbergia: M.* subg. *Bealia* (Scribn.) P.M. Peterson, *M.* subg. *Clomena* (P. Beauv.) Hack., *M.* subg. *Muhlenbergia*, *M.* subg. *Pseudosporobolus* (Parodi) P.M. Peterson, and *M.* subg. *Trichochloa* (P. Beauv.) A. Gray. Formerly, subtribe Muhlenbergiinae included 10 genera but based on DNA-derived phylogenies nine of these genera were subsumed within *Muhlenbergia* (Giraldo-Cañas and Peterson 2009; Columbus and Smith 2010; Peterson et al. 2010b). The phylogeny of *Muhlenbergia* was revisited in Peterson et al. (2018, 2021) and was based on 150 of the 183 (82%) species in the genus. To show the affinities of the taxa treated in this revision we include a phylogenetic tree generated previously in Peterson et al. (2021).

Biogeographical reconstruction of *Muhlenbergia* suggests the genus originated 9.3 mya in the Sierra Madre (Occidental and Oriental) in México, splitting into six lineages, with *M. ramulosa* (Kunth) Swallen diverging 8.2 mya, *M*. subg. *Muhlenbergia* at 5.9 mya, *M*. subg. *Pseudosporobolus* at 5.9 mya, *M*. subg. *Clomena* at 5.4 mya, *M*. subg. *Bealia* at 4.3 mya, and *M*. subg. *Trichochloa* at 1 mya, each of these with a high probability of Sierra Madrean origin (Peterson et al. 2021). Founder-event speciation from Sierra Madre to Central America occurred independently multiple times in four of the five subgenera during the Pleistocene and late Pliocene (Peterson et al. 2021).

The most comprehensive treatment of *Muhlenbergia* for Central America appears in Flora Mesoamericana where Reeder (1994) recognized 36 species. In addition, *Aegopogon* Humb. & Bonpl. ex Willd. with two species (Pohl 1994a), *Lycurus* Kunth with a single species (Davidse 1994), and *Pereilema* J. Presl with three species (Pohl 1994b) appear in Flora Mesoamericana, all now included within *Muhlenbergia* (Peterson et al. 2010a, b). All of these genera, as then understood, were treated in the subtribe Sporobolinae Benth. (Davidse and Pohl 1994).

Here we present a phylogeny, classification, and a taxonomic revision of 38 species of *Muhlenbergia* for Central America Central (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama; and Campeche, Chiapas, Quintana Roo, Tabasco, and Yucatán, México). Since the Flora Mesoamericana (Davidse and Pohl 1994) included the Yucatán Peninsula and Chiapas in addition to Central America (political region), we also include in our treatment Campeche, Chiapas, Quintana Roo, Tabasco, and Yucatán, a region that harbors species of *Muhlenbergia*.

Materials and methods

Phylogenetic analyses

The phylogram (Fig. 1) was generated using existing data from Peterson et al. (2021). The methods for DNA extraction, primers, amplification, sequencing, and phylogenetic analysis are given in Peterson et al. (2010b, 2016, 2018, 2021). We estimated the phylogeny among members of *Muhlenbergia* based on the analysis of six DNA sequence markers (ITS 1&2 and plastid *ndhA* intron, *rpl32-trnL*, *rps3*, *rps16* intron, and *rps16-trnK*).We sampled 150 species of *Muhlenbergia* (82%) within subtribe Muhlenbergiinae, and included outgroups: *Distichlis scoparia* (Nees ex Kunth) Arechav. (Monanthochloinae Pilg. ex Potztal), *Willkommia sarmentosa* Hack. (Traginae P.M. Peterson & Columbus), and *Sporobolus indicus* L. (Zoysieae Benth., Sporobolinae Benth.). Voucher information with GenBank numbers and characteristics of the six regions along with parameters used in Bayesian analyses can be found in Peterson et al. (2021) or are available upon request.

Taxonomy

Specimens of *Muhlenbergia* from Central America were reviewed in the following herbaria: CAS, CIIDIR, CR, DS, ENCB, INB (now part of CR), ITC, LAGU, MEXU, MHES, MICH, MO, NY, SLPM, TAES, TEFH, US, and USJ (Thiers 2023). Distribution information for each species is based on a review of the literature and on specimens cited in this treatment. Additional synonyms accepted by us can be found in the Catalogue of New World Grasses web site (http://www.tropicos.org/Project/CNWG) that is continually updated within TROPICOS (http://www.tropicos.org).

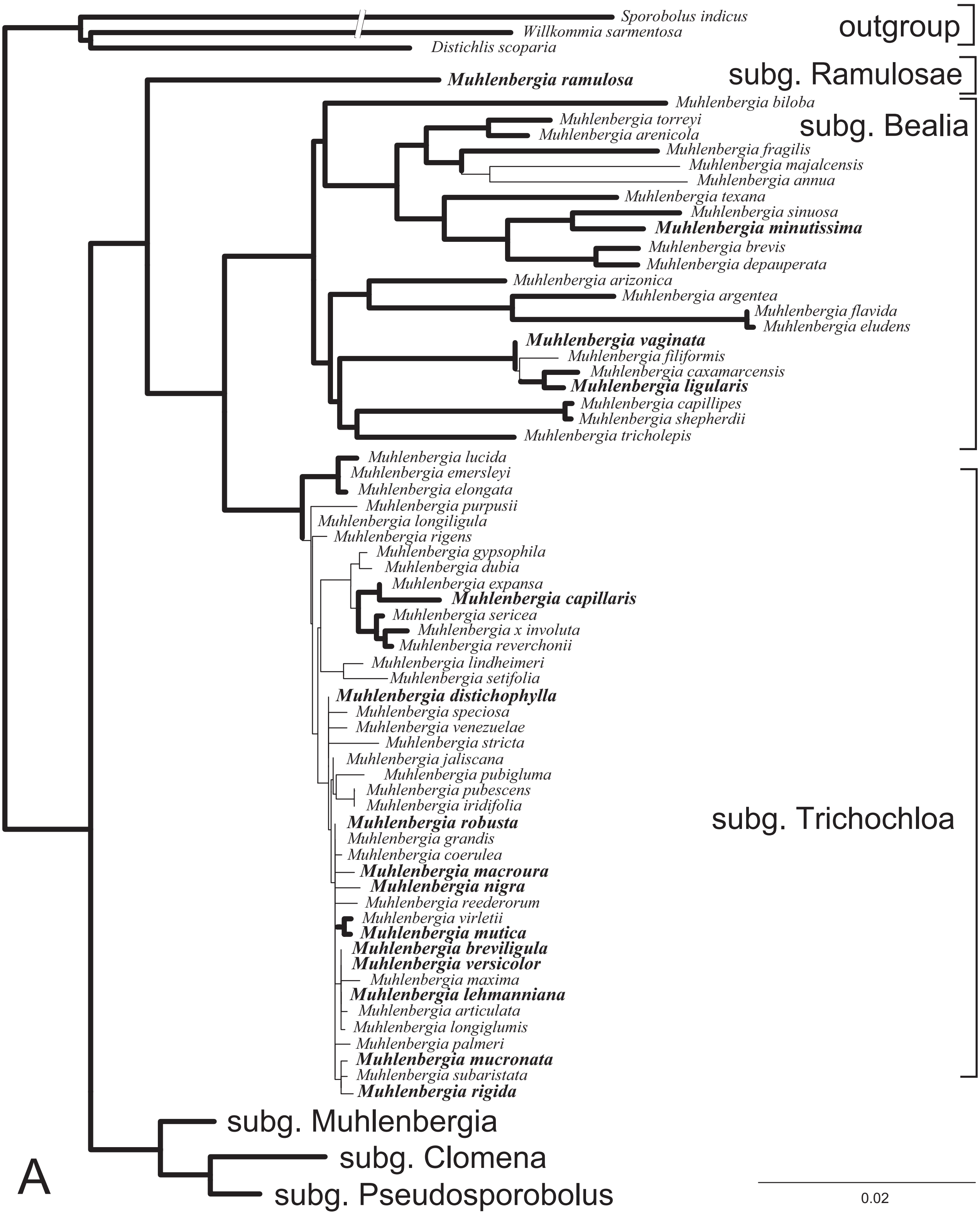

Figure 1. A, B Bayesian tree inferred from combined plastid (*ndhA* intron, *rps16-trnK*, *rps16* intron, *rps3*, and *rpl32-trnL*) and ITS sequences. Thick branches indicate posterior probabilities of 0.95–1; species in bold occur in Central America; Scale bar: 2%.

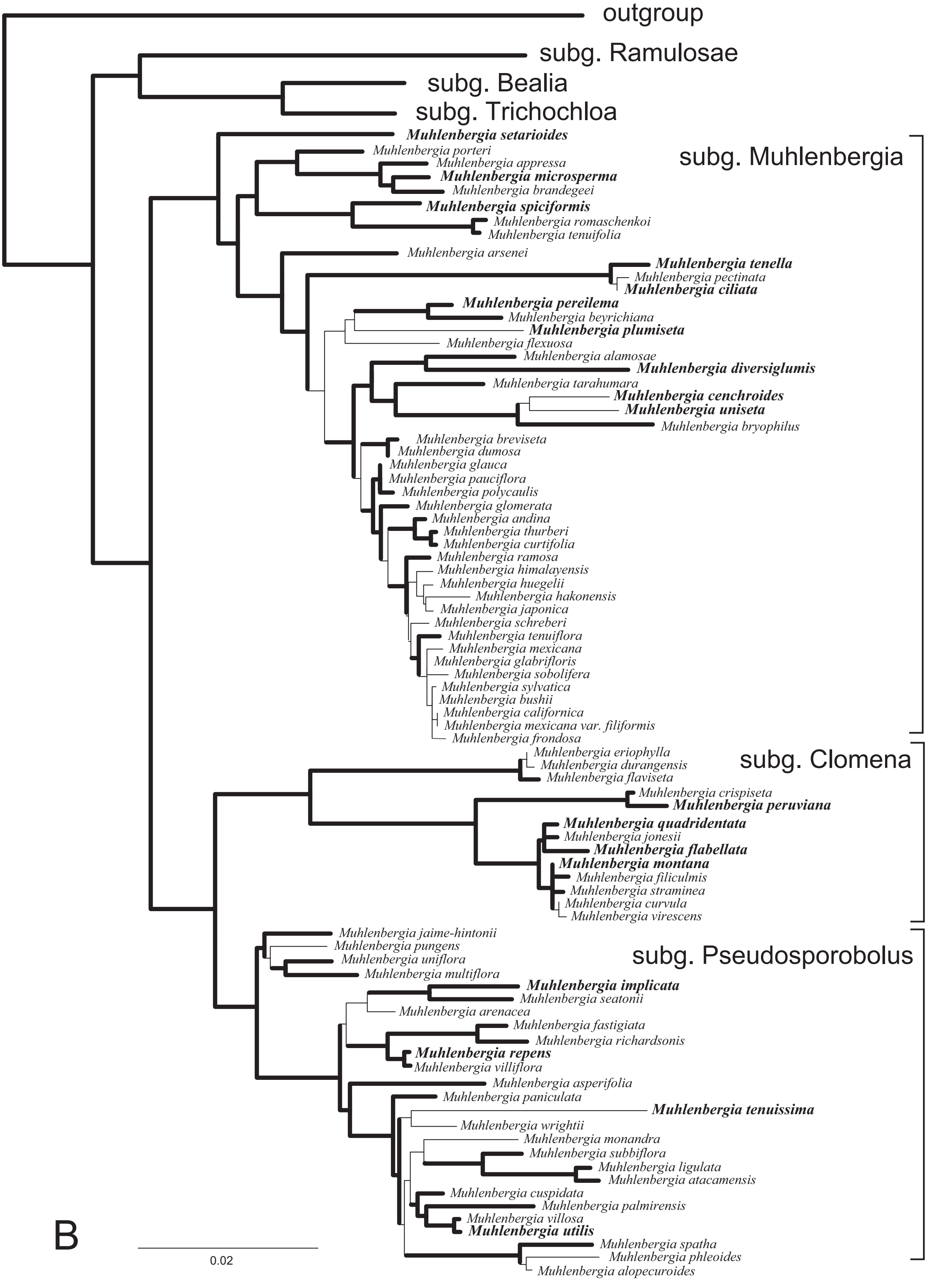

Figure 1. Continued.

When counting culm nodes it is best to start counting 1 cm above the base. Blade width is measured from margin to margin on a flat blade but not when the blade is tightly involute. Glabrous refers to without pubescence. Smooth indicates no prickle-hairs with broad bases and/or hooked or pointed apices (i.e. pubescence can occur on a smooth surface, and a scabrous surface can be glabrous). Excluded species and an infrageneric classification of the accepted species of *Muhlenbergia* in Central America are presented at the end prior to the references.

Results and discussion

Phylogeny

The Bayesian tree from the combined analysis of ITS and five plastid regions is well resolved with strong support for the monophyly of *Muhlenbergia*, including *M. ramulosa* (Kunth) Swallen sister to *M.* subg. *Bealia* + *M*. subg. *Trichochloa*, these all in one clade that is sister to *M*. subg. *Clomena* + *M*. subg. *Pseudosporobolus* sister to *M*. subg. *Muhlenbergia*. (Fig. 1; posterior probability, PP = 0.95–1, shown with thick branches). Each of the six major clades, corresponding to the six subgeneric divisions, five of these clades recognized previously (Peterson et al. 2010b; 2018), include species that occur in Central America (shown in **bold**). The species in each of these subgenera share salient morphological characteristics or trends.

Species of *Muhlenbergia* subg. *Bealia* are strongly caespitose, never rhizomatous, annuals or perennials with pubescent margins or midveins at least on the lower ½ of the lemma (only *M. ligularis* is without pubescence), and round, equal primary, secondary, and tertiary vascular bundles without well-developed sclerenchyma (Peterson and Herrera Arrieta 2001; Peterson 2003; Peterson et al. 2010b). *Muhlenbergia minutissima* (Steud.) Swallen and *M. vaginata* Swallen (two species included in our revision) are members of this subgenus.

Although the clade of species representing *Muhlenbergia* subg. *Trichochloa* is strongly supported in our analyses (Fig. 1), there is little resolution among members, indicative of low levels of genetic divergence in the studied markers among the species in this subgenus. The low level of divergence may be a consequence of rapid speciation events. Within *Muhlenbergia*, species within this group are by far the most difficult to determine because there are few morphological differences among the taxa and discrete (nonplastic) characteristics are few. Species of *M*. subg. *Trichochloa* consist of robust perennials up to three meters tall with compressed-keeled or rounded basal sheaths, 1-veined glumes, and unequal rectangular or obovate/elliptic secondary and tertiary vascular bundles with well-developed sclerenchyma girders, these usually with sclerosed phloem (Peterson and Herrera Arrieta 2001; Herrera Arrieta and Peterson 2007, 2017, 2018; Peterson et al. 2010b). Thirteen of the species in Central America are placed in *M*. subg. *Trichochloa: M. aurea* Swallen (endemic to Guatemala), *M. breviligula* Hitchc., *M. capillaris* (Lam.) Trin., *M. distichophylla* J. Presl) Kunth, *M. lehmanniana* Henrard, *M. macroura* (Kunth) Hitchc., *M. mucronata* (Kunth) Trin., *M. mutica* (Rupr. ex E. Fourn.) Hitchc., *M. nigra* Hitchc., *M. rigida* (Kunth) Kunth, *M. robusta* (E. Fourn.) Hitchc., *M. versicolor* Swallen, and *M. xanthodas* Soderstr.

Species of *Muhlenbergia* subg. *Clomena* have 3-veined upper glumes that are often 3-toothed, densely caespitose non rhizomatous culms with lower leaf sheaths that often flat and somewhat papery at maturity, and lemmas with flexuous awns [only *M. jonesii* (Vasey) Hitchc., an endemic to California, lacks an awn but the apex is mucronate] (Reeder and Reeder 1995; Herrera Arrieta 1998; Peterson 2003; Peterson et al. 2010b). Of the Central America species, *Muhlenbergia flabellata* Mez (endemic to Costa Rica and Panama), *M. montana* (Nutt.) Hitchc., *M. peruviana* (P. Beauv.) Steud., and *M. quadridentata* (Kunth) Trin. are members of this subgenus.

Members of *Muhlenbergia* subg. *Pseudosporobolus* usually have plumbeous spikelets, well-developed adaxial and abaxial sclerenchyma in their primary vascular bundles, narrow to loosely open panicles, unawned, mucronate or short-awned lemmas [long-awned in *M. implicata* (Kunth) Trin.], and the plants are rhizomatous when perennial (Peterson and Herrera Arrieta 2001; Peterson 2003; Peterson et al. 2010b). In Central America, *M. implicata*, *M. phalaroides* (Kunth) P.M. Peterson, *M. plumbea* (Trin.) Hitchc., *M. tenuissima* (J. Presl) Kunth, and *M. utilis* (Torr.) Hitchc. are placed in *M*. subg. *Pseudosporobolus*.

Morphologically, species of the *Muhlenbergia* subg. *Muhlenbergia* clade have broad, flat leaf blades, most have well-developed, scaly, and creeping rhizomes, and panicles that are usually narrow at maturity (Peterson et al. 2010b). This is the only subgenus where the PCK subtype of C_4 photosynthesis has been found. PCK species contain chlorenchyma composed of tabular cells that are indistinctly radiate and continuous between bundles [PCK type, defined as centrifugal/evenly distributed photosynthetic carbon reduction (PCRD) cell chloroplasts (with grana). The major veins are surrounded by two bundle sheaths, an inner mestome sheath of elongate nonchlorenchymatous cells and an outer chlorenchymatous sheath of shorter PCRD cells (designated XyMS+structural type; Hattersley and Watson 1976, 1992; Dengler et al. 1986). In addition, the leaf blades of these species contain fan- to shield-shaped bulliform cells that do not form a column of colorless cells from the adaxial to the abaxial surface, and they generally have four or more secondary and/or tertiary vascular bundles between consecutive primary vascular bundles (Gutierrez et al. 1974; Brown 1977; Peterson and Herrera Arrieta 2001). In Central America, *M. cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson, *M. ciliata* (Kunth) Trin., *M. diandra* (R.W. Pohl) Columbus (endemic to Costa Rica), *M. diversiglumis* Trin., *M. microsperma* (DC.) Kunth, *M. pereilema* P.M. Peterson, *M. plumiseta* Columbus, *M. setarioides* E. Fourn., *M. spiciformis* Trin., *M. tenella* (Kunth) Trin., *and M. uniseta* (Lag.) Columbus are placed in *M*. subg. *Muhlenbergia*.

In our study, and all previous molecular studies, *M. ramulosa* does not align within an existing subgenus of *Muhlenbergia*. Instead, it is sister to *M* . subg. *Bealia* and *M* . subg. *Trichochloa* in plastid and combined phylograms and sister to all Muhlenbergiinae in ITS phylograms (Columbus et al. 2010; Peterson et al. 2010b, 2018, 2021). Morphologically, *M* . *ramulosa* is similar to many of the small delicate annual or perennial species classified in *M* . subg. *Bealia*. *Muhlenbergia ramulosa* differs from most species of *M*. subg, *Bealia* in having awnless, mottled (greenish-black and greenish-white areas) lemmas, obtuse to subacute and glabrous glumes that are shorter than the lemma, panicles that are exserted and loosely contracted, ovoid or deltoid in outline 0.6–2.7 cm wide, and individuals with erect or spreading culms that do not root at the lower nodes (Peterson and Annable 1991; Herrera Arrieta and Peterson 2018). We describe a new subgenus below to include this enigmatic species.

Taxonomic treatment

***Muhlenbergia* Schreb., Gen. Pl. 1: 44. 1789.**

Dilepyrum Michx., Fl. Bor.-Amer. 1: 40. 1803. Type: *Dilepyrum minutiflorum* Michx. (= *Muhlenbergia schreberi* J. F. Gmel.). (*M*. subg. *Muhlenbergia*).

Aegopogon Humb. & Bonpl. ex Willd., Sp. Pl. 4 (2): 899. 1805 [1806]. Type: *Aegopogon cenchroides* Humb. & Bonpl. ex Willd. [≡ *Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson]. (*M*. subg. *Muhlenbergia*).

Podosemum Desv., Nouv. Bull. Sci. Soc. Philom. Paris 2: 188. 1810. Type: *Podosemum capillare* (Lam.) Desv. [≡ *Muhlenbergia capillaris* (Lam.) Trin.]. (*M*. subg. *Trichochloa*).

Clomena P. Beauv., Ess. Agrostogr. 28. 1812. Type: *Clomena peruviana* P. Beauv. [≡ *Muhlenbergia peruviana* (P. Beauv.) Steud.]. (*M*. subg. *Clomena*).

Tosagris P. Beauv., Ess. Agrostogr. 29. 1812. Type: *Tosagris agrostidea* P. Beauv. [= *Muhlenbergia capillaris* (Lam.) Trin.]. (*M*. subg. *Trichochloa*).

Trichochloa P. Beauv., Ess. Agrostogr. 29. 1812. Type: *Trichochloa purpurea* P. Beauv. [= *Muhlenbergia expansa* (Poir.) Trin.]. (*M*. subg. *Trichochloa*).

Podosaemum Kunth, Mem. Mus. Hist. Nat. 2: 72. 1815; orth. var. *Podosemum*. (*M*. subg. *Trichochloa*).

Hymenothecium Lag., Gen. Sp. Pl. 4. 1816. Lectotype: *Cynosurus tenellus* Cav. ex DC., designated by Hitchcock 1920: 169 [≡ *Lamarckia tenella* DC. ≡ *Hymenothecium tenellum* (Cav. ex DC.) Lag. = *Muhlenbergia uniseta* (Lag.) Columbus]. (*M*. subg. *Muhlenbergia*).

Lycurus Kunth, Nov. Gen. Sp. 1: 141. 1815 [1816]. Lectotype: *Lycurus phleoides* Kunth, designated by Hitchcock 1920: 139 [≡ *Muhlenbergia phleoides* (Kunth) Columbus]. (*M*. subg. *Pseudosporobolus*).

Anthipsimus Raf., J. Phys. Chim. Hist. Nat. Arts 89: 105. 1819. Type: *Anthipsimus gonopodus* Raf. (= *Muhlenbergia schreberi* J.F. Gmel.). (*M*. subg. *Muhlenbergia*).

Sericrostis Raf., Neogenyton 4. 1825. Lectotype: *Stipa sericea* Michx, designated by Pfeiffer 1874: 1142 [≡ *Muhlenbergia sericea* (Michx.) P.M. Peterson]. (*M*. subg. *Trichochloa*).

Pereilema J. Presl, Reliq. Haenk. 1 (4–5): 233.1830. Type: *Pereilema crinitum* J. Presl (≡ *Muhlenbergia pereilema* P.M. Peterson). (*M*. subg. *Muhlenbergia*).

Epicampes J. Presl, Reliq. Haenk. 1 (4–5): 235. 1830. Type: *Epicampes stricta* J. Presl [= *Muhlenbergia robusta* (E. Fourn.) Hitchc.]. (*M*. subg. *Trichochloa*).

Dactylogramma Link, Hort. Berol. 2: 248. 1833. Type: *Dactylogramma cinnoides* Link [= *Muhlenbergia glomerata* (Willd.) Trin.]. (*M*. subg. *Muhlenbergia*).

Calycodon Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 23. 1848. Type: *Calycodon montanum* Nutt. [≡ *Muhlenbergia montana* (Nutt.) Hitchc.]. (*M*. subg. *Clomena*).

Pleopogon Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 25. 1848. Type: *Pleopogon setosum* Nutt. [≡ *Lycurus setosus* (Nutt.) C.G. Reeder = *Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus]. (*M*. subg. *Pseudosporobolus*).

Schedonnardus Steud., Syn. Pl. Glumac. 1: 146. 1854. Type: *Schedonnardus texanus* Steud. [= *Lepturus paniculatus* Nutt. ≡ *Rottboellia paniculata* (Nutt.) Spreng. ≡ *Schedonnardus paniculatus* (Nutt.) Branner & Coville ≡ *Spirochloe paniculata* (Nutt.) Lunell ≡ *Muhlenbergia paniculata* (Nutt.) Columbus]. (*M*. subg. *Pseudosporobolus*).

Vaseya Thurb., Proc. Acad. Nat. Sci. Philadelphia 15: 79. 1863. Type: *Vaseya comata* Thurb. [= *Muhlenbergia andina* (Nutt.) Hitchc.]. (*M*. subg. *Muhlenbergia*).

Chaboissaea E. Fourn., Mexic. Pl. 2: 112. 1886. Type: *Chaboissaea ligulata* E. Fourn. [≡ *Muhlenbergia ligulata* (E. Fourn.) Scribn. & Merr.]. (*M*. subg. *Pseudosporobolus*).

Crypsinna E. Fourn., Mexic. Pl. 2: 90. 1886. Lectotype: *Crypsis macroura* Kunth, designated by Hitchcock 1920: 144. [≡ *Crypsinna macroura* (Kunth) E. Fourn.≡ *Muhlenbergia macroura* (Kunth) Hitchc.]. (*M*. subg. *Trichochloa*).

Redfieldia Vasey, Bull. Torrey Bot. Club 14: 133. 1887. Type: *Graphephorum flexuosum* Thurb. ex A. Gray [≡ *Redfieldia flexuosa* (Thurb. ex A. Gray) Vasey ≡ *Muhlenbergia multiflora* Columbus]. (*M*. subg. *Pseudosporobolus*).

Bealia Scribn., True Grasses 104, f. 45a. 1890. Type: *Bealia mexicana* Scribn. (≡ *Muhlenbergia biloba* Hitchc.). (*M*. subg. *Bealia*).

Blepharoneuron Nash, Bull. Torrey Bot. Club 25(2): 88. 1898. Lectotype: *Vilfa tricholepis* Torr., designated by Peterson and Annable 1990: 522 [≡ *Blepharoneuron tricholepis* (Torr.) Nash ≡ *Muhlenbergia tricholepis* (Torr.) Columbus]. (*M*. subg. *Bealia*)

Schaffnerella Nash, N. Amer. Fl. 17(2): 141. 1912. Type: *Schaffnera gracilis* Benth. [≡ *Schaffnerella gracilis* (Benth.) Nash ≡ *Muhlenbergia spatha* Columbus]. (*M*. subg. *Pseudosporobolus*).

Description. Plants ***annual*** or ***perennial***; usually synoecious, infrequently andromonoecious; sometimes rhizomatous, often cespitose, sometimes mat-forming, rarely stoloniferous. ***Culms*** 2–300 cm, erect, geniculate, or decumbent, usually herbaceous, sometimes becoming woody. ***Sheaths*** open; ***ligules*** membranous or hyaline (rarely firm or coriaceous), acuminate to truncate, sometimes minutely ciliolate, sometimes with lateral lobes longer than the central portion; ***blades*** narrow, flat, folded, or involute, sometimes arcuate. ***Inflorescences*** **(synflorescence)** terminal, sometimes also axillary, open to contracted, racemelike or spikelike panicles; **disarticulation** usually above the glumes, occasionally below the pedicels. ***Spikelets*** mostly perfect with 1 (2–6) florets, sometimes staminate or sterile, occasionally paired or in groups of threes then the central spikelet perfect and the lateral ones staminate or sterile; chasmogamous, rarely cleistogamous; ***glumes*** usually (0)1(2–3)-veined, apices entire, erose, or toothed, truncate to acuminate, sometimes mucronate or awned from the midvein, occasionally awned from the lateral veins; ***lower glumes*** sometimes rudimentary or absent, occasionally bifid; ***upper glumes*** shorter than to longer than the florets; ***calluses*** poorly developed, glabrous or hairy, the hairs up to 3.5 mm long, straight; ***lemmas*** glabrous, scabrous, or with short hairs, 3-veined (rarely appearing 5-veined), apices awned from the midvein, mucronate, or unawned; **awns**, if present, straight, flexuous, sinuous, or curled, sometimes borne between 2 minute teeth, lateral veins occasionally extended into awns; ***paleas*** shorter than or equal to the lemmas, 2-veined, apices; ***lodicules*** 2, cuneate, fleshy, sometimes with a narrow membranous apex, apex truncate and slightly lobed, glabrous; ***anthers*** (1–2) 3, purple, orange, yellow, olivaceous, or whitish; ***ovary*** with 2 styles (rarely 1), glabrous, stigmas plumose. ***Caryopses*** an achene,elongate, fusiform or elliptic, slightly dorsally compressed, rarely laterally compressed, free threshing; ***grain*** solid without lipid. ***Cleistogamous panicles*** sometimes present in the axils of the lower cauline leaves, enclosed by a tightly rolled, somewhat indurate sheath. ***Chromosome base number*** is x = (8 or 9) 10, and these are relatively small in size when compared to chromosomes in the Pooideae.

Distribution. The genus is primarily distributed in the Western Hemisphere in North, Central, and South America (Peterson 2003; Peterson and Giraldo-Cañas 2012; Peterson et al. 2018, 2021). There are also eight species known to occur in southeastern Asia; six of these are found in China (Wu and Peterson 2006) and five in India (Tiwari et al. 2023).

Ecology. The species occur in open habitats in deserts, grasslands, sclerophyllous scrubland, and margins of forests often in xeric to meso-xeric habitats from near sea level to more than 4000 m.

Etymology. Named for Gotthilf Henry Ernest Muhlenberg (1753–1815), a Lutheran minister and pioneer botanist of Pennsylvania, USA.

Key to the species of *Muhlenbergia* in Central America

1 Spikelets in clusters of three to five or more; lemmas usually with lateral veins excurrent into awns **2**
– Spikelets not in clusters of three to five, or if in clusters, then in pairs; lemmas with lateral veins not excurrent into awns **6**
2 Spikelets subtended by an involucre of bristles; leaf blades with prominent auricles **3**
– Spikelets not subtended by an involucre of bristles; leaf blades without auricles **5**
3 Involucres deciduous with feathery bristles; panicles 0.2–0.6 cm wide .... **25. *Muhlenbergia plumiseta* Columbus**
– Involucres persistent with scabrous bristles, panicles 1–3 cm wide **4**
4 Leaf blades 5–9 mm wide; lemma awns straight; stamens 2, anthers 0.7–1 mm long, purple .... **6. *M. diandra* (R.W. Pohl) Columbus**
– Leaf blades 2–3(–5) mm wide; lemma awns flexuous; stamens 3, anthers 0.4–0.7 mm long, yellow .... **21. *M. pereilema* P.M. Peterson**
5 Glumes with acute lobes, central vein extending as an awn 2–4 mm long; plants perennial usually caespitose .... **4. *M. cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson**
– Glumes with obtuse or rounded lobes, central vein usually extending as a mucro 0.2–1 mm long; plants annual sprawling or caespitose .... **34. *M. uniseta* (Lag.) Columbus**
6 Annual plants **7**
– Perennial plants **17**
7 Glumes and lemmas awnless, the lemma sometimes mucronate with a mucro up to 1.2 mm long **8**
– Glumes and/or lemmas awned, the awns (1.5–)5–30 mm long **11**
8 Glumes sparsely short pilose at least near the apex; pedicels 2–7 mm long, longer than the spikelets; panicles open, ovate with spreading branches, often capillary .... **15. *M. minutissima* (Steud.) Swallen**
– Glumes glabrous; pedicels 1–3 mm long, mostly shorter than the spikelets; panicles contracted, narrow **9**

9 Panicles contracted, narrow, linear, usually partially included in the uppermost sheath, 0.3–0.7 cm wide; branches ascending or appressed; culms geniculate or decumbent, often rooting at the lower nodes........................ ....**36. *M. vaginata* Swallen**
– Panicles loosely contracted, exerted, 0.5–2.7 cm wide; branches usually open, extended or reflexed to closely appressed; culms erect or decumbent, not rooting in the lower nodes..**10**
10 Lemmas 0.8–1.3 mm long, oval, plump; ligules 0.2–0.5 mm long; anthers 0.2–0.3 mm long ....**27. *M. ramulosa* (Kunth) Swallen**
– Lemmas 1.5–3.0 mm long, lanceolate, slender; ligules 0.6–2.5 mm long; anthers 0.8–1.1 mm long .... **12. *M. ligularis* (Hack.) Hitchc.**
11 Upper glumes apex wide and truncate, usually 2 or 3-toothed; lemma awns irregularly flexuous, purple....................**22. *M. peruviana* (P. Beauv.) Steud.**
– Upper glumes apex acuminate, acute or obtuse but never 2 or 3-toothed; lemma awns straight or flexuous, greenish to purplish **12**
12 Lemmas up to 2.5(–2.7) mm long **13**
– Lemmas 2.5–7.6 mm long **15**
13 Ligules acute or rounded, sometimes lacerate, membranous, 0.6–1.5 mm long; lemmas indistinctly 3-veined with no intermediate veins visible .... **33. *M. tenuissima* (J. Presl) Kunth**
– Ligules truncate, a ciliate membrane, 0.2–0.9 mm long; lemmas prominently 3-veined with the appearance of 5 veins, these intermediate veins are rows of short barbs on top of folded epidermal ridges.......................**14**
14 Primary panicle branches spreading or reflexed at maturity up to 90° from the culm axis; awns of lemma (1.5–)5–11(–18) mm long; leaf blades alternately inserted along the culm; plants found in moist to dry habitats usually beneath taller vegetation..........................**5. *M. ciliata* (Kunth) Trin.**
– Primary panicle branches tightly appressed and ascending; awns of the lemma 12–26 mm long; leaf blades commonly secund or lying to one side of the culm; plants restricted to moist drainages or perennially wet, rocky cliffs..**32. *M. tenella* (Kunth) Trin.**
15 Glumes dimorphic, those from proximal spikelets of each branch, often awnless, those of distal spikelets often one or both awned; ligules up to 0.8 mm long; primary panicle branches appearing secund or lying to one side of the culm axis .... **8. *M. diversiglumis Trin.***
– Glumes similar in all spikelets, awnless; ligules 1.0–2.5(–3) mm long; primary panicle branches alternately inserted along the culm.....................**16**
16 Panicles diffuse at maturity; pedicels capillary and flexuous, smooth; cleistogamous spikelets absent; lemmas pubescent only on the callus .... **10. *M. implicata* (Kunth) Trin.**
– Panicles not diffuse; pedicels stiff and stout, antrorsely scabrous; cleistogamous spikelets usually present in the axils of the lowermost culm branches; lemmas pubescent along margins, midvein, and callus .... **14. *M. microsperma* (DC.) Kunth**
17 Plants rhizomatous, rhizomes slender or stout, scaly and creeping **18**
– Plants not rhizomatous...**20**
18 Upper glumes (3–)3.2–4 mm long, apex truncate, obtuse or acute, often with 3 or 4 small teeth less than 1/6th the length; ligules 2–8 mm long,

apex acuminate often lacerate; leaf sheaths 10–30 cm long, basal sheaths becoming flattened with age; spikelets 3.4–4.7 mm long, plumbeous; rhizomes short and stout ....**26. *M. quadridentata* (Kunth) Trin.**
– Upper glumes 0.5–1.6(–1.8) mm long, apex acute without any teeth; ligules 0.2–0.8 mm long, apex truncate; leaf sheaths 0.3–5 cm long, basal sheaths not becoming flattened with age; spikelets 1.4–2.4(–3.5) mm long, plumbeous, green or purplish; rhizomes slender and scaly **19**
19 Panicles open, usually well exerted from upper sheaths, 4–9(–14) cm long, 0.5–4(–8) cm wide; primary branches 2–8 cm long, ascending to spreading up to 50° from the rachis; spikelets 2.5–3.2(–3.5) mm long; paleas 2–2.8(–3.1) mm long, apex acuminate; anthers 1.4–2 mm long .... **24. *M. plumbea* (Trin.) Hitchc.**
– Panicles narrow, contracted, partially included in the upper sheaths, 1–5 cm long, 0.1–0.4 cm wide; primary branches 0.1–1.2 cm long, appressed, rarely spreading 30° from the rachis; spikelets 1.4–2.4 mm long; paleas 1–2 mm long, apex acute; anthers 0.7–1.4 mm long ....**35. *M. utilis* (Torr.) Hitchc.**
20 Upper glumes 3-veined; old sheaths flattened below and sometimes spirally twisted near base **21**
– Upper glumes 1-veined, rarely 2 or 3-veined; old sheaths not flat and/or spirally twisted near base **23**
21 Upper glume apices 3 or 4-toothed, the teeth 1/6th the length of the glume; internodes mostly scabrous ....**26. *M. quadridentata* (Kunth) Trin.**
– Upper glume apices usually 3-toothed, occasionally 2-toothed, the teeth about 1/3 the length of the glume; internodes smooth **22**
22 Sheaths much overlapping or flabellately arranged below; leaf blades mainly basal 2–5 cm long; leaf blades mainly basal; glumes unawned....... ....**9. *M. flabellata* Mez**
– Sheaths not overlapping nor flabellately arranged below; leaf blades basal and cauline, 5–30 cm long; glumes mucronate or short-awned.................. .... **15. *M. montana* (Nutt.) Hitchc.**
23 Panicles diffuse, branches capillary; pedicels 4–40(–50) mm long, much longer than the spikelets..**24**
– Panicles not diffuse, branches not capillary branches; pedicels ≤ 3 mm long, shorter than the spikelets or equal in length **26**
24 Culms 12–30 cm tall; leaf blades 5–8 cm long; spikelets 3–3.5 mm long, plumbeous to dark-green turning golden brown with age; ligules 0.3–0.5(–1) mm long, truncate, membranous....................... **20. *M. orophila* Swallen**
– Culms 40–100 (–150) cm tall; leaf blades 10–35(–80) cm long; spikelets 3–5 mm long, usually purple to reddish-purple, occasionally green, brown or stramineous; ligules (1–) 1.8–6 (–8) mm long, obtuse to acute, firm below..**25**
25 Panicles 8–30 (–41) cm wide; pedicels 10–40(–50) mm long; primary branches widely divergent, diverging up to 100° from the culm axis........... ....**3. *M. capillaris* (Lam.) Hitchc.**
– Panicles (2–)3–5(–12) cm wide; pedicels ≤ 10 mm long; primary branches ascending and spreading, diverging up to 80° from the culm axis ....**28. *M. rigida* (Kunth) Kunth**

26 Culms rounded near base, the base appearing terete in transverse section **27**
– Culms compressed-keeled near base, appearing elliptic in transverse section.. **32**
27 Lower glumes 2 or 3-veined, usually 2-awned, the awns 1–3 mm long; upper glumes usually 1-awned, the awns 1–2.5 mm long; spikelets usually in pairs, the lower spikelet short- pedicelled perfect, staminate or sterile and the upper spikelet longer-pedicelled and usually perfect; culms 10–30 cm tall and decumbent sprawling near base.......... **23. *M. phalaroides* (Kunth) P.M. Peterson**
– Lower glumes 1-veined and unawned; upper glumes unawned; spikelets not in pairs and all spikelets perfect; culms 30–200 cm tall and erect, rarely geniculate near base **28**
28 Plants sprawling along the ground, culms geniculate and rooting at the lower nodes; lemmas with 3 prominent, green veins; anthers yellowish...... .... **30. *M. setarioides* E. Fourn.**
– Plants with culms caespitose and rooting only at the base; lemmas 3-veined, the veins not green nor prominent; anthers reddish-purple, purplish, greenish, or greenish-gray to whitish-gray **29**
29 Glumes 3.4–8 mm long, usually as long or longer than the lemmas, strongly laterally compressed; ligules (5–)8–40(–50) mm long, strongly decurrent, often splitting into broad auricles 10–35(–50) mm long; panicles dense and spikelike, 5–12 mm wide, plumbeous with a hint of green or greenish–gray, with primary branches 1–12 mm long **30**
– Glumes ≤ 2 mm long, ½ as long or less than the lemmas, not laterally compressed; ligules 1–8 mm long, not decurrent and without auricles; panicles narrow and contracted to loosely contracted and spreading, (0.6–)1–5(–12) cm wide, purple, reddish-purple or purplish-green, with primary branches 0.4–10 cm long.. **31**
30 Spikelets 3.4–5.6(–6) mm long; lemmas 3.4–5 mm long; glumes 3.4–5.6 mm long, unawned and without a mucro; basal leaf sheaths keeled; anthers 1.5–2.2 mm long .... **13. *M. macroura* (Kunth) Hitchc.**
– Spikelets (5.3–)6–8 mm long; lemmas 5–6.5 mm long; glumes (5.3–)6–8 mm long, sometimes mucronate or short-awned; basal leaf sheaths flattened; anthers 2.5–3.2 mm long.............................. **19. *M. nigra* Hitchc.**
31 Culms with 4–8 nodes per culm; leaf blades 2–12 cm long; glumes 0.3–1 mm long; anthers 0.9–1.6 mm long............. **31. *M. spiciformis* Trin.**
– Culms with 1 or 2 nodes per culm; leaf blades 12–40 cm long; glumes 1–2 mm long; anthers 1.7–2.3 mm long **32**
32 Lemmas awned, awns 10–22 mm long; glumes 1–1.7(–2) mm long, apex obtuse to subacute, sometimes erose............. **28. *M. rigida* (Kunth) Kunth**
– Lemmas mucronate or shortly awned, awns or mucros 0.5–1(–2) mm long; glumes 1.5–2 mm long, apex acute, scabrous .... **17. *M. mucronata* (Kunth) Trin.**
33 Panicles and spikelets golden yellow to yellowish-brown......................... **34**
– Panicles dark green, plumbeous, greenish-gray, silvery-gray, greenish-brown, purple, purplish-brown, purplish-green, reddish-purple or brownish-purple but never yellowish **37**

34 Lemmas 1.8–2 mm long, hyaline, indistinctly 3-veined; paleas 1.7–1.8 mm long, glabrous between the veins; glumes 1.7–2.2 mm long, mucronate, the mucro up to 0.6 mm long; known only from Guatemala ... **1. *M. aurea* Swallen**
– Lemmas (2–)2.1–3.3 mm long, membranous, distinctly 3-veined; paleas 2–2.9 mm long, hairy between the veins; glumes 2–3.8 mm long, sometimes mucronate; more wide-ranging in Central America **35**
35 Glumes unveined, smooth, translucent, somewhat lustrous and shining, apex acute without a mucro; ligules hyaline, delicate, frayed in age, becoming somewhat firm at base (3–)6–13 mm long...........**38. *M. xanthodas* Soderstr.**
– Glumes 1-veined, occasionally 2-veined or rarely 3-veined; apex acute to acuminate, usually mucronate; ligules membranous to chartaceous 6–25 mm long or 0.1–2 mm long and truncate on culm leaves.........................**36**
36 Ligules 0.1–2 mm long on culm leaves, usually 6–13 mm long on the innovations, apex truncate; basal sheaths becoming brown, curled and fibrillose or shredded; leaf blades usually abruptly narrowed at base (sheath and blade junction)..**2. *M. breviligula* Hitchc.**
– Ligules 10–25 cm long on the culm leaves and lower innovations, apex acuminate; basal sheaths golden yellow with age and not fimbrillose or basally shredded; leaf blades not abruptly narrowed at the based (sheath and blade junction).. **11. *M. lehmanniana* Henrard**
37 Lemmas unawned or mucronate, the mucro, if present, less than 1 mm long; culms 100–300 cm tall **38**
– Lemmas awned, the awns 4–20(–25) mm long; culms 70–150(–167) cm tall...**39**
38 Panicles (8–) 15–30 cm wide, purple or brown-purplish; auricles absent; primary panicle branches pendulous to flexuous spreading, 6–25 cm long, usually 15–20 cm long below.......**18. *M. mutica* (Rupr. ex E. Fourn.) Hitchc.**
– Panicles (2–)3–8 cm wide, greenish-gray to silvery-gray or purplish; auricles present, (1–)2–4(–10) mm long; primary panicle branches closely appressed to spreading 40° from the axis, 1–15(–17) cm long ....
....**29. *M. robusta* (E. Fourn.) Hitchc.**
39 Sheath auricles lacking or rudimentary, less than 0.5 mm long................**40**
– Sheath auricles present, 1.5–64 cm long **41**
40 Ligules 0.1–2 mm long on culm leaves, usually 6–13 mm long on the innovations, apex truncate; basal sheaths becoming brown, curled and fimbrillose or shredded; leaf blades usually abruptly narrowed at base (sheath and blade junction)..**2. *M. breviligula* Hitchc.**
– Ligules 10–25 mm long on the culm leaves and lower innovations, apex acuminate; basal sheaths golden yellow with age and not fimbrillose or basally shredded; leaf blades not abruptly narrowed at the based (sheath and blade junction).. **11. *M. lehmanniana* Henrard**
41 Lemmas villous on lower 1/2–2/3 and pilose along the margins near base, (2.5–)3–3.5 mm long; panicles dark-greenish to plumbeous; upper glumes mostly awned, the awns 1–1.2 mm long; culms strigulose below the nodes .... **37. *M. versicolor* Swallen**
– Lemmas glabrous with short pubescence along the margins and midvein on the lower 1/2–2/3, 1.4–2.8 mm long; panicles greenish-brown,

purplish-brown to reddish-purple; upper glumes unawned or mucronate, the mucro up to 0.4 mm long; culms glabrous, puberulent or pubescent below the nodes **42**

42 Ligules 0.1–2 mm long on the culm leaves, apex truncate; sheath auricles 1.5–6 mm long; leaf blades usually abruptly narrowed at base (sheath and blade junction), 2–3 mm wide ....**2. *M. breviligula* Hitchc.**

– Ligules 4–15 mm long on culm leaves, apex lacerate; sheath auricles (6–)10–26 mm long below and up to 64 mm long above; leaf blades not abruptly narrowed at the base (sheath and blade junction), 2–7 mm wide. .... **7. *M. distichophylla* (J. Presl) Kunth**

1. *Muhlenbergia aurea* Swallen, Contr. U.S. Natl. Herb. 29(9): 411. 1950.
Fig. 2A–E

Type. Guatemala. Quezaltenango, in thickets at base of vertical slopes along railroad, Finca Pirineos, lower S facing slopes of Volcán Santa María, between Santa Maria de Jesus and Calahuache, 1300–1500 m, 31 Dec 1939, *J.A. Steyermark 33175* (holotype: F-1057948 [image 64109!]; isotype: US-2236470 fragm. ex F!).

Description. Strongly caespitose ***perennials***. ***Culms*** 70–80 cm tall, stout, compressed-keeled near base, glabrous below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** glabrous below becoming scabrous near the collar; ***ligules*** 3–10 mm long, hyaline, apex attenuate, appearing shredded and withering with age; ***sheath auricles*** 4–8 mm long, often rudimentary and withering with age; ***blades*** 25–42 cm long, 2.5–5 mm wide, flat, conduplicate near base, scaberulous above, scabrous below, margins saw-toothed. ***Panicles*** 28–36 cm long, 5–10 cm wide, nodding, dense, golden yellow; ***primary branches*** 10–17 cm long, ascending, appressed to spreading up to 30° from the culm axis, without spikelets on the lower half; pedicels 1.5–2 mm long, scabrous. ***Spikelets*** 1.7–2.2 mm long, erect, yellow; ***glumes*** 1.7–2.2 mm long, as long as the floret, the upper glumes slightly longer than the lower, apex acute, scabrous, mucronate, the mucro up to 0.6 mm long; ***lemmas*** 1.8–2 mm long, hyaline, indistinctly 3-veined, pubescent on the lower 1/3 of the margins and midvein, awned, awns 10–20 mm long, flexuous borne just below the apex; ***paleas*** 1.7–1.8 mm long, a little shorter than the lemma, hyaline, glabrous; ***anthers*** not seen. ***Caryopses*** not seen.

Phenology. Flowering December and January.

Distribution. Known only from two collections in Guatemala, the type locality on the south facing slopes of Volcán Santa Maria in Departamento Quezaltenango between the cities of Quezaltenango and Retalhuleu (Peterson et al. 2001).

Ecology. *Muhlenbergia aurea* occurs on slopes between 1300 and 1500 meters.

Comments. Swallen (1950) suggested *M. aurea* is related to *M. scoparia* Vasey “which differs in having narrower sheaths and blades, an elongate ligule, a narrow, less densely flowered, purple panicle, and longer awns.” Not much is known about *M. aurea* and currently it has not been investigated using molecular methods. However, based on morphology it is placed in *M*. subg. *Trichochloa*.

Specimens examined. Guatemala. **Quetzaltenango**: Finca Pirineos, lower south-facing slopes of Volcán Santa María, between Santa María de Jesús and Calahuaché, *J.A. Steyermark 33175* (MO); Quezaltenango–Retalhuleu, 1480 m, 1954, *M. de Koninck 241* (US-2182672).

Figure 2. A–E *Muhlenbergia aurea* Swallen **A** habit **B** inflorescence **C** ligule **D** Spikelet **E** immature lemma **F–H** *Muhlenbergia xanthodas* Soderstr. **F** ligule **G** spikelet **H** lemma. **A** drawn from *J.A. Steyermark 33175* (F-1057948) **B–E** drawn from *M. de Koninck 241* (US-2182672) **F–H** drawn from *E. Matuda 4003* (US-1817864).

2. *Muhlenbergia breviligula* Hitchc., N. Amer. Flora 17(6):458. 1935.
Fig. 3A–E

Type. Guatemala, Guatemala City, collected on clay hill, 1500 m, 2 Dec 1911, *A.S. Hitchcock 9063* (holotype: US-995888!).

Description. Densely caespitose ***perennials***. ***Culms*** 70–140 tall, erect, stout, compressed-keeled near base, puberulent to glabrous below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** 8–26 cm long, mostly longer than the lower internode, scaberulous to glabrous, basally becoming brown, curled and fibrillose or shredded, margins entire, apex pubescent on abaxial surface; ***ligules*** 0.1–2 mm long on the culm leaves, of innovations 6–13 mm long, membranous to chartaceous with a rim of hairs, lacerate, apex truncate; ***sheath auricles*** 1.5–6 mm long, whitish when present, often lacking; ***blades*** 20–50 cm long, 2–3 mm wide, usually abruptly narrowed at base (sheath and blade junction), flat to folded, scabrous above, sometimes pubescent near throat and scaberulous below. ***Panicles*** 30–51 cm long, 3–10 cm wide, nodding, somewhat dense, yellowish to purplish brown or purplish green; ***primary branches*** mostly 3–12 cm long, ascending, lax and nodding, appressed to spreading up to 40° from the culm axis; ***pedicels*** 0.5–3 mm long, scaberulous. ***Spikelets*** 2–3.5 mm long, erect, yellowish to purplish-brown; ***glumes*** 2–3.5 mm long, equal or a little longer than the floret, equal in length, lanceolate to oblong-lanceolate, 1-veined, occasionally the upper 2-veined, apex acute to acuminate, often scaberulous, sometimes mucronate, the mucros up to 0.2 mm long; l**emmas** 2.1–2.8 mm long, lanceolate to oblong-lanceolate, awned, midvein and margins pubescent to sparsely pilose on the proximal 2/3, the hairs up to 0.3 mm long, apex acute to acuminate; awns 6–18 mm long, straight or flexuous, borne just below the apex; ***callus*** sparsely pilose; ***paleas*** 2–2.7 mm long, oblong, the proximal 2/3 pubescent to sparsely pilose between the veins, apex acute; **anthers** 1–1.7 mm long, purple or yellow. ***Caryopses*** 1–1.3 mm long, fusiform, light brownish.

Phenology. Flowering October through December.

Distribution. Chiapas, México, southeast to Guatemala, Honduras, El Salvador, and Nicaragua (Peterson et al. 2001; Menjívar Cruz et al. 2021).

Ecology. *Muhlenbergia breviligula* occurs on rocky slopes, along drainages, and in open pine-oak woodlands; 650–2530 m.

Comments. This species is morphologically similar to *M. emersleyi* Vasey, a species common in southwestern USA and northern México. However, *M. breviligula* differs in having culms with a short ligule 0.2–2 mm long (ligules 10–25 mm long in *M. emersleyi*), leaf blades 2–3 mm wide (2–6 mm wide in *M. emersleyi*), and persistent fimbrillose basal sheaths (not as persistent in *M. emersleyi*) [Soderstrom 1967; Peterson 2003]. *Muhlenbergia breviligula*, a member of *M.* subg. *Trichochloa*, has been found in an unsupported clade with three other species, distributed in North America (México), Central America, and South America (Columbia, Ecuador, and Peru) [*M. lehmanniana*, *M. versicolor*, and *M. maxima* Lægaard & Sanchez Vega] (Fig. 1A; Peterson et al. 2021).

Specimens examined. El Salvador. **Chalatenango**: San Fernando, creciendo a orilla de la calle, *J. González 398* (MO). Honduras. **Choluteca**: San Marcos de Colón, pine forest area near San Marcos [de Colón], *L.O. Williams & A. Molina R. 10921* (MO). **El Paraíso**: Guinope, Galeras, along road ca 10 km S of El Zamorano, open pine forest. [Originally reported from Francisco Morazán], *R.W. Pohl 12527* (MO); Alauca, Las Manos, 5 km N of Las Manos, near Los Limones, *R.W. Pohl & M. Gabel 13430* (MO). **Francisco Morazán**: Tatumbla, 24 km E de Tegucigalpa, bosque húmedo subtropical, *I. Cruz P. 75* (MO); In mountains along highway, 30 km W of Tegucigalpa, *W.A. Archer 3846* (US); Drainage of the Rio Yaguare, floresta de pino roble, acueducto de la EAP, Zamorano, *A. Molina R. 1593* (US); foothills of Mt. Uyuca, beyond Las Floras, overhanging steep bank in pine forest, *J.R. Swallen 11323* (US); San Antonio de Oriente, El Zamorano, *R.W. Pohl 12509* (MO); San Antonio del Oriente, overhanging bank, small shady canyon, about 2 km above San Antonio, *J.R. Swallen 10968* (US); Distrito Central, El Picacho, carretera en el Picacho, *Villatoro et al. 137* (MO). **Lempira**: Gracias, Río Mejocote [Rio Grande de Mejocote], 9 km de Gracias, pinares, *C. Nelson et al. 252* (MO). **Ocotepeque**: Santa Fe, about 8 km southwest of Santa Fé, near the Guatemala border, *R.A. Molina et al. 31271*(MO). **Olancho**: Jutiapa, mountain above a fire tower, Jutiapa Forest Station, between Concordia and Salamáa, pine forest on a steep slope, *R.W. Pohl & M. Gabel 13493* (MO). **Santa Bárbara**: Quimistán, Cofradia, ca. 8 km S of Cofradia, along Highway 18, open pine savana on a hill, *R.W. Pohl & M. Gabel 13392* (MO). **El Paraíso**: Dry hillsides along the Quebrada de Dantas, Rio Choluteca Valley about 16 km north of Yuscaran, *L.O. Williams & R.P. Williams 18652* (US). Guatemala. **Chiquimula**: along Rio Taco, between Chiquimula and Montana Barriol, 3–15 mi NW of Chiquimula, *J.A. Steyermark 30649* (US). Alta Verapaz: vicinity of Secanquim, *O.F. Cook & C.B. Doyle 60* (US). **Guatemala**: Guatemala City, *A S. Hitchcock 9063* (MO), *A.S. Hitchcock 9064* (US). *A.S. Hitchcock 9109* (US). **Huehuetenango**: Mountains wet of Aguacatan, on the road to Huehuetenango, open bank, *P.C. Standley 81190* (US). **Zacapa:** 13 km east of El Lobo, North-facing slope of open field and thickets, Quercus and Pinus on drier slopes, *W.E. Harmon & J.A. Fuentes 1851* (MO). Mexico. **Chiapas**: **Arriaga:** At La Mina Microwave Station, *D.E. Breedlove 56328* (CAS, MO); **Chiapa de Corso:** Above El Chorreadero, *D.E. Breedlove & R.F. Thorne 20499* (CAS, MO); 30 miles W of San Cristobal de las Casas on Mex 190 *J. N. Brunken & C. H. Perino 354* (MEXU); **Cintalapa:** Crest of the Sierra, near the microwave station of La Mina, 12 km S of Mexican Highway 190, near Rizo de Oro, *D.E. Breedlove & R.F. Thorne 20555* (CAS, MO); **Comitán de Domínguez:** 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54872* (CAS, MO); 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54870* (CAS, MO); **Huistán:** 10 km E of Huistán. [Tenejapa Mpo. (Huistan), *D.E. Breedlove & G. Davidse 55186* (CAS, MO); Comitán de Domínguez: 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54872* (CAS, MO); 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54870* (CAS, MO); **Ixtapa:** near the Zinacantán Paraje of Muctajoc. Slope with tropical deciduous forest, *D.E. Breedlove & G. Davidse 54005* (MEXU, CAS, MO), *54006* (CAS, MO), *54008* (MEXU, CAS, MO), *54009* (MEXU, CAS, MO), *54011* (CAS, MO); Intersection of the Tuxtla Gutiérrez-San Cristobal de las Casas and the Villahermosa highways, *G. Davidse et al. 30101* (MO); along road from Zinacantán center to Ixtapa near Paraje Vo Bits, *D.E. Breedlove 40709* (CAS, MO); **Jiquipilas**: Ejido Tierra y Libertad, *A. Reyes-García 5556* (MEXU); **La Independencia:** 6–10 km NNE of La Soledad along logging road from Las Margaritas to Campo Alegre, *D.E. Breedlove & B.M. Bartholomew 55670* (CAS, MO); **La Trinitaria:** a 12 km al S de la Trinitaria, camino a Cd. Cuauhtemoc, *E.M. Martínez S. & W.D. Stevens 23905a* (MEXU); 6–7 km

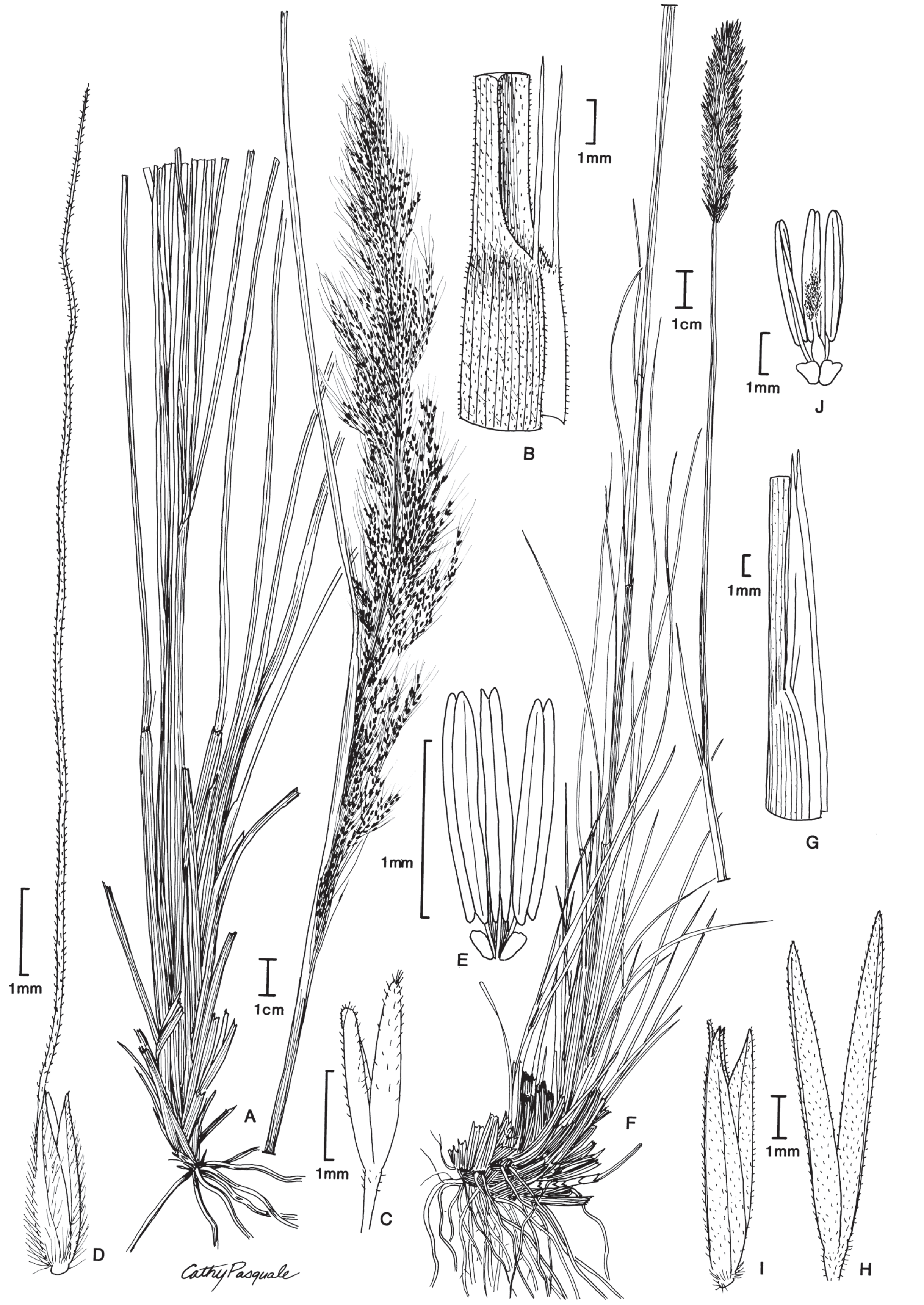

Figure 3. A–E *Muhlenbergia breviligula* Hitchc. **A** habit **B** ligule with auricles **C** glumes **D** floret **E** stamens and lodicules **F–J** *Muhlenbergia nigra* Hitchc. **F** habit **G** ligule **H** glumes **I** floret **J** stamens, pistil, and lodicules. **A–E** drawn from *A. Molina R. 25227* (US-2942492) **F–J** drawn from *S.D. Koch 76255* (US-2824590).

S of La Trinitaria, *G. Davidse et al. 29938* (MO); 6 km south of La Trinitaria on Mexican Highway 190, *D.E. Breedlove & G. Davidse 55074* (CAS, MO); 20 km south of La Trinitaria, *D.E. Breedlove & G. Davidse 55067* (CAS, MO); *D.E. Breedlove 4216* (CAS, MO); **Oxchuc:** 5 km east of Oxchuc, *D.E. Breedlove & F. Almeda 57120* (CAS, MO); **San Cristóbal las Casas:** NE edge of San Cristóbal las Casas, *D.E. Breedlove 54721 & G. Davidse* (CAS, MEXU, MO); Northeast edge of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 54746* (CAS, MEXU, MO); San Fernando: Parque Nacional del Sumidero, 20–22 km NW of Tuxtla Gutiérrez, along the road to the canyon Outlook, *G. Davidse et al. 29764* (MO); Northeast edge of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 54728* (CAS, MO); **San Juan Chamula**, *C. Santíz Ruíz 222* (MEXU); **Tuxtla Gutiérrez:** 22 km north of Tuxtla Gutiérrez. Cliff faces and limestone bluffs with Seasonal Evergreen Forest, Calycophyllum, Zanthoxylum, Bursera, Quercus, Ficus and Erythrina at El Sumidero, *D.E. Breedlove & B.M. Bartholomew 55482* (CAS, MO); 16 km north of Tuxtla Gutiérrez on road to El Sumidero, *D.E. Breedlove & Bruce M. 55494* (CAS, MO); t El Sumidero, 22 km north of Tuxtla Gutiérrez, *D.E. Breedlove & A.R. Smith 21557* (CAS, MO); **Venustiano Carranza:** Wooded slope near the town, along the road to Pugiltic, *R. M. Laughlin 2702* (ENCB); 3 mi S of Aguacatenango along road to Pinola Las Rosas, *D.E. Breedlove & P.H. Raven 13135* (ENCB); **Villa Corzo:** Above Colonia Vincente Guerrero on road to Finca Cuxtepec [Custepec], *D.E. Breedlove 54599 & G. Davidse* (CAS, MO); near Paraje Navenchauk, *D.E. Breedlove & G. Davidse 53899* (CAS MO); Near Colonia Vincente Guerrero, *D.E. Breedlove 48584* (CAS, MO); **Zinacantán:** near Paraje Zinacantán, *D.E. Breedlove 53901 & G. Davidse* (MEXU); near the Zinacantán Paraje of Muctajoc, *D.E. Breedlove & G. Davidse*, (MEXU); *D.E. Breedlove 13807* (DS, MO). Nicaragua. **Nueva Segovia**: Santa María, km 242, 1 km al W de Santa María, *P.P. Moreno 25214* (MO).

3. ***Muhlenbergia capillaris*** (Lam.) Trin., Gram. Unifl. Sesquifl. 191–192, 296, t. 5, f. 15. 1824.

Fig. 4A–D

Stipa capillaris Lam., Tabl. Encycl. 1: 158. 1791. Type: USA, E. Carolina, *D. Fraser s.n.* (holotype: P-LAM!; isotypes: MPU-026956 [image!], US-A866136 fragm. ex P-LAM!). ≡ *Podosaemum capillare* (Lam.) Desv., Nouv. Bull. Sci. Soc. Philom. Paris, sér 2 2: 188. 1810. ≡ *Trichochloa capillaris* (Lam.) DC., Cat. Pl. Horti Monsp. 152. 1813. Basionym.

Description. Caespitose ***perennials***. ***Culms*** 60–100(–150) cm tall, erect from the base, not conspicuously branched; ***internodes*** mostly glabrous, sometimes puberulent below the nodes. ***Leaf sheaths*** glabrous or puberulent, basal sheaths terete, often becoming fibrous, but never spirally coiled, at maturity; ***ligules*** 1.8–5(–10) mm long, membranous, firm, strongly decurrent, obtuse; ***blades*** 10–35(–80) cm long, 2–4 mm wide, flat or involute, smooth abaxially, scabrous adaxially. ***Panicles*** 15–50(–60) cm long, 8–30(–41) cm wide, longer than wide, diffuse; ***primary branches*** 2–20 cm long, capillary, diverging 30–100° from the culm axis, naked basally, lower branches with 5–20 spikelets; ***pedicels*** 10–40(–50) mm long, longer than the spikelets, capillary, flexible.

Figure 4. A–C *Muhlenbergia capillaris* (Lam.) Trin. **A** habit **B** glumes **C** floret. **A–C** drawn from *F. Lamson Scribner s.n.* (US-746068) used in Hitchcock (1935).

Spikelets 3–5 mm long, usually purple, occasionally green, brown, or stramineous; ***glumes*** (0.3–)1–1.5(–2) mm long, usually less than 1/2 as long as the lemmas, subequal, glabrous; ***lower glumes*** 1-veined, usually unawned, rarely awned, awns 1–3 mm long; ***upper glumes*** 1-veined, rarely 3-veined, acute to acuminate, often erose, usually unawned, rarely awned, awns 1–3(–5) mm long; ***lemmas*** 3–5 mm long, lanceolate, not shiny, calluses short pubescent, apices scabrous, acuminate, sometimes with 2 setaceous teeth, teeth to 1 mm long, unawned or awned, awns 2–13(–18) mm long, clearly demarcated from the lemma bodies; ***paleas*** 2–4.5 mm long, lanceolate, acuminate, usually unawned; ***anthers*** 1.5–2 mm long, purple. ***Caryopses*** 2–2.5 mm long, narrowly elliptic, brownish.

Distribution. *Muhlenbergia capillaris* ranges from the southeastern United States, the Caribbean coast of México (Quintana Roo), extending to Guatemala, Bahamas, and various Caribbean islands (Peterson et al. 2001). It is also grown as an ornamental. This species was reported from the Yucatán (Dávila et al. 2018) but we have been unable to locate a specimen to verify this record.

Ecology. *Muhlenbergia capillaris* occurs in open woodlands, pine-oak forests, savannahs and on rock outcrops; 0–2020 m.

Comments. *Muhlenbergia capillaris* can be separated morphologically from *M. rigida* in having panicles 8–30(–41) cm wide with open, diffuse branches that are strongly divergent, whereas *M. rigida* has loosely contracted panicles 2–5(–12) cm wide with appressed to ascending branches spreading up to 80° from the culm axis. *Muhlenbergia capillaris*, a member of *M*. subg. *Trichochloa*, is found in a strongly supported clade sister to *M. expansa* (Poir.) Trin., a species from the southeastern USA (Fig.1; Peterson et al. 2021).

Specimens examined. Guatemala. **Guatemala**: Guatemala City, open prairie, *A.S. Hitchcock 9141* (US-995855); **Huehuetenango**: Rocky dry slopes above San Ildefonso, Ixtahuacan, *J.A. Steyernmark 50673* (US-1935074, US-2208677); **Quiché**: Chichicastenango, 1 km north of Chichicastenango. Small “prairie” next to a milpa, shallow soil on sandstone, *W.E. Harmon 4364* (MO), mts. E of Quiche, *V. Grant 645* (US-1818233). Mexico. **Chiapas**: near ranch house on S edge of Teopisca, *D.E. Breedlove & P.H. Raven 13097* (MICH); Marsh near Teopisca, *D.E. Breedlove & G. Davidse 54803* (MICH, CAS, MO); Teopisca, slope at W edge of Teopisca, *D.E. Breedlove & J.L. Strother 46373* (CAS, MO). **Quintana Roo**: **José María Morelos**: Lake Chichancanab (Laguna Chan-kabnab), 28–29 July 1932, *J.R. Swallen 2726* (MO, US-1537112, US-3090503).

4. ***Muhlenbergia cenchroides*** (Humb. & Bonpl. ex Willd.) P.M. Peterson, Caldasia 31(2): 280, f. 2 C–D. 2009.

Fig. 5A, B

Aegopogon cenchroides Humb. & Bonpl. ex Willd., Sp. Pl. 4(2): 899. 1806. Type: Venezuela, Sucre, Cumaná, *F.W.H.A. Humboldt & A.J.A. Bonpland 3002* (holotype: B-W-01637-020 [image!]). Basionym.

= *Hymenothecium quinquesetum* Lag., Gen. Sp. Pl. 4. 1816. *Aegopogon quinquesetus* (Lag.) Roem. & Schult., Syst. Veg. 1:805. 1817. Type: México, México Iperio, *Ludovicus Nee* (holotype: MA; isotype: BAA-00002156 [image!]).

= *Hymenothecium trisetum* Lag., Gen. Sp. Pl. 4. 1816. *Aegopogon trisetus* (Lag.) Roem. & Schult., Syst. Veg. 2:805. 1817. *Aegopogon cenchroides* var. *trisetus* (Lag.) E. Fourn., Mexic. Pl. 2:72. 1886. Type: México, México Imperio (holotype: MA; isotype: BAA-00002158 [image!]).

= *Aegopogon setifer* Nees, Linnaea 19(6):691. 1847. Type: México, *A. Aschenborn 132* (holotype: B; isotypes: FR-0036375 [image!], FR-0036376 [image!], US-75953 fragm. ex B!).

= *Aegopogon cenchroides* var. *multisetus* E. Fourn., Mexic. Pl. 2: 72. 1886. Type: México, Moran. in rupibus, 1840, *H. Galeotti 5808* (lectotype: BR! designated by Peterson et al., Contr. U.S. Natl. Herb. 41: 10. 2001; isolectotypes: P!, US-75958 fragm. ex P!).

Description. Caespitose ***perennials*** often sprawling, occasionally with stolons. ***Culms*** (10–)25–55 cm tall, glabrous below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** mostly 0.8–8 cm long, shorter than the internodes, glabrous; ***ligules*** 1–2 mm long, apex acute, lacerate; ***blades*** 1.5–6 cm long, 0.5–2 mm wide, flat, scaberulous above, smooth beneath. ***Panicles*** 2–8 cm long, 0.5–1.2 cm wide, open, loosely-flowered with recemosely arranged branches; ***primary branches*** 2–4 mm long, excluding the awns, one per node, often purplish. ***Spikelet*** fascicles of three with one sessile perfect spikelet (lateral staminate or sterile), the ***pedicels*** less than 0.2–0.5 mm long and the other two spikelets short-pedicelled, the ***pedicels*** about 0.7–1.2 mm long; ***glumes*** (1–)1.5–2.8 mm long, oblong and wider distally, 1-veined, apex deeply notched, awned, the awns 2–4 mm long, lobes triangular, acute; ***lemmas*** 2.5–3 mm long, fusiform, 3-awned, the central awns 5–13 mm long, lateral awns 2–3 mm long; ***paleas*** 2.5–3 mm long, puberulent, apex awned, the awns 1–2 mm long; ***anthers*** 1.6–1.8 mm long, yellowish to purplish. ***Caryopses*** 1–1.4 mm long, fusiform. 2*n* = 40, 60, 80.

Distribution. *Muhlenbergia cenchroides* ranges from throughout México, throughout Central America (Costa Rica, El Salvador, Guatemala, Honduras, México, Nicaragua, and Panama) to South America in Bolivia, Brazil, Colombia, Ecuador, Peru, Guyana, and Venezuela (Pohl 1994a; Peterson et al. 2001).

Ecology. *Muhlenbergia cenchroides* occurs on rocky slopes, canyons, cliffs, roadcuts, arroyos, seeps, and meadows, often associated with *Baccharis* spp., *Salvia* spp., *Eupatorium*, *Festuca*, *Schizachyrium*, *Muhlenbergia* spp., *Hyptis*, *Oxalis*, *Aristida*, *Bidens*, *Sporobolus*, *Carex*, *Eragrostis*, *Lupinus*, *Lycopodium*, *Jarava*, *Nassella*, *Agave*, *Thalictrum*, and *Chusquea*; 1430–3850 m.

Comments. *Muhlenbergia cenchroides* can be separated from its South American sister, *M. bryophilus* (Döll) P.M. Peterson (South American) in having anthers 1.6–1.8 mm long, the perennial habit with (10–)25–55 cm tall culms, and sessile or inconspicuously pedicelled perfect spikelets usually associated with two staminate or sterile pedicelled spikelets (Tovar 1993; Giraldo-Cañas and Peterson 2009). In addition to being perennial, *Muhlenbergia cenchroides* differs from *M. uniseta* in having glumes with acute lobes and central veins extending as an awn 2–4 mm long.

Muhlenbergia cenchroides, a member of *M*. subg. *Muhlenbergia*, lies in a strongly supported trichotomy with *M. bryophilus* and *M. uniseta*, and this trichotomy is sister to *M. tarahumara* P.M. Peterson & Columbus (Sierra Madre Occidental, México) in *M*. subg. *Muhlenbergia* (Peterson et al. 2010b; Peterson et al. 2021).

Figure 5. A, B *Muhlenbergia cenchroides* (Humb. & Bonpl. ex Willd.) P.M. Peterson **A** habit **B** spikelets **C–G** *Muhlenbergia diandra* (R.W. Pohl) Columbus **C** habit **D** ligule with auricles **E** glumes **F** floret **G** stamens and pistil. **A, B** drawn from *S. Beck 7464* used in Renvoize (1998) **C–G** drawn from *P.C. Standley 44066* (US-1307162)

Specimens examined. Costa Rica. **Alajuela**: SW of Palmira, *A. Weston 3076* (USJ); 1 km S of Carrizal, *R.W. Pohl & G. Davidse 11499* (CR); 6.5 km W of Varablanca, *R.W. Pohl & C. Calderón 10278* (CR); 0.5 km W of Varablanca, roadside, *R.W. Pohl & C. Calderón 10257* (CR). **Cartago**: Reserva Biológica Tres de Junio, *J. Gómez-L. & D. Rivera 1221* (USJ); Interamerican Highway, about km 82, *L. Clark et al. 1570* (USJ, MO, US); Cordillera Central, lower slopes of Volcán Irazú, 1 km below San Juan de Chicoa, *R.W. Pohl & G. Davidse 11421* (CR); Reserva Forestal Río Macho, Cuenca del Savegre, Cerro de la Muerte, Carretera Interamericana, entre km 93/94, *A. Rodríguez 4227* (CR, INB); Estación Cuericí, camino a la Auxiliadora, 2 km E de Villa Mills, *B. Gamboa R. 753* (INB); Salsipuedes, bosque secundario y turberas en las cabeceras del rio Humo, *J.F. Morales 6223* (INB, MO); Santa Rosa, *E. Alfaro 5132* (INB); San Ramón de Tres Ríos, Westl. Talhang des Río Tiribí, untere Nebelwaldregion, Weg Einschmitt, vollsonniger Lehmhang ohne Gehölze, *H. Kuhbier 214* (CR); **Heredia:** *P. Döbbeler 2010* (MO); San José de la Montaña, *M. Montiel s.n.* (USJ); Monte de la Cruz, R. Ocampo 1251 (CR); 2 km N of Porrosatí, *R.W. Pohl & M. Gabel 13673* (CR); San José de la Montaña, D. Santamaría 3092 (INB); Parque Nac. Braulio Carrillo Porrosatí, Río Ciruelas, *R. Rivera 457* (MO). **San José**: Santa Maria de Dota, *J. Bustamante 218* (INB); Hda. Tiquires, Bosque primario, robledales y potreros en la Fila Aguabuena cerca de la Laguna, *J.F. Morales 4232* (MO, INB); Bosque secundario en la cima del Cerro Pico Alto, cabeceras del rio Poas, El Cidral, *J.F. Morales 1725* (INB); Copey, Cerro Vueltas, bosques enanos transición a páramo y páramos en la cima, *L. G. Clark 1570* (INB); Carretera Interamericana, ruta al Cerro de la Muerte, 2 km después de los Chespiritos dirección a Pérez Zeledón, entre km 80–81, *A. Rodríguez 3276* (INB, MO); Dota, Reserva Ftal Los Santos, Estación Ojo de Agua, Calle a Providencia, *E. Alfaro 2223* (INB); along Carretera Interamericana between km 103 and km 106, ca. 7.7–9.7 km beyond La Georgina toward San Isidro de El General, *M. Grayum 8154* (INB); Bajo Gamboa, 1 km sobre el camino que conduce al Cerro Caraigres, *J.F. Morales 6718* (CR, INB); R.F. Los Santos. Providencia Dota, Fila Cerro Vueltas, *J.F. Morales 8412* (INB); Salsipuedes, km 69, Carretera Interamericana, *B. Hammel 5132* (INB); Direct line from Hotel La Georgina to Cerro Frío of the Cerro Buenavista complex (Cerro de la Muerte), area with television and radio towers, *G. Davidse 25028* (MO); along Carretera Interamericana between km 103 and km 106, ca. 7.7–9.7 km beyond La Georgina toward San Isidro de El General, *M. Grayum & J. Affolter 8154* (MO); Z.P. Cerros de Escazú, Cerros Escazú-La Carpintera, *J.F. Morales 1725* (MO); Cuenca Térraba-Sierpe. Estación Cuericí, camino a la Auxiliadora, bosque secundario en orillas del camino, *B. Gamboa R. 753* (MO); Los Santos, Est. Ojo de Agua, colectando en bosque y orillas del tendido eléctrico, *E. Alfaro & M. Alfaro 2223* (MO); Cerro León, camino hacia Fila Aguabuena, *A. Quesada et al. 751* (CR); Cerro León, camino hacia Fila Aguabuena, *A. Quesada et al. 755* (CR); Los Cuadros, O. Jiménez 710 (CR); Cordillera de Talamanca, 26 km N of San Isidro del General along the Carretera Interamericana, *R.W. Pohl & G. Davidse 10755* (CR); along carretera Interamericana, ca. 10 km N of San Isidro del General roadsides, *R.W. Pohl & C. Calderón 10064* (CR); Montane forest formations with open landslides and road cuts and swamps, about 22 km SE of Empalme, along the Interamericcan Highway, *G. Davidse 6452* (CR); Z.P. Cerros de Escazú Río Londres y Río Agres, bosque ripario secundario, *G. Vargas & J. Sánchez 940* (CR); Los Santos Ca. 4 km due S of La Georgina at Villa Mills off the Interamerican

Hwy., *F. Almeda & K. Nakai 4824* (CR); R.F. Los Santos Camino entre San Gerardo y Carretera Interamericana, *A. Estrada et al. 2782* (CR); Cerro León, camino hacia Fila Aguabuena, *R. Chacón et al. 188* (CR); San Antonio, *S. Lobo 908* (CR); Rivas, *A. Rodríguez 6509* (INB); Páramo, *D. Santamaría 3151* (INB); Páramo, *S. Lobo 1656* (CR); Carretera interamericana Sur, *J. Gómez. 6342* (CR); 71 km from San Isidro del General on Cartago road, *H.S. McKee 11221* (US). El Salvador: **Santa Ana**, Cerro Monte Cristo, NE of Metapan, *R.W. Pohl 12581* (CR); Montecristi, *R. Villacorta & J. González 1158* (MO); Volcán de Santa Ana, *G. Davidse & R.W. Pohl 2050* (MO); Parque Nacional Montecristo, camino a Miramundo, *R.A. Carballo & J. Aldana RAC00590* (MO). **Usulutan**: Laguna de Alegría, por la entrada, *D. Williams & R.W. Williams 356* (MO). Guatemala. **Alta Verapaz:** *H. von Turckheim s.n.* (MO).). **Chimaltenango**: Vegetación del volcán de Acatenango, *M. Vélz 93.2751* (MO). **Guatemala**: Guatemala city, *A.S. Hitchcock 9108* (US). **Huehuetenango:** Carretera a la Sierra de los Cuchumatanes, M. Véliz, 96.5778 (MO); Dry oak-pine forest and ravines about 6 km S of Huehuetenango, *L.O. Williams et al. 22038* (US). **Izabal:** Between Los Amates and Izabal, Sierra del Mico, *W.A. Kellerman*, *6230* (MO). **Quetzaltenango**: Mountains above Ostucalco, *P. C. Standley 66407* (US); vicinity of Zunil, dry brushy hillside, *P.C. Standley 83211* (US).**Sololá**: Volcan Atitlán, *J. Viñals*, *s.n.* (MO). Honduras. **Comayagua**: vicinity of Siguatepeque, *P.C. Standley 56214* (US). **El Paraíso**: Mansaragua, *G. Davidse et al. 35031*(MO). **Intibucá**: Cerro San Cristóbal, *C. Nelson & R. Andino 10605* (MO). **Ocotepeque**: Nueva Ocotepeque, *W.E. Harmon & J.D. Dwyer 4123* (MO). Mexico. **Chiapas**: **Cintalpa:** Hacienda Monserrat, *C.A. Purpus 467* (MO). Larráinzar, Muctahuitz. Región Los Altos, *L. Soto-Pinto 1543* (MEXU). **Huixtlán**: Chilil, *B.Y. López-Santos 217*, *218* (MEXU). **Tenajapa**: In the Paraje of Pahal Ton, *D.E. Breedlove 12591* (MEXU). **Mapastepec**: Reserva El Triunfo, polígono 1, Dry area above Cañada Honda, *M. Heath & A. Long 1043* (MEXU). **San Cristóbal**: 10 km de la carr. San Cristóbal-Ocosingo, *Borrego 6* (MEXU); entrada a Zacualpa, 500 m carr San Cristóbal-Comitán, *S. Ochoa-Gaona et al. 4258* (MEXU). **San Juan Chamula**: Los Altos, Bautista Chico, *L. Soto-Pinto 1236*, *1264* (MEXU); *Yalchín*, *B.Y. López-Santos & F. Martínez 735* (MEXU). **Unión de Juárez**: en el camino de Talquián a Chiquihuite, *E. Martínez et al. 193976* (MEXU). **Venustiano Carranza**: Ejido "Laja tendida", km 17 de carr. Venustiano Carranza-Tuxtla Gutíerrez, aprox. 2 km a Flores Magón, *A. Miranda S. 1237* (MEXU); *G. Davidse 9449* (MO). Nicaragua. **Chontales**: 3 miles southeast of Juigalpa, route 7, roadside and swampy woods [Seymour series], *D.A. Dudey 1602* (MO). **Estelí**: Mechapa, *D.A. Hamblett 992* (MO). **Rivas:** Southwest of La Virgen and northeast of San Juan del Sur, route 16 where road crossed brook, km 136 [Seymour series], *F.C. Seymour1228* (MO); Peñas Blancas, *F.C. Seymour1853* (MO). Panama. **Chiriquí**: Volcán Barú, on road to towers at top; near towers at summit, *G. McPherson 15064* (MO); 3 km S of Boquete along Rio Caldera, *P.M. Peterson & C.R. Annable 7387* (MO); Steep forested slope to W of Río Caldera, ca. 2 km NW of Bajo Mono (Boquete region), *M. Grayum et al. 6450* (MO); Camino de acceso al Parque Nacional Volcán Barú (vertiente oriental), *M. Vega & R. Rincon 194* (MO); Baru/Potrero Muleto, *G. Davidse & W.G. D'Arcy 10257* (MO); Volcán Chiriquí, *A. Weston 12375A* (CR); Volcán Chiriquí, *A. Weston 6216* (CR); Side of Barú Mt., *J.S. McCorkle 156* (US); 8 km NW of Boquete on road to Volcán Barú, slopes above Quebrada Grande, *P.M. Peterson & C.R. Annable 7361* (US); Chiriqui Volcano, *A.S. Hitchcock 8218* (US); Chiriquí Volcano, *A.S. Hitchcock 8206* (US).

5. *Muhlenbergia ciliata* (Kunth) Trin., Gram. Unifl. Sesquifl. 193. t.5, f.16. 1824.
Fig. 6A–D

Podosemum ciliatum Kunth, Nov. Gen. Sp. (quarto ed.) 1:128–129. 1816. Type: México, Michoacán, Volcán de Jorullo, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (**lectotype, designated here**: P-00077293 [image!]; isolectotypes: BAA-1619 ex P!, BM!, P-00129654 [image!], US-91918 fragm. ex P!). ≡ *Trichochloa ciliata* (Kunth) Roem. & Schult., Syst. Veg. 2:386. 1817. ≡ *Polypogon ciliatus* (Kunth) Spreng., Syst. Veg. 1:243. 1825. Basionym.

= *Muhlenbergia adspersa* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(3-4):291. 1841. Type: Peru, Lima, ex herb. *C.H. Mertens s.n.* (**lectotype, designated here**: LE-TRIN-1486.01 fragm. ex LE herb. Mertens!; isolectotype: US-87236 fragm. ex LE herb. Mertens!).

Description. Sprawling, slender ***annuals***. ***Culms*** 8–30(–50) cm tall, glabrous, filiform, often tufted, freely branching at lower nodes; 0.2–0.5 mm diameter just below the inflorescence; ***internodes*** 6–42 mm long. ***Leaf sheaths*** (8–)20–44 mm long, glabrous or sparsely pilose along the margins, shorter than the internodes; ***ligules*** 0.2–0.8 mm long, a ciliate membrane; apex truncate; margin with a tuft of hairs up to 1 mm long; ***blades*** 1–4 cm long, 0.6–1.4 mm wide, flat or loosely involute, often sparsely pilose above, glabrous below. ***Panicles*** 4–12 cm long, 1.8–5.0 cm wide, terminal, densely flowered; ***primary branches*** 1.5–3.7 cm long spreading and reflexed at maturity up to 90° from the rachises, one per node; ***pedicels*** 0.5–3 mm long, glabrous, appressed, erect; nodes 6–13 per panicle. ***Spikelets*** appressed to the branches, overlapping; ***glumes*** 0.7–1.7 mm long, subequal, glabrous, 1-veined; apex acuminate, often mucronate; the mucro up to 0.5 mm long; ***lower glumes*** 0.7–1.5 mm long; ***upper glumes*** 0.8–1.7 mm long; ***lemmas*** 1.8–2.5 mm long, lanceolate, slender, awned, strongly 3-veined but appearing five-veined, the intermediate "nerves" actually rows of short barbs on top of folded epidermal ridges, sometimes with prominent short hairs (scabers) along the lateral veins, often appearing glabrous without magnification, awns (1–)5–11(–18) mm long, flexuous; ***callus*** minutely short pubescent; ***paleas*** 1.6–2.4 mm long, narrowly lanceolate, glabrous; ***anthers*** 0.3–0.5 mm long, yellowish. ***Caryopses*** 0.8–1.8 mm long, narrowly fusiform, brownish. 2*n* = 20.

Distribution. *Muhlenbergia ciliata* is found throughout México and Central America (Costa Rica, El Salvador, Guatemala, Honduras, México, Nicaragua, and Panama) to Ecuador, Peru, Brazil, Bolivia, and Argentina (Peterson and Annable 1991; Peterson et al. 2001).

Ecology. *Muhlenbergia ciliata* is found on moist to dry soils usually beneath taller vegetation, sandy drainages, steep rocky slopes, rock outcrops, and disturbed roadsides in woodlands with *Acacia*, *Agave*, *Andropogon*, *Bidens*, *Baccharis* spp., *Bothriochloa*, *Eupatorium*, *Melinus minutiflora* P. Beauv., *Muhlenbergia bryophilus*, *M. flexuosa*, *M. rigida*, *Puya*, and *Salvia*; 1000–2400 m.

Comments. *Muhlenbergia ciliata* can be differentiated from *M. tenella* in having lemmas with ciliate margins (not ciliate in *M. tenella*), reflexed and spreading panicles branches (tightly appressed panicle branches in *M. tenella*), regular, alternating leaf blade insertion (secund in *M. tenella*) [Peterson and Annable 1991; Peterson and Giraldo-Cañas 2011, 2012].

Muhlenbergia ciliata is closely related to *M. pectinata* C.O. Goodd. (North America) and *M. tenella* (Kunth) Trin. (North America, Central America, and Colombia) [Peterson and Annable 1991]. These three species form a strongly supported clade in *M.* subg. *Muhlenbergia* (Fig.1; Peterson et al. 2010b; Peterson et al. 2021).

Specimens examined. Costa Rica. **San José**: *J.F. Morales 6707A* (MO); Cerro de Piedra Blanca, above Escazú, *P.C. Standley 32486* (US); Cord. Talamanca, 14 km S of Division along the Interamerican Highway, roadside through oak forest, road fill, *R.W. Pohl & G. Davidse 11616* (US). El Salvador. **San Salvador**: Volcano of San Salvador, *A.S. Hitchcock 8938* (US). Guatemala. **Alta Verapaz**: Coban, Unter Kiefernwald, *H. Von Turckheim 3989* (US). **Guatemala**: Guatemala city, dry hill, *A.S. Hitchcock 9061* (US). Quetzaltenango: km 15.5, *M. de Koninck*, *M. 227* (US). **Huehuetenango**: San Juan Ixcoy, Sierra de los Cuchumatanes, 3 mi N of San Juan Ixocy on Hwy 9N, *P.M. Peterson & C.R. Annable 4689* (MO); Huehuetenango, *P.M. Peterson & C.R. Annable 4681* (MO). **Sacatepequez:** Magdalena, *W.A. Archer 3865* (US); Volcano Agua, open ground near Antigua, *A.S. Hitchcock 9135* (US); Volcano Agua, *A.S. Hitchcock 9136* (US). **Totonicapán**: San Francisco El Alto, *W.E. Harmon 4555* (MO). **Zacapa**: Forested slopes, Sierra de las Minas, near summit of mountain, between Rio Hondo and Finca Alejandria, *J.A. Steyermark 29683* (US). Honduras. **Copan**: Sta. Rosa de Copan, *W.A. Archer 3838* (US). **Francisco Morazán:** Santa Lucía, Quebrada Hierba Buena, *R. Clotter 87* (MO); Tatumbla, Cerro Uyuca, *I. Cruz 93* (MO); Tatumbla, Cerro Uyuca, *R.W. Pohl & M. Gabel 13414* (MO); Distrito Central, El Hatillo, *R.W. Pohl & M. Gabel 13463* (MO); Distrito Central, between El Hatillo and Los Jutes, *R.W. Pohl & M. Gabel 13790* (MO); Valle Angeles, *R. Ramos 99* (MO); Valle de los Angeles, El Balmoral, *C. Román 23* (MO); Drainage of the Rio Yeguare, *L. O. Williams 17001* (US); Cerro de Uyuca, along trail from Las Flores to La Labranza, *P.C. Standley 27380* (US); San Antonio del Oriente, *J.R. Swallen 10916* (US); Mt. Uyuca, *J.R. Swallen 11177* (US). Mexico. **Chiapas: Cacahoatán:** 3 km NE of Huixtla on hwy to Motozintla, *W.D. Stevens & E.M. Martínez 25671* (MO). **Ocozocoautla de Espinosa:** 13 km E of Ocozocoautla on Rte. 190, then N on road to Aguacera, *M.J. Huft el al. 2252* (MO). **Ixtapa:** 1 km W of Ixtapa, *F.W. Gould 12713* (ENCB). **Jitotol**: about 10 mi NE of Bochil on Hwy 195, *J.R. Reeder & C.G. Reeder 6075* (ARIZ, ENCB, MO); 4 km SE of Jitotol along road to Bochil, *G. Davidse et al. 29663* (MEXU); Slope, 10 km N of Jitotol near Rio Hondo, *D.E. Breedlove & G. Davidse 55155* (CAS); Santa Isabel near Jitotol, *A. A. Beetle M-4091* (MEXU). **Ruíz:** camino de El Zopilote a San Juan Corapan, *A. Ramos 291* (MEXU). **Teopisca:** Belem, 8 km NW of Teopisca along hwy. to San Cristobal de las casas, *G. Davidse et al. 29771* (MEXU); 8.2 mi SE de San Cristóbal de las Casas, *P.M. Peterson & C.R. Annable 4679* (US); 10.5 mi SE of San Cristobal de las Casas, *P.M. Peterson & C.R. Annable 4717* (ENCB, MEXU, US); **Venustiano Carranza:** 3 mi S of Aguacatenango along rd to Pinola Las Rosas, *D. E. Breedlove & P. H. Raven 13458* (US). Nicaragua. **Estelí:** Darailí, *W.D. Stevens 15913* (MO). Panama. **Chiriquí:** vicinity of Boquete, from Boquete to 3mi N, *W.H. Lewis et al. 332* (MO).

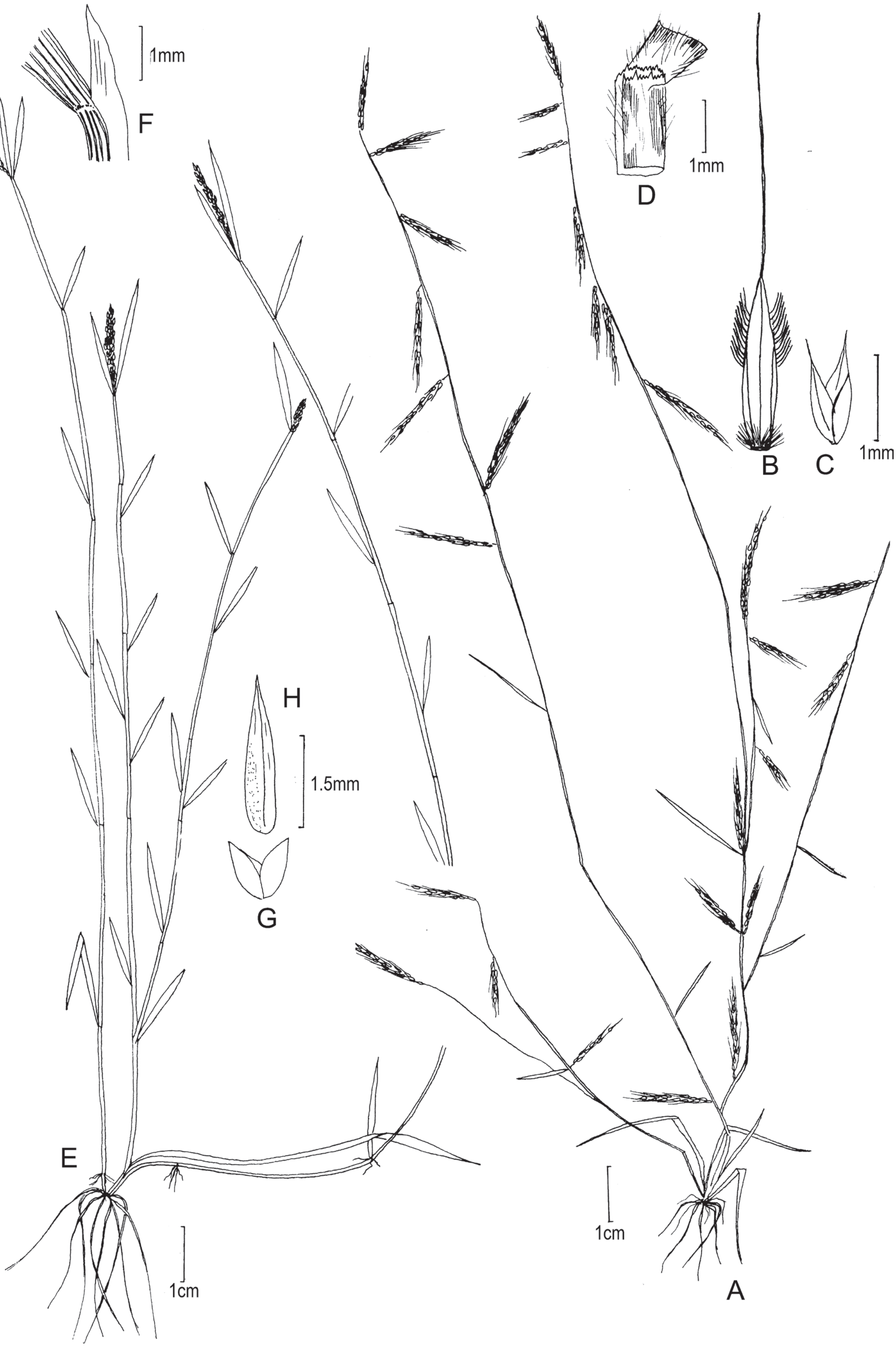

Figure 6. A–D *Muhlenbergia ciliata* (Kunth) Trin. **A** habit **B** floret **C** glumes **D** ligule **E–F** *Muhlenbergia vaginata* Swallen **E** habit **F** ligule **G** glumes **H** floret. **A–D** drawn from *P.M. Peterson & C.R. Annable 4541* (US, WS) **E–F** drawn from *P.M. Peterson & C.R. Annable 4111* (US, WS) both used in Peterson and Annable (1991).

6. *Muhlenbergia diandra* (R.W. Pohl) Columbus, Aliso 28: 66. 2010 (21 May).
Fig. 5C–G

Pereilema diandrum R.W. Pohl, Novon 2(2): 102. 1992. Type: Costa Rica, Heredia: Puente Mulas, S of San Antonio, canyon of Río Virilla, 850 m, 28 Nov 1968, *R.W. Pohl & G. Davidse 11482* (holotype: ISC-277884!; isotypes: CR-46688!, K-000308951 [image!], MO-356265 fragm. ex ISC!, US-3054594!). ≡ *Muhlenbergia diandra* (R.W. Pohl) P.M. Peterson, Amer. J. Bot. 97(9): 1543. 2010 (1 Sep), isonym. Basionym.

Description. Caespitose ***annuals***. ***Culms*** 35–90 cm tall, erect to somewhat decumbent and rooting at the lower nodes, smooth and glabrous below the nodes; internodes 1–2 mm diameter, glabrous or slightly scabrous, often reddish. ***Leaf sheaths*** shorter than the internodes, scabrous or smooth; prophyll**s** 2–3 cm long, prominent, bifid; ***ligules*** 0.7–1 mm long, membranous, thick, apex truncate; ***blades*** 9–22 cm long, 5–9 mm wide, flat, scabrous, auriculate near base, the **auricles** 1–2 mm long, ciliate, clasping. ***Panicles*** 10–22 cm long, 1–2.5 cm wide, cylindrical, solitary, exserted or included in the sheaths below; ***primary branches*** 1–3.5 cm long, ascending mostly appressed, spreading up to 70° from the culm axis with dense fascicles of florets; ***pedicels*** 0.1–0.3 mm long, the spikelets arising just above the sterile spikelets or bristles, the **bristles** 3–5 mm long. ***Spikelets*** (fertile) 1.8–2.8 mm long; ***glumes*** 0.7–1.5 mm long, subequal, oblong to ovate, 1-veined, awned, the awns 1.5–4 mm long; ***lemmas*** 1.8–2.6 mm long, lanceolate, scabrous 3-veined, awned, the awns 10–24 mm long, straight, callus hairy, the hairs 0.6–1 mm long; ***paleas*** 1.8–2.8 mm long, slightly longer than the lemma, apex bidentate; ***stamens*** 2, ***anthers*** 0.8–1 mm long, often purple. 2*n* = 80 (Pohl and Davidse 1971).

Distribution. The species is endemic to Costa Rica and is known from Provincias Alajuela, Heredia, Puntarenas, and San José (Peterson et al. 2001; Morales 2003).

Ecology. *Muhlenbergia diandra* occurs on dry to moist roadsides and disturbed sites on the margins of humid forests; 500–1800 m.

Comments. *Muhlenbergia diandra* differs from *M. pereilema* in having wide leaf blades 4–9 mm long (2–3 mm wide in *M. pereilema*), lemmas with straight awns (flexuous in *M. pereilema*), and chromosome number (Davidse and Pohl 1992; Morales 2003). This species probably forms a clade with *M. beyrichiana* Kunth, *M. pereilema*, and *M. plumiseta* Columbus within *M.* subg. *Muhlenbergia* (Peterson et al. 2021).

Muhlenbergia beyrichiana is only known to occur in Brazil, Ecuador, and Peru as determined here. Earlier, it was reported in México and Central America but these are in error (Espejo Serna et al. 2000; Lægaard and Peterson 2001; Peterson et al. 2001, 2018).

Specimens examined. Costa Rica. *Hoffmann 465* (US); Río Tiliri, *A. Tonduz 3121* (MO, CR). **Alajuela**: Poás, Carrillos de Poás, *A.M. Brenes 14606* (CR, US); Naranjo, puente sobre el Rio Colorado donde el Tropical Bungee, *B. Hammel 20587* (INB, CR); Naranjo, open areas on upper slopes of Cerro Espíritu Santo, 1–3 km SW of Naranjo, *A.S. Weston et al. 3852* (CR). **Heredia**: Puente de Mulas, S of San Antonio, Canyon of the Río Virilla, *R.W. Pohl & G. Davidse 11482* (MO, CR). **Puntarenas**: Monteverde, 10 km S Monteverde on road to Inter-American Highway, area of spring, *W. Haber & W. Zuchowski 9639* (MO, INB); Cordillera de Tilarán, 10 km SW Santa Elena on road from Monteverde to Inter American Highway, dry ridges and cut banks, *W. Haber & W. Zuchowski 10305* (MO, INB, US). **San José**: San Francisco de Guadalupe, *A. Tonduz 9817* (CR, MO, US); Mora, Llano Grande Puriscal, *O. Jiménez 890* (US, CR); Orillas del camino a San Juan, *O. Jiménez 161* (US); vicinity of Santa Maria de Dota, *P.C. Standley 41769* (US), *43224* (US), *44066* (US); Bordes del rio Torres, San Francisco de Guadalupe, *A. Tonduz 7198* (US).

7. ***Muhlenbergia distichophylla*** (J. Presl) Kunth, Enum. Pl. 1: 202. 1833.
Fig. 7F–I

Podosemum distichophyllum J. Presl, Reliq. Haenk. 1(4–5): 231. 1830. Type: México, 1831, *T.P.X. Haenke* s.n. (holotype: PRC-450429 [image!]; isotypes: MO-1837831!, US-90711 fragm ex PR!, W-0002571!). ≡ *Epicampes stricta* var. *distichophylla* (J. Presl) M.E. Jones, Contr.W. Bot. 14: 6. 1912. Basionym.
= *Muhlenbergia angustifolia* Swallen, N. Amer. Fl. 17(6): 457. 1935. Type: México, near Guadalajara, on rocky hills, 11 Nov 1889, *C.G. Pringle 2346* (holotype: US-822822!; isotypes: BR-0000006863357 [image!], BR-0000006884116 [image!], CM-2819 [image!], KFTA-0002830 [image!], LE!, MEXU-00005188 [image!], MO-1837815!, UC-122455 [image!], US-995828!, US-3274342!, W-18900000582 [image!], W-19160027683 [image!]).

Description. Caespitose ***perennials***. ***Culms*** 100–180 cm tall, erect, glabrous to pubescent below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** 8–42 cm long, longer than basal internodes, glabrous, the keels prominent, sometimes coiled to shredded below, basal sheaths compressed-keeled; ***sheath auricles*** 6–26 mm long, on lower portions and to 6.4 cm above, apex acuminate; ***ligules*** 4–15 mm long, membranous, apex finely lacerate sometimes almost to the base; ***blades*** 18–90 cm long, 2–7 mm wide, flat or folded, scaberulous to scabrous on both sides, the margins and keel saw-toothed. ***Panicles*** 35–70 cm long, 4–15 cm wide, densely-flowered, oblong, sometimes lax near apex, greenish-brown, sometimes reddish-purple; ***primary branches*** 2–15 cm long, without spikelets near the base, appressed to loosely spreading up to 60° from the rachises; ***pedicels*** 0.2–4 mm long, glabrous to scaberulous. ***Spikelets*** 1.5–2.8(–3) mm long, erect, greenish-brown, to reddish-purple; ***glumes*** 1.2–2.8 mm long, longer, as long or a little shorter than the lemma, subequal, oblong to narrowly-oblong, faintly 1-veined, hyaline, glabrous to scaberulous, usually with faint, widely scattered hairs, the hairs less than 0.1 mm long, apex acute to acuminate**;** ***upper glumes*** rarely mucronate, the mucro to 0.4 mm long; ***lemmas*** 1.4–2.7 mm long, lanceolate to linear-lanceolate, awned, glabrous or sometimes the margins on the lower 1/3 pubescent, the hairs to 0.2 mm long, rarely the lower 1/3 with scattered hairs, apex acute, minutely bifid, the teeth to 0.5 mm long, the awn 4–16 mm long, flexuous, often reddish-purple near base; ***callus*** usually short pilose; ***paleas*** 1.3–2.7 mm long, glabrous or with few hairs between the veins on the lower 1/3, apex acute; ***anthers*** 1.2–1.5 mm long, yellowish, sometimes reddish tinged. ***Caryopses*** not seen.

Distribution. The species ranges from central México in Jalisco, Guerrero, México, Oaxaca, and Chiapas to Guatemala (Peterson et al. 2001).

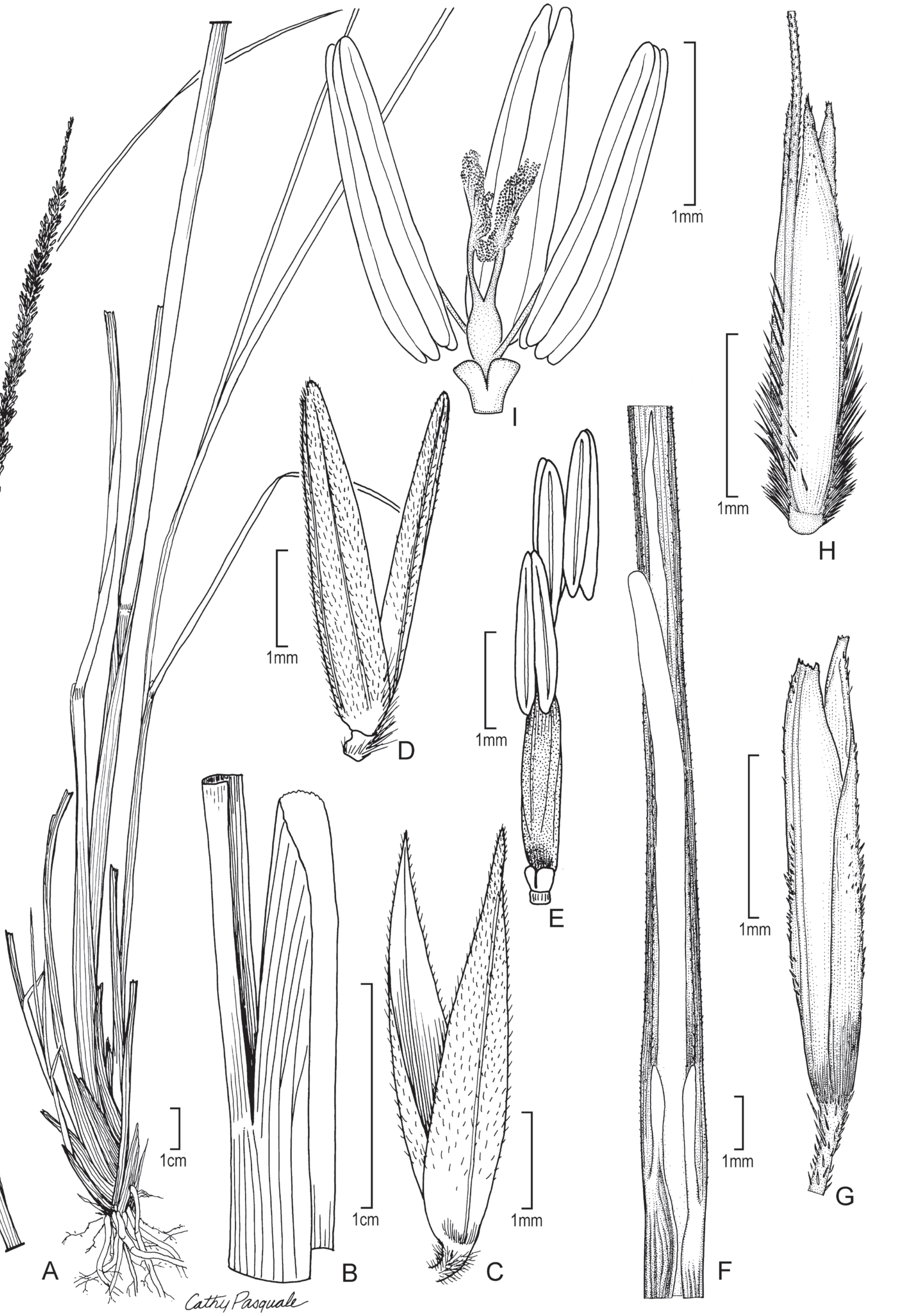

Figure 7. A–E *Muhlenbergia macroura* (Kunth) Hitchc. **A** habit **B** ligule **C** glumes **D** floret **E** stamens, pistil, and lodicules **F–I** *Muhlenbergia distichophylla* (J. Presl) Kunth **F** ligule **G** glumes **H** floret **I** stamens pistil, and lodicules. **A–E** drawn from *P.M. Peterson & C.R. Annable 5970* (US) **F–I** drawn from *L.O. Williams*, *A. Molina R. & T.P. Williams 22309* (US) and *F.W. Gould 12666* (US).

Ecology. *Muhlenbergia distichophylla* occurs in open pine-oak forests and tropical deciduous forests on rocky slopes, canyons, and ravines; 400–2000 m.

Comments. This species can be separated from other members of *M*. subg. *Trichochloa* in having long, acuminate sheath auricles up to 6.4 cm long on the culm, usually greater than 2 cm long on the lower innovations (Herrera Arrieta and Peterson 2018). *Muhlenbergia distichophylla*, a member of *M*. subg. *Trichochloa*, has been found in an unsupported clade with nine other species, distributed in North America (Eastern USA, western USA, México) and Central America [*M. lindheimeri* Hitchc., *M. setifolia* Vasey, *M. dubia* E. Fourn., *M. gypsophila* Reeder & C. Reeder, *M.* x *involuta* Swallen, *M. reverchonii* Vasey & Scribn., *M. sericia* (Michx.) P.M. Peterson, *M. expansa* (Poir.) Trin. and *M. capillaris*] (Fig. 1; Peterson et al. 2021).

Specimens examined. Guatemala. **Escuintla**: Rio Coyolate, near Highway CA-2, thickets on banks of Río Coyolate, *W.E. Harrmon & J.A. Fuentes 4721* (MO). **Huehuetenango:** On dry bank about 5 km. west of Huehuetenango, *L.O. Williams*, *A. Molina R. & T.P. Williams 22309* (US); Sierra de los Cuchumatanes, *P.C. Standley 81480* (US). Mexico. **Chiapas**: Escuintla, *E. Matuda 319* (MEXU); Monte Ovando, *E. Matuda 322* (MO).

8. *Muhlenbergia diversiglumis* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4):298. 1841.

Fig. 8A–D

Type. México, Porto Pedro, *Karwinsky 1393* (**lectotype, designated here**: LE-TRIN-1497.01!; isolectotypes: LE-TRIN-1497.02!, LE-TRIN-1497.03!, US-84831 fragm. ex LE-TRIN!, W-0002564!).

Description. Sprawling ***annuals***. ***Culms*** 16–50 cm tall, decumbent, rooting at the lower nodes; **nodes** retrorsely pilose; ***internodes*** smooth or scabridulous. **Leaf** s**heaths** 1.5–8.5 cm long, sparsely or densely pilose, hairs to 3 mm long, papillose-based; ***ligules*** 0.5–0.8 mm long, membranous, apex truncate, erose; ***blades*** 2–6 cm long, 1.5–4 mm wide, flat, bases distinctly narrowed to the junction with the sheath, surfaces scabridulous and sparsely pilose, hairs papillose-based. ***Panicles*** 6–10.5 cm long, 2.0–4.5 cm wide, open; ***primary branches*** 0.8–3.5 cm long, secund, spreading at right angles or somewhat reflexed usually lying to one side with 2–5 spikelets; ***secondary branches*** not developed; ***pedicels*** 1–5 mm long, scabrous or shortly pilose, hairs papillose-based; **disarticulation** at the base of the primary branches where there is a weak and contorted stipe. ***Spikelets*** 4–8 mm long, dimorphic with respect to the glumes, proximal spikelets on each branch almost sessile; ***glumes* of proximal *spikelets*** on each branch subequal, 0.2–0.7 mm long, orbicular, truncate, often erose or irregularly toothed, unawned; ***glumes* of distal *spikelets*** on each branch markedly unequal; ***lower glumes*** to 8 mm long, 1-veined, acute, usually awned, awns 0.5–3 mm; ***upper glumes*** orbicular, acute, sometimes awn-tipped; ***lemmas*** 4.0–7.6 mm long, linear to broadly lanceolate, light greenish, smooth or scabrous, usually with greenish veins, apices acuminate, awned, awns 6–19 mm long, usually straight, scabrous; ***paleas*** 3.7–6.8 mm long, narrowly lanceolate, coarsely papillate or almost smooth, 2-keeled, the veins prominent, scabrous, greenish, sometimes extending as minute awns, acuminate; ***anthers*** 0.4–0.8 mm long, yellowish. ***Caryopses*** 1.8–3 mm long, oblong-ovoid, flattened, brownish. 2*n* = 20.

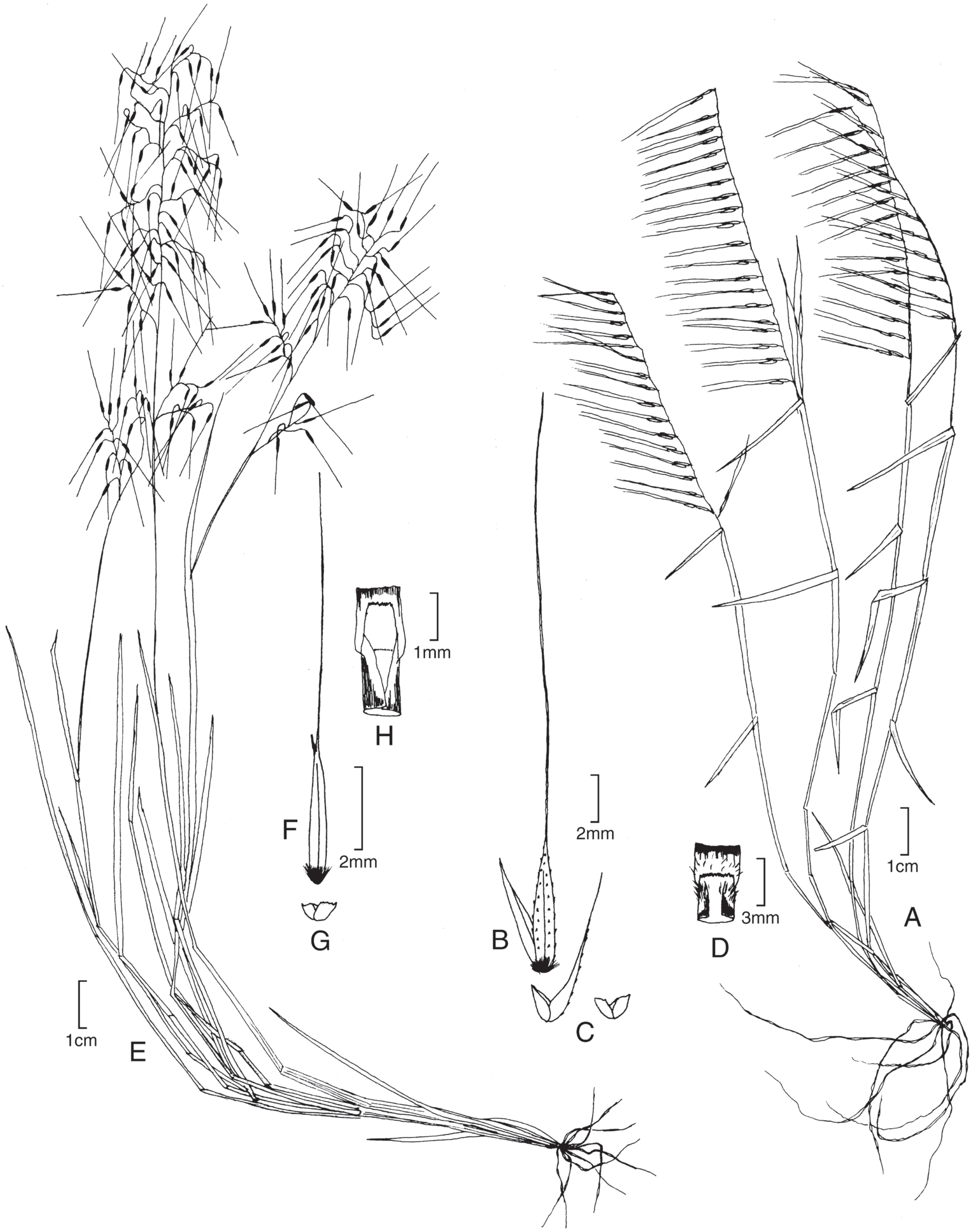

Figure 8. A–D *Muhlenbergia diversiglumis* Trin. **A** habit **B** floret **C** glumes **D** ligule **E–H** *Muhlenbergia implicata* (Kunth) Kunth **E** habit **F** floret **G** glumes **H** ligule. **A–D** drawn from *P.M. Peterson & C.R. Annable 4158* (US, WS). **E–H** drawn from *P.M. Peterson & C.R. Annable 4598* (US, WS).

Distribution. The species is native to North America, Central America, Colombia, Venezuela, Ecuador, Peru, and Argentina (Peterson and Annable 1991; Peterson et al. 2001).

Ecology. *Muhlenbergia diversiglumis* grows on moist cliffs, along water courses, sandy slopes, and road cuts, primarily in moist shaded environments of broadleaf evergreen forests and pine-oak forests; 600–2500 m.

Comments. *Muhlenbergia diversiglumis* can be differentiated from *M. ciliata*, *M. microsperma*, and *M. romaschenkoi* in having secund panicles (versus not secund in the latter three species) with each primary branch consisting of 2–5 dimorphic spikelets where the proximal spikelets have short orbicular glumes less than 1 mm long, and the distal spikelets have glumes up to 8 mm long (Peterson and Annable 1991; Giraldo-Cañas and Peterson 2009).

Muhlenbergia diversiglumis is a member of *M.* subg. *Muhlenbergia* and is sister to *M. alamosae* Vasey, a species from México (Peterson et al. 2021).

Specimens examined. Costa Rica. **Alajuela**: 1 km S of Carrizal, *R.W. Pohl & G. Davidse 11500* (US). **Cartago**: San Ramón, E of San José, open grassy roadside, *R.W. Pohl & Mark Gabel 13678* (MO); Road crossing of Río Reventado between Llano Grande and Tierra Blanca, gravelly river banks, *R.W. Pohl & M. Lucas 13092* (MO). **Heredia**: Porrosati, 2 km by road N of Porrosati, *R.W. Pohl & M. Gabel 13672* (MO); Carrizal, *H. Pittier 786* (US); Barba, cultures a La Esmeralda, *A. Tonduz 1692* (US). **Puntarenas**: Cordillera de Tilarán, *W. Haber & W. Zuchowski 10891* (MO, INB). **San José**: Aserri, Cuenca del Pirris-Damas, Cerros Caraigres, Falda S, Quebrada Concha, en el camino viejo a Bijagual, *J.F. Morales 5913* (MO, INB); León Cortés Castro, Z.P. Caraigres, Cuenca del Pirris-Damas, Fila El Alto. *J.F. Morales 5933* (MO, INB), Pérez Zeledón, P. N. Chirripó camino a Chirripó a orilla del sendero, Cuenca Térraba- Sierpe, *E. Alfaro*, *et al. 966* (CR, INB); Hacienda La Esperanza, La Palma, *O. Jiménez 963* (CR). San Francisco de Guadalupe, cultivos, *O. Jiménez s.n.* (US); Jardines de San Francisco de Guadalupe, *H. Pittier 9068* (US); 11 km N of San Isidro de El General along the Carretera Interamericana, *R.W. Pohl & G. Davidse 11570* (US); Between Aserrí and Tarbaca, *P.C. Standley 41352* (US); vicinity of Santa María de Dota, moist forest, *P.C. Standley 41831* (US); vicinity of Santa María de Dota, *P.C. Standley & J. Valerio 43215* (US); La Verbena de Alajuelita, *A. Tonduz 9084* (US). El Salvador. **Ahuachapán**: Parque Nacional El Imposible: San Benito, al S del enganche de los ríos Venado y Escalares, *E. Sandoval & F. Pérez 1470* (MO). **San Salvador**: Volcán San Salvador, el Boqueron, disturbed secondary forest bordering pasture and cafetale, *A. Monro et al. 2179* (MO); Volcano of San Salvador, *A.S. Hitchcock 8929* (US); Volcano of San Salvador, *A.S. Hitchcock 8939* (US); Volcano of San Salvador, *A.S. Hitchcock 8940* (US). Guatemala. **Alta Verapaz**: near San Cristóbal Verapaz, wet thickets and second growth forest, *L.O. Williams et al. 42228* (MO); Coban, *H. Von Turckheim s.c.* (US); Coban, Maisfeldem. unter Kiefernald, *H. Von Turckheim 3988* (US). **Guatemala**: Guatemala City, *A.S. Hitchcock 9049* (US). **Huehuetenango:** 21 mi NW of Huehuetenango on Pan American Hwy. 1, *P.M. Peterson & C.R. Annable 4682* (MO). **Jalapa:** Mountains along the road between Jalapa and Paraiso, *P.C. Standley 77358* (US). **Jutiapa:** Volcan Chingo, *W.C. Shannon 3699* (US). **Quiche**: Chichicastenango, 4 km S of Chichicastenango, steep wooded hillside dominated by pine and oak, *W.E. Harmon 4613* (MO). **San Marcos**: Wet mountain forest near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, west facing slope of the Sierra Madre Mountains, *L.O. Williams et al. 25993; L.O. Williams et al. 25971* (US); Montane cloud forest area on outer slopes of Tajumulco Volcano, Sierra Madre Mountains about 8–10 km west of San Marcos, *L.O. Williams et al. 26928* (US). Honduras. **Francisco Morazán**: Tatumbla, Cerro Uyuca, *R.W. Pohl 12493* (MO); San Antonio del Oriente, *J.R. Swallen 10975* (US); forest with with *Pinus* and *Liquidambar* entre Peña Blanca y Lo de Ponce, *L.O. Williams & A. Molina R. 17126* (US). Mexico. **Chiapas. Angel Albino Corzo:** slopes of Río Cuxtepec. along stream below Finca Cuxtepec, *D.E. Breedlove & J.L. Strother 46692* (CAS, MO). **Motozintla:** Sierra Madre de Chiapas 5 mi NW of Motozintla de Mendoza on road to El Porvenir, *P.M. Peterson & C.R. Annable 4707* (ENCB, MEXU, US, MO); W side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, *D.E. Breedlove & B.M. Bartholomew 55714* (CAS, MO). **Zinancantán:** Hwy 190, 10 mi SE of the road to Simojovel paraje of Granadia, *D.E. Breedlove 7276* (ENCB).

9. *Muhlenbergia flabellata* Mez, Repert. Spec. Nov. Regni Veg. 17: 213. 1921. Fig. 9A–E

Type. Costa Rica, San José, Cerro de Buena Vista, 3000m, 19 Jan 1891, *H. Pittier 3372* (**lectotype, designated here**: G-00192109 [image!]; isolectotypes G-00192054 [image!], US-577110!).

Description. Caespitose and sprawling ***perennials***. ***Culms*** 25–45 cm long, densely branched near base, decumbent and rooting below; ***internodes*** glabrous. ***Leaf sheaths*** much overlapping, flabellately arranged, glabrous, margins membranous, old sheaths flattened and papery; ***ligules*** (2.5–)3–8 mm long, membranous, hyaline, margins entire, decurrent, apex acute; ***blades*** 2–5 cm long, 1–2 mm wide, flattened to folded or involute, mainly basal, strongly ridged above with short stiff hairs, scabrous below. ***Panicles*** 3–9(–15) cm long, 2–3 cm wide, few-flowered, narrow, short-exserted, dark green; ***primary branches*** mostly 1–2 cm long, sometimes purplish with loosely appressed and ascending branches, spreading up to 30° from the culm axis, central axis slightly flattened, 2-ribbed, scabrous; ***pedicels*** 0.2–1 mm long, scabrous. ***Spikelets*** 3–4 mm long, erect, plumbeous to dark olivaceous; ***glumes*** 1.2–2 mm long, subequal, scabrid, apex obtuse to truncate, unawned; ***lower glumes*** 1.2–1.6 mm long, ovate, usually 1-veined, sometimes unveined; ***upper glumes*** 1.6–2 mm long, half as long as the lemma, oblong-obovate, usually 3-veined, but sometimes very faint, 2 or 3-toothed, the teeth 0.3–0.6 mm long, about 1/3 the length of the glume; ***lemmas*** 3–4 mm long, lanceolate, pilose below and along margins, the hairs mostly less than 1 mm long, the callus hairy, apex awned, the awns 4–8 mm long, flexuous, scabrous, olive-green, arising from a bifid apex, the teeth up to 0.5 mm long; ***paleas*** 3–4 mm long, as long as the lemma, olive-green, scabrous; ***anthers*** 1.8–2.1 mm long, fusiform, purple.

Distribution. The species is endemic to Costa Rica and Panama (Peterson et al. 2001).

Ecology. *Muhlenbergia flabellata* occurs in páramos between 3100–3500 m often associated with *Chusquea subtessellata* Hitchc., *Hypericum*, spp., *Comaristaphylos arbutoides* Lindl., *Garrya laurifolia* Hartw. ex Benth., and *Buddleja nitida* Benth.

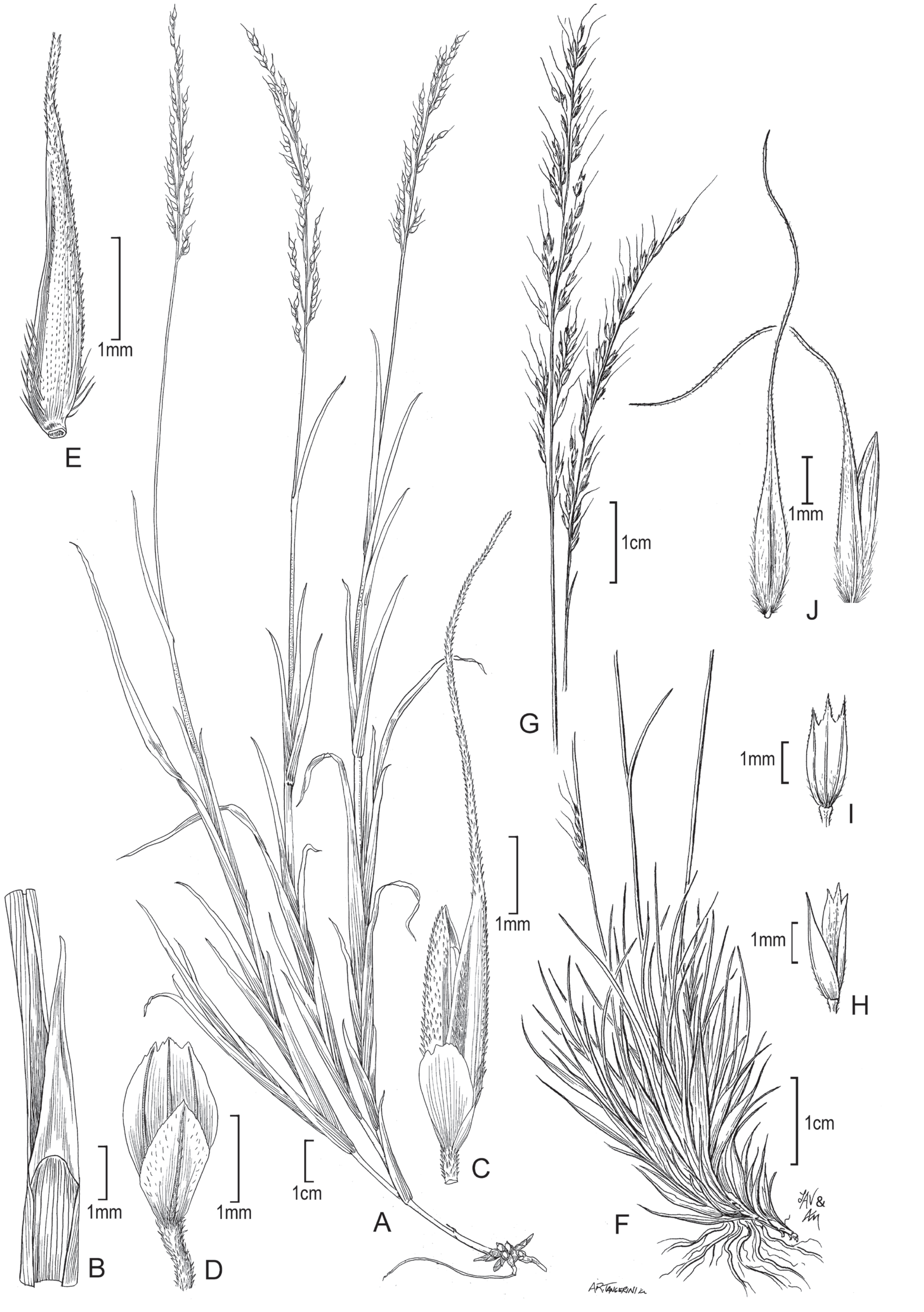

Figure 9. A–E *Muhlenbergia flabellata* Mez. **A** habit **B** ligule **C** glumes **D** floret **E** floret **F–J** *Muhlenbergia montana (Nutt.) Hitchc* **F** habit **G** inflorescence **H** glumes **I** upper glume **J** florets. **A, B, D, E** drawn from *W.C. Burger & L. Gomez P. 8309* (US-2695054) **C** drawn from *G. Davidse 24971* (US-3014559) **F–J** drawn from *A.S. Hitchcock 3143* (US-995116).

Comments. *Muhlenbergia flabellata* is a member of *M.* subg. *Clomena* and within this clade it is sister to *M. quadridentata*, a species primarily restricted to higher elevations that is common in México and extends into Guatemala (Peterson et al. 2021). *Muhlenbergia flabellata* can be separated from *M. quadridentata* in having short leaf blades 2–5 cm long (5–15 cm long in *M. quadridentata*), short upper glumes 1.6–2 mm long [versus (3–)3.2–4 mm long in *M. quadridentata*], and paleas scabrous throughout (versus pilose on the proximal ½ in *M. quadridentata*) [Peterson et al. 2007b; Herrera Arrieta and Peterson 2018].

Specimens examined. Costa Rica. **Cartago**: Paraíso, Cerro de la Muerte, Cordillera de Salamanca, near summit of Cerro Sátira, *S. Horn 35* (CR); Paraíso, Cerro de la Muerte, *M. Kappelle et al. 2377*(CR). **Pérez Zeledón:** R. F. Los Santos, Cerro Bubis, *A. Estrada et al. 2769* (CR); P. N. Chirripó, parte superior (norte) del Valle de los Conejos, *J. Gómez 5339* (CR); R.F. Los Santos Alrededores de las torres de TV, cerro Buenavista, *L. Gómez 6354* (CR); P. N. Chirripó, alrededores de refugio, parte inferior del valle de los Conejos, *J. Gómez-L. 4503* (USJ); P. N. Chirripó, Cordillera de Salamanca, S facing slope of the Valle de los Conejos, about 1 km S of Cerro Nuevo, *S. Horn 59* (CR); P.N. Chirripó, Valle de los Conejos, *R. Ocampo 1466* (CR); P.N. Chirripó, Valle de los Conejos, *R. Ocampo 1489* (CR); Rivas, *A. Rodríguez 6422* (INB); Pérez Zeledón, Rivas, *A. Rodríguez 6541* (INB); P.N. Chirripó, refugio Los Crestones, *G. Vargas et al. 340* (USJ); disturbed paramo, Cerro de la Muerte, *R. Chazdon 447* (CR); Cordillera de Talamanca, Cerro de la Muerte, summit of Cerro Buvis, *R.W. Pohl & G. Davidse 11621* (US); Direct line from Hotel La Georgina to Cerro Frio of the Cerro Buenavista complex (Cerro de la Muerte), area with television and radio towers, G. *Davidse 24971* (US, MO); Open paramo formation with stands of *Chusquea* bamboo 1–2.5 m tall and areas of short-burned forest and original forest 5–15 m tall in protected sites, along the trail to the Valle de los Leones and the lower part of theValle de los Conejos along the upper Rio Talari, *W. Burger & L.D. Gomez 8309* (US). **San Jose**: *W.C. Burger & R. Liesner 7467* (MO); Chirripó, *G. Davidse & R. W. Pohl 1541* (MO); Buenavista, *A. Jiménez 2666* (MO); Parque Nacional Chirripó, Páramo near Albergues de los Crestones, along Río Talari near trail to Valle de los Conejos, *J. G. Pruski et al. 3904* (MO); Buenavista, *A. Weston 5846* (MO); Cerro Buenavista, *P.M. Peterson*, *S. Lobo*, *J. Sánchez & R. Chacón 22855* (CR, US); P. N. Chirripó Open paramo formation with stands of Chuquea bamboo 1–2.5 m tall on slopes and in the valley, short grasses and very short (30 cm) shrubs on the exposed ridges, Valle de los Conejos (upper río) Talari and trails to Cerro Chirripó and the Valle de Los Lagos, *W.C. Burger & R. Liesner 7353* (CR); P. N. Chirripó, *A. Chaverri et al. 1026* (CR); P. N. Chirripó Valle de los Conejos, *A. Chaverri et al. 1172* (CR), Panama. **Bocas del Toro**: Fábrega, A. *Weston 10190* (MO).

10. ***Muhlenbergia implicata*** (Kunth) Trin., Gram. Unifl. Sesquifl. 193: t. 5a, f. 26. 1824.

Fig. 8E–H

Podosemum implicatum Kunth, Nov. Gen. & Sp. 1: 127. 1815 (1816). Type: México, Michoacán, near Lake Cuiseo and Puerto de Andaracuas, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n*. (holotype: B-W!; isotype: P!). ≡ *Trichochloa implicata* (Kunth) Roem. & Schult., Syst. Veg. 2: 385. 1817 ≡ *Agrostis implicata* (Kunth) Spreng., Syst. Veg. 1: 262. 1825. Basionym.

= *Muhlenbergia erecta* J. Presl, Reliq. Haenk. 1:231. 1830, nom illeg. hom., non *Muhlenbergia erecta* Schreb, 1807. Type: México, *Haenke s.n.* (holotype: PR!).

Description. Caespitose slender ***annuals***. ***Culms*** 15–50(–70) cm tall, mostly branched below and lax spreading or erect, scaberulous to short-pubescent below the nodes, the nodes 0.4–0.6 mm in diameter just below the inflorescence; ***internodes*** 3–9.5 cm long. ***Leaf sheaths*** 1.4–9.1 mm long, mostly shorter than the internodes, glabrous to scaberulous; ***ligules*** 1–2.5(–3) mm long, membranous to hyaline; ***blades*** 3–5(–10) cm long, 1–2.5 mm wide, flat or loosely involute, short pubescent above and mostly glabrous below, margins scabrous. ***Panicles*** 7–12(–26) cm long, 3–5(–9.2) cm wide, open, diffuse, with the peduncle included in the sheath, axis scaberulous; ***primary branches*** ascending and spreading up to 90° from the culm axis; ***pedicels*** 7–11 mm long, capillary, flexuous, delicate, smooth, nodding to reflexed, mostly purplish, thickened just below the spikelet. ***Spikelets*** 2.5–3(–4) mm long, purple; ***glumes*** 0.2–0.6 mm long, unequal, glabrous, apex truncate to broadly obtuse, often erose; ***lower glumes*** 0.2–0.4 mm long, veinless; ***upper glumes*** 0.3–0.6 mm long, 1-veined; ***lemmas*** 2.5–3(–4.5) mm long, 3-veined, appearing 5-veined because the margins are folded with rows of barbs that resemble extra veins, narrowly lanceolate, scabrous, apex awned and 2-toothed, the teeth to 1 mm long, the awns 8–26 mm long; ***callus*** with whitish appressed or spreading pubescence, the hairs up to 0.7 mm long; ***paleas*** 2.9–4 mm long, narrowly lanceolate, glabrous, apex acuminate; ***anthers*** 0.4–0.9 mm long, purple. ***Caryopses*** 1.8–2.7 mm long, narrowly fusiform, brownish. *2n* = 20 (Peterson and Annable 1991).

Distribution. *Muhlenbergia implicata* ranges from México to Central (Costa Rica, El Salvador, Guatemala, Honduras, México, Nicaragua, and Panama) and South America (Peterson and Annable 1991; Peterson et al. 2001). In Mexico, *M. implicata* is known from Chiapas and Campeche (Sanchez-Ken 2018).

Ecology. This species grows on cliffs, canyon walls, and dry to rocky roadsides in open vegetation associated with oak-pinyon-juniper woodlands; (5–) 600–2550 m.

Comments. *Muhlenbergia implicata* is a member of *M.* subg. *Pseudosporobolus* and is sister to a central Mexican endemic, *M. seatonii* Scribn. (Fig. 1; Peterson et al. 2021).

Specimens examined. Costa Rica. **Alajuela**: San Ramón, San Pedro de San Ramón, *A.M. Brenes 14966* (CR); San Ramón, Colinas de San Pedro de San Ramón, *A.M. Brenes 16704* (CR); San Ramón, San Juan cerca de San Ramón, *A. M. Brenes 16852* (CR); Orillas de camino, *O. Jiménez 44* (US); Canoas, *O. Jiménez s.n.* (US); 4 km NW of San Jose, Dry road bank in coffee plantation, *R.W. Pohl & G. Davidse 11366* (US); 1 km S of Carrizal. Open roadside in coffee plantation, *R.W. Pohl & G. Davidse 11501* (US). **Cartago**: *R.W. Pohl & M. Lucas 13152* (MO). **Heredia**: *M. Grayum 9600* (MO). **San José:** *R.W. Pohl & M. Lucas 12997* (MO); Puriscal, 10 km antes de Puriscal, *R. Ocampo1123* (CR); San José, *J.J. Cooper 5996* (US); along railway, *A.S. Hitchcock 8511* (US); San José, *A.S. Hitchcock 8459* (US); San Francisco de Guadalupe, sobre paredón, *O. Jiménez 5* (US); 13 km N of San Isidro de El General along the carretera interamericana, busy roadside in forest, *R.W. Pohl & G. Davidse 11628* (US); vicinity of Santa Maria de Dota, in potrero, *P.C. Standley 41586* (US); vicinity of Santa Maria de Dota, in cafetal, *P.C. Standley 41608* (US); vicinity of Santa Maria de Dota, brushy slope, *P.C. Standley & J. Valerio 43218* (US). El

Salvador. **La Libertad**: Volcán San Salvador, *P. Bernhardt & E.A. Montalvo 79* (MO); Volcano of San Salvador, *A.S. Hitchcock 8948* (US). Guatemala. **Alta Verapaz**: Coban, *H. Von Turckheim 3990* (US); Coban, *H. Von Turckheim s.n.* (US). **Chimaltenango**: along road from Chimaltenango to San Martin Jilotepeque, *P.C. Standley 57892* (US); along road between Chimaltenango and San Martin Jilotepeque, oak forest, *P.C. Standley 80877* (US). **Guatemala**: Guatemala City, *A. S. Hitchcock 9030* (US); Guatemala City, *A.S. Hitchcock 9013* (US); Barranca north of Guatemala City, *W. Popenoe 736* (US). **Huehuetenango**: Sierra los Cuchumatanes. 8 mi N of Huehuetenango on Pan American hwy CA 1, slopes above Rio, Quercus forest, *P.M. Peterson & C.R. Annable 4701* (MO, US); About Laguna de Ocubila, east of Huehuetenango, dry open bank, *P.C. Standley 82631* (US); Pine-oak forest region, canyon at head of Rio Chixoy, about 10 km southwest of Huehuetenango, *L.O. Williams et al.22548* (US); Barranco in oak forest near Ocubila, 10 km west of Aguacatan, *L.O. Williams & T.P. Williams 21785* (US); Open, wet, boggy meadow 3 km S of Huehuetenango, *L.O. Williams et al. 22105* (US). **Jalapa**: Jalapa, *P.C. Standley 76829* (MO); vicinity of Jalapa, damp thicket, *P.C. Standley 76399* (US); vicinity of Jalapa, *P.C. Standley 76410* (US). **Sacatepequez**: Magdalena, *W. A. Archer 3867* (US); Above Pastores, sand along stream, *P.C. Standley 60846* (US). Mountains near Santa Maria, *Weatherwax 173* (US). Honduras. **El Paraíso**: Guinope, drainage of the Rio Yeguare, en el pantano, llanos y potreros empantanados de Galeras y Llano de Lizapa, *A. Molina 3367 (*MO); Cumbre on Yuscaran road, rocky slope in pine forest, *P.C. Standley 29360* (US). **Francisco Morazán**: Distrito Central, Colonia Miraflores, *A. Díaz 244A* (MO); San Antonio de Oriente, Las Mesas, *R.W. Pohl 12521* (MO); Distrito Central, between El Hatillo and Los Jutes, *R.W. Pohl & M. Gabel 13791* (MO); Las Casitas, L. *Villela 129* (MO); Cerro la Uyuca, La Labranza and vicinity, along trail to summit, moist thicket, trail to La Labranza, *P.C. Standley 28299* (US); vicinity of Suyapa, *J.R. Swallen 11271* (US); San Antonio del Oriente, *J.R. Swallen 10915* (US); Drainage of the Rio Yeguare, *L.O. Williams 16905* (US). Mexico. **Campeche**: **Campeche**: 2.5 km al oeste de San Francisco Kobén, 5m, 20 Sep 2003, *C. Gutiérrez Báez 7909* (MEXU-1338596). **Chiapas**: 10.5 mi SE of San Cristobal de las Casas, *P.M. Peterson & C.R. Annable 4721* (ENCB, MEXU, US); near San Cristóbal, *A.A. Beetle 3963* (MEXU); W edge of San Cristóbal de las Casas, *D.E. Breedlove 53975* (NY); 2 mi S of Tuxtla Gutiérrez along road to Villa Flores, *D.E. Breedlove & P.H. Raven 13357* (US). **La Trinitaria:** 20 km S of La Trinitaria, *D.E. Breedlove & G. Davidse 55055* (CAS, MO); 6–7 km S of La Trinitaria, *G. Davidse et al. 29972* (MO). **Ixtapa:** near the Zinacantán Paraje of Muctajoc, *D.E. Breedlove & G. Davidse 54021* (CAS, MO); near Ixtapa, *D.E. Breedlove & G. Davidse 54298* (CAS, MO); near the Zinacantán Paraje of Muctajoc, *D.E. Breedlove & G. Davidse 53991* (CAS, MO). **Pueblo Nuevo Solistahuacán**: Clínica Yerba Buena, 2 km NW de Pueblo Nuevo Solistahuacán, *D.E. Breedlove & P.H. Raven 19825* (ENCB, TAES, US). **San Cristobal de las casas:** S end of the valley of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 54374* (CAS, MO). **Teopisca:** N of Teopisca, *D.E. Breedlove & G. Davidse 54770* (CAS, MO); 7 km NW of Teopisca along hwy. to San Cristobal de las Casas, *G. Davidse*, *M. Sousa*, *O. Téllez*, *E. Martinez & J. Davidse 29826* (MO, US); 6 km W of Teopisca, *F.W. Gould & S.L. Hatch 14420* (US). Nicaragua. **Estelí**: Las Pilas, *P.P. Moreno 22341* (MO). **Jinotega**: Mountain slopes and wooded ravines of Cordillera Central de Nicaragua, 2–4 km S of Jinotega, grass in clearing, *L.O. Williams et al. 23554* (MO); Jinotega, *L. O. Williams et al. 27924* (MO). Panama. **Chiriquí**: *G. Davidse & W.G. D´Arcy 10382* (MO); *J.A. Duke 9197* (MO); *M. Nee 14135* (MO).

11. *Muhlenbergia lehmanniana* Henrard, Meded. Rijks-Herb. 40: 49. 1921.
Fig. 10G–K

= *Muhlenbergia attenuata* Swallen, Ann. Missouri Bot. Gard. 30 (2): 138. 1943. Type: Panamá, Chiriquí, El Boquete, foothills, 1000–1300 m, *A.S. Hitchcock 8174* (holotype: US-995843!).
= *Muhlenbergia multinodis* Aspl., Bot. Not. 1939: 796. 1939. Type: Colombia, Cauca, Popayán, El Tambo, 1700 m, 22 Jun 1938, *Sneidern 1323* (holotype: S-R-3665 [image!]; US-2383833 fragm. ex S!).

Type. Colombia, Cauca, Popayán, *F.C. Lehmann 1267* (holotype: L-0044745 [image!]; isotypes: K-000308934 [image!], NY-00381489 [image!], US-72979 fragm. ex L!, US-72977 fragm. ex L!, US-72978 fragm. ex K!).

Description. Caespitose ***perennials*** covered in old sheaths. ***Culms*** (72–)90–130(–167) cm tall, erect, compressed-keeled near base, glabrous to scaberulous below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** tightly imbricate below, golden yellow with age, not basally shredded; ***ligules*** 10–25 mm long, membranous, somewhat firm below; apex acuminate; ***sheath auricles*** lacking or rarely rudimentary up to 0.1 mm long; ***blades*** 20–40 cm long, 1–4 mm wide, flat to folded, scaberulous to scabrous, apex becoming narrow and threadlike. ***Panicles*** 19–45 cm long, 3–6 cm wide, dense and narrow, golden, golden-brown or purplish-green; ***primary branches*** mostly 3.5–14 cm long, and up to 19 cm long below, ascending and appressed, naked below; ***pedicels*** 0.7–3.5 mm long, scaberulous. ***Spikelets*** 2.5–3.8 mm long, erect; ***glumes*** 2.5–3.8 mm long, about equal, sometimes the upper glume, both longer than the lemmas, 1-veined, occasionally 2 or 3-veined, hispid; apex obtuse to dentate, usually mucronate, the mucro up to 0.3 mm long; ***lemmas*** 2–3.3 mm long, pilose along the veins and margin on lower 2/3, awned from just below the apex; apex obtuse, the awns 10–20 mm long, flexuous and minutely scabrid; ***callus*** with short hairs; ***paleas*** 2.3–3.2 mm long, usually shorter than the lemma, hairy between the veins on the lower ½; ***anthers*** 1.4–1.6 mm long. ***Caryopses*** 1.2–1.3 mm long, fusiform, glabrous, light brown. $2n$ = 20 +2b (Reeder 1994).

Distribution. *Muhlenbergia lehmanniana* ranges from Central America in Costa Rica, Honduras, and Panama to South America in Columbia, Ecuador, and Venezuela (Giraldo-Cañas and Peterson 2009).

Ecology. This species occurs on gentle to steep slopes, ravines, gravelly sites, and disturbed sites in humid tropical forests with *Pinus* and *Quercus*; 600–2200 m.

Comments. *Muhlenbergia lehmanniana* is morphologically similar to *M. máxima* Lægaard & Sánchez Vega, a Peruvian endemic. However, *M. lehmanniana* differs from *M. máxima* in having longer lemmatal awns (12–20 mm long versus 4–9 mm long in *M. máxima*) and longer ligules (10–25 mm long versus 3–5 mm long in *M. máxima*) [Peterson et al. 2018].

Muhlenbergia lehmanniana is a member of *M.* subg. *Trichochloa* (Peterson et al. 2010b; 2021). There is not much genetic variation among all members of *M.* subg. *Trichochloa* in Peterson et al. (2018, 2021).

Specimens examined. Costa Rica. Basamento de Fila Lleskila, *L.D. Gómez et al. 23244* (MO). **Alajuela**: San Ramón, San Pedro de San Ramón, cerca del Río Barranca, *A.M. Brenes 21415* (CR); 6 km S of Los Cartagos by road, *R.W. Pohl &*

Figure 10. **A–F** *Muhlenbergia versicolor* Swallen **A** habit **B** ligule **C** glumes **D** lemma **E** palea **F** stamens, pistil, and lodicules **G–K** *Muhlenbergia lehmanniana* Henrard **G** habit, **H** ligule **I** glumes **J** floret **K** stamens, pistil, and lodicules. **A** drawn from *G.B. Hinton 2324* (US-1840807) **B–F** drawn from *G.B. Hinton 14808* (US-1842654) **G–K** drawn from *H. Pittier 1468* (US).

G. Davidse 11504 (US); 12 km SW of San Ramon along the Carretera Interamericana, *R.W. Pohl & G. Davidse 11511* (US). **Cartago**: El Guarco, *F. Solís 618* (CR); Oreamuno, in Monte Irazú, *A.S. Oersted 14012* (US), *14471* (US); Paraíso, Las Concavas, *C.H. Lankester 676* (US); 5 km E of Paraíso, *R.W. Pohl & G. Davidse 11390* (US). **Puntarenas**: Coto Brus, Z.P. Las Tablas. Cuenca Terraba-Sierpa, el tajo, colectando a orillas del camino, *E. Alfaro 2593* (MO); Coto Brus, Z.P. Las Tablas, Cuenca Térraba-Sierpe, Cerro Pando, colecta en bosque y orillas de potreros *E. Alfaro et al. 925* (MO); Coto Brus, Z.P. Las Tablas. Cuenca Térraba-Sierpe, Cerro Pando, colecta en bosque y orillas de potreros, *E. Alfaro et al. 931* (MO); Coto Brus, Z.P. Las Tablas, *E. Alfaro 925* (INB); Coto Brus, Z.P. Las Tablas, *E. Alfaro 931* (INB); Coto Brus, Finca Cafrosa, 2.5 km al E del Progreso, Cerro Pelón, *E. Alfaro 2593* (INB); Buenos Aires, Ujarras, El Carmen, Sabanas de Murur Bisuk, estribaciones de Cerro Amu, *G. Herrera 3593* (INB); Buenos Aires, P.N. La Amistad, Cuenca térraba-Sierpe, Violey, Sabanas Esperanzas, *L. González & A. Garita 1196* (MO); Buenos Aires, R.I. Ujarrás-Salitre-Cabagra, Cuenca Térraba-Sierpa, Salitre, Cerro Sipar, *L. González & A. Garita 1215* (MO); Monteverde, 10 km S Monteverde on road to InterAmerican Highway, area of spring, *W. Haber & W. Zuchowski 9660* (MO); Golfito, P.N. Corcovado, Península de Osa, Dos Brazos de Río Tigre, Jiménez, Cuenca superior del Río Madrigal, margen derecha, *G. Herrera & C. Fallas 4710* (MO, INB); Buenos Aires, Ujarrás, El Carmen, Sabanas de Murur Bisuk, estribaciones de Cerro Amú, *G. Herrera & W. Gamboa 3593* (MO); Buenos Aires, Violey, Sabanas Esperanzas, *L. González 1196* (INB); Buenos Aires, Salitre, Cerro Sipar, *L. González 1215* (INB); Parrita, Cuenca del Naranjo y Paquita, Fila Chonta, La Virgen, sector SE, Fila entre la *vuelta del Pallo*, cabeceras Río Palo Seco y Fila Chonta, *J. F. Morales & R.J. Abarca 6294* (MO); Buenos Aires, Potrero Grande, *A. Rodríguez 9744* (INB); Buenos Aires, Potrero Grande, *A. Rodríguez 9835* (INB); Boruca, Savanes de Boruca, *Soc. ex. San José 449* (CR); Buenos Aires, Potrero Grande, *D. Solano 2871* (INB); Buenos Aires, *M. Valerio 873* (CR); Monteverde, 10 km S Monteverde on road to Inter American Highway, area of spring, *W. Haber 9960* (INB); Coto Brus, Savanas de Cañas Gordas, *H. Pittier 7355* (US); Coto Brus, Savanes de Cañas Gordas, *H. Pittier 11019* (MO); Coto Brus, Savanas de Cañas Gordas, *H. Pittier 7358* (US); Borde de chemin de Mano de Tigre, *H. Pittier 4630* (US); **San José:** Perez Zeledón, along Carretera Interamericana, S slope Cerro de la Muerte, between km 125 and km 117, *M. Grayum & B. Hammel 9580* (MO, INB); Aserri, bosque primario y tacotales en la Fila El Alto, *J.F. Morales 3390* (INB); Aserri, Faldas SE Fila Aguabuena, entre Quebrada Ceniza y Quebrada Sopapo, camino a Bijagual, *J.F. Morales 6863* (INB, CR); Acosta, Alto Reflis, Falda NE, Fila de Cal, *J.F. Morales 8764* (INB); Escazú, San Antonio, *J. González 2886* (INB); Aserri, Cuenca del Pirris-Damas, Cerros Caraigres, Falda S, Quebrada Concha, en el camino viejo a Bijagual, *J.F. Morales 5915* (MO); Aserri, Cuenca del Pirris-Damas. Ceiba Alta, Cuest Pacayas, Quebrada Pacayas, charrales residuales, *J.F. Morales 6759* (MO, INB); 6 km by road N of San Pablo, N of San Marcos, open dry pasture on a hilltop, *R.W. Pohl & M. Lucas 13142* (MO); Acosta, Cerro León, camino hacia Fila Aguabuena, *R. Chacón et al. 190* (CR); Santa Ana, Z.P. Cerros de Escazú, Alto Caña Quemada, *A. Estrada et al. 3241* (CR); Cercanías de División, Carretera Interamericana Sur, *J. Gómez-L. 3460* (USJ); Acosta, Cuenca del Río Pírris-Damas, Fila del Naranjal, sendero a la Escuadra, *J.F. Morales 7459* (CR, INB, MO); Acosta, Cerro León. Camino hacia Fila Aguabuena, *A. Quesada et al. 741* (CR); Acosta, Cerro León. Camino hacia Fila Aguabuena, *J. Sánchez* *et al. 1170* (CR); 3 km SSE of Villa Colon, *R.W. Pohl & G. Davidse 11399* (US); 13 km N of San Isidro de El General along the Carretera Interamericana, *R.W. Pohl & G. Davidse 11631* (US). Honduras. **Comayagua:** Ojo de Agua, orilla Río Humuya, 30 km N de ciudad Comayagua, bosque de vega tropical rodeado de pinares, *C. Nelson et al. 6818* (MO). Panama. **Chiriquí**: In bare clay of steep artificial roadside bank below coffee finca. Western slope of first ridge east of Quebrada Zumbona, opposite east side of Cerro Pando, 7 km (by air) northwest of El Hato Del Volcán, *T.S. Cochrane et al. 6327* (MO); Boquete, ca. 26 km N of David along the road to Boquete, Curatella-Byrsonima-Trachypogon savanna on old lava flow, *G. Davidse & W.G. D'Arcy 10138* (MO); Boquete, eastern slope of Volcán de Chiriquí (Barú), WNW of Boquete. Partially cleared slopes with patches of original oak forest and mostly secondary growth, *G. Davidse & W.G. D'Arcy 10170* (MO); Large old lava flow ca. 3 km NE of El Hato del Volcán at base of Volcán de Chiriquí (Barú), 1–3 km E of highway, *G. Davidse & W.G. D'Arcy 10332* (MO); Llanos E of El Hato de Volcán, savannah and woods on lava flow, *B. Hammel et al. 6811* (MO); Grassy slopes on lava flow about 16 km above town at Volcan, *B. Hammel 1585* (MO); Volcán Barú, summit to llanos at base of W slope, along trail, *B. Hammel et al. 6576* (MO); Lava fields near the town of Volcan, *J.A. Duke 9143* (MO); Western slopes of Volcan de Chiriqui (Baru), on lava flow, *S. Mori & J. Kallunki 5714* (MO); Bambito, in savanna 1 mile south, *M. Partch 69-31* (MO); Alto Boquete, savanna, *M. Partch 69-62* (MO); 2 km S of Boquete above the Río Caldera near a small flood control dam. Disturbed roadside, *P.M. Peterson & C.R. Annable 7349* (MO, US); Between Río Quebrado El Velo and Río Caldera, W of San Ramon and NW of Boquete, gravel pit with very steep sandy slopes, *P.M. Peterson & C.R. Annable 7372* (MO, US); 1 km NW of Boquete on road towards Volcan Baru, dry roadcut in bare soil, *P.M. Peterson & C.R. Annable 7376* (MO, US); S end of Boquete, dry open slopes, *P.M. Peterson & C.R. Annable 7385* (MO, US); NW of Boquete, between Finca Lerida and San Ramon, *P.M. Peterson & C.R. Annable 7371* (MO, US); S end of Boquete, *P.M. Peterson & C.R. Annable 7386* (MO, US); Ca 1.5 mi. northeast of El Hato del Volcan, grassy plain with occasional patches of forest, *S. McDaniel 10199* (MO); Foothills, vicinity of El Boquete, *A.S. Hitchcock 8241* (US); foothills, vicinity of El Boquete, *A.S. Hitchcock*, *8242* (US); Cerro Vaca, eastern Chiriqui, in savannas, *H. Pittier 5360* (US); Cerro Vaca, eastern Chiriqui, in savannas, *H. Pittier 5362* (US). **Cocle**: hills S of El Valle de Antón, *P.H. Allen 2812* (MO);vicinity of Ola, *H. Pittier 5062* (US), *H. Pittier 5042* (US). **Veraguas**: Cerro Campana, savannas S of radio tower, *B. Hammel 5528* (MO).

12. ***Muhlenbergia ligularis*** (Hack.) Hitchc., Contr. U.S. Natl. Herb. 24(8):388. 1927.

Fig. 11F–J

Sporobolus ligularis Hack., Oesterr. Bot. Z. 52(2):57. 1902. Type: Ecuador, Pichincha, 23 Jan 1899, *Sodiro 23/1* (holotype: W-19160026304 [image!]; isotypes: BAA-2905! ex W, US-3274313! ex W, US-1163183!). Basionym.

= *Muhlenbergia calcicola* Swallen, Contr. U.S. Natl. Herb. 29(9):407. 1950. Type: Guatemala, Huehuetenango, Chemal, Sierra de los Chuchumatanes, 3300 m, 31 Dec 1940, *P.C. Standley 81703* (holotype: US-1910686!; isotypes: F-1200274 [image!], US-2236500US!).

= *Muhlenbergia breviculmis* Swallen, Contr. U.S. Natl. Herb. 29(9):408. 1950. Type: Guatemala, Huehuetenango, Cerro Chemalito, Sierra de los Cuchumatanes, 3.5 mi W of Santa Eulalia, 3100–3150 m, 2 Aug 1942, *J.A. Steyermark 49905* (holotype: US-1935054!; isotypes: F, US-2208654!).

= *Muhlenbergia minuscula* H. Scholz, Willdenowia 14:393. 1984. Type: Bolivia, Canton Ulla-Ulla, Pampa von Ulla-Ulla, Apolobamba Cordillera, 4450 m, 26 Feb 1983, *X. Menhofer X-1974* (holotype: B-10-0249104!; isotype: LPB-0000293 [image!]).

Description. Loosely tufted ***annuals*** to short-lived ***perennials***. ***Culms*** 2–12 cm tall, 0.2–0.4 mm diameter just below the panicle, erect or decumbent, slender, glabrous, sometimes flowering the first year, up to 15 cm broad, dying in the center, profusely branched below, a short branchlet with fascicled leaves borne at each node, with 4–6 nodes; ***internodes*** 2–20 mm long. ***Leaf sheaths*** 2–20 mm long, generally shorter than the internodes, glabrous, ridged, flattened by the densely fascicled branches; ***ligules*** 0.6–2.5 mm long, membranous to hyaline, apex truncate to rounded; ***blades*** 0.3–2.2 cm long, 0.8–1.5 mm wide, flat or folded, prominently veined, thick, firm, usually with whitish-thickened midvein and margins, conspicuously crystalline or spiculate on both surfaces, otherwise glabrous below, sparsely scaberulous above and along margins, tapering to a boat shaped tip. ***Panicles*** 1.0–3.0 cm long, 0.3–1.4 cm wide, long exerted or included in the uppermost sheath, loosely contracted; ***primary branches*** 5–9 mm long, one per node, appressed or reflexed at maturity up to 70° from the culm axis; ***pedicels*** 1–3 mm long, stiff, densely scabrous, spiculate, erect. ***Spikelets*** 1.5–3.0 mm long, often plumbeous to reddish-purple; ***glumes*** 1.0–1.9 mm long, subequal, glabrous, apex acute to obtuse, often minutely erose, greenish-gray; ***lower glumes*** 1.0–1.7 mm long, 1-veined; ***upper glumes*** 1.1–1.9 mm long, 1-veined or occasionally 3-veined; ***lemmas*** 1.5–3.0 mm long, lanceolate, 3-veined, keeled, glabrous, mottled with greenish-black areas or dark greenish mottles on a pale background, apex minutely scaberulous, acuminate, entire or mucronate; mucro rarely more than 1(–1.2) mm long; ***paleas*** 1.4–2.9 mm long, lanceolate, glabrous; ***anthers*** 0.8–1.1 mm long, purplish becoming pale. ***Caryopses*** 0.8–1.2 mm long, elliptic to fusiform, brownish.

Distribution. This species ranges from Guatemala and Costa Rica to Colombia, Venezuela, Ecuador, Bolivia, Peru, and Argentina (Pohl 1980; Peterson and Annable 1991; Peterson et al. 2001; Giraldo-Cañas and Peterson 2009).

Ecology. *Muhlenbergia ligularis* occurs in grassy flats, moist depressions, wet meadows, gravelly banks, ridgetops, and gravelly roadsides often derived from calcareous substrates, associated with *Achnatherum*, *Aciachne*, *Agrostis*, *Alnus*, *Anatherostipa*, *Baccharis*, *Berberis*, *Bidens*, *Buddleja*, *Caiophora*, *Carex*, *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone, *Colletia spinosissima* J.F. Gmel., *Eleocharis*, *Festuca*, *Gaultheria*, *Hypericum*, *Jarava*, *Juncus*, *Lepidophyllum*, *Lupinus*, *Margyricarpus*, *Muhlenbergia*, *Nassella*, *Plantago*, *Poa*, *Puya*, *Rumex*, *Salvia*, and *Senecio*; 2320–4650 m.

Comments. *Muhlenbergia ligularis* is morphologically similar to the widespread South American, *M. fastigiata* (J. Presl) Henrard. It can be separated from the latter by possessing flat leaf blades, 0.8–1.5 mm wide, and a rather loosely tufted habit without wiry creeping rootstocks and scaly rhizomes. Morphologically, *M. ligularis* differs from the Peruvian endemic *M. caxamarcensis* Lægaard & Sánchez Vega in having glabrous lemmas (sericeous hairs on lower 1/2–3/4 of the lemma in the latter) [Peterson et al. 2018].

Molecular DNA sequence analysis indicates *M. ligularis* falls within the *M.* subg. *Bealia* clade in a subclade with *M. filiformis* (Thurb. ex S. Wats.) Rydb. and *M. vaginata* (Fig. 1; Peterson et al. 2021).

Specimens examined. Costa Rica. **San José**: Valle de los Conejos (upper Río Talari) and trails to Cerro Chirripó and the Valle de los Lagos, open paramo formation with stands of *Chusquea* bamboo 1–2.5 m tall on slopes and in the valley, short grasses and very short (30 cm), shrubs on the exposed ridges, *W.C. Burger & R.L. Liesner 7470* (CR); Perez Zeledón, Paramo en el Sendero al Valle de los Conejos, *E. Alfaro 415* (INB, MO); Perez Zeledon, Rivas, sendero Valle Los Conejos y Cerro Chirripo en Paramo, *E. Alfaro 572* (INB); Perez Zeledón, Valle de los Conejos, *E. Alfaro 3873* (INB); P. N. Chirripó Alrededores del refugio, parte inferior (sur) del Valle de los Conejos, *J. Gómez 5344* (CR); P.N. Chirripó A la vera del Río Talari, parte inferior (Sur) del Valle de los Conejos, *J. Gómez 5382* (CR); P.N. Chirripó Valle de los Conejos, *R. Ocampo 1500* (CR); Pérez Zeledón, Rivas, *A. Rodríguez 6414* (INB); P.N. Chirripó Valle de los Conejos, *R. Soto s.n.* (CR). Guatemala. **Huehuetenango:** along road in region of Chémal, Sierra de los Cuchumatanes, at km 36, *P.C. Standley 81703* (MO); Sierra de los Cuchumatanes, 6.6 mi NW of Santa Eulalia on road to San Mateo Ixtatán, *P.M. Peterson & C.R. Annable 4691* (ARIZ, ENCB, GH. MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 3.6 mi NW of Paguix on hwy 9N and 16.2 mi S of San Juan Ixcoy, *P.M. Peterson & C.R. Annable 4686* (GH, MO, NY, US, WS); 15.1 mi S of San Juan Ixcoy on hwy. 9N, *Peterson & Annable 4688* (GH, MO, NY, RSA, US, WS); Meadow at Tojiah on hwy. 9N, *P.M. Peterson & C.R. Annable 4695* (GH, MO, NY, RSA, UC, US, WS); 13 mi NW of Santa Eulalia on road to San Mateo Ixtatán, *P.M. Peterson & C.R. Annable 4692* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); Meseta alta Sierra de los Cuchumatanes, *R. López s.n.*, (MO); Cerro Chemalito, Sierra de Cuchumatanes, 3.5 miles W of Santa Eulalia, *J.A. Steyermark 49905* (MO); Sierra de los Cuchumatanes, at Chemal at km 318 on Ruta Nacional 9N, *J.H. Beaman 3068* (US); Sierra de los Cuchumatanes, immediately north of Tojiah at km 322 on Ruta Nacional 9N, *J.H. Beaman 3920* (US); Region of Chemal, Sierra de los Cuchumatanes, *P.C. Standley 81115* (US); Sierra de los Cuchumatanes, 3.6 mi NW of Paguix on hwy 9N and 16.2 mi S of San Juán Ixcoy, *P.M. Peterson & C.R. Annable 4686* (GH, MO, NY, RSA, US, WS); 15.1 mi S of San Juan Ixcoy on hwy 9N, *P.M. Peterson & C.R. Annable 4688* (GH, MO, NY, RSA, US, WS); 6.6 mi NW of Santa Eulalia on road to San Mateo Ixtatán, *P.M. Peterson & C.R. Annable 4691* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 13 mi NW of Santa Eulalia on road to San Mateo Ixtatán, *P.M. Peterson & C.R. Annable 4692* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); Meadow at Tojiah on hwy 9N, *P.M. Peterson & C.R. Annable 4695* (GH, MO, NY, RSA, UC, US, WS); SW of Tojiah on Hwy 9N, *P.M. Peterson & C.R. Annable 4700* (NY, US, WS). **Chimaltenango:** Cerro Chichoy near Chichoy, *L.O. Williams & A. Molina R.15317* (US). **Totonicapan**: On the Tecum Uman Ridge at km 154 on Ruta Nacional N1, ca 20 km east of Totonicapan, *J.H. Beaman 4156* (UC, US); Desconsuelo, potrero natural, Flora alpine, *M. de Koninck 116* (US); Region of Desconsuelo, *P.C. Standley 62736* (US); Region of Chiu Jolom, mountains above Totonicapan, on road to Desconsuelo, *P.C. Standley 84418* (US); Totonicapan, En pastizal dominado por *Agrostis exserta* y *Geranium alpicola*, muy sobrepastoreado; plano; plena sol, *Smith & Nelson 768* (MO).

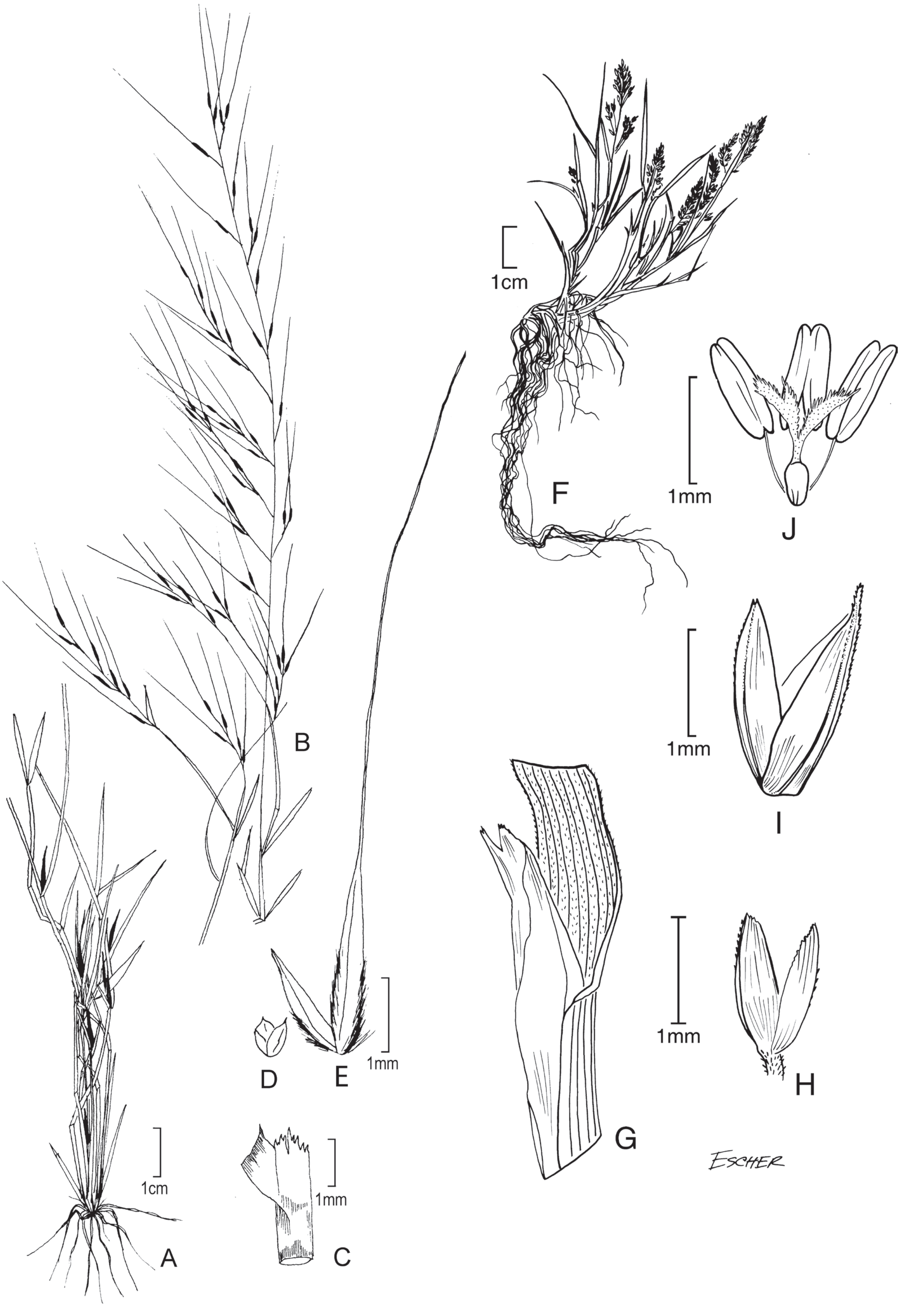

Figure 11. A–E *Muhlenbergia microsperma* (DC.) Kunth **A** habit **B** inflorescence **C** ligule **D** glumes **E** floret **F–J** *Muhlenbergia ligularis* (Hack.) Hitchc. **F** habit **G** ligule **H** glumes **I** floret **J** stamens and pistil. **A–E** drawn from *P.M. Peterson 4185* (US, WS) **F–J** drawn from *P.M. Peterson*, *C.R. Annable*, *S. Lægaard & R.J. Soreng 12684* (US-3275569).

13. *Muhlenbergia macroura* (Kunth) Hitchc., N. Amer. Fl. 17(6): 468. 1935.
Fig. 7A–E

Crypsis macroura Kunth, Nov. Gen. Sp. (quarto ed.) 1: 140–141. 1816 Type: México. Toluca, in apricis montanis regio Mexicane, 1760 m, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n*. (holotype: P-00669403[image!]; isotypes: BAA-00003297 [image!], P-00077291 [image!]). ≡ *Cinna macroura* (Kunth) Kunth, Révis. Gramin. 1: 67. 1829. ≡ *Phleum macrourum* (Kunth) Willd. ex Steud., Nomencl. Bot. (ed. 2) 1: 365. 1840. ≡ *Epicampes macroura* (Kunth) Benth., J. Linn. Soc., Bot. 19: 87. 1881. ≡ *Crypsinna macroura* (Kunth) E. Fourn., Mexic. Pl. 2: 90. 1886. Basionym.

Description. Caespitose ***perennials*****.** ***Culms*** 75–200 cm tall, erect, terete near base, forming dense clumps of 100 culms or more and up to 1 m in diameter, pubescent below the nodes, usually 1 or 2 nodes per culm; ***internodes*** mostly glabrous. ***Leaf sheaths*** 15–40 cm long, shorter than the internodes, glabrous to scaberulous, the basal persistent and keeled with age; ***ligules*** (5–)8–40(–50) mm long, strongly decurrent, splitting into broad **auricles** 10–35(–50) mm long, membranous to chartaceous above, brownish, firm, the veins evident below and near margins, apex truncate to obtuse; ***blades*** 20–60 cm long, 2–5 mm wide, mostly flat and apically involute, scabrous above and below. ***Panicles*** (15–)20–40 cm long, 5–12 mm wide, dense, spikelike, erect, exserted and surpassing the blades in height, greenish to greenish-gray; ***primary branches*** 0.1–1.2 cm long, ascending and tightly appressed, unexposed, imbricate; ***pedicels*** 0.1–1.7 mm long, shorter than the spikelets, scaberulous to hispidulous. ***Spikelets*** 3.4–5.6(–6) mm long, erect, strongly laterally compressed, greenish-gray; ***glumes*** 3.4–5.6 mm long, linear-elliptic to linear-ovate, usually longer than the lemma, 1-veined, scabrous along the keel, subequal, awnless, the upper slightly longer, apex acute to acuminate, scabrous; ***lemmas*** 3.4–5 mm long, elliptic to linear-elliptic, scabrous, greenish-gray; callus pilose, the hairs 0.1–0.3 mm long, apex acute, rarely mucronate, the mucro less than 0.4 mm long; ***paleas*** 3.4–5 mm long, about as long as the lemma, scabrous, apex acute; ***anthers*** 1.5–2.2 mm long, pale greenish. ***Caryopses*** 2–3 mm long, fusiform, brownish. $2n$ = 20, 24, 28.

Distribution. *Muhlenbergia macroura* occurs in the Sierra Madre Occidental in northern México from Chihuahua to Chiapas and Guatemala (Herrera Arrieta and Peterson 2018).

Ecology. This species can be found growing on upland slopes, mountain meadows, in pine or pine-oak forests often in deep humid soils; 1500–3400 m.

Comments. *Muhlenbergia macroura* is morphologically similar to *M. nigra* but differs in having spikelets 3.4–5.6(–6) mm long [(5.5–)6–8 mm long in *M. nigra*] and greenish to greenish-gray panicles (15–)20–40 cm long [dark green to blackish panicles 6–15(–17) cm long in *M. nigra*]. *Muhlenbergia macroura* is a member of *M*. subg. *Trichochloa*, and in a recent study was found to be sister to *M. rigida* (Peterson et al. 2021).

Specimens examined. Guatemala. **Chimaltenango**: Plains near Tecpam, *A.F. Skutch 610* (US). **Guatemala**: Guatemala City, *A.S. Hitchcock 9140* (US). **Huehuetenango**: La Sierra (Tujimach), across river from San Juan Atitlan, Sierra de los Cuchumatanes, *J.A. Steyermark 51968* (US); Paquix, San Juan Ixcoy, Sierra de los Cuchumatanes between Paquix and San Juan Ixcoy, *A.A. Molina et al. 30017* (MO); San Juan Ixcoy, Sierra de los Cuchumatanes, along road to Huehuetenango, 5 miles S of San Juan Ixcoy, *D.E. Breedlove 8569* (MO, DS); San Juan Ixcoy, Jolomhuitz, Aldea Jolomhuitz, *M. Véliz 95.4470* (MO). **Quetzaltenango**: Mountains near Santa Maria, near Quetzaltenango, *Weatherwax 177* (US); La Esperanza, *M. de Koninck 18* (US); Cuesta El Caracol, Sierra Madre Mountains, about 5–8 km N of San Juan Ostuncalco, *L.O. Williams et al. 22770* (US); Oak pine forest, above Los Vahos, Cerro Quemado, *P.C. Standley 86171* (US). **Quiche:** Chichicastenango, 1 km N of Chichicastenango, *W.E. Harmon 4369* (MO). **Sacatepequez**: Santa Maria de Jesús, Mal Paso, Volcán de Agua, Mal Paso, *M. Véliz et al. 8529* (MO); Volcan Agua, *W.A. Kellerman 4764* (US). **San Marcos**: Tajumulco, Volcan Tajumulco, *M. Véliz et al. 10622* (MO), *M. Véliz et al. 10638* (MO); El Boqueron, in the mountains at the summit of the road between San Antonio Sacatepequez and Palestina, *P.C. Standley 85307* (US). **Solola**: Volcan Atitlan, near summit of mountain, *J. H. Beaman 4053* (US); NW of Los Encuentros, *L.O. Williams*, *A. Molina R. & T.P. Williams 25404* (F, US). **Totonicapán**: near San Francisco El Alto, *P.C. Standley 83123* (US); along road between San Francisco El Alto and Momostenango, *P.C. Standley 84011* (US); *O. F. Cook 35* (US); Hochland von Calel, *s.n. 2703* (US). México. **Chiapas**: Vol. Tacana, Chiquihuite, *E. Matuda 2829* (ARIZ, MO); Mt. Tacana, *E. Matuda 2420* (DS). Amecatlán, Paraje Navenchauk, along mexican Hwy 190, *R. M. Laughin 1506* (ENCB). **La Grandeza**: La Grandeza to Ojo de Agua, *E. Hernandez X-1445* (US). **Larráinzar**: Muctahuitz. Región Los Altos, *L. Soto s/n* (MEXU). **Motozintla:** On the N and W slope of Cerro Mozotal below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, *D.E. Breedlove & R.F. Thorne 31173* (MO). **San Juan Chamula**: near school house of yal Ichin, *D.E. Breedlove 7147* (ENCB, DS); Yut Bax, *C. Santoz Ruíz 179* (ENCB). Motozintla, NW slope of cerro Mozotal, along the road from Huixtla to El Porvenir and Siltepec, *D.E. Breedlove 31175* (NY); Slope near the school house of Yal Ichin, *D.E. Breedlove 10471* (DS). **Tenajapa**: Paraje Matsbad, *Alush Shilon Ton 999*, (ENCB, DS); Paraje Shohieh, *Alush Shilon Ton 548* (ENCB, DS); near Tenejapa Center, *Alush Shilon Ton 63* (DS). **Venustiano Carranza**: Ejido "Laja Tendida" km 17 carr. Venustiano Carranza-Tuxtla Gutiérrez, aprox. 2 km a Flores Magón, *A. Miranda S. s/n* (MEXU). **Zinacantán:** near Paraje Nachij [Nachig], *D.E. Breedlove & G. Davidse 53871* (CAS, MO); Steep NE slope of Zontehuitz near Summit, *D.E. Breedlove 12348* (DS); near Zinacantán Center, *R.M. Laughlin 2241* (DS); at paraje Navenchauk along Mexican Highway 190, *R.M. Laughlin 1506* (DS); alley floor in Zinacantán Center, *R.M. Laughlin 630* (DS).

14. ***Muhlenbergia microsperma*** **(DC.) Kunth, Révis. Gramin. 1:64. 1829.**
Fig. 11A–E

Trichochloa microsperma DC., Cat. Pl. Horti Monsp. 151. 1813. Type: México, cultivated at botanical garden at Montpellier from seeds collected in México and distributed by the Botanical Garden of Madrid, *M. Sésse & J.M. Mociño s.n.* (holotype: MPU; isotypes: G-00099434 [image!], P!, US fragm. ex P!). ≡ *Muhlenbergia microsperma* (DC.) Trin., Gram. Unifl. Sesquifl. 193. 1824, *nom. inval*. Basionym.

= *Agrostis microsperma* Lag., Gen. Sp. Pl. 2. 1816. Type: México, plants grown at H.R. Matritensis (= Herbario del Real Jardín Botánico de Madrid) from seeds collected by M. Sessé & J.M. Mociño in Nueva Espania, Oct, 1806, *M. Sessé & J.M. Mociño s.n.* (**lectotype, designated here**: SEL-H10620 [image!]).

= *Podosemum debile* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 128. 1816. Type: Ecuador, Prov. Pichincha, Quito, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-Bonpl!; isotypes: B-W, P!, US-91924 fragm. ex P-Bonpl!). ≡ *Trichochloa debilis* (Kunth) Roem. & Schult., Syst. Veg. 2:385. 1817. ≡ *Muhlenbergia debilis* (Kunth) Trin., Gram. Unifl. Sesquifl. 193, t. 5, f. 18. 1824.

= *Podosemum setosum* Kunth, Nov. Gen. Sp. (quarto ed.) 1:129. 1816. Type: México, between Gueguetoque and Tula, Aug, *F.W.H.A. Humboldt & A.J.A. Bonpland 4174* (holotype: P-Bonpl!; isotypes: B-W, US-91917 fragm. ex P-Bonpl!). ≡ *Trichochloa setosa* (Kunth) Roem. & Schult., Syst. Veg. 2:386. 1817. ≡ *Agrostis setosa* (Kunth) Spreng., Syst. Veg. 1:262. 1825. ≡ *Muhlenbergia setosa* (Kunth) Trin., Gram. Unifl. Sesquifl. 193, t. 5, f. 22. 1824. ≡ *Muhlenbergia setosa* (Kunth) Kunth, Révis. Gramin. 1:63. 1829, *isonym*.

= *Muhlenbergia purpurea* Nutt., J. Acad. Nat. Sci. Philadelphia, ser. 2, 1:186. 1848. Type: USA, California, Santa Barbara Co., Santa Barbara and Santa Catalina Island, *Gambel s.n.* (holotype: K!).

= *Muhlenbergia ramosissima* Vasey, Bull. Torrey Bot. Club 13(12):231. 1886. Type: México, Chihuahua, SW Chihuahua, Aug–Nov 1885, *E. Palmer 158* (lectotype: NY! designated by Hitchcock, N. Amer. Fl. 27:441. 1935, but without indicating the specific specimen; Peterson and Annable, Syst. Bot. Monogr. 31:61. 1991, indicated the specific specimen; isotypes: LE!, MO-2974152!, P!, US-995580!).

Description. Caespitose ***annuals***, sometimes appearing as short-lived perennials. ***Culms*** 10–80 cm tall, often geniculate at the base, slender, often striate, much branched near the base, scaberulous below the nodes; ***internodes*** 1.8–8.6 mm long, mostly scaberulous or smooth. ***Leaf sheaths*** 2.2–6.6 mm long, commonly shorter than the internodes, glabrous, smooth or scaberulous; ***ligules*** 1–2 mm long, membranous to hyaline, decurrent, margins often extended, apex truncate to obtuse; ***blades*** 3–8.5(–10) cm long, 1–2.5 mm wide, flat or loosely involute, scabrous below, strigulose above, often deciduous with age. ***Panicles*** 6.5–13.5 cm long, 1–6.5 cm wide, open and not densely flowered, often purplish; ***primary branches*** 1.6–4 cm long, ascending or diverging up to 80° from the rachises, spikelet-bearing to the base; ***pedicels*** 2–6 mm long, appressed to divaricate, antrorsely scabrous. ***Cleistogamous panicles*** with 1–3 spikelets present in the axils of the lower sheaths. ***Spikelets*** 2.5–5.3 mm long; ***glumes*** 0.4–1.3 mm long, exceeded by the florets, 1-veined, obtuse, often minutely erose; ***lower glumes*** 0.4–1 mm long; ***upper glumes*** 0.6–1.3 mm long; ***lemmas*** 2.5–3.8(–5.3) mm long, narrowly lanceolate, mostly smooth, scaberulous distally, hairy on the lower 1/2 of the margins and midveins, the hairs 0.2–0.5 mm long, the callus hairy, apices acuminate, often bidentate, awned, awns 10–30 mm long, straight to flexuous; ***paleas*** 2.2–4.8 mm long, narrowly lanceolate, acuminate; ***anthers*** 0.3–1.2 mm long, purplish. ***Caryopses*** 1.7–2.5 mm long, fusiform, reddish-brown. 2n = 20, 40, 60.

Distribution. *Muhlenbergia microsperma* occurs in Hawaii, southwestern USA, México, Guatemala, Colombia, Venezuela, Ecuador (including the Galapagos Islands), Peru, and Bolivia (Peterson and Annable 1991).

Ecology. Rocky slopes, rock outcrops, sandy drainages, cliffs, and disturbed roadsides usually in desert scrub vegetation with *Acacia*, *Aristida adscensionis* L., *Baccharis*, Bombacaceae, Cactaceae, *Dodonaea viscosa* (L.) Jacq., *Fucraea*, *Heliotropium*, *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., *Lantana*, *Pitcairnia*, *Prosopis*, *Puya*, *Salvia*, *Schinus molle* L., and *Schizachyrium*; 1150–3500 m.

Comments. *Muhlenbergia microsperma* can sometimes be confused with *M. romaschenkoi* known only from Peru and differs from it by having cleistogamous panicles in the axils of the lower sheaths and shorter, obtuse glumes, 0.4–1.3 mm long (glumes acute to acuminate, 2–2.8 mm long in *M. romaschenkoi*) [Peterson et al. 2018].

In a molecular DNA sequence study, *M. microsperma* forms a strongly supported clade with two other annuals, *M. appressa* C.O. Goodd. and *M. brandegei* C.G. Reeder, all members of *M*. subg. *Muhlenbergia* (Fig. 1; Peterson et al. 2010b). In addition, these three species produce cleistogamous spikelets in the axils of the lower culm branches, enclosed by a sheath (Peterson and Annable 1991). Cleistogamous spikelets appear to have evolved twice within *Muhlenbergia*, once in *M*. subg. *Muhlenbergia* within the *M. appressa*–*M. brandegei*–*M. microsperma* clade and once in *M*. sect. *Pseudosporobolus* in *M. cuspidata* (Torr. ex Hook.) Rydb. (Morden and Hatch 1984; Peterson et al. 2010b).

Specimens examined. Guatemala. **Sacatepequez**: Above Pastores, wet thicket, *P.C. Standley 60819* (US); Volcano Agua, near Antigua, shady bank, *A.S. Hitchcock 9130* (US); Antigua, *W.A. Kellerman 7301* (US).

15. *Muhlenbergia minutissima* (Steud.) Swallen, Contr. U.S. Natl. Herb. 29(4):207. 1947.

Fig. 12E–H

Agrostis minutissima Steud., Syn. Pl. Glumac. 1:171. 1854 Type: U.S.A., New México, 1847, *A. Fendler 986* (holotype: not located; isotypes: F-72158 [image!], MO!, NY-327637!, S-29780 [image!], US-825378!, US-997292!, W-0030511 [image!]). ≡ *Sporobolus minutissimus* (Steud.) Hitchc, Proc. Biol. Soc. Wash. 41:161. 1928. Basionym.

= *Milium microspermum* Lag., Gen. Sp. Pl. 2. 1816, Type:: México, Habitat in Nova Hispania, *D. Sesse s.n*. (holotype: MA; isotype: US-91019! fragm.). non *Muhlenbergia microsperma* (DC.) Trin. 1824. ≡ *Panicum microspermum* (Lag.) E. Fourn., Mexic. Pl 2: 492. 1886. ≡ *Sporobolus microspermus* (Lag.) Hitchc, J. Wash. Acad. Sci. 23(10):453. 1933.

= *Vilfa confusa* E. Fourn., Mexic. PL 2: 101. 1886. Type: México, Jalicingo, *C.].W. Schiede & Deppe 913* (syntype: US-998282! fragm. ex P); Orizaba, *Botteri 117* (syntypes: P!, US! fragm.); Orizaba, *Schaffner 93* (syntypes: P!, US! fragm. ex P); Orizaba, *Schajfner 125* (syntype: P!); Nevado de Toluca, Sep, *Hahn s.n.* (syntype:: P!); U.S.A., *Hall & Harbour 643* (syntype: P!). ≡ *Sporobolus confusus* (E. Fourn.) Vasey, Bull. Torrey Bot. Club 15:293. 1888. ≡ *Muhlenbergia confusa* (E. Fourn.) Swallen, Contr. U.S. Natl. Herb. 29(4): 207. 1947.

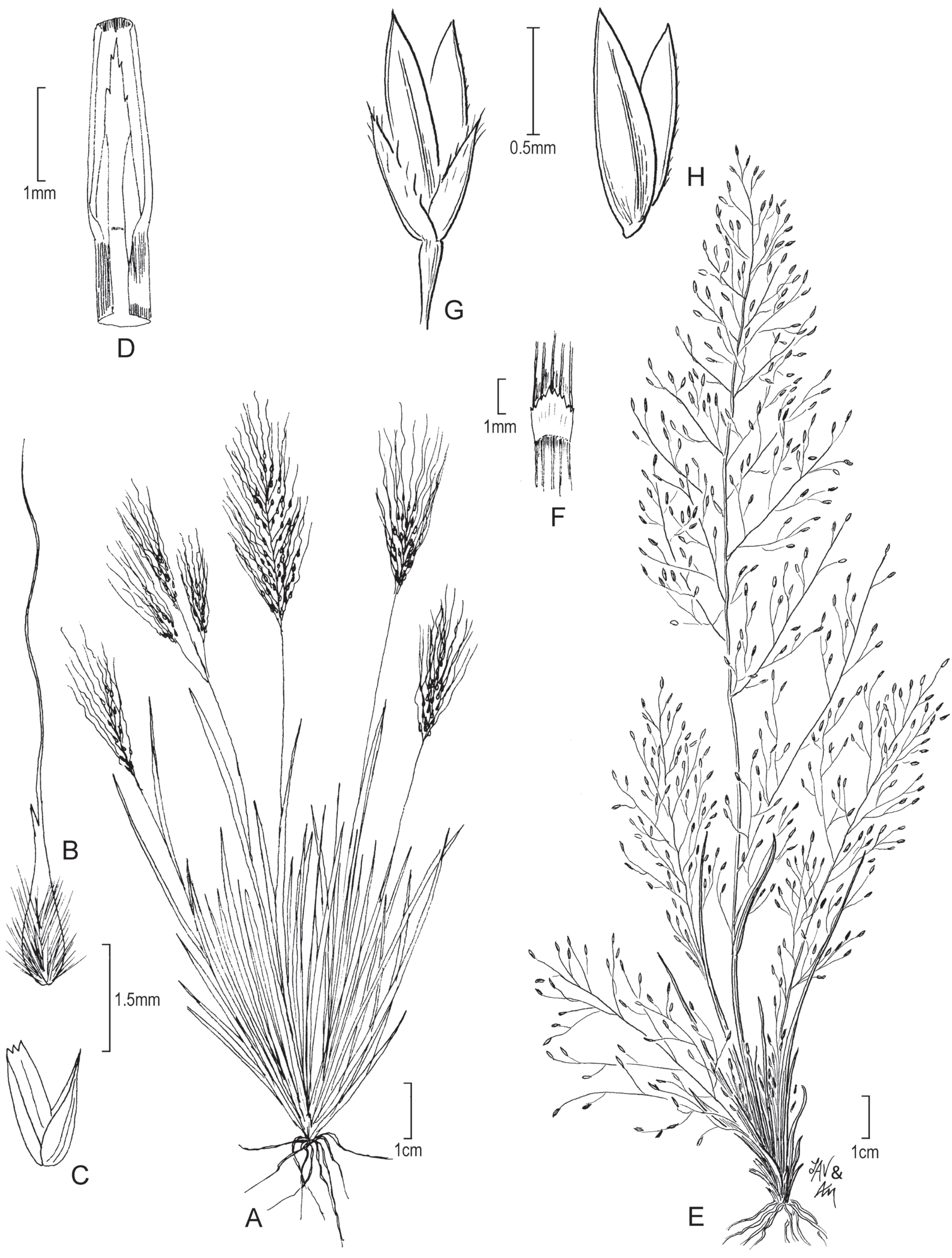

Figure 12. A–D *Muhlenbergia peruviana* (P. Beauv.) Steud. **A** habit **B** floret **C** glumes **D** ligule **E–H** *Muhlenbergia minutissima* (Steud.) Swallen **E** habit **F** ligule **G** spikelet **H** floret. **A–D** drawn from *P.M. Peterson & C.R. Annable 4067* (US, WS) **E, G, H** drawn from *P.M. Peterson & C.R. Annable 5601* (US-3182908) **F** drawn from *P.M. Peterson & C.R. Annable 4675* (US, WS).

Description. Delicate ***annuals*. *Culms*** 5–40 cm tall, erect or spreading, slender, scaberulous to strigulose below the nodes, 0.3–0.7 mm diameter just below the inflorescence; ***internodes*** 8–25 mm long. ***Leaf sheaths*** 4–52 mm long, shorter to longer than the internodes, glabrous or scaberulous, margins hyaline; ***ligules*** 1–2.6 mm long, hyaline, apex irregularly toothed to lacerate, truncate to obtuse, margins entire, sometimes splitting off to form auricles which are not longer than the body of the ligule; ***blades*** 0.5–4.0(–10) cm long, 0.8–2.0 mm wide, flat or involute, short pubescent above and scabrous below. ***Panicles*** 5.0–16.2(–21) cm long, 1.5–6.5 cm wide, open, ovate, nodes 12–35 per inflorescence; ***primary branches*** 8–42 mm long, one or two per node, spreading 25–80° from the rachis; ***pedicels*** 2–7 mm long, slender often capillary, erect. ***Spikelets*** 0.8–1.5 mm long, erect; ***glumes*** 0.5–0.9 mm long, subequal, 1-veined, sparsely short-pilose at least near apex; ***lower glumes*** 0.5–0.8 mm long, obtuse to acute; ***upper glumes*** 0.6–0.9 mm long, obtuse, usually broader than the first glume; ***lemmas*** 0.8–1.5 mm long, lanceolate, with short appressed silky pubescence located along the midvein and margins to glabrous, unawned, apex obtuse to subacute; ***paleas*** 0.8–1.4 mm long, about as long as lemma, with short appressed silky pubescence between the veins or glabrous; ***anthers*** 0.2–0.7 mm long, purplish. ***Caryopses*** 0.6–0.9 mm long, fusiform to elliptic, brownish. 2*n* = 60, 80.

Distribution. Western North America from central Washington to Montana south to Texas, U.S.A. and throughout México to Guatemala (Peterson and Annable 1991).

Ecology. Sandy and gravelly drainages, rocky slopes, flats, road cuts, and open sites most commonly in yellow pine forests, oak-pine forests with *Arctostaphylos*, thorn scrub forests with *Acacia*, pinyon-juniper woodlands, and oak-gramma grass (*Bouteloua*) savannahs; 1200–3000 m.

Comments. Morphologically, *Muhlenbergia minutissima* can be separated from other annual species of *Muhlenbergia* in Central America in having sparsely short-pilose glumes near the apex and open, ovate, panicles with pedicels that are longer than the spikelets (2–7 mm long [Peterson and Annable 1991].

Based on DNA sequence analysis, *Muhlenbergia minutissima* is a member of *M*. subg. *Bealia* and shares a most recent common ancestor with *M. sinuosa* Swallen, a species known to occur in Arizona and New Mexico, USA and Chihuahua and Sonora, México (Peterson and Annable 1991; Peterson et al. 2021).

Specimens examined. GUATEMALA. **Quetzaltenango**: Santa Maria, Volcano Agua, *A.S. Hitchcock 9130* (MICH, US-998503). **Quiché**: *W.A. Archer 3858* (US-1646054). **Totonicapán**: E of San Cristóbal Totonicapán, *Harmon 4570* (ENCB, NY).

16. *Muhlenbergia montana* (Nutt.) Hitchc., U.S.D.A. Bull. (1915–23) 772: 145, 147. 1920.

Fig. 9F–J

Calycodon montanum Nutt., J. Acad. Nat. Sci. Philadelphia ser. 2. 1:186. 1848. Type:United States, New Mexico, Santa Fe Co., in the Rocky Mountains near Santa Fe, *W. Gambel s.n.* (holotype: BM!; isotypes: GH, MO-992590!, PH). Basionym.

= *Muhlenbergia gracilis* var. *enervis* Scribn. ex Beal, Grass. N. Amer. 2: 242. 1896. Type: México, Chihuahua, dry ledges, Sierra Madre, 7 Oct 1887, *C.G.*

Pringle 1413 (holotype: MSC; isotypes: GH-00024024 [image!], US-995814!, UVMVT-024031 [image!], W-1916-27712!). ≡ *Muhlenbergia enervis* (Scribn. ex Beal) Hitchc., Contr. U.S. Natl. Herb. 17(3): 302. 1913.

= *Muhlenbergia trifida* Hack., Repert. Spec. Nov. Regni Veg. 8: 518. 1910. Type: México, Michoacán, vicinity of Morelia, Quinceo, 9 Nov 1909, *Bro. Arséne 3217* (holotype: W-1916-32145!; isotypes: BM, MO-843315!, MPU-026951 [image!], US!, US-86637! fragm.).

Description. Densely caespitose ***perennial***. ***Culms*** 10–80(–90) cm tall, erect, terete near base, glabrous below the strictly basal nodes; ***internodes*** mostly glabrous, occasionally glaucous. ***Leaf sheaths*** 2–35 cm long, longer than the lower internode, glabrous to scaberulous, often glaucous, becoming flat, loose and papery, and occasionally spirally twisted near the base; ***ligules*** 4–14(–20) mm long, membranous, decurrent, apex acute to acuminate, often lacerate; ***blades*** 6–30 cm long, 1–2.5(–3) mm wide, flat becoming loosely involute to subfiliform, somewhat stiff, scabrous below and hirsute above. ***Panicles*** 5–25 cm long, (1–)2–6 cm wide, narrow to somewhat open, loosely flowered, not dense; ***primary branches*** 0.5–10 cm long, ascending, appressed or spreading to 40° from the rachises; ***pedicels*** 2–7 mm long, longer than the spikelets, flattened, scabrous, occasionally stiffly reflexed. ***Spikelets*** 3–4.5(–7) mm long, erect, occasionally reflexed; ***glumes*** (1–)1.5–3.2(–4) mm long, ⅓ to ⅔ as long as the lemma, subequal, glabrous to scaberulous above; ***lower glumes*** 1-veined, sometimes mucronate, the mucro less tan 1 mm long; ***upper glumes*** 3-veined, 3-toothed and 3-awned, the teeth (including the awns) ⅓ to the length of the glume, and the awns up to 1.7 mm long, apex truncate to acute; ***lemmas*** 3–4.5 mm long, lanceolate, awned, often greenish or yellowish with dark green or purple mottles, scaberulous above, loosely to densely appressed-pubescent to pilose along the midvein, margins, and proximal. to ⅘, the hairs up to 0.8 mm long, occasionally glabrous, apex acute to acuminate, the awn (2–)6–25 mm long, flexuous; ***paleas*** 3–4.5 mm long, lanceolate, loosely to densely appressed-pubescent to pilose between the veins on the proximal ⅓ to ⅘, apex acute to acuminate, scaberulous; ***anthers*** 1.5–2.3 mm long, purplish. ***Caryopses*** 1.8–2 mm long, fusiform, light brown. 2*n* = 20, 40 (Herrera Arrieta 1998).

Distribution. This species ranges from southwestern USA throughout western México to Guatemala (Peterson et al. 2001).

Ecology. *Muhlenbergia montana* grows on rocky slopes, dry meadows, ridgetops, and open grasslands, primarily in upland and mountain habitats in pine and oak forests, at elevations of 1400–3000 m.

Comments. *Muhlenbergia montana* is morphologically similar to *M. quadridentata* but can be separated from the latter in having 3-toothed and 3-awned upper glumes with teeth 1/3 to ½ the length of the glume (the teeth are small <1/6 the length of the glumes in *M. quadridentata*), lemmas that are greenish or yellowish with green mottles or purple mottles (the lemmas are greenish-plumbeous to mottled plumbeous in *M. quadridentata*), and the anthers are usually 1.5–2 mm long (2–2.5 mm long in *M. quadridentata*) [Herrera Arrieta and Peterson 2007, 2018].

Muhlenbergia montana is a member of *Muhlenbergia* subg. *Clomena*, a lineage hypothesized to have originated in the Sierra Madre of México about 5.4 mya (Peterson et al. 2021).

Specimens examined. Guatemala. **Huehuetenango**: La Sierra (Tujimach), across river from San Juan Atitlan, Sierra de los Cuchumatanes. Open upper slopes, *J.A. Steyermark 51989* (US); About Laguna de Ocubila, east of Huehuetenango, dry open oak woods, *P.C. Standley 82722* (US); Chiantla, cerca del cementerio, Llano de San Nicolás, *D.N. Smith 442* (MO)¸ Aldea San Nicolás, Chiantla, *D.N. Smith 491* (MO). **Quetzaltenango**: La Esperanza, lugares secos, esteriles, *M. de Koninck 132* (US). **Quiche**: Between Quiche and San Pedro Jocopilas, on dry rolling hills with pine and oak forest, *P.C. Standley 62453* (US). Mexico. **Chiapas**: Amatenango del Valle: S of the center of Amatenango del Valle, *Alush Shilom Ton 1531*, (ENCB). **San Cristóbalde las Casas:** "El Banco" sobre el libramiento E a San Cristobal, km 4 carr. San Cristobal de Las Casas-Tenejapa, *A. Miranda S. s/n* (MEXU); *D.E. Breedlove & G. Davidse 55174* (CAS) cited in Reeder (1994).

17. ***Muhlenbergia mucronata*** (Kunth) Trin., Gram. Unifl. Sesquifl. 194, t. 5, f. 23. 1824.
Fig. 13H

Podosemum mucronatum Kunth, Nov. Gen. Sp. 1:129. 1815 (1816). Type: México, Guanajuato, crescit in mountains prope Cerro de Serna, Santa Rosa et Los loares, 1270–1360 hexap (2318-2482 m). Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotypes: BAA-00003945 [image!], BM-000938659 [image!], US-91925! fragm. ex P-Bonpl. y photo). ≡ *Agrostis mucronata* (Kunth) Spreng., Syst. Veg. 1:262. 1825 ≡ *Trichochloa mucronata* (Kunth) Roem. & Schult., Syst. Veg. 2:387. 1817. Basionym.

= *Muhlenbergia laxiflora* Scribn., Zoë 4:389. 1894. Type: México, Baja California Sur, La Chuparrosa, 17 Oct 1893, *T.S. Brandegee 74* (lectotype designated by A.S. Hitchcock, Contr. U.S. Natl. Herb. 17: 298. 1913: UC-122474!; isolectotypes: NY-00381444 [image!], US! fragm.ex UC).

Description. Densely caespitose ***perennials***. ***Culms*** 75–100(–120) cm tall, erect, scabrous or strigulous below the nodes, rounded near base. ***Leaf sheaths*** shorter than internodes, glabrous or scaberulous, purplish in part, rounded below; ***ligules*** (2–)5–8 mm long; ***blades*** 20–40 cm long, 2–3 mm wide, flat or loosely involute, scabrous abaxially, scabrous on ribs adaxially, attenuate into a long apex. ***Panicles*** (5–)10–15(–20) cm long, 1–3(–6) cm wide, oblong-cylindrical, spreading, purple, rarely purplish-green; ***primary branches*** 4–8(–10) cm long, ascending or appressed; ***pedicels*** 1–3 mm long, usually shorter than the spikelets, slender, scabrous below spikelets. ***Spikelets*** (4–)4.5–5 mm long; ***glumes*** 1.5–2 mm long, acute, subequal, scabrous near the apex; ***lemmas*** (4–)4.5–5 mm long, scaberulous between veins, mucronate or shortly awned from 2 minute teeth, the mucro or awn 0.5–1(–2) mm long; ***callus*** hairy, the hairs 0.5–0.7 mm long; ***paleas*** about as long as the lemma, scabrous between the veins, apex acute or acuminate; ***anthers*** 2–2.2 mm long, purplish. ***Caryopses*** 2–2.5 mm long, about 0.5 mm wide, ellipsoid, reddish-brown.

Distribution. This Mexican endemic is known from: Baja California and Chihuahua in the north throughout central México to Oaxaca, Veracruz, and Chiapas in the south (Herrera Arrieta and Peterson 2018).

Figure 13. A–G *Muhlenbergia rigida* (Kunth) Kunth **A** habit **B** inflorescence (narrow) **C** inflorescence (open) **D** ligule **E** glumes **F** floret **G** stamens and pistil **H** *Muhlenbergia mucronata* (Kunth) Trin. **H** floret. **A, B** drawn from *P.M. Peterson 9659* (US) **C–I** drawn from *P.M. Peterson*, *C.R. Annable & J. Valdés-Reyna 10876* (ANSM, US) **H** drawn from *P.M. Peterson & C.R. Annable 10778* (US).

Ecology. *Muhlenbergia mucronata* grows in oak–pine forests at elevations of 1350–2650 m.

Comments. *Muhlenbergia mucronata* is morphologically similar to *M. rigida*, differing from the latter in having mucronate to short-awned lemmas, narrower panicles, and usually shorter pedicels.

Muhlenbergia mucronata is a member of *M*. subg. *Trichochloa* and pairs with *M. subaristata* Swallen in a recent biogeographical analysis based on plastid and nuclear DNA sequences (Fig. 1; Peterson et al. 2021).

Specimens examined. Mexico. **Chiapas**: **San Cristóbal de las Casas**: 7 km E of San Cristobal las Casas in road to Zontehuitz, *D.E. Breedlove 11153* (US-3113121, US-3113122). **Tenejapa**: along river Chik Ha, barrio of Yashanal, *D.E. Breedlove 11125* (US-3113120). **Zinacantán**: along hwy 190 at Granadilla, *D.E. Breedlove 10607* (US-3113119), *D.E. Breedlove 52324* (CAS) citado en Flora Mesoamercana.

18. ***Muhlenbergia mutica*** **(Rupr. ex E. Fourn.) Hitchc., N. Amer. Fl. 17(6): 459. 1935.**

Fig. 14A–I

Epicampes mutica Rupr. ex E. Fourn., Mexic. Pl. 2: 87. Type: México, Veracruz, Mirador, Zacuapan, and Cantaranas, 1840, *H.G. Galeotti 5797* (lectotype, designated by T.R. Soderstrom in Contr. U.S. Natl. Herb. 34(4): 141. 1967: P; isolectotype: US-865973! fragm. ex P). Basionym.

= *Epicampes gigantea* E. Fourn., Mexic. Pl. 2:88. 1886. *Muhlenbergia gigantea* (E. Fourn.) Hitchc., N. Amer. Fl. 17(6): 460. 1935. Type: México, Veracruz, Orizaba, Río Blanco, 30 Sep 1886, *E. Bourgeau 3137* (**lectotype, designated here**: P-02265396 [image!]; isolectotypes: G-00099412 [image!], MPU-027109 [image!], P-02265395 [image!]; S14-29388 [image!], US-865978 fragm!, US-865977 fragm!).

= *Epicampes bourgeaei* E. Fourn., Mexic. Pl. 2:88. 1886. Type: México, Veracruz, Escamala, Refrou D'Orizaba, 26 Aug 1866, *E. Bourgeau 2973* (holotype: P; isotypes: K!, US-A0865984! fragm.).

= *Epicampes bourgeaei* var. *mutica* E. Fourn., Mexic. Pl. 2:88. 1886. Type: México, Veracruz, Mirador, Nov 1841, *F.M. Liebmann 678* (lectotype: US-207466!, designated by Herrera Arrieta and Peterson, Sida, Bot. Misc. 29: 35. 2007; isolectotypes: K!, US-207465!).

= *Epicampes expansa* E. Fourn., Mexic. Pl. 2:88. 1886. Type: México, Orizaba, *M. Botteri & Sumichrast 104* (holotype: P!; isotype: US-865979! fragm).

= *Epicampes laxiuscula* E. Fourn., Mexic. Pl. 2:88. 1886. Type: México, Orizaba, *M. Botteri 155* (syntype: P?; isosyntypes: BM-000938656 [image!], US-865975! fragm.).

= *Epicampes ehrenbergii* Mez, Repert. Spec. Nov. Regni Veg. 17: 212. 1921. Type: México, Cuesta de Pinolco, *C. Ehrenberg 1156* (holotype: B?; isotype: US-A0865980! fragm.).

= *Muhlenbergia alta* Hitchc., N. Amer. Fl. 17(6): 461. 1935. Type: México, Jalisco, hills E of Zapotlán, 25 Sep 1910, *A.S. Hitchcock 7180* (holotype: US-998980!).

= *Muhlenbergia magna* Hitchc., N. Amer. Fl. 17(6): 460. 1935. Type: México, Jalisco, under cool cliffs of barranca near Guadalajara, 3 Nov 1890, *C.G.*

Pringle 3335 (holotype: US-825277!; isotypes: BR-0000006883416 [image!], BR-0000006883744 [image!], CM-2820 [image!], E-00531666, F-73213 [image!], G-00099367 [image!], G-00099368 [image!], GOET-006639 [image!], KFTA-0000246 [image!], MEXU-00004527 [image!], MEXU-00004528 [image!], MO-105133!, MO-1837821!, MU-000000018 [image!], MU-000107304 [image!], US-998977!), W-18910001067 [image!].

Description. Strongly caespitose ***perennials***. ***Culms*** 120–300 cm tall, erect, compressed-keeled near the base, glabrous below the nodes to sometimes scaberulous. ***Leaf sheaths*** 12–32 cm long, shorter than internodes, sometimes purplish near base, often changing to brown with age, keels prominent and glabrous, lacking auricles; ***ligules*** (5–)8–15 mm long, membranous, apex lacerate; ***blades*** 35–110 cm long, 5–10 mm wide, flattened, scaberulous adaxially and glabrous abaxially, margins and keels serrate. ***Panicles*** 35–100 long, (8–)15–30 cm wide, purple or brown-purplish, branches ascending or pendulous spreading up to 60° from culm axis; ***primary branches*** 6–25 cm long, usually 15–20 cm long below, naked near the base, pendulous to flexuous; ***pedicels*** 0.2– 2.5 mm long, generally shorter than spikelets, scaberulous. ***Spikelets*** 1.3–2.6(–3) mm long, erect, purple to brownish-purple; ***glumes*** 1.3–2.6(–3) mm long, ovate, generally longer than florets, subequal, 1-veined, often translucent, usually glabrous to scaberulous, apex acute to obtuse; ***lemmas*** 1.3–2.3 mm long, oblong, awnless, rarely mucronate, glabrous; ***paleas*** 1.3–2.3 mm long, glabrous, apex acute to obtuse; ***anthers*** 0.9–1.3 mm long, yellow to purplish. ***Caryopses*** 1–1.3 mm long, fusiform, reddish-brown. 2*n* = 20, 24.

Distribution. *Muhlenbergia mutica* ranges from Chihuahua, Sinaloa, and Durango, México south to Oaxaca, Veracruz, and Chiapas (Herrera Arrieta and Peterson 2007, 2018).

Ecology. The species grows among pines or pine–oak forests and tropical forests with *Liquidambar*, *Nyssa*, and *Sabal*; 600–2300 m.

Comments. *Muhlenbergia mutica* can be separated morphologically from *M. robusta* in having wider panicles (8–)15–30 cm wide (2–8 cm wide in *M. robusta*) and non-auriculate leaf sheaths [auricles 2–4(–10) mm long in *M. robusta*] (Herrera Arrieta and Peterson 2018). *Muhlenbergia mutica* is a member of *M*. subg. *Trichochloa*, and in a recent study was found sister to *M. virletii* (E. Fourn.) Soderstr., another Mexican endemic (Peterson et al. 2021).

Soderstrom (1967) chose to recognize *M. mutica* and *M. gigantea*, stating, “The only character to separate the two is the length of the glumes in relation to the floret. It (*M. mutica*) is most closely related to and doubtfully distinct from *M. gigantea*.” After careful study of the isolectotypes attributed to *M. mutica* and *M. gigantea* (both housed at US), we find no differences in glume length, and they appear to represent specimens of a single species. Therefore, we place *M. gigantea* (younger name) as a synonym of *M. mutica* in our treatment.

Specimens examined. Mexico. **Chiapas. Cintalapa**: 12 km S of’ Mexican hwy 190 near Rizo de Oro, Crest of the Sierra near the microwave station of La mina, *D.E. Breedlove 20641*(ENCB); 23 km W of Las Cruces along road to La Mina Microwave Station, *D.E. Breedlove & G. Davidse 54111* (CAS, MO); Slope, near La Cienega de Leon 30 km N of Las Cruces, *D.E. Breedlove & F. Almeda 48041* (CAS, MO). **Ixtapa**: near Ixtapa, *D.E. Breedlove & G. Davidse 54301* (CAS, MO); Near the

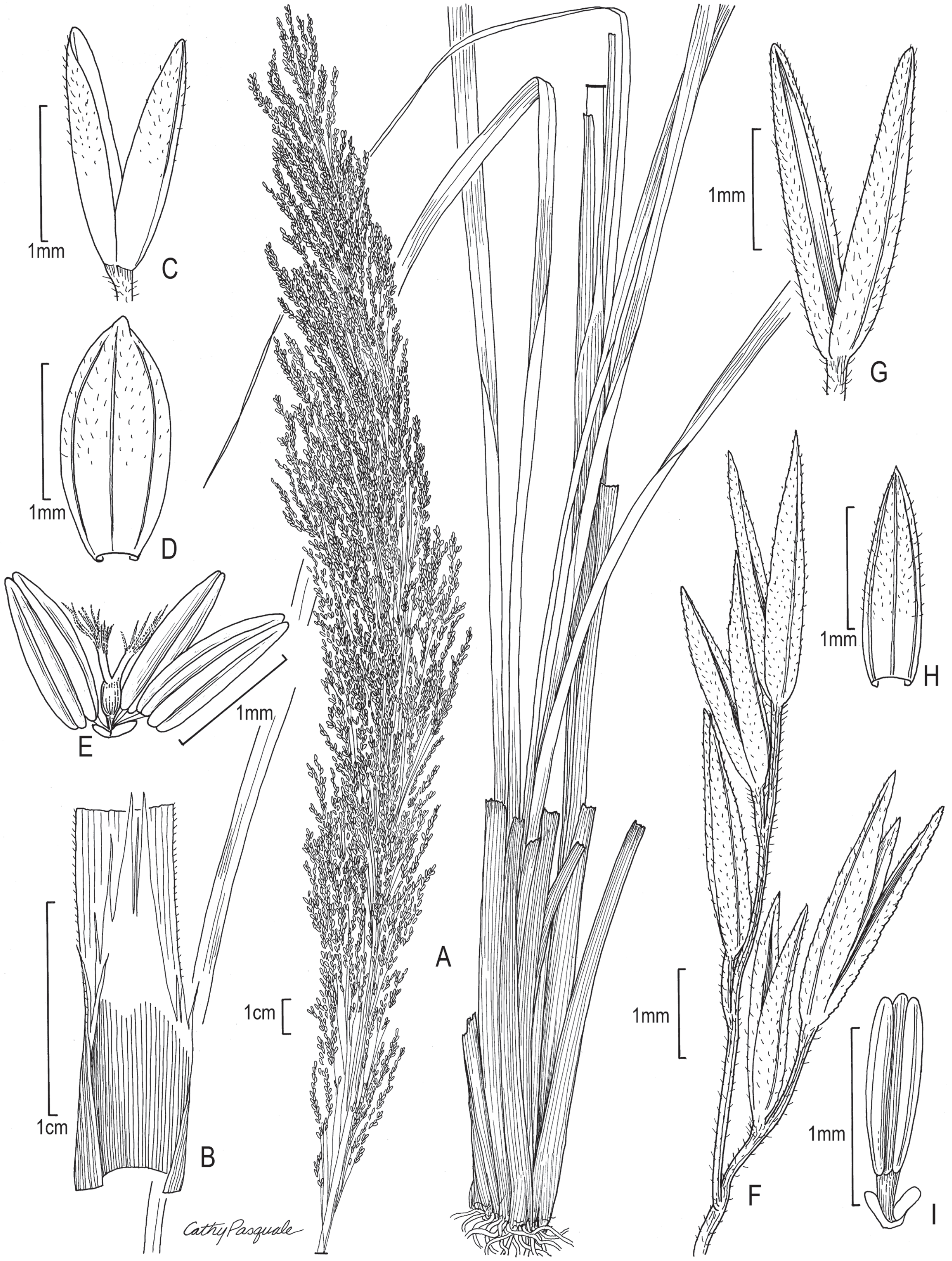

Figure 14. A–I *Muhlenbergia mutica* (Rupr. ex E. Fourn.) Hitchc. **A** habit **B** ligule **C** glumes **D**. lemma **E** stamens, pistil, and lodicules **F** inflorescence branch **G** glumes **H** lemma **I** stamens and lodicules. **A–E** drawn from *P.M. Peterson & C.R. Annable 6051* (US) **F–I** drawn from *Carl Mez Herbarium 3370* [*Botteri & Sumichrast 104*] (US-1720166).

Zinacantán Paraje of Muctajoc, *D.E. Breedlove & G. Davidse 54007* (CAS, MO); at Escopetazo, *D.E. Breedlove & G. Davidse 53947* (CAS, MO). **Jitotol**: 10 km N of Jitotol, *D.E. Breedlove 55152* (NY); near Colonia El Laurel, ca. 5 km N of Jitotol, *G. Davidse et al. 29600* (MO). **La Trinitaria**: *E.M. Martínez S. & W.D. Stevens 23903* (MEXU, MO). Paraje of Mahben Chauk, *D.E. Breedlove 7677* (ENCB); Paraje of Yehts 'Uk'um, *D.E. Breedlove 7504* (ENCB); in the Paraje of Mahosik', *D.E. Breedlove 14861* (ENCB). **cozingo**: Estación Chajul, reserva Montes Azules, 4 km NE del poblado de Chajul, *S. Sinaca-Colín s/n* (MEXU). Tenejapa: In the Paraje of Mahosik', *A.S. Ton 1187* (ENCB). Tenejapa: Kulaktik, *A.M. Ton 4570* (ENCB). **San Juan Cancuc**: El Pozo to Oxchuc, *E. Hernández & Sharp X-616* (US). **Tenejapa:** slopes, near Paraje Kulak'tik, *D.E. Breedlove 53057* (CAS, MO); lopes west of Tih Ha' in the Barrio of Kurus Pilal. Paraje of Mahben Chauk, *D.E. Breedlove 6282* (DS). **Zinacantán**: from Zinacantán paraje of Paste' to San Lucas, *R.M. Laughlin 2583* (ENCB); ear Paraje Sequentic, *D.E. Breedlove & G. Davidse 53910* (CAS, MO).

19. ***Muhlenbergia nigra*** Hitchc., N. Amer. Fl. 17(6): 468. 1935.
Fig. 3F–J

Type. México, México, Nevado de Toluca, cool slopes under pines, 2 Sep 1892, *C.G. Pringle 4211* (holotype: US-746689!; isotypes, F!, MO-2974170!, MSC, US-821929!).

Description. Caespitose ***perennials***. ***Culms*** 45–110 cm tall, erect, rounded near base, pubescent below the nodes, internodes glabrous to scaberulous. ***Leaf sheaths*** 3–17 cm long, shorter than the internodes, glabrous to scaberulous, the basal persistent, papery and flattened with age; ***ligules*** (5–)8–20 mm long, strongly decurrent, occasionally splitting into auricles, membranous to chartaceous above, firmer below near margins, apex truncate to obtuse; ***blades*** 5–25(–35) cm long, 2–3 mm wide, involute, scabrous and short pubescent above and mostly glabrous below. ***Panicles*** 6–15(–17) cm long, 5–10 mm wide, dense, spikelike, erect, exserted and surpassing the blades in height, plumbeous with a hint of green; ***primary branches*** 1–6 mm long, tightly appressed and ascending, imbricate, unexposed; ***pedicels*** 0.1–1.3 mm long, densely hispidulous. ***Spikelets*** (5.3–)6–8 mm long, erect, laterally compressed, plumbeous with a hint of green; ***glumes*** (5.3–)6–8 mm long, linear-elliptic to linear-ovate, usually longer than the lemma, 1-veined, sometimes mucronate or awn-tipped, scabrous along the keel, subequal; apex acuminate, scabrous, the awn up to 1.8 mm long; ***lemmas*** 5–6.5 mm long, broadly lanceolate, the margins involute, scabrous, unawned, mucronate or awned greenish-gray; apex acute, sometimes awn-tipped, the awn up to 1.3 mm long sometimes borne between two minute lobes, the lobes 0.1–0.3 mm long; ***callus*** sparingly pilose, the hairs 0.1–0.3 mm long; ***paleas*** 4.5–6 mm long, shorter than the lemma, scabrous; apex acute; ***anthers*** 2.5–3.2 mm long, grayish-green to whitish-gray. Caryopses 3–3.5 mm long, fusiform, brownish. Chromosome number unknown.

Distribution. *Muhlenbergia nigra* occurs in central México south to Guatemala and Costa Rica (Peterson et al. 2001).

Ecology. This species is found in mountain meadows, lava fields, and open pine forests; 2300–4000m.

Comments. *Muhlenbergia coerulea* (Griseb.) Mez from the Cordillera de los Andes in South America is morphologically similar to *M. nigra*. However, in recent molecular studies *M. nigra* and *M. coerulea*, both members of *M.* subg. *Trichochloa*, do not share an immediate common ancestor but lie in a poorly resolved clade with 10 other species in the subgenus (Fig. 1; Peterson et al. 2018, 2021).

Specimens examined. Costa Rica. **San José:** Sabana, south fork of Rio Talarí, *A.S. Weston 12372* (CR, ISC); Pérez Zeledón, sendero a la Sabana los Leones, 700m. S del Puesto, *A. Rodríguez 6461* (INB); Pérez Zeledón, P.N. Parque Nacional Chirripó, Cuenca Chirripó, Cuenca Terraba-Sierpe, sendero a Valle Los Leones, *E. Alfaro 1770* (INB, MO); Pérez Zeledón, Paramo en Las Sabanas Chirrido, *E. Alfaro 424* (INB, MO); Pérez Zeledón: bosques quemados y bosque enano camino al Rio Terbi y Sabana de Los Leones, *J.F. Morales 5174* (INB); Pérez Zeledón, Parque Nacional Chirripó. Del Puesto Los Crestones, 2.5 km al Sur, camino a Sabana Leones, *R. Robles 1784* (INB, MO); Rivas. P.N. Chirripó. Sabana de los Leones, *J. Sánchez el al. 2870* (MO); P.N. Chirripó, Valle de los Conejos, *R. Ocampo 1492* (CR); Parque Nacional Chirripó, Frente a refugio Los Crestones, *G. Vargas et al. 540* (USJ); P.N. Chirripó, Sabana de los Leones, *A. Weston 10114* (CR). Guatemala. **Huehuetenango**: Todos Santos, Cuchumatan, Tuicoy, *R. Flores & M. Véliz 94.4308* (MO); Todos Santos Cuchumatan, camino a la Torre, *M. Véliz et al. 14030* (MO); Sierra de los Cuchumatanes, ca. 28 mi from Huehuetenango, slopes of Cerro Chemal, *J.G. Hanokes 1453* (US); Cerro Chémal, *J.A. Steyermark 50305* (US-1935065, US-2208671). **Quetzaltenango**: Volcan Santa Maria, near summit of mtn., in open somewhat weedy and disturbed meadow above timberline, *J.H. Beaman 4119* (US). **Sacatepequez**: Volcano Agua, open pine woodland on steep northern slopes, *W.E. Harmon 3595* (MO); Santa Maria de Jesús, *M. Véliz et al. 2M.8512* (MO); Acatenango, Volcán de Acatenango, *M. Véliz et al. 10351* (MO); Volcan de Agua, summit of south rim of crater. In open, gravelly soil, *J.H. Beaman 2931* (US); Volcano Agua, *A.S. Hitchcock 9117* (US); Volcan de Agua, *W.A. Kellerman 7416* (US); Antigua, Volcan de Agua, *W.A. Kellerman s.n.* (US); Volcan de Agua, *G. Salas 538* (US).

20. ***Muhlenbergia orophila*** Swallen, Contr. U.S. Natl. Herb.29(9): 408. 1950.
Fig. 15F–J

= *Muhlenbergia matudae* Sohns, J. Washington Acad. Sci. 46(12): 382, f. 32–38. 1956. Type: México, Morelos, Lago de Zempoala, collected en madera humeda, orilla de bosque mixto de pinos y oyamel, 3000 m, 7 Oct 1951, *E. Matuda 25601* (holotype: US-2079186!; isotype: US-2119930!).

Type. Guatemala, Dept. Huehuetenango, Cerro Chémal in alpine meadow, summit of Sierra de los Cuchumantanes, 3700–3800 m, 8 Aug 1942, *J.A. Steyermark 50309* (holotype: F-1202399!; isotypes: F-73211!, G-00099366 [image!], US-132785!, US-132784!, US-1935066!, US-2208672!).

Description. Densely caespitose ***perennials***. ***Culms*** 12–30 cm tall; ***leaf sheaths*** longer than the internodes, glabrous, smooth or scabrous; ***ligules*** 0.3–0.5(–1) mm long, apex truncate and erose; ***blades*** 5–8 cm long, 1–1.6 mm wide, flat or loosely folded to involute, scaberulous, apearing glabrous below with widely-spaced, stiff, short ascending hairs more common towards the apex,

Figure 15. A–E *Muhlenbergia quadridentata* (Kunth) Trin. **A** habit **B** ligule **C** glumes **D** floret **E** stamens, pistil, and lodicules **F–J** *Muhlenbergia orophila* Swallen **F** habit **G** ligule **H** glumes **I** floret **J** stamens, pistil, and lodicules. **A–E** drawn from *P.M. Peterson & C.R. Annable 6201* (US) **F–J** drawn from *P.M. Peterson & C.R. Annable 11105* (US).

margins scabrous towards apex. ***Panicles*** 5–25(–30) cm long, open, diffuse, capillary, the base often partially enclosed by the sheath; ***primary branches*** 2–8 cm long, scabrous, naked below with very few spikelets, spreading 60–90° from the culm axis; ***pedicels*** 4–15 mm long, straight, scabrous; **disarticulation** above the glumes. ***Spikelets*** 3–3.5 mm long, plumbeous to dark-green turning golden brown with age; ***glumes*** 1.5–2.2 mm long, subequal, the lower a little shorter than the upper, 1-veined, apex acute, erose, often mucronate, the mucro less than 0.3 mm long; ***lemmas*** 3–3.5 mm long, lanceolate, 3-veined, puberulous, apex acute, minutely bifid, mucronate or awned between the teeth, the awn up 1.3 mm long, straight or slightly curled near apex, scaberulous; ***callus*** sparsely hairy; ***paleas*** 3–3.6 mm long, often slightly longer than the lemma, 2-veined; ***anthers*** about 1.2–1.6 mm long, purple. ***Caryopses*** not seen.

Distribution. This species has been reported in Chiapas and the type was collected in Guatemala (Villaseñor Ríos 2016). It is also known from central México and has been reported in Ciudad de México, Hidalgo, Morelos, México, Puebla, and Tlaxcala (Espejo Serna et al. 2000; Villaseñor Ríos 2016; Sanchez-Ken 2018).

Ecology. *Muhlenbergia orophila* is found along creeks and wet areas in pine-fir forests; 3000–3860 m.

Comments. Affinities of *M. orophila* are unknown and it has not yet been included in a DNA molecular study.

Specimen examined. GUATEMALA. **Huehuetenango**: Chemal, vicinity of Chémal, summit of Sierra de los Cuchumatanes, *J.A. Steyermark 50309* (MO).

21. *Muhlenbergia pereilema* P.M. Peterson, Caldasia 31(2): 293. 2009.
Fig. 16A–E

Pereilema crinitum J. Presl, Reliq. Haenk. 1(4–5): 233, t. 37, f. a–f. 1830. Type: Panama, *T. Haenke s.n.* (holotype: PR-198058!; isotypes: BR-0000006886257 [image!], HAL-0107173 [image!], LE-TRIN-1519.01!, M, MO-123263!, PR-849!, W-0029492 [image!], W-0029493 [image!], W-18890238189 [image!]). Basionym.

= *Pereilema crinitum* var. *cirratum* E. Fourn., Mexic. Pl. 2: 93. 1886. Type: México, Veracruz, Escamella, Orizaba, 24 Oct 1866, E. Bourgeau 3272 (**lectotype, designated here**: P-00751681 [image!]; isolectotypes: L-0062313 [image!], S14-29644 [image!], US-996097! ex P).

Description. Delicate, caespitose, ***annuals***. ***Culms*** 15–90 cm tall, decumbent, rooting from flower nodes, mostly smooth and glabrous below the nodes; internodes usually glabrous to scaberulous. ***Leaf sheaths*** longer than the internodes, smooth or scaberulous; **ligule**s 0.5–1 mm long, membranous, eciliate, irregularly erose; ***blades*** 5–15 cm long, 2–3(–5) mm wide, flat, acuminate, auriculate near base; **auricles** 1–1.5 mm long, falcate. ***Panicles*** 5–20 cm long, 1–3 cm wide, spiciform, linear, continuous or interrupted; ***primary branches*** 0.5–3.5 cm long, appressed, the spikelets arising just above the sterile spikelets or bristles; **bristles** 2–4 mm long, antrorsely scabrous; ***pedicels*** 0.1–0.2 mm long, oblong, arising just above the bristles. ***Spikelets*** 1.5–2.6 mm long, greenish to stramineous, subtended by an involucre of persistent bristles, disarticulation below the glumes; ***glumes*** 0.8–1.5 mm long, equal, narrowly awl-shaped, awned, the awns 1–3 mm long; ***lemmas*** 1.5–2.6 mm long, ovate, keeled, 3-veined, with appressed hairs below, lateral veins close to margins, scabrous, apex acuminate, awned, the awns (15–)20–30 mm long, flexuous, callus hairy, the hairs 0.3–1 mm long; **palea** similar to lemma; ***stamens*** 3, ***anthers*** 0.5–0.7 mm long, yellow; **style** 1. ***Caryopses*** 0.8 mm long, ellipsoid, with adherent pericarp. *2n* = 20 (Pohl and Davidse 1971).

Distribution. *Muhlenbergia pereilema* ranges from throughout México to Central (Costa Rica, El Salvador, Guatemala, Honduras, México, Nicaragua, and Panama) and South America (Peterson et al. 2001).

Ecology. This species occurs on grassy slopes and rocky roadsides, ravines, and barrancas in tropical and oak-pine forests; 50–2450 m.

Comments. *Muhlenbergia pereilema* can be separated from *M. plumiseta* in having persistent, scabrous bristles (plumose in *M. plumiseta*) and wider panicles (1–3 cm in *M. pereilema* and 0.2–0.6 cm wide in *M. plumiseta*) [Pohl 1994B; Herrera Arrieta et al. 2010; Herrera Arrieta and Peterson 2018]. This species forms a clade with *M. beyrichiana* Kunth and *M. plumiseta* within *M.* subg. *Muhlenbergia* (Peterson et. al. 2021).

Specimens examined. Costa Rica. **Alajuela**: Atenas, Balsa, alrededores de las Escuela Centroamericana de Gandería, *J. Gómez-L 6127* (CR); 1 km S Carrizal, open roadside in coffee plantation, *R.W. Pohl & G. Davidse 11502* (US, CR); La Garita, dam in the canyon of the Rio Grande de Tarcoles, *R.W. Pohl & G. Davidse 11494* (US, CR); 1 km N of Grecia, *R.W. Pohl & G. Davidse 11523* (US, CR). **Cartago**: Roadside N of Puente Negro, N of Orosi, *R.W. Pohl & M. Lucas 13153* (MO, CR); Turrialba, Près de la station de Juan Viñas, *H. Pittier 1759* (CR); San Juan Norte, *R. W. Pohl & G. Davidse 11435* (US, CR); vicinity of Finca Las Concavas, *P.C. Standley 41551* (US). **Heredia**: Orillas de la vía férrea a Heredia, *A.M. Brenes 13284* (CR); Barva, bordes del Río Segundo, *J. León 415* (CR); El Gallito de Heredia, *M. Valerio 540* (CR). **Puntarenas**: Paturage a Boruca, *A. Tonduz 3689* (CR); Savannas de Boruca, *H. Pittier (Tonduz, A.) 4450* (US, CR); Boca de Barranca, *M. Montiel s.n.* (USJ); Bord du chemin a Mano de Tigre, *H. Pittier (Tonduz, A.) 4627* (US, CR). **San José**: Acosta, camino a Bajo Palma, *J.F. Morales 7439* (INB, MO); Puriscal, Alto La Escalera, a lo largo del camino entre San Ignacio y Guaitil, cuenca del Pirris-Damas. Valle del Candelaria, Alto La Escalera en el camino a Bajo Arias y La Cruz, *J.F. Morales & B. Hammel 6049* (MO, INB, CR); Acosta, Cuenca del Pirris-Damas, Cerros de Caraigres, cabeceras del Río La Mesa, cerca Ceiba Este, *J.F. Morales & J.F. Corrales 6032* (MO, INB); Mora, Colón, le long des chemins dans la vallée du rio Jaris, prés de Pacaca, *H. Pittier 3329* (CR); Mora, Colón, en la orilla del camino de lastre que va de Brasil a Ciudad Colón, *S. Lobo 2309* (CR); Escazú, San Antonio, *D. Santamaría 3648* (INB, MO); Bordes líneas férreas San José-Guadalupe, *A. Tonduz 709* (CR); Hacienda La Esperanza, La Palma, *O. Jiménez 973* (US, CR); Sur un rocher au bord du rio Virilla, sous le pont du F. C. R., près San Juan, *A. Tonduz 17556* (CR); 13 km N of San Isidro de El General along carretera interamericana, *R. W. Pohl & G. Davidse 11626* (US, CR); San Pedro, *W.A. Archer 3888* (US); Tibas, collected along the Río Virilla about 1 km S of Santo Domingo, *J. Taylor 17313* (MO). El Salvador. **Ahuachapán**: Ahuachapán, *S.A. Padilla 134* (US); San Benito, al N de la cima del cerro La Olla, *E. Sandoval & Chinchilla 767* (LAGU, MO). **La Libertad**: Nueva San Salvador, Jardin Botanico La Laguna, *W.G. Berendsohn 1003* (LAGU, MO); Boqueron del Volcán de San Salvador, *L. E. González 1851* (MO, ITIC). **San Salvador**: San Salvador, *S. Calderón 494* (MO); San Martin, *S. Calderón 1902* (US); Cerro el Guayabal, *S. Calderón 1964* (US). Guatemala. **Alta Verapaz**, Coban,

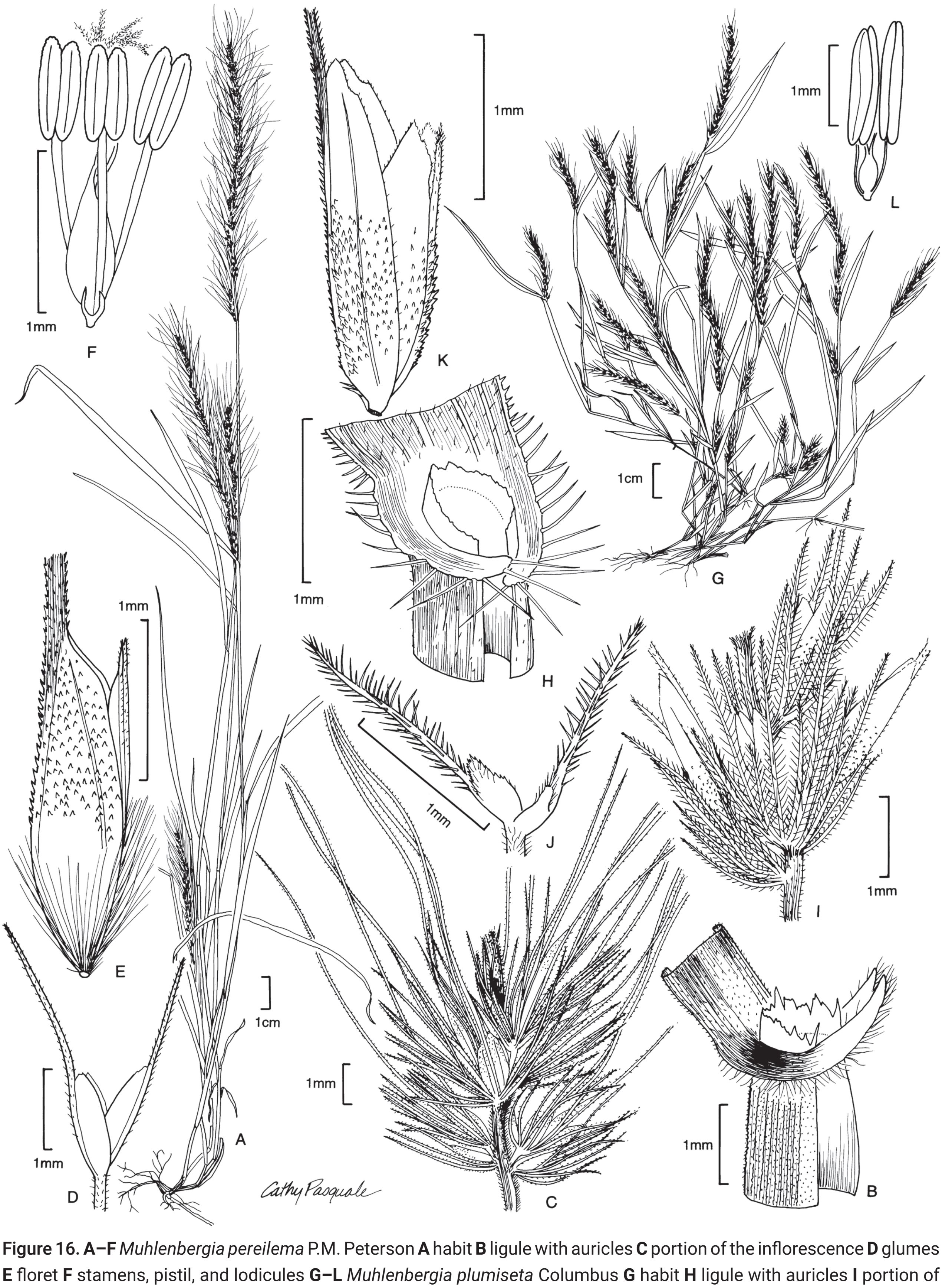

Figure 16. A–F *Muhlenbergia pereilema* P.M. Peterson **A** habit **B** ligule with auricles **C** portion of the inflorescence **D** glumes **E** floret **F** stamens, pistil, and lodicules **G–L** *Muhlenbergia plumiseta* Columbus **G** habit **H** ligule with auricles **I** portion of the inflorescence **J** bristles **K** floret **L** stamens and pistil. **A–F** drawn from *A.S. Hitchcock 9050* (US) **G–L** drawn from *C.G. Pringle 5962* (US).

H. von Türckheim 743 (MO); Cobán, *H. von Türckheim 1362* (MO); *H. von Türckheim 1509* (MO, US); Area of mixed forest and clearings, hills about 10 km south of Coban, *L. O. Williams et al. 40051* (US); Finca aved near Coban, *W. Popenoe 903* (US). **Chimaltenango**: along road from Chimaltenango to San Martin Jilotepeque, *P.C. Standley 57894* (US). **Chiquimula**: Volcan Ipala, near Amatillo, bordering lake on top, *J.A. Steyermark 30491* (US). **Huehuetenango**: Thickets and forest in deep canyon of a tributary of Rio Blanco, about 5 km W of Aguacatan, *L.O. Williams et al. 22338* (US). **Jalapa**: vicinity of Jalapa, pine-oak forest, *P.C. Standley 76749* (US). Jutiapa: Volcan Chingo, *J. Donnell Smith 3673* (US). **Guatemala**: Guatemala City, *A.S. Hitchcock 9050* (US); Guatemala City, rocky hill, *A.S. Hitchcock 9031* (US); Guatemala City, barranca north of Guatemala city, *W. Popenoe 733* (US); San Antonio, Las Roces, *Rojas 385* (US). **Santa Rosa**: Chupadero, *J. Donnell Smith 3914* (US); Cerro Redondo, *J. Donnell Smith 6274* (US). **Solola**: Mixed forest area, mountain slopes above Lake Atitlan, about 3–5 km W of Panajachel, *L.O. Williams et al. 25278* (US). Honduras. **El Paraíso**: Yuscarán, la Piedra de Apaguiz, 3.5 km al SE de Danlí, *N.P. Estrada 137* (MO, CR, TEFH); Arauca, Las Manos, 5 km N of Las Manos, near Los Limones, *R.W. Pohl & M. Gabel 13429* (MO, CR); Road to Danlí, near Río San Francisco, *J. R. Swallen 11196* (MO); Road to Yuscaran, *J.R. Swallen 11347* (US). **Francisco Morazán**: Distrito Central, Cerro el Hatillo, 15 km al NE de Tegucigalpa; bosque premontano húmedo, *L.M. Ordóñez 67* (MO); San Antonio de Oriente, quarry above El Zamorano, on road to San Antonio de Oriente, *R.W. Pohl & G. Davidse 12505* (MO, CR); vicinity of El Zamorano, along "Wood Road", *J.R. Swallen 10821* (US); In pine woods near Piedra Herrada, Mt. Uyuca region, *L.O. Williams 18543* (US); Drainage of the Rio Yeguare, Moist rocky bank near Agua Amarilla, in oak-pine forest, *L.O. Williams & A. Molina R. 14723* (US). **Olancho**: Jutiapa Forest Camp, near Salamá. Pine forest on a steep slope above a stream, *R.W. Pohl & M. Gabel 13749* (MO, CR). Mexico. **Chiapas: Angel Albino Corzo:** slopes of Río Cuxtepec, below Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54676* (MEXU, CAS). Arriaga: 13 km N of Arriaga along Mex. Hwy. 195, *D.E. Breedlove & G. Davidse 54149* (CAS, MO); slope at El Sumidero, 22 km N of Tuxtla Gutierrez, *D.E. Breedlove & P.H. Raven 13387* (DS); along ravines 13 km N of Arriaga along Mexican Highway 195, *D.E. Breedlove 28278* (MO). **Cintalapa:** 23 km W of Las Cruces along road to La Mina Microwave Station, *D.E. Breedlove & G. Davidse 54092* (CAS, MO). Chiapa de Corzo: above El Chorreadero, *D.E. Breedlove & G. Davidse 54032* (MEXU, CAS, MO); 36 km E of Tuxtla Gutierrez, *F.W. Gould & S. Hatch 14374* (ISC, DS); Ixhuatán: 2 km al N of Ishuatan, *G. Davidse et al. 29641* (MEXU, MO). Ixtapa: intersection of Tuxtla Gutiérrez-San Cristobal de las Casas and Villahermosa, *G. Davidse et al. 30104* (MEXU, MO); near Ixtapa, *D.E. Breedlove & G. Davidse 54264* (CAS, MO); along Mex Hwy 190 in the Zinacantan paraje of Muctajoc, *D.E. Breedlove 13819* (DS). **Motozintla:** Motozintla de Mendoza, 25–27 km NE of Huixtla along rd to Motozintla SW of Toliman, *D.E. Breedlove 28593* (CHAPA, MEXU, DS, MO); Ejido Toliman, sobre la carr. Huixtla-Motozintla. Vega de Arroyo, *Gómez et al. 185* (MEXU). **Tenejapa:** In the paraje of Mahosik', *D.E. Breedlove 16146* (DS). **Villa Corzo:** Above Colonia Vicente Guerrero on road to Finca Cuxtepec, *D.E. Breedlove & L. Strother 46573* (CAS, MO); Above Colonia Vicente Guerrero on road to Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54567* (MEXU, CAS, MO). San Fernando: Parque Nacional del Sumidero, 20–22 km NW of Tuxtla Gutiérrez, *G. Davidse et al. 29767* (MEXU, MO). Nicaragua. Rivas, Volcán Concepción, Isla Ometepe, plantas propias de la lava, *W. Robleto T. 157* (MO, CR). Panama. Coclé, vicinity of Ola, *H. Pittier 5046* (US).

22. *Muhlenbergia peruviana* (P. Beauv.) Steud., Nomencl. Bot. (ed. 2) 1:41. 1840.
Fig. 12A–D

Clomena peruviana P. Beauv., Ess. Agrostogr. 28, t. 7, f. 10; t. 3, f. 20. 1812. *Agrostis peruviana* (P. Beauv.) Spreng., Syst. Veg. 1:262. 1825. Type: Peru, *M. Thibaut s.n.* (holotype: P!; isotype: E-00373717 [image!]). Basionym.

= *Clomena peruviana* var. *pulvinata* Nees, Gramineae 12–13. 1841. *Muhlenbergia peruviana* var. *pulvinata* (Nees) Nees & E. Mey. ex Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Peru, Lago Titicaca, Apr, *J.F.J. Meyen s.n.* (holotype: B; isotype: US-3376134 fragm. ex B!).

= *Muhlenbergia nana* Benth., Pl. Hartw. 262. 1846. Type: Ecuador, Mt. Cotopaxi, 1843, *Hartweg 1458* (holotype: K!; isotypes: BAA-1629!, K!, LE!, P!, US-91916 fragm. ex P!, US-995896 fragm. ex P-STEUD & fragm. ex BR!).

= *Muhlenbergia pusilla* Steud., Syn. Pl. Glumac. 1:177. 1854. Type: México, México, Valley of Toluca, Oct. 1827, J.*L. Berlandier 1141* (holotype: P!; isotypes: BAA-1635!, K!, MO-2974185!, P!, US-1084517!, US-2561239!, US-91910 fragm. ex P!).

= *Epicampes bourgeaei* E. Fourn., Mexic. Pl. 2: 88. 1886. Type: México, Veracruz, Escamala, Refrou D'Orizaba, 26 Aug 1866, *E. Bourgeau 2973* (holotype: P!; isotype: US-A0865984 fragm ex P!).

= *Muhlenbergia bourgeaei* E. Fourn., Mexic. Pl. 2:86. 1886. Type: México, Valle de México, Desierto Viejo, 3 Nov 1865, *M. Bourgeau 1309* (lectotype: P! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991; isotype: US-87243 fragm. ex P!). ≡ *Epicampes bourgeaei* (E. Fourn.) M.E. Jones, Contr. W. Bot. 14:7. 1912, *nom. illeg. hom.*

= *Muhlenbergia pulcherrima* Scribn. ex Beal, Grass. N. Amer. 2:240. 1896. Type: México, Chihuahua: Sierra Madres, dry ledges of porphyry, 30 Sep 1887, *C.G. Pringle 1416* (holotype: MSC!; isotypes MO-3727978!, NY!, US-995494!, VT!).

= *Muhlenbergia peruviana* var. *elatior* Kuntze, Revis. Gen. Pl. 3(2): 357. 1898. Type: Bolivia, Tunarigebirge, 3000 m, May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991: isotype: fragm. & photo US!).

= *Muhlenbergia peruviana* var. *subcaespitosa* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Tunari Mts., 4600 m, 4 May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991).

= *Muhlenbergia peruviana* fo. *versicolor* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Tunarigebirge, 3000 m, May 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991; isotype: US fragm. ex NY!).

= *Muhlenbergia peruviana* fo. *viridis* Kuntze, Revis. Gen. Pl. 3(3):357. 1898. Type: Bolivia, Puna, 4000 m, 11 Mar 1892, *Kuntze s.n.* (lectotype: NY! designated by Peterson and Annable, Syst. Bot. Monogr. 31:73. 1991).

= *Muhlenbergia herzogiana* Henrard, Meded. Rijks-Herb. 40:58. 1921. Type: Bolivia, Cordillera de Santa Bonita, Jun 1911, *T. Herzog 2226* (holotype: L!; isotypes: US-87248 fragm. ex L!, US-1161342!, W-1926-23724!).

Description. Tufted ***annuals***. ***Culms*** 3–27 cm tall, erect, glabrous. ***Leaf sheaths*** usually longer than the internodes, smooth or scabridulous; ***ligules*** 1.5–3 mm long, membranous, acute; ***blades*** 1–5 cm long, 0.6–1.5 mm wide, flat to involute, smooth or scabridulous abaxially, sometimes shortly pubescent adaxially. ***Panicles*** 2–8 cm long, 0.3–3.4 cm wide, contracted or open; ***primary branches*** 1–5 cm long, diverging up to 80° from the rachises; ***pedicels*** 0.4–5 mm long, smooth or scabrous. ***Spikelets*** 1.4–4.2 mm long, 1-flowered; ***glumes*** smooth or scabridulous; ***lower glumes*** 0.8–2.8 mm long, narrow to broadly lanceolate, 1-veined, acute, often awn-tipped; ***upper glumes*** 0.9–3 mm long, wider than the lower glumes, lanceolate, 3(2)-veined, truncate to acute, 2- or 3-toothed; ***lemmas*** 1.4–4.2 mm long, ovate, widest near the base, purplish mottled with dark green areas, hairy on the calluses and lower 2/3 of the lemma bodies, hairs to 0.5 mm long, apices acuminate, usually bifid and awned from between the teeth, teeth to 0.5 mm long, awns 3–10 mm long, flexuous, purplish; ***paleas*** 1.3–3.8 mm, narrowly lanceolate, acuminate to subacute; ***anthers*** 0.5–1 mm long, purplish to yellowish. ***Caryopses*** 1–1.6 mm long, fusiform, brownish. 2*n* = 30.

Distribution. *Muhlenbergia peruviana* occurs in Arizona and New Mexico, U.S.A, throughout México to Guatemala, and then in Argentina, Bolivia, Chile, Ecuador, and Peru (Peterson and Annable 1991).

Ecology. Grassy flats, open gravelly flats, rock outcrops, sandy washes, gravelly drainages, wet or dry meadows, canyons, gravelly or sandy slopes, valleys, shores along lakes, open ridgetops, and disturbed road cuts associated with *Aciachne pulvinata* Benth., *Anatherostipa*, *Berberis*, *Colletia spinosissima*, *Ephedra*, *Festuca orthophylla* Pilg., *Festuca* spp., *Jarava*, *Juncus*, *Lepidophyllum*, *Luzula*, *Margyricarpus*, *Monnina*, *Muhlenbergia* spp., *Nassella*, *Plantago*, *Poa* spp., *Polylepis*, *Puya*, *Pycnophyllum*, *Salvia oppositiflora* Ruiz & Pav., *Stevia*, *Tagetes*; 3000–4900 m.

Comments. As treated here, *Muhlenbergia peruviana* includes (as synonyms) what was sometimes identified as *M. pulcherrima* Scribn. ex Beal (southwestern USA and northern México) and *M. pusilla* Steud. (central México to Guatemala). There are many more morphological forms than just these, and since the only chromosome count of this species suggests triploidy (2*n* = 3*x* =30), perhaps this species is apomictic (Reeder 1968). We believe apomixis is occurring in this species but that it is not obligate, and that gene flow takes place sporadically to form intermediates maintained by asexual seed formation (Peterson and Annable 1991).

In a molecular DNA sequence analysis *Muhlenbergia peruviana* is sister to *M. crispiseta* Hitchc., another annual known only from Texas and north central México, and this pair is embedded in the strongly supported *M*. subg. *Clomena* clade (Peterson et al. 2010b, Peterson et al. 2021). Members of *M*. subg. *Clomena* possess spikelets with upper glumes that are 3-veined and often 3-toothed and have a densely caespitose habit (Peterson et al. 2010b). *Muhlenbergia peruviana* can be separated from *M. crispiseta* in having purplish irregularly flexuous, purplish awns (versus sinuous-wavy, crisped and curled, olive-green awns in *M. crispiseta*) and narrow, gradually acuminate lemmas (versus lemmas that are plump near middle) [Peterson and Annable 1991].

Specimens examined. Guatemala. **Huehuetenango**: La Capellania, Sierra de los Cuchumatanes, 1.0 miles NW of La Capellania on hwy 9N and 12.3 miles N of Huehuetenango, *P.M. Peterson & C.R. Annable 4683* (GH, MEXU, MICH, MO, NY, RSA, UC, US, WS); Tojiah, Sierra de los Cuchumatanes, 3 miles SW of Tojiah on hwy 9 N., *P.M. Peterson & C.R. Annable 4698* (GH, MO, NY, RSA, US, WS); Treeless paramo-like plain near Calaveras, *L.O. Williams et al. 21961* (US). **San Marcos**: Tacana, Volcán Tacaná, *M. Véliz et al. 10587* (MO). Mexico. Chiapas:

NW de Motozintla de Mendoza on road to El Porvenir, *P.M. Peterson & C.R. Annable 4712* (US); 13 mi NW de Motozintla de Mendoza off road to El Porvenir at top of cumbre below tower, *P.M. Peterson & C.R. Annable 4714* (US).

23. *Muhlenbergia phalaroides* (Kunth) P.M. Peterson, Caldasia 31(2): 294–296, f. 7 A–B. 2009.

Fig. 16A–B

Lycurus phalaroides Kunth, Nov. Gen. Sp. (quarto ed.) 1: 142. 1815 (1816). Type: México, Michoacán, near Valladolid, Alberca de Palangeo and Patzcuaro, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-00669405 [image!]; isotypes: B-W-1630, BM!, BAA-1530!, US-91988 fragm. ex P-BONPL!, US-610837 fragm. ex LE-TRIN!). Basionym.

= *Muhlenbergia lycuroides* Vasey ex Beal, Grass. N. Amer. 2: 239. 1896. Type: México, Jalisco, Guadalajara, Jul–Oct 1886, *E. Palmer 489* (holotype: MSC; isotypes: GH-00023916 [image!], LE, MEXU, MO-2972929!, NDG-07247 [image!], NY, P-00644181 [image!], P-00644182 [image!], S14-29628 [image!], US-822925!, US-81642!, YU-000898 [image!]).

= *Lycurus phleoides* var. *brevifolius* Scribn. ex Beal, Grass. N. Amer. 2: 271. 1896. Type: México, Jalisco, plains of Guadalajara, 23 Oct 1889, *C.G. Pringle 2470* (lectotype: MSC, designated by C. Reeder, Phytologia 57(4): 288. 1985; isolectotypes: BAA!, GH, MEXU, MO-2972926!, NY!, P-00644183 [image!], P-00644184 [image!], US-996049!, W-18900000580 [image!], W-19160029092 [image!]).

Description. ***Perennials***, intricately branched near base. ***Culms*** 10–30 cm tall, erect, mostly glabrous, usually decumbent and sprawling below, bent at the pubescent to short pilose nodes; ***internodes*** 0.4–10(–15) cm long, pubescent to short pilose. ***Leaf sheaths*** much shorter than the internodes above, hyaline near the margins, pilose near summit; ***ligules*** 0.4–1 mm long, membranous, apex truncate to deltoid, often erose and lacerate; ***blades*** 0.5–6.5 cm long, 0.5–1.2 mm wide, shorter near the base of culms, flat, folded or loosely involute, lanate above and glabrous or with scattered, short appressed hairs below, margins whitish-thickened, apex navicular, occasionally with a short seta, seta usually less than 2 mm long. ***Panicles*** 1.5–6.5 cm long, 3–8 mm wide, spiciform and spikelike, densely flowered, often interrupted below with only a few spikelets, terminal or axillary; **rachis** lanate to hispid, the short hairs antrorse, appressed; ***primary branches*** 1.5–7 mm long, very short, the spikelets usually in pairs, rarely 1 or 3 per terminal branch, when in pairs the lower short-pedicelled spikelet perfect, staminate or sterile and the upper longer-pedicelled spikelet usually perfect; ***pedicels*** 0.3–1.4 mm long; **disarticulation** usually at the base of the pedicel, each spikelet falling as a unit leaving a small cuplike tip. ***Spikelets*** 3–4 mm long, stramineous with plumbeous mottles, sometimes additionally with purplish mottles; ***glumes*** 1–2.1 mm long, shorter than the lemma, subequal, 1–3-veined; ***lower glumes*** commonly 2 or 3-veined, usually 2-awned, occasionally 1 or 3 awned, the awns 1–3 mm long, equal or subequal, scabrous, recurved; ***upper glumes*** commonly 1-veined, usually 1-awned, the awns 1–2.5 mm long; ***lemmas*** 3–4 mm long, narrowly lanceolate, 3-veined,

Figure 17. A, B *Muhlenbergia phalaroides* (Kunth) P.M. Peterson **A** culm with inflorescence **B** spikelet **C–F** *Muhlenbergia tenella* (Kunth) Trin. **C** habit **D** ligule **E** glumes **F** floret. **A, B** drawn from *S. Lægaard 71419* (AAU) **C–F** drawn from *P.M. Peterson & C.R. Annable 4755* (US, WS).

margins hirsute to lanate and occasionally the lower ½ sparsely hairy, the hairs 0.1–0.3 mm long, apex usually awned, occasionally unawned or mucronate, the awns 1–3 mm long; ***paleas*** 2.8–3.8 mm long, hairy between the veins, the veins occasionally extending as mucros; anthers 1.3–2 mm long, yellowish. ***Caryopses*** 1.7–2 mm long, fusiform, brownish.

Distribution. *Muhlenbergia phalaroides* ranges from México to South America where it is found in Argentina, Bolivia, Columbia, Ecuador, and Peru (Reeder 1985; Sánchez and Rúgolo de Agrasar 1986; Davidse and Pohl 1994).

Ecology. This species occurs in open grasslands and savannahs on steep rocky slopes flats, and along disturbed irrigation canals in deep clayish-loam to sandy soils associated with *Baccharis*, *Berberis*, *Cheilanthes*, *Condalia*, *Dodonaea viscosa*, *Eragrostis*, *Jarava ichu Opuntia*, *Muhlenbergia cenchroides*, *M. rigida*, *Nassella*, *Plantago*, *Puya*, and *Sporobolus indicus* (L.) R. Br.; 2800–3500 m.

Comments. *Muhlenbergia phalaroides* is morphologically similar to *M. phleoides* (Kunth) Columbus known in the southwestern USA and México, and *M. alopecuroides* (Griseb.) P.M. Peterson & Columbus found in the southwestern USA, México, and disjunct in Argentina and Bolivia (Reeder 1985; Davidse and Pohl 1994, Renvoize 1998; Peterson and Giraldo-Cañas 2012). *Muhlenbergia alopecuroides* differs from *M. phalaroides* in having leaf blades with terminal seta (3–)4–7(–12) mm long and ligules (2–)3–12 mm long whereas *M. phleoides* differs in having auriculate ligules 1–2 mm long (Reeder 1985; Peterson 2003). These morphological differences are perhaps better recognized at the subspecific level but there are no population studies comparing these three species, other than Peterson and Morrone (1997) who investigated populations of only the amphitropical, *M. alopecuroides* [as *Lycurus setosus* (Nutt.) C. Reeder].

Muhlenbergia phalaroides probably lies within *M*. subg. *Pseudosporobolus*, although the species has not been included in a DNA-derived phylogeny, aligning with *M. alopecuroides* and *M. phleoides* (Peterson et al. 2021). Many members of this subgenus have narrow panicles, plumbeous spikelets with unawned, mucronate or short-awned lemmas (Peterson et al. 2010b).

Specimens examined. GUATEMALA. **Quetzaltenango**: Chiquilaja, potreros naturales y secos, *M. de Koninck 63* (US). MEXICO. **Chiapas**: **San Cristóbal:** NE edge of San Cristóbal de Las Casas, *D.E. Breedlove & G. Davidse 46039*, *54734* (MEXU). **Teopisca:** N of Teopisca, *D.E. Breedlove & G. Davidse 54768* (MEXU).

24. *Muhlenbergia plumbea* (Trin.) Hitchc., Contr. U.S. Natl. Herb. 17(3): 296. 1913.

Fig. 18A–E

Vilfa plumbea Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(1–2): 98. 1840. Type: México, Mineral del Monte, *Schlechtendal s.n.* (holotype: TRIN-1724.01!; isotype US-557435! fragm. ex LE). ≡ *Sporobolus plumbeus* (Trin.) Hemsl.. Biol. Cent.-Amer., Bot. 3(19): 546–547. 1885. Basionym.

= *Sporobolus pooides* Hack., Repert. Spec. Nov. Regni Veg. 10(243–247): 167. 1912[1911]. Type: México, Puebla, Rancho Posada, 2194m, Aug 1910, *F.G. Nicolas 5423* (holotype: W1916-0032028 [image!]; isotype: US-87219! fragm. ex W).

Description. ***Perennials*** with slender, scaly rhizomes; **rhizome scales** 7.5–16 mm long, acute often deteriorating with age. ***Culms*** 10–40(–50) cm tall, erect, decumbent near base, little or much branched below, glabrous; ***internodes*** 0.4–6 cm long, glabrous, smooth to nodulose-roughened, the nodes green or purple, constricted. ***Leaf sheaths*** 1–5 cm long, mostly longer than the internodes, glabrous, margins hyaline; ***ligules*** 0.3–0.5(–0.7) mm long, membranous, truncate, decurrent; ***blades*** 2–10(–12) cm long, 1–2.4(–3.0) mm wide, flat or folded, glabrous. ***Panicles*** 4–9(–14) cm long, 0.5–4(–8) cm wide, open, usually well exerted with 6–12 branches; ***primary branches*** mostly 2–8 cm long, ascending and spreading up to 50° from the culm axis, with 3–30 spikelets, widely spaced, naked below, one per node, scabrid; ***pedicels*** 0.5–2 mm long, shorter than the spikelets, scaberulous. ***Spikelets*** 2.5–3.2(–3.5) mm long, plumbeous; ***glumes*** 1–1.6 (–1.8) mm long, shorter than the florets, equal or subequal, the upper often slightly longer than the lower, 1-veined, apex acute; ***lemmas*** 2.2–3(–3.3) mm long, lanceolate to ovate, glabrous or occasionally scabrous, faintly 3-veined, dark green, apex acute; ***paleas*** 2–2.8(–3.1) mm long, about as long as the lemma, glabrous, faintly 2-veined, apex acuminate; ***anthers*** 1.4–2 mm long, dark green or purplish turning yellow with age. ***Caryopses*** 1.4–1.6 mm long, ellipsoid, greenish-brown. 2*n* = 40 (Reeder 1967).

Distribution. In Central America *M. plumbea* is known only from a single specimen collected in Guatemala. The species is wide ranging in México having been reported in Baja California, Chihuahua, Ciudad de México, Coahuila, Durango, Guanajuato, Hidalgo, México, Michoacán, Puebla, San Luis Potosí, Sonora, Tlaxcala, and Zacatecas. (Dávila et al. 2018; Sanchez-Ken 2018).

Ecology. This species occurs in wet depressions and alkaline meadows associated with pine and fir forests but is often collected near cultivated fields; 1800–3050m.

Comments. *Muhlenbergia plumbea* is morphologically similar to *M. utilis*, in Central America known only from Chiapas, the former having longer panicles [4–9(–14) cm versus 1–5 cm] that are usually well exserted (partially included in the upper sheath in *M. utilis*) with longer primary branches (2–8 cm versus 0.2–1.2 cm], longer spikelets [2.5–3.2(–3.5) mm versus 1.4–2.4 mm], and longer anthers [1.4–1.6 mm versus 0.7–1.4 mm].

This species has not been included in a molecular DNA sequence study to date but based on morphology it appears allied with the *M. filiformis–M. ligularis–M. vaginata* clade in *M*. subg. *Bealia* or the *M. repens* (J. Presl) Hitchc.–*M. utilis–M. villifora* Hitchc. clade in *M*. subg. *Pseudosporobolus* (Fig. 1; Peterson et al. 2021).

Specimens examined. Guatemala. Tan abundante como el "Zacachiquin", 19 Jun 1954, *M. de Koninck 31* (US-2151621).

25. ***Muhlenbergia plumiseta*** Columbus, Aliso 28: 66. 2010.
Fig. 16 G–L

Pereilema ciliatum E. Fourn., Mexic. Pl. 2: 93. 1886. Type: México, region Orizaba, 8 Nov 1866, *E. Bourgeau 3328* (**lectotype, designated here**: P-00751680!; isolectotypes: K-000308948 [image!], L-0062312 [image!], MPU-026837 [image!], US-996083!). ≡ *Muhlenbergia plumosa* P. M. Peterson, Amer. J. Bot. 97(9): 1546. 2010, isonym. Basionym.

Description. Delicate, caespitose, ***annuals***. ***Culms*** 15–50 cm tall, decumbent, rooting at the lower nodes, smooth and glabrous below the nodes; internodes usually glabrous to scaberulous. **Leaf** s**heaths** shorter than the internodes, scaberulous or smooth; ***ligules*** 0.2–0.4 mm long, membranous, apex truncate, erose; ***blades*** 4–10 cm long, 1.5–3 mm wide, flat, acuminate, auriculate near base, the **auricles** 0.5–1 mm long, clasping, ciliate. ***Panicles*** (2–)3–8 cm long, 0.2–0.6 cm wide, spiciform, linear, continuous; ***primary branches*** 0.2–0.8 cm long, tightly appressed, pilose, ascending, frequently glandular, the spikelets arising just above the sterile spikelets or bristles, the **bristles** 1–4 mm long, plumose, deciduous; ***pedicels*** 0.1–0.2 mm long, arising just above the bristles. ***Spikelets*** 2–3 mm long, stramineous to mottled with gray areas, subtended by an involucre of deciduous bristles; ***glumes*** 1–3 mm long, narrowly awl-shaped, 1-veined, plumose, difficult to separate from the bristles; ***lemmas*** (1.8–)2–3 mm long, lanceolate, scabrous, 3-veined, usually awned, the awns (1–)5–25 mm long, straight or flexuous, callus hairy, the hairs 0.2–0.4 mm long; ***paleas*** (1.8–)2–3 mm long, as long as the lemmas, apex bidentate; ***stamens*** 3, ***anthers*** 0.6–1.4 mm long, yellow or purplish; **styles** 2. ***Caryopses*** about 0.8 mm long, ovoid. 2*n* = 40 (Reeder 1968).

Distribution. *Muhlenbergia plumiseta* ranges from northwestern México to Guatemala and El Salvador (Peterson et al. 2001).

Ecology. This species occurs on open hillsides, ravines, and margins of forests in tropical deciduous forests and pine forests in shaded, often dry sites; 700–1800 m.

Comments. *Muhlenbergia plumiseta* can be separated from *M. pereilema* in having deciduous, plumose bristles (bristles not plumose in *M. Pereilema*) subtending the spikelets and spiciform panicles (2–)3–8 cm long, 0.2–0.6 cm wide (10–22 cm long, 1–3 cm wide in *M. Pereilema*) [Herrera Arrieta et al. 2010). This species forms a clade with *M. Beyrichiana* and *M. Pereilema* within *M.* Subg. *Muhlenbergia* (Peterson et al. 2021).

Specimens examined. Guatemala. **Huehuetenango**: Rio Selgua, from wooded slopes above Río Selegua, *W.E. Harmon & J.D. Fuentes 4807* (MO). Mexico. **Chiapas**: **Chiapa de Corzo:** above El Chorreadero, *D.E. Breedlove 53812* (CHAPA). **Chicoasén:** Mirador "Manos que imploran", 10 km al SW de Chicoasén, *A. Reyes G. 911* (MEXU). **Jitotol:** 3 km NE de Jitotol, en la carr. 195, *F.W. Gould 12707* (ENCB, MEXU, US). **Ocozocoautla de Espinosa:** 14.8 mi de Ocozocoautla, en la carr. Méx., *J. Brunker & C. Perino 314* (ENCB). **Tenejapa:** Paraje de Kotol Te´, *D.E. Breedlove 7363* (ENCB, US). **Tuxtla Gutiérrez:** 2 mi S of Tuxtla Gutiérrez along road to Villa Flores, *D.E. Breedlove & P.H. Raven 13334* (US); 11 km al NE de Tuxtla Gutierrez, Cañon del Sumidero, *R. Torres*, *E. Cabrera & M. Huft 6348* (MEXU); 17 km al NE de Tuxtla Gutierrez, Cañon del Sumidero, *R. Torres*, *E. Cabrera & M. Huft 6405* (MEXU). **Zinacantán:** along Mexican Hwy 190 at paraje Sequentic, *D.E. Breedlove 28688* (MEXU).

26. ***Muhlenbergia quadridentata*** (Kunth) Trin., Gram. Unifl. Sesquifl. 194, t. 5b, f. 14. 1824.

Fig. 15A–E

Podosemum quadridentatum Kunth, Nov. Gen. Sp. (quarto ed.) 1:130–131. 1816. Type: México, México, near Toluca, Sep, *F.W.H.A. Humboldt & A.J.A.*

Bonpland s.n. (lectotype: P-BONPL!, designated by McVaugh p. 253. 1983; isolectotypes: GH, US-2557456!, US-86634 fragm. ex P!, US-86635!). ≡ *Agrostis quadridata* (Kunth) Spreng., Syst. Veg. [Sprengel] 1: 263. 1825 (1824). ≡ *Muhlenbergia quadridentata* (Kunth) Kunth, Révis. Gramin. 1:64. 1829, isonym. ≡ *Trichochloa quadridentata* (Kunth) Roem. & Schult., Syst. Veg. 2:388. 1817. ≡ *Muhlenbergia virescens* subsp. *quadridentata* (Kunth) Y. Herrera, Amer. J. Bot. 81(8):1043. 1994. Basionym.

= *Podosemum gracile* Kunth, Nov. Gen. Sp. (quarto ed.) 1:131–132. 1816. Type: México, Michoacán, Volcán de Jorullo, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-BONPL!; isotypes: LE-TRIN-1501.02!, US-86636 fragm. ex P-BONPL!). ≡ *Muhlenbergia gracilis* (Kunth) Trin., Gram. Unifl. Sesquifl. 193, t. 5a, f. 6. 1824. ≡ *Trichochloa gracilis* (Kunth) Roem. & Schult., Syst. Veg. (ed. 15 bis) 2: 389. 1817. ≡ *Muhlenbergia gracilis* (Kunth) Kunth, Révis. Gramin. 1:64. 1829, isonym.

Description. Caespitose ***perennials*** with short, stout rhizomes. ***Culms*** 20–70 cm tall, erect, mostly glabrous below the nodes, the nodes basal, flattened, 1 node per culm; ***internodes*** mostly scabrous. ***Leaf sheaths*** 10–30 cm long, shorter than the internodes, scabrous to smooth; **basal *sheaths*** densely pubescent to glabrous abaxially, smooth and shiny adaxially, becoming flattened and usually not spirally twisted with age; ***ligules*** 2–8 mm long, membranous to hyaline above, firm and often brownish with evident veins near the margins below, decurrent, apex acuminate often lacerate; ***blades*** 5–15 cm long, 0.6–2 mm wide, flat or usually tightly involute, scaberulous below, short-spiculate and often villous above, the hairs 0.2–0.5 mm long, usually appressed, the spicules shiny to whitish. ***Panicles*** 5–20 cm long, 0.5–2 cm wide, narrow, loosely-contracted, interrupted below, mostly plumbeous; **central axis** flattened with 2 ribs, scabrous; ***primary branches*** 0.5–5(–6) cm long, appressed and ascending to spreading up to 30° from the rachises; ***pedicels*** 0.5–2 mm long, shorter than the spikelets, scabrous. ***Spikelets*** 3.4–4.7 mm long, mostly plumbeous; ***glumes*** 1.8–4 mm long, shorter to almost as long as the floret, unequal, mostly greenish-plumbeous, scabrous, usually with a few short hairs below; ***lower glumes*** 1.8–2.5 (–3) mm long, 1-veined, apex obtuse to acute, often with 2 small teeth; ***upper glumes*** (3–)3.2–4 mm long, 3-veined, apex truncate, obtuse or acute, often with 3 or 4 small teeth, the teeth less than 1/6 the length of the glumes; ***lemmas*** 3–4.7 mm long, lanceolate, terete, usually awned, greenish-plumbeous to mottled-plumbeous, sparsely pilose near base and margins on lower ½, apex acuminate, scabrous, the awns 1–20 mm long, flexuous, scabrous, greenish-plumbeous; ***paleas*** 2.8–4.3 mm long, shorter than the lemma, pilose on the proximal ½; ***anthers*** 1–2.5 mm long, purple. ***Caryopses*** 1.8–2 mm long, fusiform, brownish. 2*n* = 20.

Distribution. This species is found throughout México in the higher mountains extending to Guatemala (Peterson et al. 2001).

Ecology. *Muhlenbergia quadridentata* occurs on open to forested slopes derived from calcareous and volcanic rocks, and is associated with *Pinus* spp., *Abies* sp., *Holodiscus discolor* (Pursh) Maxim., *Populus tremuloides* Michx., *Pseudostuga*, and *Quercus* spp.; (1900–) 2500–4100 m.

Comments. The distinction between *M. quadridentata* and *M. virescens* (Kunth) Kunth is minimal and it has been suggested that quite possibly they

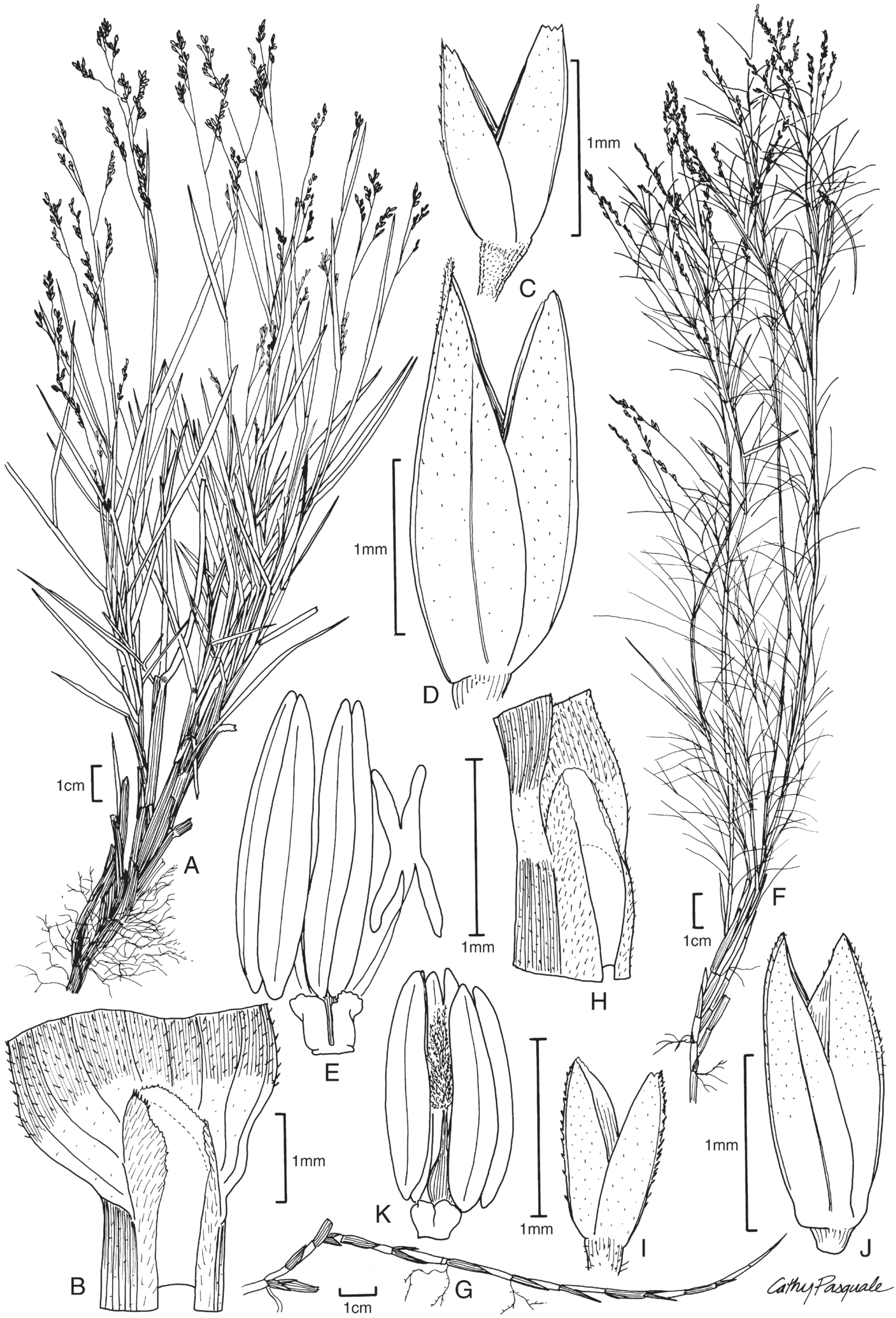

Figure 18. A–E *Muhlenbergia plumbea* (Trin.) Hitchc. **A** habit **B** ligule **C** glumes **D** floret **E** stamens and lodicules **F–L** *Muhlenbergia utilis* (Torr.) Hitchc. **F** habit **G** rhizome **H** ligule **I** glumes **J** floret **K** stamens, pistil, and lodicules. **A–E** drawn from *C.G. Pringle 9581* (US-396634) **F–L** drawn from *A,S. Hitchcock 5652* (US).

represent different morphological forms of a single species corresponding to different habitats (McVaugh 1983). Generally, the plumbeous spikeleted forms (*M. quadridentata*) are found above 2500 m whereas the whitish-hyaline to grayish-green forms (*M. virescens*) are found between 1600–2700 m. Even this color distinction can break down since intermediate individuals are not uncommon. One character that seems to be fairly consistent within each species is the presence of hairs at the base of the glumes. In addition to having dull, scabrous glumes, most individuals of *M. quadridentata* have a few short hairs near the base, whereas individuals of *M. virescens* have whitish or stramineous glumes that are glabrous and shiny near the base. Usually the upper glume apices of *M. quadridentata* are truncate with 3 or 4 teeth whereas the glume apices of *M. virescens* are acute and entire (Herrera Arrieta and Peterson 2018).

Muhlenbergia quadridentata is a member of *M.* subg. *Clomena* and it pairs with *M. flabellata* in a recent DNA molecular sequence analysis (Peterson et al. 2021). However, *M. virescens* aligns in a clade with *M. montana*, *M. straminea* Hitchc., and *M. curvula* Swallen [the latter two species treated as synonyms of *M. virescens* in Herrera Arrieta and Peterson (2018)].

Specimens examined. Guatemala. **Huehuetenango**: San Juan Ixcoy, Ul-xemal, *M. Véliz 98.689* (MO); Pine-Juniperus woodland near Tojquia, summit of Sierra de los Cuchumatanes, *J.A. Steyermark 50229* (US); Sierra de los Cuchumatanes, between Tojiah and Chemal at km 319.5 on Ruta Nacional 9N, in grassy meadow, *J.H. Beaman 3874* (US). Mexico. **Chiapas**: **Cintalapa:** 1 km al E de Rizo de Oro, *P. Dávila s.n.* (MEXU).

27. ***Muhlenbergia ramulosa*** (Kunth) Swallen, Contr. U.S. Natl. Herb. 29(4): 205. 1947.

Fig. 19A–D

Vilfa ramulosa Kunth, Nov. Gen. & Sp. 1: 137. 1815. Type: México, Jorulla, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (lectotype: P-HBK! designated in Peterson and Annable, Syst. Bot. Monographs 31: 77. 1991; isolectotypes: B-WILLD!, US! fragm ex P). ≡ *Sporobolus ramulosus* (Kunth) Kunth, Rev. Gram. 1: 68. 1829. Basionym.

= *Sporobolus wolfii* Vasey, Bull. Torrey Bot. Club 10: 52. 1883. Type: U.S.A., Colorado, Twin Lakes, 1873, *J. Wolf 1077* (holotype: US!; isotypes: MO!, NY!, US!). ≡ *Muhlenbergia wolfii* (Vasey) Rydberg, Bull. Torrey Bot. Club 32: 600. 1905.

Description. ***Annuals***; delicate, slender, often purplish. ***Culms*** (3–)5–25 cm tall, erect or spreading, geniculate, branched at the base, glabrous to minutely scaberulous below the nodes, branching below, striate, 0.2–0.3 mm in diameter just below the inflorescence; internodes 3–40 mm long. ***Leaf sheaths*** 3–30 mm long, usually shorter than the internodes, glabrous to minutely scaberulous, margins hyaline, scaberulous; ***ligules*** 0.2–0.5 mm long, hyaline, apex truncate, ciliate, without lateral lobes (auricles), margins entire; ***blades*** 5–30 cm long, 0.8–1.2 mm wide, involute or flat, minutely puberulent above, glabrous below. ***Panicles*** (1–)2–9 cm long, 0.6–2.7 cm wide, ovoid or deltoid, sparsely flowered; ***primary branches*** (0.5–)1–3.2 cm long, ascending to spreading (open) or closely appressed; ***pedicels*** 1–3 mm long, glabrous or scabrous, rigid. ***Spikelets*** 0.8–

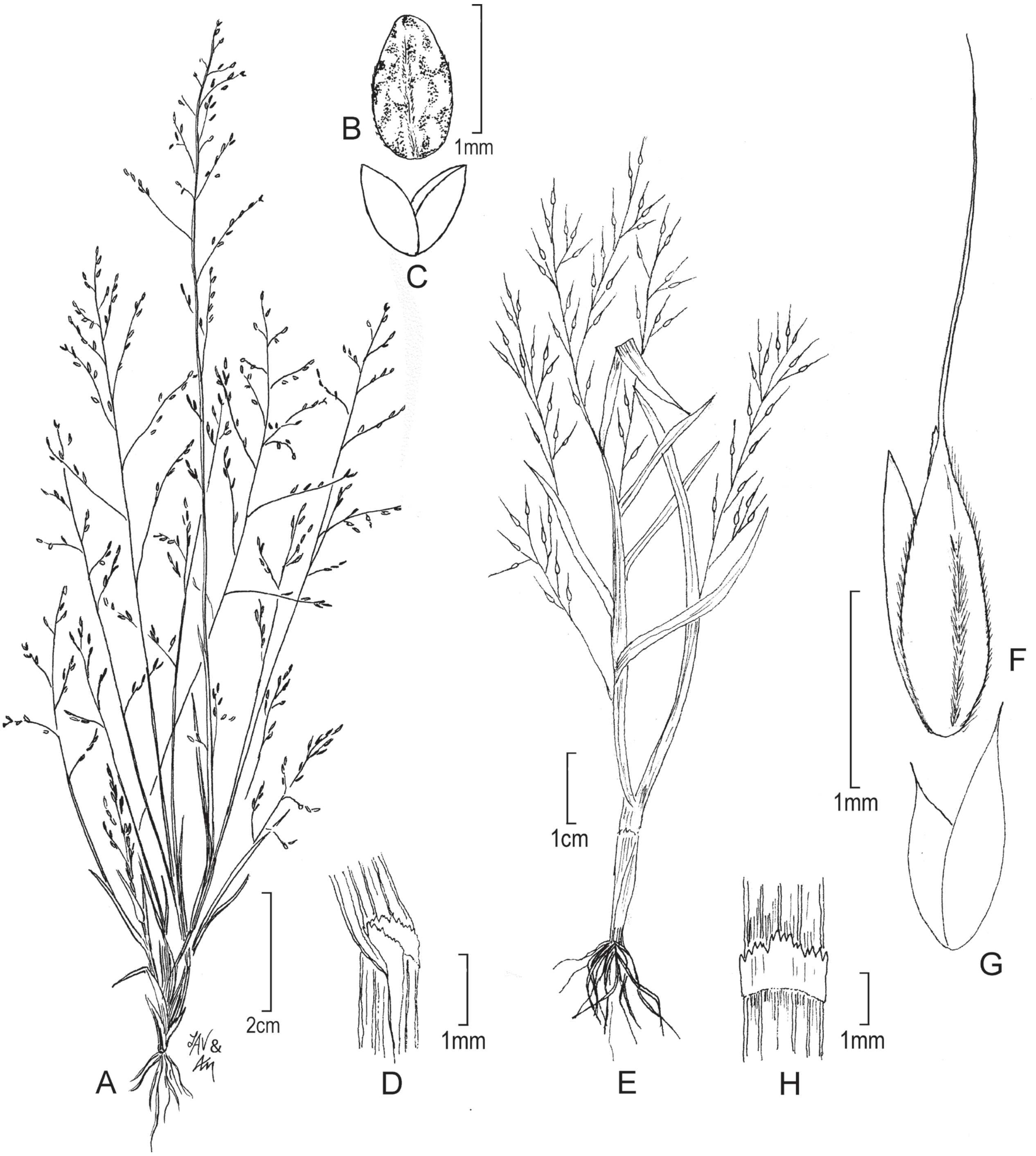

Figure 19. A–D *Muhlenbergia ramulosa* (Kunth) Swallen **A** habit **B** floret **C** glumes **D** ligule **E–H** *Muhlenbergia tenuissima* (J. Presl) Kunth **E** habit **F** floret **G** glumes **H** ligule. **A** drawn from *P.M. Peterson & C.R. Annable 5602* (US-3182911) **B–D** drawn from *P.M. Peterson & C.R. Annable 4661* (US, WS) **E–H** drawn from *P.M. Peterson & C.R. Annable 4751* (US, WS).

1.3 mm long, erect; ***glumes*** 0.4–0.7 mm long, equal, 1-veined, glabrous, whitish, obtuse or subacute, awnless; ***lemmas*** 0.8–1.3 mm long, oval, plump, with mottled with dark greenish-black areas and greenish-white or ochroleucous areas, inflated at maturity, glabrous or appressed-pubescent on margins and midvein, apex acute, awnless; ***paleas*** 0.7–1.3 mm long, oval; ***anthers*** 0.2–0.3 mm long, purplish. ***Caryopses*** 0.5–1 mm long, ellipsoid, brownish to purplish. *n* = 10.

Distribution. *Muhlenbergia ramulosa* ranges from the southwestern United States, México, Central America (Guatemala and Costa Rica), and Argentina (Peterson and Annable 1991).

Ecology. It occurs in open pine-oak and tropical forests; 1620–3400 m.

Comments. *Muhlenbergia ramulosa* does not align within the five existing subgenera but is instead sister to the common ancestor shared between the well supported clades of all species in *M*. subg. *Bealia* and in *M*. subg. *Trichochloa* (Peterson et al. 2021). We place *M. ramulosa* in a separate subgenus, *M.* subg. *Ramulosae* P.M. Peterson below.

Specimens examined. Costa Rica. **Cartago**: Oreamuno, Volcán Iraza, devastated area at end of Park Road above Sanitario Duran, growing on ash *R.W. Pohl 14209* (MO); Cordillera Central, lower slopes of Volcan Irazu, 1 km below San Juan de Chicoa, *R.W. Pohl & G. Davidse 11417* (US, CR); Cráter del Volcan Irazú, *O. Jimenez 1151* (US, CR). Guatemala. **Chimaltenango**: Chichavac, *A.F. Skutch 665* (US). **Huehuetenango**: Santa Eulalia, Sierra de los Cuchumatanes, 13 mi NW of Santa Eulalia on road to San Mateo Ixtatán, moist meadow, associates: *Sibbaldia* and *Deschampsia*, *P.M. Peterson & C.R. Annable 4693* (GH, MO, NY, US, WS); meadow at Tojiah on Hwy 9N, *P.M. Peterson & C.R. Annable 4696* (NY, US. WS); 3mi SW of Tojiah on Hwy 9N, *P.M. Peterson & C.R. Annable 4699* (NY, US, WS); Todos Santos Cuchumatan, cerca de la Torre, *J.R. Gálvez et al. 96.5812* (MO); between Tojiah and Chemal at km 319.5 on Ruta Nacional 9N, *J.H. Beaman 3876* (US). **Quetzaltenango**: Cerro Calel, *M. de Koninck* 153 (US). **Sacatepequez**: Volcán de Acatenango, *M. Véliz et al. 10292* (MEXU, MO); Volcano de Agua, *A.S. Hitchcock 9125* (US). Mexico. **Chiapas**: NW de Motzintla de Mendoza on road to El Porvenir, *P.M. Peterson & C.R. Annable 4711* (US, MO); 13 mi NW of Motozintla de Mendoza off road to El Porvenir, *P.M. Peterson & C.R. Annable 4715* (GH, MICH, MO, NY, RSA, UC, US, WS). Sierra Madre, *C.G. Pringle 1425* (MEXU).

28. *Muhlenbergia rigida* (Kunth) Kunth, Révis. Gramin. 1: 63. 1829.
Fig. 13A–G

Podosemum rigidum Kunth, Nov. Gen. Sp. (quarto ed.) 1: 129. 1816. Type: México, Guanajuato, near Guanajuato, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotypes: BAA!, US-91920 fragm. ex P!). ≡ *Trichochloa rigida* (Kunth) Roem. & Schult., Syst. Veg. 2: 386. 1817. ≡ *Agrostis rigida* (Kunth) Spreng., Syst. Veg. 1: 262. 1825. Basionym.

= *Podosemum elegans* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 130. 1816. Type: Ecuador, Chimborazo, Paramo de las Puntas & Pomallacta, Jun, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P!; isotype: BAA!). ≡ *Trichochloa elegans* (Kunth) Roem. & Schult., Syst. Veg. 2: 387. 1817. ≡ *Agrostis quitensis* Spreng., Syst. Veg. 1: 262. 1825.

= *Podosemum glabratum* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 130. 1816. Type: México, Santa Rosa de la Sierra and Cañada de Acabuca, Sep, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-Bonpl!; isotype: US-91921 fragm. ex P-Bonpl!). ≡ *Trichochloa glabrata* (Kunth) Roem. & Schult., Syst. Veg. 2: 387. 1817. ≡ *Agrostis glabrata* (Kunth) Spreng., Syst. Veg. 1: 262. 1825.

= *Muhlenbergia berlandieri* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3-4): 299. 1841. Type: México, Distrito Federal, Mountains near México, Aug 1827, *J.L. Berlandier 676*, *684* (lectotype: LE-TRIN-1487.01! designated by Peterson et al. in PhytoKeys 114: 195. 2018; isolectotypes [all *Berlandier 676*]: COL-000006382 [image!]; P-00644117 [image!], P-00644119 [image!], US-2557457!, US-87241 fragm!, W-239604!, W-0029177 [image!]).

= *Muhlenbergia affinis* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3-4): 301. 1841. Type: México, México, Toluca, *J.L. Berlandier 1083* (lectotype: P-00644141 [image!] designated by Peterson et al. in PhytoKeys 114: 195. 2018; isolectotypes: G-00099411 [image!], G-00099410 [image!], G-00099409 [image!], LE-TRIN-1485.01 fragm.!, P-00644142 [image!], US-87237 fragm.!). ≡ *Podosemum affine* (Trin.) Bush, Amer. Midl. Naturalist 7(2):40. 1921.

= *Muhlenbergia phragmitoides* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 255. 1874. Type: Argentina, Tucumán: Cuesta de Anfama, Sierra de Tucumán, 23 Mar 1872, *P.G. Lorentz 79* (lectotype: GOET-006649 [image!] designated by Peterson et al. in PhytoKeys 114: 195. 2018; isolectotypes: BAA-00002225 [image!], CORD-00004622 [image!], GOET-006648 [image!], SI-002780 [image!], US-91911 fragm. ex GOET!).

= *Muhlenbergia elegans* var. *atroviolacea* Kuntze, Revis. Gen. Pl. 3(3): 357. 1898. Type: Bolivia, Cochabamba, 3000 m, 26 Mar 1892, *O. Kuntze s.n.* lectotype: NY-00381485 [image!] designated by Peterson et al. in PhytoKeys 114: 195. 2018.

= *Muhlenbergia elegans* var. *subviridis* Kuntze, Revis. Gen. Pl. 3(3): 357. 1898. Type: Bolivia, Tunari Mts, 1600 m, *O. Kuntze* (lectotype: NY-00381486 [image!] designated by Peterson et al. in PhytoKeys 114: 195. 2018).

= *Muhlenbergia metcalfei* M.E. Jones, Contr. W. Bot. 14: 12. 1912. Type: USA, New Mexico: Grant Co., Santa Rita Mountains, in and around S end of the Black Range, 7000 ft, 9 Oct 1904, *O.B. Metcalf 1485* (holotype: POM-116640!; isotypes: GH-00023980 [image!], MO!, US!).

= *Muhlenbergia holwayorum* Hitchc., Contr. U.S. Natl. Herb. 24(8): 389. 1927. Type: Bolivia, Sorata, 16 Apr 1920, *E.W.D. Holway & M.M. Holway 530* (holotype: US-1108445!).

Description. Densely caespitose ***perennials***. ***Culms*** 40–100 cm tall, stiffly erect, glabrous to scaberulous below the basal, terete nodes, usually 1 node per culm; ***internodes*** mostly glabrous. ***Leaf sheaths*** 2–30 cm long, longer than the internodes, glabrous to scaberulous, rounded near base; ***ligules*** (1–)3–6(–8) mm long, often lacerate, firmer below, strongly decurrent, apex obtuse to acute; ***blades*** 12–35 cm long, 1–3 mm wide, flat or involute, glabrous to scaberulous below and scaberulous to hirsutulous above. ***Panicles*** (4–)10–35 cm long, (2–)3–5(–12) cm wide, loosely contracted to open and lax, sometimes diffuse, reddish-purple; ***primary branches*** 0.4–10 cm long, sometimes capillary, ascending and spreading up to 80° from the rachises; ***pedicels*** 1–10 mm long, mostly longer than the spikelets. ***Spikelets*** 3.5–5 mm long, reddish-purple; ***glumes*** 1–1.7(–2) mm long, much shorter than the floret, about equal, 1-veined, unawned, apex obtuse to subacute, sometimes hirsutulous, rarely mucronate; ***lemmas*** 3.5–5 mm long, narrow lanceolate, scaberulous to scabrous, purple, awned, callus with hairs up to 0.5 mm long, apex acuminate, the awns (8–)10–

22 mm long, flexuous; ***paleas*** 3.5–5 mm long, narrow lanceolate, purple, scaberulous, apex acuminate; ***anthers*** 1.7–2.3 mm long, reddish-purple. ***Caryopses*** 2–3.5 mm long, fusiform, brownish. 2*n* = 40, 44.

Distribution. *Muhlenbergia rigida* ranges from Arizona, New Mexico, and southwestern Texas, throughout México, Guatemala, and Honduras to South America where it occurs along the Andes from Columbia, Venezuela, Ecuador, Bolivia, Peru, and Argentina (Peterson et al. 2001).

Ecology. This species occurs on rocky slopes, ravines, and sandy, gravelly slopes derived from granitic and calcareous substrates associated with *Acacia*, *Agave*, *Aristida*, *A. adscensionis*, *Baccharis*, *Berberis*, *Bidens*, *Bouteloua curtipendula* (Michx.) Torr., *Caesalpinia*, *Colletia spinosissima*, *Cortaderia bifida*, *C. jubata*, *Desmodium*, *Dodonaea viscosa*, *Ephedra*, *Eragrostis*, *Eucalyptis*, *Eupatorium*, *Festuca*, *Fucaria*, *Hypericum*, *Jarava*, *Krameria*, *Lepechinia*, *Lupinus*, *Lycium*, *Melinus minutiflora*, *Mirabilis*, *Opuntia*, *Paspalum*, *Cenchrus clandestinus*, *Peperomia*, *Puya*, *Salvia*, *Schinus molle* L., *Schizachyrium*, *Sporobolus*, *Tillandsia*, and *Trichocereus*; 2000–3650 m.

Comments. This species is highly variable and is one of the most common upland bunchgrasses forming almost pure stands in northern México, less common in Peru and South America where it is usually found in smaller populations.

Molecular DNA sequence analysis indicates *M. rigida* lies within *Muhlenbergia* subg. *Trichochloa* and genetically is highly variable (Peterson et al. 2010b; Peterson et al. 2021).

Specimens examined. Guatemala. **Huehuetenango**: upper and off canyon near Huehuetenango, *A.A. Beetle 6* (MEXU). Honduras. **Francisco Morazán**: along road 13 km W of Mateo, *R.W. Pohl 12737* (CR). Mexico. **Chiapas**: **Ococingo:** a 4 km al S de Ejido Benemérito de las Américas camino a Flor de Cacao, *E. Martínez 10785* (ENCB); Arroyo del Rancho Pellizzi, al E de San Cristóbal, *A. Méndez 9158* (CIIDIR, MEXU). **San Cristóbal de las Casas:** 7 km E of San Cristóbal de las Casas, along the road to Zontehuitz, *D.E. Breedlove 11155* (ENCB); NE edge of San Cristobal de las Casas, *D.E. Breedlove 53858* (NY); Northeast edge of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 54745* (CAS, MO); East side of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 52327* (CAS, MO). **San Fernando:** Sobre cerro ubicado al E de la subestación de CFE, entrada por la zona de extración de arena, carretera Tuxtla-San Fernando, *A. López C. 1359* (HEM, MO). **Tenejapa:** barrio of Yashanal, paraje of Mastab, steep slope along the river of Chik Ha', *D.E. Breedlove 11125* (ENCB). **Teopisca:** about 15 mi SE of Teopsca on a heavily grazed slope, *J.R. Reeder & C.G. Reeder 2029* (ENCB); S edge of Teopisca, *D.E. Breedlove & P.H. Raven 13097* (ENCB). **Zinacantan:** near paraje Nachij, *D.E. Breedlove 54703* (NY).

29. ***Muhlenbergia robusta*** (E. Fourn.) Hitchc., N. Amer. Fl. 17(6): 462. 1935.
Fig. 20A–E

Epicampes robusta E. Fourn., Mexic. Pl. 2:89. 1886. Type: México, Distrito Federal, Santa Fe, 2 Oct 1865, *M. Bourgeau 1153* (lectotype: P!, designated by Hitchcock, N. Amer. Fl. 17(6): 462. 1935; isolectotypes: K!, US-999036!, US-999031! fragm., US-90734! fragm.). Basionym.

= *Epicampes stricta* J. Presl, Reliq. Haenk. 1(4-5):235, t. 39. 1830. Type: México, *T. Haenke s.n.* (holotype: PRC?; isotypes: LE-TRIN-1558.01! fragm., US-865970! fragm.). ≡ *Muhlenbergia presliana* Hitchc., N. Amer. Fl. 17(6): 462. 1935b, *nom. nov.*

= *Epicampes berlandieri* E. Fourn., Mexic. Pl. 2:89. 1886. Type: México, México, Feb 1839, *J.L. Berlandier 670* (lectotype: P! designated by Hitchcock, N. Amer. Fl. 17(6): 462. 1935; isolectotypes: BM-000938652 [image!], G-00099371 [image!], US-1127013!). ≡ *Muhlenbergia fournieriana* Hitchc., J. Wash. Acad. Sci. 23(10): 453. 1933.

= *Epicampes macrotis* Piper, Proc. Biol. Soc. Wash. 18:144. 1905. Type: México, Zacatecas, Sierra Madre Mountains, ca. 40 km W of San Juan Capistrano, 7 Aug 1897, *J.N. Rose 3528* (holotype: US-302505!). ≡ *Muhlenbergia macrotis* (Piper) Hitchc., N. Amer. Fl. 17(6): 463. 1935.

= *Epicampes minutiflora* Mez, Repert. Spec. Nov. Regni Veg. 17:212. 1921. Type: México, Michoacán, near El Canizal, 600m, 15 Jan 1899, *E. Langlassé 750* (isotype: US-386160!). ≡ *Muhlenbergia meziana* Hitchc., N. Amer. Fl. 17(6): 461. 1935, *nom. nov.*

Description. Caespitose ***perennials***. ***Culms*** 100–230(–300) cm tall, erect, compressed-keeled near base, glabrous to sometimes pubescent below the nodes; ***internodes*** glabrous. ***Leaf sheaths*** 15–70 cm long, longer than the internodes, glabrous, becoming brownish below, sometimes shredded; ***sheath auricles*** present, (1–)2–4(–10) cm long, linear subulate to broadly triangular, longer above, straight or twisted, firm below; ***ligules*** 2–10(–12) mm long, membranous, lacerate throughout; ***blades*** 40–100 cm long, 4–7 mm wide, folded sometimes involute toward tip, scaberulous above and below, the margins and keel saw-toothed. ***Panicles*** 30–80 cm long, (2–)3–8 cm wide, narrow to loosely contracted, greenish-gray to silvery gray or purplish; ***primary branches*** 1–15(–17) cm long, naked near base, ascending and closely appressed to spreading up to 40° from the rachises; ***pedicels*** 0.3–1.1 mm long, shorter than the spikelets, erect, scaberulous; central axis prominently ribbed, scabrous. ***Spikelets*** (1.8–)2–3 (–3.2) mm long, erect, greenish-gray or purplish; ***glumes*** 1.8–3.2 mm long, usually longer than the floret, subequal, narrowly oblong to elliptic, veinless to indistinctly 1-veined, hyaline to greenish-gray, glabrous to scaberulous, apex acute to obtuse occasionally erose; ***lemmas*** 1.7–2.6 mm long, linear-oblong, unawned or rarely mucronate, greenish to yellowish-brown, glabrous or pubescent with scattered hairs on lower, the hairs up to 0.3 mm long, ***callus*** glabrous or with few hairs, apex acute, the mucro when present up to 1 mm long; ***paleas*** 1.7–2.6 mm long, glabrous to sparingly pilose between the veins on lower, apex acute; ***anthers*** 1.1–2 mm long, purplish. ***Caryopses*** 1.2–1.7 mm long, fusiform, brownish. $2n = 40$.

Distribution. *Muhlenbergia robusta* occurs in mountainous areas from Sinaloa and Chihuahua south to Chiapas, Guatemala, Honduras, and Nicaragua in Central America (Peterson et al. 2001).

Ecology. It is found on rocky slopes, along barrancas (canyons), in pine and pine–oak forests, and in tropical deciduous forests; 850–3000 m.

Comments. Morphologically, *M. robusta* is similar to *M. mutica* but can be separated from the latter in having narrow panicles (2–)3–8 cm wide [(8–)15–30 cm wide in *M. mutica*] and auriculate leaf sheaths (not auriculate in *M. mutica*), the auricles 2–4(–10) mm long.

Figure 20. A–E *Muhlenbergia robusta* (E. Fourn.) Hitchc. **A** habit **B** ligule **C** glumes **D** floret **E** stamens, pistil, and lodicules **F, G** *Muhlenbergia uniseta* (Lag.) Columbus **F** habit **G** primary inflorescence branch with three spikelets. **A–E** drawn from *P.M. Peterson & C.R. Annable 6131* (US) **F, G** drawn from *F.W. Gould 10391* (US-3000113).

In DNA sequence studies, *Muhlenbergia robusta* is found to align in a large polytomy with other species in *M.* subg. *Trichochloa* (Fig. 1; Peterson et al. 2010b; Peterson et al. 2021).

Specimens examined. Guatemala. **Chimaltenango**: near finca La Alameda, near Chimaltenango, *P.C. Standley 59136* (US); Above Santa Maria, Volcano Agua, *A.S. Hitchcock 9129* (US). **Guatemala**: Guatemala City, 21 km W of Guatemala on CA-1, along road in oak forest, *W.E. Harmon& J.A. Fuentes 4865* (MO); Guatemala City, Eureka, *A.S. Hitchcock 9081* (US); Guatemala City, *A.S. Hitchcock 9035* (US), *9063 (1/2)* (US). **Huehuetenango**: Barranco "Palo Negro" in oak-pine forest about 10 km west of Aguacatan, *L.O. Williams et al. 21844* (US), *21848* (US); km 101 between El Mirador and Chintla, Sierra Cuchumatanes, rocky slopes, *A. Molina 21176* (US). Santa Rosa: Taxisco, Naranjo, *J. Donnell Smith 3932* (US, MO). **Quiche**: Nebaj, NE of Nebaj, *M.J. Metzler 17* (MO). **Sacatepequez**: near Antigua, *P C. Standley 61698* (US); *P.C. Standley 76942* (US). **Santa Rosa**: Taxisco, Naranjo, *Heyde & Lux 3932* (MO). **Sololá**: 5 km W of Patzún, collection from deep ravine covered with pine and oak, *W.E. Harmon & J.D. Dwyer 2646* (MO); Cerca del Lago Atitlán, *M. de Koninck 145* (US). Honduras. **Intibucá**: La Esperanza, Intibucá, Cerro San Cristóbal, bosque mixto premontano húmedo, *T. M. Mejía O. 87* (MO). Mexico. **Chiapas**: Camino de San Cristobal a Ocosingo, 31 km suroeste de Ocosingo, *R. Banda S. et al. 73117* (DS). **Amatenango del Valle**: 14 km SE of Teopisca along hwy. to Comitán, *G. Davidse et al. 29800* (MO). **Angel Albino Corzo:** slopes of Río Cuxtepec below Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54699* (CAS, MO). **Bochil**: 5 km east of Bochil on road to Pichucalco, *D.E. Breedlove & G. Davidse 55164* (CAS, MO). Comitán de Domínguez: 6 km N of Comitán along Mexican hwy 190, 1770 m, *D.E. Breedelove & G. Davidse 54873* (SLPM, CAS, MO); 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54877* (CAS, MO); 6 km N of Comitán along Mexican Highway 190, *D.E. Breedlove & G. Davidse 54869* (CAS, MO). **Ixtapa**: at Escopetazo, *D.E. Breedlove & G. Davidse 53948* (CAS, MO); along Mexican Highway 190 at the Zinacantán paraje of Muctajoc, *Laughlin 1559* (DS). **La Independencia**: above and SW of La Soledad on road to Las Margaritas, *D.E. Breedlove 53126* (CAS, MO). **La Trinitaria**: 6–7 km S of La Trinitaria, *G. Davidse et al. 29950* (MO); 10 km south of La Trinitaria on Mexican Highway 190, *G. Davidse et al. 55070* (CAS, MO). **Rayón**: 9 miles NW of Pueblo Nuevo Solistahuacá along the road between Rincon Chamula and Rayón, *H. Zuill 609* (DS). near summit of Zontehuitz, *A. Shilom Ton 30* (DS). **Teopizca**: 7 km NW of Teopisca along hwy. to San Cristobal de las Casas, *G. Davidse et al. 29829* (MO); North of Teopisca, *D.E. Breedlove & G. Davidse 54765* (CAS, MO). **Tuxtla Gutiérrez:** 31 km al W de Tuxtla Gtz y 13 km NE de Chiapa de Corzo, 1050 m, *J. C. Soto 13361 con D. Sutton*, *R. Hampshire*, *R. Lira y A. Reyes* (MEXU); km 11.5 de la carr. Tuxtla Gutierrez-Cañon del Sumidero, en el lugar denominado El Zacabastal, *E. Rodríguez s/n* (MEXU); 16 km N of Tuxtla Gutiérrez on road to El Sumidero, *D.E. Breedlove & B.M. Bartholomew 55491* (CAS, MO). **Venustiano Carranza**: 3 miles S of Aguacatenango along the road to Pinola Las Rosas, *D.E. Breedlove & P.H. Raven 13433* (DS). **Villa Corzo**: above Colonia Vincente Guerrero on the road to Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54600* (CAS, MO); near Revolucion Mexicana, *D.E. Breedlove & G. Davidse 54520* (CAS, MO). **Zinacantán**: near Paraje Sequentic [Zequentic], *D.E. Breedlove & G. Davidse 53909*

(CAS, MO); Along Mexican Highway 190, 10 miles southeast of the road to Simojovel. Paraje of Granadia, *D. E. Breedlove 7274* (DS); at Kampana Ch'en along Mexican Highway 190, 3 miles west of paraje Navenchauk, *R.M. Laughlin 2279* (DS); along road from Zinacantán center to Ixtapa near Paraje Vo Bits, *D.E. Breedlove 40725* (MO). Nicaragua. **Managua**: Sierra de Managua, *H.A. Garnier 1953* (GH, US).

30. *Muhlenbergia setarioides* E. Fourn., Mexic. Pl. 2: 84. 1886.
Fig. 21F–J

= *Muhlenbergia polypogonoides* Hack., Ann. K. K. Naturhist. Hofmus. 17: 255. 1902. Type: México, *A. Schmitz 862* (holotype: W-18890124080!; isotypes: US-3412356! fragm. ex W, W-19160029073!

Type. México, Orizaba, Borrego, 14 Nov 1865–1866, *M. Bourgeau 3362* (**lectotype, designated here**: MPU-026952 [image!]; isolectotypes: G-00099164 [image!], GH-0024047 [image!] ex P, K-000308906 [image!], MO-2974294!, US-0091990! ex P & ex LE, S-14-29487 [image!]. ≡ *Muhlenbergia sylvatica* var. *setarioides* (E. Fourn.) Beal, Grass. N. Amer. 2: 249. 1896.

Description. Sprawling ***perennials***, rooting at the lower nodes. ***Culms*** 30–70(–100) cm tall, geniculate, usually glabrous, with many branches, about 1.5 mm thick near base. ***Leaf sheaths*** shorter or longer than internodes, terete, striate, glabrous or scaberulous; ***ligules*** 1.5–3.5 mm long, hyaline, becoming yellowish-brown or brownish, erose; ***blades*** 4–12(–17) cm long, 3–6(–9) mm wide, flat, thin, dark green, scaberulous above, narrowing to the base, central vein whitish, prominent. ***Panicles*** 6–13.5(–15) cm long, 1–2 cm wide, yellowish-brown to greenish, densely flowered, interrupted below; ***primary branches*** 1–3.5 cm long, appressed or ascending, flowered to the base; ***pedicels*** 0.2–1.7 mm long, shorter than the spikelets, hispidulous. ***Spikelets*** (2–)2.5–3 mm long; ***glumes*** 1–2(–2.5) mm long, unequal, 1-veined, green and prominent, apex acute to acuminate; ***lower glumes*** 1–1.5 mm long; ***upper glumes*** 1.5–2(–2.5) mm long; ***lemmas*** (2–)2.5–3 mm long, lanceolate, pale, awned, mottled with dark green spots, the 3-veins green and prominent, scabrous along the veins, pilose over the central vein and margins on the lower 1/3–1/2, the awns 5–14 mm long, somewhat flexuous, purplish; ***paleas*** about as long as the lemma, pilose between the veins on lower ½; ***anthers*** 1–1.2 mm long, yellowish. ***Caryopses*** 1.3–1.5 mm long, narrowly-ellipsoid, dark reddish-brown. $2n = 40$.

Distribution. *Muhlenbergia setarioides* ranges from Puebla, Oaxaca (*Peterson & Annable 9897*, 1.4 mi E of Ayutla on Mex 179), Tlaxcala,Veracruz, and Chiapas in México to Central America from Guatemala to Panama (Sanchez-Ken 2018).

Ecology. This species is found in tropical-wet forests, shaded banks, near cornfields, and along barrancas; 1500–2400 m.

Comments. Morphologically, *M. setarioides* resembles *M. spiciformis* but differs from the latter in having wider leaf blades 3–6(–9) mm wide (1–3 mm wide in *M. spiciformis*), shorter spikelets (2–)2.5–3 mm long (versus 3–4 mm long), acute to acuminate (obtuse to acute in *M. spiciformis*) glumes, upper glumes 1.5–2(–2.5) mm long (versus ≤ 1mm long), and lemmas with awns 5–14 mm long [versus (10–)20–40 mm].

Muhlenbergia setarioides is a member of *M*. subg. *Muhlenbergia* and is sister to all remaining species in the subgenus (Fig. 1; Peterson et al. 2021).

Specimens examined. Costa Rica. **Alajuela**: along road below Los Cartagos, 5 km above Carrizal, wet bank of roadside, in shade of herbs, *R.W. Pohl & G. Davidse 11735* (CR, US). **Cartago**: River crossing of Río Reventado between Llano Grande and Tierra Blanca, *R.W. Pohl & M. Lucas 13097* (MO, CR); Cerro de La Carpintera, in potrero, *P.C. Standley 34502* (US). **San José**: along Rio Maria Aguilar, near San José, *P.C. Standley 38976* (US); Vazquez de Coronado, Quebrada Corralillo, 2 km E of Rancho Redondo, moist mossy canyon walls in shade and along roadsides, *R.W. Pohl & G. Davidse 11701* (CR, MO, US); La Palma, wet forest, *P.C. Standley 33006* (US); San Gabriel, orillas de un arroyo, *O. Jiménez 173* (US). El Salvador. **La Libertad**: Volcan San Salvador, near bottom of crater of Volcán San Salvador, *N.C. Fassett 28595* (MO, ITIC, US); Volcan San Salvador, Boquerón de San Salvador, *L.E. González 1852* (MO, ITIC). **San Salvador**: San Salvador, *A.S. Hitchcock 8927* (US). **Sonsonate**: *A. R. Molina et al. 21747* (LAGU). Guatemala. **Escuintla**: San José, *W. A. Kellerman 5115* (MO, US). **Guatemala:** Near San Rafael, *W.A. Kellerman 6239* (US). **Huehuetenango**: Thickets and forest in deep canyon of tributary of Rio Blanco, about 5 km W of Aguacatán, *L.O. Williams*, *A. Molina R. & T.P. Williams 22329* (US). **Quetzaltenango**: Mountains near Santa Maria, just S of Quetzaltenango, *Weatherwax 161 (1679)* (US); Region of Las Nubes, south of San Martin Chile Verde, densely forested barranco, *P.C. Standley 83711* (US); Ravine below Fuentes Georginas, just above Zunil, *J.A. Steyermark 34480* (US); Retalhuleu, *M. De Koninck 226* (US); Mountains above Rio Samala, Sierra Madre Mountains, 2 km west of Zunil, *L. O. Williams*, *A. Molina R. & T.P. Williams 22987* (US). **Sacatepequez**: near Pastores, damp ravine, *P.C. Standley 59936* (US); Volcano Agua, near Antigua, shady bank, *A.S. Hitchcock 9134* (US); Nacimiento del Cangrejal, cuesta de Las Cañas, *A. Molina R. 15439* (US). **San Marcos**: Barrancos 6 mi south and west of town of Tajumulco, northwestern slopes of Volcan Tajumulco, moist thickets in quebrada, *J.A. Steyermark 36594* (US); Barranco Eminencia, above San Rafael Pie de la Cuesta, wet meadow, *P.C. Standley 68464* (US). **Sololа**: Mixed forest area, mountains slopes above Lake Atitlan, about 3–5 km west of Panajachel, *L.O. Williams*, *A. Molina R. & T.P. Williams 25264* (US). Mexico. **Chiapas. Motozintla:** along road from Toilman to Niquivil, near Ojo de Agua, *D.E. Breedlove 42616* (MO). **Siltepec**: On the ridge above Siltepec on the road to Huixtla, *D.E. Breedlove & Almeda 58258* (CAS, MO). **Tenejapa:** along trail from Tenejapa center to San Cristóbal de las Casas, in the paraje of Balum K' anal, *D.E. Breedlove 9350* (ENCB, DS, US); La Punta del Cerro Cruz Ch'en, *A. Shilom Méndez Ton 5088* (MEXU, MO). **Unión Juárez:** En el volcán Tacaná a 500 m al E de Talquián, *E.M. Martínez S. & A Reyes-García 20293* (MO). Panama. **Chiriquí**: Rio Caldera, 1–2 mi above El Boquete, *E.P. Killip 4513* (US).

31. ***Muhlenbergia spiciformis*** **Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg. Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 288. 1841. (Fig. 14, E-I).** Fig. 21A–E

= *Muhlenbergia acutijolia* E. Fourn., Mexic. Pl. 2:86. 1886. Type: México, Veracruz, Orizaba, 8 Nov 1866, *M. Bourgeau 3327* (holotype: P!; isotypes: MO-2974301!, US-87235! fragm! US-2561240!).

= *Muhlenbergia parviglumis* Vasey, Contr. U.S. Natl. Herb. 3(1):71. 1892. Type: U.S.A., Texas, 1887, *G.C. Nealley s.n.* (holotype: US-81638!; isotype: US-994967!).

Type. México, "Southern México," *Karwinsky s.n.* (lectotype: W-0002567! designated by Peterson et al. 2007b in J. Bot. Res. Inst. Texas 1(2): 989; isolectotype: LE fragm!).

Description. Caespitose ***perennials***, often short-lived and appearing as annuals. ***Culms*** 25–80 cm tall, erect, slender and wiry, freely branching at the base, strigose to glabrous below the nodes; ***internodes*** mostly glabrous, usually 4–8 nodes per culm. ***Leaf sheaths*** 3.5–12 cm long, shorter than the internodes, scaberulous; ***ligules*** 1–3 mm long, deeply lacerate, margins hyaline, apex acuminate; ***blades*** 2–12 cm long, 1–3 mm wide, flat to involute, hirsutulous to scabrous above and scaberulous below. ***Panicles*** 4–18(–20) cm long, (0.6–)l–2.8 cm wide, narrow, contracted, sometimes interrupted below, loosely flowered; ***primary branches*** 0.6–5 cm long, ascending and appressed occasionally spreading up to 30° from the rachises; ***pedicels*** 0.1–3.0 mm long. ***Spikelets*** 2.8–4 mm long, erect; ***glumes*** 0.3–1.0 mm long, less than 1/2 as long as the lemma, 1-veined, unequal, apex obtuse to acute, sometimes erose; lower glumes shorter than the upper glumes; ***lemmas*** 2.8–4 mm long, narrowly lanceolate, awned, purplish, scabrous roughened, sparsely appressed-pubescent on the calluses and lower 1/4 of the midveins and margins, the hairs less than 0.3 mm long, apex acuminate, the awn (10–)20–40 mm long, straight to flexuous; ***paleas*** 2.6–3.9 mm long, narrowly lanceolate, sparsely pubescent between the veins on the basal 1/3, apex acuminate, scabrous; ***anthers*** 0.9–1.6 mm long, purplish. ***Caryopses*** 2–2.6 mm long, fusiform, brownish. 2*n* = 40.

Distribution. This species ranges from the southwestern United States south to México (Chiapas, Chihuahua, Coahuila, Hidalgo, Nuevo León, Oaxaca, Puebla, Queretaro, San Luis Potosí, Tamaulipas, Tlaxcala, Veracruz) [Peterson et al. 2007b; Sanchez-Ken 2018)].

Ecology. *Muhlenbergia spiciformis* grows on rocky slopes, cliffs, and calcareous rock.

outcrops, often in thorn-scrub and open woodland communities associated with *Quercus* spp., *Pinus* spp., *P. cembroides*, *Juniperus deppeana*, *Pseudotsuga menziesii*, *Abies*, *Cupressus*, *Agave*, *Ceanothus*, *Acacia*, *Salvia*, *Arbutus*, *Opuntia* and *Fraxinus*; 450–2800 m.

Comments. In addition to being morphologically similar to *M. setarioides* (see earlier comments under *M. setarioides*), *M. spiciformis* can be confused with *M. microsperma* but differs in not having cleistogamous spikelets in the axils of the lower culm branches, panicles narrow, contracted, 0.6–2.8 cm wide (1–6.5 cm wide in *M. microsperma*) primary branches spreading up to 30° from the rachises (primary branches spreading up to 80° from the rachises in *M. microsperma*), and ligules acuminate (truncate to obtuse in *M. microsperma*) [Peterson et al. 2007b].

Muhlenbergia spiciformis is a member of *M*. subg. *Muhlenbergia* and is sister to the *M. romaschenkoi*–*M. tenuifolia* pair in a recent biogeographical study based on DNA sequence analysis (Peterson et al. 2021).

Specimens examined. Mexico. **Chiapas: Comitán de Domínguez:** Laguna Chamula microwave station, 4 km SW of Highway 190 between Comitán and Amatenango del Valle, *D.E. Breedlove & G. Davidse 54857* (CAS, MO). **Jilotol:** 10 km N of Jitotol near Rio Hondo, *D.E. Breedlove & G. Davidse 55151* (CAS, MO).

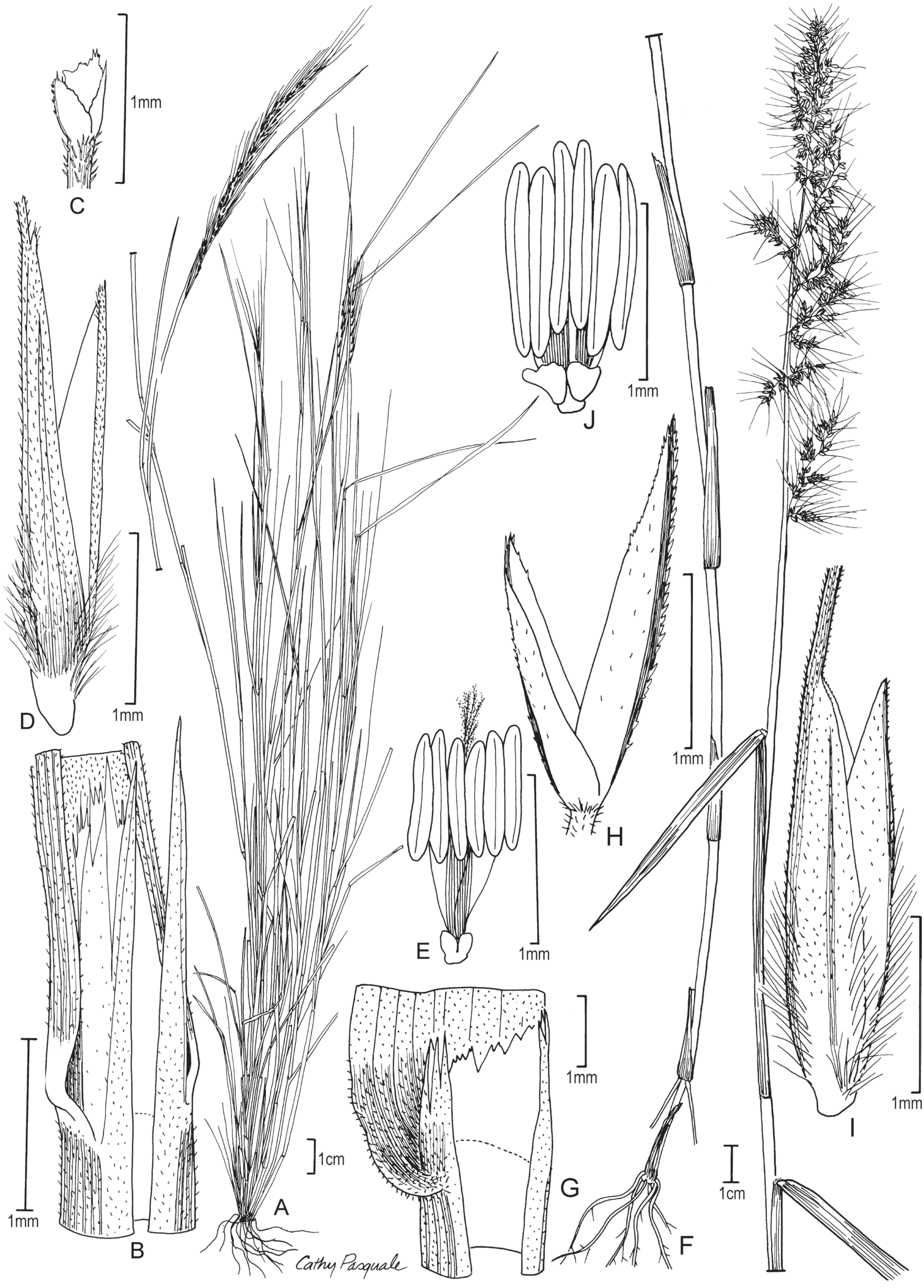

Figure 21. A–E *Muhlenbergia spiciformis* Trin. **A** habit **B** ligule **C** glumes **D** floret **E** stamens, pistil, and lodicules **F–J** *Muhlenbergia setarioides* E. Fourn. **F** habit **G** ligule **H** glumes **I** floret **J** stamens, pistil, and lodicules. **A–E** drawn from *P.M. Peterson & C. R. Annable 8361* (US) **F–J** drawn from *D.E. Breedlove 9350* (US).

La Trinitaria: along Mexican Highway 190, 3 miles south of La Trinitaria, *D.E. Breedlove & P.H. Raven 13235* (DS, US). **San Cristobal de las Casas:** NE edge of San Cristobal de las Casas, *D.E. Breedlove & G. Davidse 54748* (NY, CAS, MO); Northeast edge of San Cristóbal Las Casas, *D.E. Breedlove & G. Davidse 54722* (CAS, MO); W edge of San Cristobal Las Casas, *D.E. Breedlove & G. Davidse 53980* (CAS, MO, US); About 2 miles SE of San Cristóbal, *J.R. Reeder & C.G. Reeder 6066* (MO); Grassy slope of Cerro San Cristóbal, *R.M. Laughlin 1761* (DS).

32. *Muhlenbergia tenella* (Kunth) Trin., Gram. Unifl. Sesquifl. p. 192. 1824.
Fig. 17C–F

Podosemum tenellum Kunth, Nov. Gen. Sp. (quarto ed.) 1: 128. 1816. 1817. Type: México,Veracruz, inter Río Frío et Barranca Honda, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n.* (holotype: P-Bonpl!; isotypes P!, US-91922! fragm. ex P). ≡ *Trichochloa tenella* (Kunth) Roem.& Schult., Syst. Veg. 2: 385. 1817. ≡ *Polypogon tenellus* (Kunth) Spreng., Syst. 1: 243. 1825. ≡ *Polypogon gracilis* (Kunth) Spreng., Syst. 5: 558 (index).1828. Basionym:

= *Muhlenbergia sprengelii* Trin., Gram. Unifl. Sesquilfl. 189. 1824. Type: México, *F.W.H.A. Humboldt & A.J.A. Bonpland s.n*. (holotype: B-W!). ≡ *Arundo tenella* Spreng., Pl. Min. Cogn. Pug. 2: 6. 1815, *nom. Illeg. hom*.

= *Muhlenbergia exilis* E. Fourn., Mexic. Pl. 2: 84. 1886. Type: México, Barranca près Cuernavaca, Iturbide, 14 Nov 1865, *E. Bourgeau 1298* (**lectotype, designated here**: P-00644178 [image!]; isolectotypes: G-00099415 [image!], MPU-026954 [image!], P-00644177 [image!], US-87216!).

Description. Slender, delicate ***annuals***, sometimes in small tufts. ***Culms*** 10–30 cm tall, erect or sprawling, glabrous, branching from the lower and middle nodes; 0.3–0.4 mm diameter just below the inflorescence; ***internodes*** 17–36 mm long. ***Leaf sheaths*** 12–37 mm long, mostly shorter than the internodes, glabrous or sparsely pilose especially near the apex and along the margins; ***ligules*** 0.3–0.9 mm long, a ciliate membrane; apex truncate; margin with a tuft of hairs up to 1 mm long; ***blades*** 2–5 cm long, 0.5–2.0 mm wide, flat, often secund or lying to one side of the culm, sparsely appressed pilose pubescent on both surfaces to almost glabrous. ***Panicles*** 3.0–12.6 cm long, 0.5–2.5 cm wide, slender, usually included in the upper sheath, terminal, with 7–12 nodes; ***primary branches*** 2–4.8 mm long, 1 per node, ascending and appressed to the culm axis, bearing spikelets to their base; ***pedicels*** 1–3 mm long, glabrous, to minutely scaberulous, appressed. ***Spikelets*** 1.7–2.7 mm long, overlapping, erect; ***glumes*** 0.5–1.8 mm long, unequal, mostly glabrous, 1-veined, the single greenish vein antrorsely scabrous; apex acute to acuminate, sometimes minutely pubescent, usually mucronate, the mucro up to 1 mm long; ***lower* glume** 0.5–1.3 mm long; ***upper* glume** 0.7–1.8 mm long, narrower; ***lemmas*** 1.7–2.7 mm long, slender, narrow lanceolate, awned, whitish, strongly 3-veined, veins greenish, the appearance of intermediate "veins" actually rows of short barbs on top of folded epidermal ridges, occasionally ciliate on the lateral veins on upper part but mostly glabrous, the awns 12–26 mm long, flexuous; ***callus*** minutely short pubescent; ***paleas*** 1.8–2.8 mm long, a little longer than the lemma, narrow lanceolate, glabrous to minutely antrorsely scabrous; ***anthers***

0.4–0.5 mm long, yellowish. ***Caryopses*** 1.4–1.6 mm long, narrowly fusiform, light brownish. Cleistogamous spikelets absent. 2*n* = 20.

Distribution. *Muhlenbergia tenella* occurs throughout México ranging to Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama) and extending into Columbia (Peterson and Annable 1991; Peterson et al. 2001).

Ecology. Individuals of *M. tenella* are usually restricted to perennial wet rocky cliffs, rock walls, and sandy or rocky places along water courses in tropical and subtropical forests and moist pine-oak woodlands; 250–2400 m.

Comments. *Muhlenbergia tenella* can be separated from *M. ciliata* in having long-awned [12–26 mm long versus (1–)5–11(–18) mm long in the latter), mostly eciliate lemmas, appressed panicle branches, secund leaf blade insertion, and its affinity for perennially wet rocky cliffs and rock walls associated with small drainages (Peterson and Annable 1991).

Based on DNA sequence analyses *Muhlenbergia tenella* forms a clade with *M. ciliata* and *M. pectinata* in *M.* subg. *Muhlenbergia* (Fig. 1; Peterson et al. 2010b, 2021).

Specimens examined. Belize. **Cayo**: Raspaculo River to Macal River near the junction of both rivers, mixed tropical hardwood forest dominated by secondary species along the side of the river, *T. Hawkins 1292* (MO). Costa Rica. **Alajuela**: Carrillos de Poás, cerca del Río Poás, *A.M. Brenes 17414* (CR); Carrillos de Poás, Old road to Poás, *A.M. Brenes 17390* (CR); San Pedro de San Ramón (orillas del Río Barranca), *A.M. Brenes 21894* (CR); Naranjo, San Juan, *R. Ocampo 764* (CR); Atenas, alrededores de las Oficinas Administrativas, Escuela Centroamericana de Ganadería, *J. Gómez 6102* (CR); La Garita, dam on the Rio Grande de Tarcoles, W of Alajuela, *R.W. Pohl & G. Davidse 11353* (US, CR); Aguacate, *A.S. Oersted 14145* (US), *A.S. Oersted 14147* (US), *A.S. Oersted 14050* (US); Grecia, *E. Anderson 1324* (US). **Cartago**: Turrialba, Terrenos del Instituto Interamericano de Ciencias Agrícolas, J. León 412 (MO); Growing on rocks along the Río Pacuare, between San Rafael and Moravia, *R.W. Pohl & G. Davidse 11476* (CR); Turrialba, Terrenos del IICA, *J. León 1485* (CR), *412* (MO); Navarro, 1 km N of Puente Negro, *R.W. Pohl & G. Davidse 11184* (US, CR); Tres Rios, *H. Pittier 3029* (US, CR). **Guanacaste**: Cañas, Finca La Pacífica, *R. Daubenmire 345* (USJ); Carrillo, *J. A. Echeverría 289* (CR); Nicoya, *R. Ocampo 757* (CR); Santa Rosa National Park, 30 km NW of Liberia, *D. H. Janzen 12267* (MO); Parque Nacional Guanacaste Sector Agua Buena, margen occidental del Río Animas, *A. Chacón et al. 667* (MO, INB, CR); Santa Rosa National Park. Nature trail, forest, *R. Liesner 4313* (MO, CR); La Cruz, Quebrada Costa Rica, Santa Rosa National Park, *E.J. Judziewicz 4286* (MO, CR); Bagaces, 7 km by road N of Bagaces. Quercus-Curtella savanna on volcanic tuff, *R.W. Pohl & M. Lucas 13077* (MO, CR); Deciduous broad-leaf forest with tress to 20 m tall. Between Liberia and Bagaces near the Rio Potrero along the Interamerican hwy, *W. Burger & W. Ramirez 4120* (US, CR). **Heredia**: 5 km al Oeste de San Joaquín de Flores, en un paredón, *M. Montiel s.n.* (CR); vicinity of horseback-riding facility at Tajo de Cariari, ca. 1 km SE of Ciudad Cariari, along Río Virilla, *M. Grayum 4294* (MO, CR); San Vicente, Bosques residuales en las vegas del Río Bermudez, *J.A. González 2485* (CR). **Limón**: Salamanca, Telire, *R. Ocampo 3893* (CR). **Puntarenas**: Montes de Oro, low cliffs along the Río Ciruelas at the Interamerican Hwy, 8 km N of the Puntarenas intersection, *R.W. Pohl & G. Davidse 11288* (CR); Cordillera de Tilarán, Monteverde, cliff edge and descending ridge below Hotel de Montaña, *W. Haber & W. Zuchowski 10893* (CR, MO, INB); Monteverde, 6 km SW Santa Elena on road to Inter American highway. Dry ridge above Río Lagarto, *W. Haber & W. Zuchowski 10155* (INB, MO, CR); Montes de Oro, Quebrada Seca, Cerro Zapotal, Miramar, *L. D. Gómez et al. 23988* (MO); Barranca, 1.5 km S of the Puntarenas intersections on the Carretera Interamericana, *R. W. Pohl & G. Davidse 11346* (CR). **San Jose**: Cul-de-sac at N. end of Calle 9, *Khan et al. 142* (MO, CR); On walls, Museo Nacional, *R.W. Pohl 14168* (MO); Sur un rocher au bord du rio Virilla, sous le pont du F. T. R., près San Juan, *A. Tonduz 17557* (CR); Techados y paredones de San José, *O. Jiménez 50* (CR) ; San Pedro, near Pulpería La Luz, along Avenida Central, *R.W. Pohl & G. Davidse 11248* (US, CR); Acosta, *R. Ocampo 1137* (CR); Sur les mur a San José, *H. Pittier 544* (CR); Sur un rocher au bord d'un ruisseau a La Verbena, pres Alajuelita, *A. Tonduz 9086* (US, CR); Toits des maisons a San Jose, *H. Pittier (Tonduz, A.) 3015* (US, CR); vicinity of La Verbena, *P. C. Standley 32288* (US); Between San Pedro de Montes de Oca and Curridabat, *P. C. Standley 32816* (US); San José, *P.C. Standley 41243* (US); Toiss des maisons a San Jose, *A. Tonduz 775* (US); Hills SW of San Jose, *E.W.D. Holway 304* (US), *408* (US); San José, *A.S. Hitchcock 8460* (US), *8501* (US), *8509* (US); San José, *H. Pittier 33* (US, CR); Acosta, San Ignacio, *R.A. Ocampo 792* (CR); Acosta. Bajo Jupa, camino a Bajo Palma, *J.F. Morales 7438* (CR. INB); Cuenca del Pirrís-Damas. Valle del Río Candelaria, Quebrada Guápiles, antes del Soslayo, *J.F. Morales 11629* (INB, MO). El Salvador. **Ahuachapán**: San Benito, al E de la vuelta del río Aguachapio, *E. Sandoval & Chinchilla 793* (MO); El Impossible, by Las Positas river, evergreen tropical moist forest, canopy height ca 30 m., *A. Monro et al. 1912* (MO); El Impossible, bosque el Pacayito, quebrada La Cascada, *W.G. Berendsohn et al. 1332* (LAGU, MO); San Fco. Menéndez, Hda. San Benito, Río Guayapa, *E. Sandoval & Chinchilla 102* (MO); Ahuachapán, *S.A. Padilla 133* (US). **Chalatenango**: La Palma, Recreo Obrero El Refugio, *P. Bernhardt & E.A. Montalvo 41* (MO, ITIC). **La Libertad**: Finca La Giralda, 5 km before Gomasagua, cafetal de sombra orgánica, hasta 12–20 m de alto, dominado por Inga, *A. Monro et al. 3080* (MO). **Morazán**: Arambala, A. P. Sapo, cantón Cumaro, camino a piedra x, *R. A. Carballo & J. Monterrosa 935* (MO); *L. Lara 240* (MHES); *J.F. Morales 14135* (LAGU, MHES); Jocoaitique, río Araute, sector Las Raices, *D. Rodríguez et al. DR-00537* (B, BM, LAGU, MO). **San Miguel**: Finca El Pacayal, Volcán Chinameca, coffee farm, shade (60%) with low diversity of shade trees, canopy to ca. 12–14 m, *A. Monro et al. 2940* (MO). **San Salvador**: vicinity of San Salvador, *P.C. Standley 22410* (MO), *21783* (MO); *19256* (MO); San Salvador, *S. Calderón 497* (MO); San Salvador, *N.L.H. Krauss 1002* (US). **San Vicente:** vicinity of San Vicente, *P.C. Standley 21208* (US). **Sonsonate**: vicinity of Sonsonate, *P.C. Standley 21783* (MO); Coastal plain, rocks along river, *A.S. Hitchcock 8974* (US). **Usulután**: Laguna de Alegría, cerca de la entrada, *D. Williams & R.W. Herrera 361* (MO), *341* (MO), *D. Williams s.n.* (MO); *J. Menjívar et al. 639* (MHES); Laguna de Alegría, *D. Williams s.n.* (MO). Guatemala. **Chiquimula**: Quebrada Shusho, above Chiquimula, *P. C. Standley 74318* (US). **Escuintla**: along Rio Guacalate, *P.C. Standley 58243* (US). **Guatemala**: San Raimundo, along National Hwy. 5, between Salamá and Guatemala City (via El Chol), 2 km past turnoff to San Raimundo (leaving paved road), dry oak forest, *T.B. Croat & D.P. Hannon 63517* (MO); Damp wooded barranca 10 km south of San Raimundo, damp shaded bank, *P.C. Standley 62868* (US); Fiscal, near Guatemala, *W.A. Kellerman 6244* (MO). Santa Rosa: Santa Rosa, *Heyde & Lux 3913* (MO). **Jutiapa**: Hills between Jutiapa and Plan de Urrutia, north of Jutiapa, *P. C. Standley*

75531 (US). Santa Rosa: Santa Rosa, *J. Donnell Smith 3913* (US, MO). **Suchitepéquez**: Mazatenango, *Bernoulli 35* (US). Honduras. **Comayagua**: Ojo de Agua, orilla Río Humuya, 30 km N de ciudad Comayagua, bosque de vega tropical rodeado de pinares, *C. Nelson et al. 6830* (MO), *7000* (MO); Chichipates, orilla del Río Yure, bosque tropical de vega; 30 km E Lago Yojoa, pinares y robledales, *C. Nelson et al. 6716* (MO); Rio Yure, unión del río Yure con el Río Humuya, 100 km NO de Ciudad de Comayagua, bosque tropical de vega húmedo, pinares y robledales, *C. Nelson et al. 6113* (MO); Agua Caliente, vaguada de Ríos Chamo y Humuya, 35 km E Lago Yojoa, pinares y robledales, bosque de vega tropical, *C. Nelson et al. 6391* (MO); In stream course of Quebrada Cana, 3 km S and W of Las Flores, *C.L. Johannessen 59* (US). **Copán**: Santa Rosa, bosque de pinos, *M.E. Villena 22* (MO); Santa Rosa, damp shady places, also rock walls, *W.A. Archer 3855* (US); Santa Rosa de Copán, *M.E. Villeda 22* (MO). **Cortés**: Orilla del Río Humuya, 40 km N Santa Cruz de Yojoa, bosque de vega tropical, *C. Nelson et al. 5840* (MO). **El Paraíso**: 9 km S of Yuscaran, *R.W. Pohl & M. Gabel 13441* (MO, CR). **Francisco Morazán**: San Antonio de Oriente, Campus of Escuela Agricola at El Zamorano, *R.W. Pohl 12482* (MO, CR); San Antonio de Oriente, Las Mesas, ca. 5 km E of El Zamorano, near Riachuelo Las Mesas, *R.W. Pohl 12520* (MO, CR); Distrito Central, Parque del Cerro El Picacho, pinares, bosque premontano húmedo, *V.L. Ochoa 83* (MO); Distrito Central, Cerro el Hatillo, 15 km al NE de Tegucigalpa; bosque premontano húmedo, *L.M. Ordóñez 58* (MO): Road toward San Antonio de Oriente, region El Jicarito, above El Zamorano, *P.C. Standley 27477* (MO); San Antonio de Oriente, Zamorano, bosque seco subtropical, *D. Aguilar S. 38* (MO); San Antonio de Oriente, near Las Mesas *L.O. Williams & A. Molina R. 10830* (MO); vicinity of El Zamorano, rocky river banks, Galeras, *J. R. Swallen 10775* (US); bosque mixto entre Cuesta de los Muertos y Monte Obscuro, La Montañita, *L. O. Williams & A. Molina R. 11161* (US); Drainage of the Rio Yaguare, Rivera del Rio Yaguare cerca de Finca San Francisco, Zamoran, *A. Molina 1581* (US); San Antonio del Oriente, moist shady bank, *J.R. Swallen 10917* (US); vicinity of Suyapa. Moist bank along road near Suyapa, *J.R. Swallen 11294* (US); Foothills of Mt. Uyuca, beyond Las Floras, moist open banks, *J.R. Swallen 11297* (US); Carretera a Valle Angeles, 15 km NO de Tega, *L. Trochez 219* (US). **La Paz**: Montaña de Opatoro, 36 km SE de Marcala, bosque húmedo subtropical, *R. Martínez 284* (MO); **Olancho**: Juticalpa, Rio Guayapa, between Jutiapa and Concordia, *R.W. Pohl & M. Gabel 13762* (MO, CR). **Santa Barbara**: Alrededores de Santa Barbara, area de Pino-roble de Rio Ulua, *A. Molina 3789* (US). **Yoro**: Victoria, orilla del Río Sulaco, bosque de vega tropical, *C. Nelson et al. 7217* (MO). Mexico. **Chiapas.** Ocozocuautla, Cañada "El Aguacero". Selva baja. En las laderas del cañón "La Venta", *J.J. Ortíz Díaz 1010* (MO). **Acala:** Wooded slope along the Río Grijalva, 10 kilometers south of Mexican Highway 190 along the road to Acala at Nandaburri, *R.M. Laughlin 2813* (DS). **Angel Albino Corzo:** slopes of Río Cuxtepec below Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54700* (CAS, MO); slopes of Río Cuxtepec below Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54675* (CAS, MO). Arriaga: 13 km N of Arriaga along Mex. Hwy. 195, *D. E. Breedlove 28273* (NY). **Chiapa de Corzo:** El Chorreadero 5.6 miles east of Chiapa de Corzo along Mexican Highway 190, *R.M. Laughlin 2608* (DS). Frontera Comalapa: S of Frontera Comalapa on Mex hwy 211 and 18 mi SW of Jtn 190 and 211, small rocky water course which feeds Rio Grijalva, *P.M. Peterson & C.R. Annable 4704* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 13 km N of Arriaga along Mex. Hwy. 195, *D.E.*

Breedlove & G. Davidse 54150 (CAS, MO). Ixtapa: 1 km W of Ixtapa, *F.W. Gould 12715* (US, MO); along Mex 190 in the Zinacantán paraje of Muctajoc, *D.E. Breedlove 13820* (US, DS); near Ixtapa, *D.E. Breedlove & G. Davidse 54265* (CAS, MO); at Escopetazo, *D.E. Breedlove & G. Davidse 54944* (CAS, MO); at Esc opetazo, *D.E. Breedlove & G. Davidse 53944* (CAS, MO). **Ocosingo:** near El Real, E of Ocosingo, *D.E. Breedlove & G. Davidse 56381* (CAS, MO). **Ocozocoautla de Espinoza:** El Aguacero, canyon of the Río La Venta, *G. Davidse et al. 30071* (MO); El Aguacero en el río La Venta, *E. Martínez 22006* (MEXU). **Tonalá:** Cerro Vernal [Cerro Bernal], 21 km S of Tonalá, *G. Davidse et al. 38123* (MO). **Tuxtla Gutiérrez:** El Zapotal, *Ruiz 017* (MEXU); 16 mi W of Pan American Hwy, *Carlson 2066* (MICH). **Villa Corzo:** 65 km S of Mexican Highway 190 on road from Tuxtla Gutiérrez to Nueva Concordia, *D.E. Breedlove & G. Davidse 54464* (CAS, MO); Above Colonia Vincente Guerrero on road to Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54595* (CAS, MO); near Colonia Vicente Guerrero, *D.E. Breedlove 48607* (CAS, MO); 58 km S of Mexican Highway 190 on road to Nueva Concordia, *D.E. Breedlove 37645* (MO). Nicaragua. **Chontales**: Hacienda Veracruz, including Cerro La Batea, pasture on rocky slopes and deciduous forest on basaltic mesas, *W. D. Stevens 23359* (MO), *23309* (MO); Hacienda San Martín, near confluence of Río El Jordán and Río La Pradera; remnant tall evergreen forest, *W.D. Stevens 22862* (MO, CR); Río El Bizcocho, along road from Juigalpa NE toward La Libertad, ca. 17.4 km NE of Río Mayales, at ford of Río El Bizcocho; pastures, gallery forest and steep cliffs S of river, *W.D. Stevens 4033* (MO). **Granada**: shore of Lago de Nicaragua, very dry soil except at water's edge [Seymour series], *J.T. Atwood 1078* (MO). **Jinotega**: Salto Kayaska, Río Bocay, among rocks along river to top of hills SW of falls, tall evergreen forest on hill, limestone, *W.D. Stevens et al. 16602* (MO). **Managua:** Tipitapa, 22 km N of Managua [Seymour series], *H. Zelaya M. 40A* (MO). **Matagalpa**: Finca La Salvadora, Vuelta del Coyolito, bordeando el Río Yasica; zona boscosa, *D. Castro C. 2217* (MO). **Nueva Segovia**: Ocotal, 3 km W of city; mostly in deep ravine along dry river bed [Seymour series], *J. T. Atwood 758* (MO), *C.E. Nichols 819* (MO). **Rivas**: Southwest of La Virgen and northeast of San Juan del Sur, route 16 where road crossed brook, km 136 [Seymour series], *J.T. Atwood 1174* (MO). Panama. **Chiriqui**: vicinity of Boquete, from Boquete to 3 mi N., second growth, cultivared areas, and roadside, *W.H. Lewis et al. 332* (MO); On rocks along Río Cuvibora ca. 5 miles N of Tolé on road past Alto Caballero, *B. Hammel 6256* (MO); Río Caldera, NW of Boquete, just S of Horqueta, near a small waterfall, volcanic cliff, *P.M. Peterson & C.R. Annable 7375* (MO, US); Cerro Vaca, eastern Chiriqui, in savannas, *H. Pittier 5308* (US); Foothills, vicinity of El Boquete, on bare rock, hilltop, *A.S. Hitchcock 8316* (US). **Cocle**: Valley of the upper Río Mata Ahogado, *P.H. Allen 137* (MO), *141* (MO); Hills south of El Valle de Antón, *P.H. Allen 2806* (MO).

33. *Muhlenbergia tenuissima* (J. Presl) Kunth, Enum. Pl. 1:198 (1833).
Fig. 19E–H

Podosemum tenuissimum Presl, Rel. Haenk. 1: 230. 1830. Type: Panama or México. *Haenke s.n.* (**lectotype, designated here**: PRC-450957 [image!]; isolectotypes: MO-2974335!, US-91923!, W-0002565!, W-0002566!, W-239298!). Basionym:

= *Muhlenbergia nebulosa* Scribn. ex Beal, Grasses N. Amer. 2: 247. 1896. Type: México, Jalisco, wet places, hills near Guadalajra, 5 Nov 1889, *C.G. Pringle 2366* (holotype: MSC-11271!; isotypes: BR-0000006883102 [image!], BR-0000006883430 [image!], E-00373720 [image!], F-73212 [image!], GH!, GOET-006642 [image!], IBUG-0179259 [image!], K!, KFTA-0000118 [image!], LL-00370119 [image!], MEXU-00005184 [image!], MEXU-00005183 [image!], UC-122478 [image!], NY!, RSA!, S-G-4200 [image!], SI-002778 [image!], US!, VT!, W-1916-29044!, W-1890-597!).

Description. Delicate, slender, ***annuals***. ***Culms*** 5–30(–38) cm tall, much branched near base and above often sprawling, glabrous or scaberulous below the nodes; 0.1–0.2 mm diameter just below the inflorescence; ***internodes*** 7–30 mm long. ***Leaf sheaths*** 4–20 mm long, glabrous or scaberulous, shorter than the internodes; margins membranous; ***ligules*** 0.6–1.5 mm long, membranous, thin, apex rounded to acute, sometimes lacerate; ***blades*** 1–5 cm long, 0.6–1.4 mm wide, flat or loosely involute, short pubescent above and glabrous to scaberulous below, margins and abaxial midvein often whitish-thickened. ***Panicles*** 6–16 cm long, 1.0–2.5(–6.0) cm wide, open, few-flowered with 9–16 nodes; ***panicle branches*** 0.5–4.0 cm long with ascending and spreading branches up to 70° from the culm axis; ***pedicels*** 1–4 mm long, scabrous, erect, ascending. ***Spikelets*** 1.3–1.9 mm long; ***glumes*** 0.4–0.8 mm long, subequal, subacute, mostly glabrous, 1-veined, minutely scabrous along veins and near apex; ***lower glumes*** 0.4–0.7 mm long, apex sometimes apiculate; ***upper glumes*** 0.6–0.8 mm long, apex sometimes mucronate, the mucro up to 0.2 mm long; ***lemmas*** 1.3–1.8 mm long, lanceolate, very thin, awned, pilose along the margins and midvein, the hairs up to 0.3 mm long, the awn 3–9 mm long, scabrous, mostly straight; callus short pilose; ***paleas*** 1.3–1.9 mm long, as long or slightly longer than the lemma, narrow lanceolate, loosely pilose between the two veins on the proximal 2/3; ***anthers*** 0.5–0.6 mm long, purplish or pale. Caryopses 0.8–1.1 mm long, fusiform, light reddish-brown.

Distribution. *Muhlenbergia tenuissima* ranges from México in Chiapas, Colima, Jalisco, Nayarit, and has been reported in Sonora and Sinaloa (Dávila et al. 2018; Sanchez-Ken 2018). It also extends into Costa Rica, Honduras, Nicaragua, and Panama.

Ecology. This species occurs in tropical forests, savannah grasslands with *Quercus* and *Acacia* often in calcareous derived soils in wet soils, moist depressions, and ephemeral moist flats; 50–1900 m.

Comments. This distinctive species is under collected and confused with other ephemeral annuals. Distinguishing features include lemmas 1.3–1.8 mm long, pilose margins and midvein, apical awns 3–9 mm long, and short anthers 0.5–0.6 mm long (Peterson and Annable 1991).

Muhlenbergia tenuissima is a member of *M*. subg. *Pseudosporobolus* where it is found to be sister to *M. wrightii* Vasey ex J.M. Coult., although the branches that unite these species are long suggesting a moderate amount of genetic divergence (Peterson et al. 2021).

Specimens examined. Costa Rica. **Guanacaste**: 5 km S of Liberia along the Carretera Interamericana, *R.W. Pohl & G. Davidse 11554* (US); 2 km E of carretera Interamericana on road to Las Animas, *R.W. Pohl & G. Davidse 11530* (CR, UD). Honduras. **Comayagua**: vicinity of Siguatepeque, *P.C. Standley 55871*

(US). Morazán: Las Mesas, *J.V. Rodriguez 3683* (US). **Olancho**: tree infested savanna called Sav. Amate, ca. 14 km NE of Catacamas, *C.L. Johannessen 964* (US). **Yoro**: Savanna of Puentecita ca. 8 km N of Yoro, *C. L. Johannessen 707* (US). Mexico. **Chiapas**: **Ixtapa:** near Ixtapa, *D.E. Breedlove & G. Davidse 54331* (CAS, MO). Nicaragua. **Chontales**: Quebrada Niscala, ca. 2.3 km SE of bridge over Quebrada Niscala along road between Acoyapa and Río Oyate; savanna, *D.W. Stevens 19067* (MO). Panama. **Panamá**: Panama City, along road between Panamá and Chepo, *C.W. Dodge et al. 16687* (MO); Juan Diaz, *M.A. Cornman 625* (US); *E.P. Killip 4214* (ARIZ); Agricultural Experiment Station at Matías Hernandez, *H. Pittier 6918* (US); Meadows, Sabana of Panama, Canal Zone, *H. Pittuer 2544* (US); Rio Tecumen, *P.C. Standley 29418* (US); along road between Panama and Chepu, *C.W. Dodge 16687* (US).

34. *Muhlenbergia uniseta* (Lag.) Columbus, Aliso 28: 66. 2010.

Fig. 20F, G

Hymenothecium unisetum Lag., Gen. Sp. Pl. 4. 1816. Type: México, cultivated from seed at MA, *D. Sessé & Mociño s.n.* (holotype: MA). ≡ *Aegopogon geminiflorus* var. *unisetus* (Lag.) E. Fourn., Mexic. Pl. 2: 71. 1886. Basionym:

= *Lamarckia tenella DC.*, Cat. Pl. Horti Monsp. 120. 1813. Type: cult. hort. Monsp., *De Candolle s.n.* (**lectotype, designated here**: US-75926! ex MPU; isolectotype: US-75925! ex MPU). ≡ *Hymenothecium tenellum* (DC.) Lag., Gen. Sp. Pl. 4. 1816. ≡ *Aegopogon tenellus* (DC.) Trin., Gram. Unifl. Sesquifl. 164. 1824.

= *Schellingia tenera* Steud., Flora 33: 232. 1850. Type: México, Oaxaca, Cordillera, 1840, *H. Galeotti 5750* (**lectotype, designated here**: P-00745714 [image!]; isolectotypes: P-00745713 [image!], P-00745715 [image!], W-18890117307 [image!], W-0001035 [image!]).

Description. Slender often sprawling, caespitose ***annuals***. ***Culms*** (2–)6–30 cm tall, glabrous below the nodes; ***internodes*** 0.6–6 cm long, glabrous to pilose. ***Leaf sheaths*** mostly 0.5–4.8 cm long, shorter than the internodes, glabrous to sparsely pilose; ***ligules*** 0.6–1.5 mm long, apex mostly truncate, lacerate; ***blades*** 1.5–6 cm long, 0.5–1.5(–1.7) mm wide, flat, scaberulent and pubescent above, smooth beneath. ***Panicles*** 2–6 cm long, 0.5–1.2 cm wide, open, loosely-flowered with racemose branches; ***primary branches*** 3–5 mm long, excluding the awns, one per node; one short-pedicelled spikelet (perfect) with ***pedicels*** 0.2–0.6 mm long and the other two spikelets (staminate or sterile) short-pedicelled, the ***pedicels*** about 0.7–1.5 mm long. ***Spikelets*** 1.5–3.2 mm long, often greenish or purplish; ***glumes*** (1–)1.3–2 mm long, oblong and wider distally, apex deeply notched, entire or mucronate, the mucro 0.2–1 mm long, lobes obtuse or rounded; ***lemmas*** 2.5–3.2 mm long, 3-awned, the central awns 3–8(–11) mm long, lateral awns usually mucronate or awned up to 2 mm long or missing; ***paleas*** 2.2–3 mm long, puberulent, apex 2-mucronate, the mucros less than 0.8 mm long; ***anthers*** 0.5–0.8 mm long, yellowish. ***Caryopses*** 1.1–1.3 mm long, obovoid, light brownish. 2n = 20, 60.

Distribution. *Muhlenbergia uniseta* ranges from southern Arizona throughout most of México and Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, México, and Panama) [Pohl 1994a; Peterson et al. 2001].

Ecology. *Muhlenbergia uniseta* grows on moist slopes, cliffs, barrancas, canyons, roadsides, and along or near springs usually in shaded areas associated with *Pinus* and *Quercus*; 1300–2860 m.

Comments. *Muhlenbergia uniseta* can be separated morphologically from *M. cenchroides* in having glumes with obtuse or rounded lobes (acute in *M. cenchroides*) that are entire or mucronate (awned 2–4 mm long in *M. cenchroides*) and by being annual (versus perennial).

Muhlenbergia uniseta is a member of *M.* subg. *Muhlenbergia* and forms a clade with *M. cenchroides* and *M. bryophilus* (Fig. 1; Peterson et al. 2021).

Specimens examined. Costa Rica. **Heredia:** San Isidro, Concepción, Calle Leones, *E. Alfaro 4724* (INB). **San José**: Dota, R.F. Los Santos. Cuenca del Pirris-Damas, Río Blanco, cabeceras Quebrada Vueltas, *J.F. Morales 7088* (MO); vicinity of Santa María de Dota, *P.C. Standley 41720* (US); Aserrí, Cuenca del Pirris-Damas, Cerros Caraigres, Falda S, Quebrada Concha, en el camino viejo a Bijagual, *J.F. Morales 5914* (MO, INB); Aserri, Z.P. Cerros Escazú, Cuenca del Tárcoles, bosques primarios y secundarios en la cima del Cerro Daser (Alto Hierbabuena), *J.F. Morales 6707* (MO,INB); Acosta, Alto Reflis, Falda NE, Fila de Cal, *J.F. Morales 7486* (CR, INB); Desamparados, Tablazo, *J.A. Echeverría 1210* (CR); Entre San Isidro y División, *s.c 3855* (CR); Cord. Talamanca, 14 km S of Division along the Interamericana Hwy., roadside through oak forest, *R.W. Pohl & G. Davidse 11615* (US). El Salvador. **La libertad**: *E. Montalvo et al. 6425* (LAGU). **Santa Ana**: *O. Rohweder 2394* (MO). **Usulután**: *J. Menjívar et al. 3591* (LAGU, MHES, MO); *G. Cerén et al. 3276* (MHES, MO). Guatemala. **Guatemala**: Volcán de Pacaya, above Las Calderas, *P. C. Standley 58340* (US); Volcán de Acatenango, *J. & M. Véliz 93.3425* (MEXU). **Sacatepéquez**: Ciudad Vieja, *H. Bethancourt & M. Véliz 94.4181* (MEXU, MO). **Sololá**: near Sololá, *A. Gentry 6504* (MO); slopes of Volcán de Agua, south of Santa Maria de Jesús, *P.C. Standley 59361* (US). Honduras. **Francisco Morazán**: El Zamorano, North side of Cerro Uyuca, near the farmhouse, *R. W. Pohl & M. Gabel 13413* (CR); On open slopes near Hoya Grande, *L.O. Williams & A. Molina 10994* (US); Open slopes in cloud forest area in mountains above San Juancito, *L.O. Williams & A. Molina 13366* (US); Santa Lucía, camino entre la montañita y Santa Lucía, *J.L. Linares & J. Alana 1901* (MEXU); Escuela Agrícola Panamericana, Faldas de La Montañita, *A. Molina R. 1612A* (US). Mexico. **Chiapas**: **Huixtlán:** 10 km E of Huistan, *D.E. Breedlove & G. Davidse 55169* (MEXU); *D.E. Breedlove & G. Davidse 53853* (MO). **Larráinzar**: NE of Bochil, *D.E. Breedlove 29276* (MEXU). **San Cristóbal de las Casas**: 16 km al NW de San Cristobal de las Casas, sobre el camino a Tenejapa, *E. Cabrera & H. de Cabrera 5733* (MEXU). **Zinacantan**: hwy 190 between paraajes of Nachic and Navenshauk, *D.E. Breedlove 7304* (US). Panama. **Chiriquí**: Large old lava flow ca. 3 km NE of El Hato del Volcán at base of Volcán de Chiriquí (Barú), 1–3 km E of highway, *G. Davidse & W.G. D'Arcy 10386* (MO).

35. *Muhlenbergia utilis* (Torr.) Hitchc., J. Wash. Acad. Sci. 23(10): 453. 1933.
Fig. 18 F–K

Vilfa utilis Torr., Pacif. Railr. Rep. 5(2):365–366. 1857. Type: U.S.A., California, Lost Mountain Spring, from Tejon to the Lost Hills, in stony places, *W.P. Blake s.n.* (holotype: NY-00431757 [image!]; isotypes: GH-00023997 [image!], MO-992072!). ≡ *Sporobolus utilis* (Torr.) Scribn., Bull. Div. Agrostol., U.S.D.A. 17:171, f. 467. 1899. Basionym.

Description. ***Perennials***; with slender, scaly rhizomes. ***Culms*** 7–30 cm tall, erect to decumbent, older plants trailing, up to 1 m long, minutely pubescent to glabrous below the nodes; ***internodes*** mostly smooth to lightly nodulose roughened. ***Leaf sheaths*** 0.3–2.4 cm long, shorter or longer than the internodes, glabrous, margins hyaline; ***ligules*** 0.2–0.8 mm long, membranous, decurrent, apex truncate; ***blades*** 0.5–4.7 cm long, 0.2–1.8 mm wide, involute, sometimes flat, straight or arcuate-spreading, the blades often at right angles to culms, mostly glabrous abaxially and hirsutulous adaxially. ***Panicles*** 1–5 cm long, 0.1–0.4 cm wide, narrow, contracted, interrupted between each branch, partially included in the upper sheaths; ***primary branches*** 0.2–1.2 cm long, appressed, rarely ascending to spreading 30° from the rachises; rachises usually visible between the branches; ***pedicels*** 0.1–1.1 mm long, glabrous. ***Spikelets*** 1.4–2.4 mm long, erect; ***glumes*** 0.5–1.4 mm long, ⅓ to as long as the lemma, subequal, unawned, glabrous, 1-veined, occasionally 2-to 3-veined, yellowish to light green, apex acute; ***lemmas*** 1.3–2.4 mm long, lanceolate, unawned, glabrous or with minute appressed pubescence along the margins and the base, the hairs about 0.1 mm long, green or purplish, apex acute; ***paleas*** 1–2 mm long, lanceolate, glabrous, apex acute; ***anthers*** 0.7–1.4 mm long, yellow to purplish. ***Caryopses*** 0.7–1.2 mm long, ellipsoid to ovoid, brown. 2*n* = 20.

Distribution. *Muhlenbergia utilis* ranges from the southern United States to México in Chiapas, Chihuahua, Durango, Guanajuato, Hidalgo, Jalisco, México, Ciudad de México, Michoacán, Puebla, Querétaro, Sonora, Veracruz, and Zacatecas, and Central America (Guatemala and México) [Herrera Arrieta and Peterson 2018].

Ecology. This species occurs in wet soils along streams, ponds, depressions in grasslands, and alkaline or gypsiferous plains associated with *Quercus spp*.; 200–2500 m.

Comments. Morphologically, *Muhlenbergia utilis* can be confused with *M. vaginata* but the former differs in having slender, scaly rhizomes, (*M. vaginata* without rhizomes but culms decumbent and rooting below can sometimes be mistaken for rhizomes) and unawned lemmas (mucronate in *M. vaginata*).

Muhlenbergia utilis is a member of *M.* subg. *Pseudosporobolus* and forms a clade with *M. repens* and *M. villiflora* Hitchc. (Fig. 1; Peterson et al. 2021).

Specimens examined. Mexico. **Chiapas**: **San Cristóbal de las Casas:** Marsh at S end of San Cristóbal de las Casas, *D.E. Breedlove 54373* (ENCB, SLPM, CAS, MO).

36. *Muhlenbergia vaginata* Swallen, Contr. U.S. Natl. Herb. 29(9): 406. 1950.

Type. Guatemala, San Marcos, road between San Sebastián and San Marcos, 2700–3800 m, 15 Feb 1940, *J.A. Steyermark 35598* (holotype: F-1046643!; isotypes: US-2240531!, US-2236472!).

Description. ***Annuals*** or short-lived ***perennials***. ***Culms*** 16–40 cm tall, lax, slender, glabrous, decumbent, rooting at the lower nodes. ***Leaf sheaths*** 0.7–1.6 cm long, shorter than the internodes, glabrous; ***ligules*** 1.3–3 mm long, hyaline, apex acute to obtuse, decurrent; ***blades*** 0.5–3.5 (–4) cm long, 0.6–1.8 (–2) mm wide, mostly cauline, flatted or folded, with navicular apex, glabrous to scabrous. ***Panicles*** 0.5–3 cm long, 3–7 mm wide, frequently partially included in the upper sheath; ***primary branches*** 3–10 mm long, ascending or appressed; ***pedicels*** 0.5–3 mm long, appressed, scabrous. ***Spikelets*** 1.6–2.5 mm long; glumes 0.6–1 mm long, subequal, glabrous, 1-veined, oblong to ovate, light green to green-grayish, apex obtuse, rounded to subacute, occasionally erose; ***lower glumes*** 0.6–0.8 mm long; ***upper glumes*** 0.6–1 mm long; ***lemmas*** 1.6–2.5 mm long, lanceolate, sparsely pubescent below and along the midvein and margins, mottled with olive-green spots, often purplish, apex scabrous, acuminate, sometimes mucronate, the mucro 0.2 mm long; ***paleas*** 1.5–2.5 mm long, lanceolate, glabrous or with a few hairs between the veins; ***anthers*** 0.5–0.8 mm long, purplish. ***Caryopses*** 1–1.2 mm long, ellipsoid to fusiform, brown. n = 9.

Distribution. *Muhlenbergia vaginata* ranges from México to Guatemala in Central America (In México it is found in Chiapas, Chihuahua, Ciudad de México, Durango, Hidalgo, Jalisco, México, Michoacán, Morelos, Puebla, Querétaro, Sinaloa, Tlaxcala, and Veracruz (Peterson and Annable 1991).

Ecology. This species is found in wet meadows, wet depressions, open flats, sandy flats along creeks, and rivers in pine or pine–oak woodlands; 1500–3800 m.

Comments. Morphologically, *M. vaginata* can be separated from *M. ligularis* in having contracted, narrow panicles up to 0.7 cm wide (0.4–1.5 cm wide in *M. ligularis*) and culms often rooting at the lower nodes (not rooting at lower nodes in *M. ligularis*) [Peterson and Annable 1991]. *Muhlenbergia ligularis* can be separated morphologically from *M. filiformis* in having inconspicuous panicles partly enclosed in the sheath (conspicuous, long-exerted panicles in *M. filiformis*) and leaf blades that are well developed along the entire length of the culm (versus leaf blades most numerous near the base of the culm) [Peterson and Annable 1991].

Based on DNA sequence analysis, *Muhlenbergia vaginata* is in *M*. subg. *Bealia* and forms a clade with *M. filiformis* and *M. ligularis* (Fig. 1; Peterson et al. 2021).

Specimens examined. Guatemala. **Huehuetenango**: La Capellania, Sierra de los Cuchumatanes, 3.3 mi NW of La Capellania on hwy 9N and 14.6 mi N of Huehuetenango, *P.M. Peterson & C.R. Annable 4685* (GH, MO, NY, RSA, UC, US, WS); El Mirador, at the summit of the road leading from Huehuetenango to Sierra de los Cuchumatanes, *P.C. Standley 81872* (US); Sierra de los Cuchumatanes. 1.1 mi E of Santa Eulalia on road to San Sebastian Coatan, *P.M. Peterson & C.R. Annable 4690* (US, WS); meadow at Tojah on hwy 9N, *P.M. Peterson & C.R. Annable 4697* (US, WS). **Quetzaltenango**: along eastern side of Rio Somala opposite Santa Maria de Jesus, *J.A. Steyermark 35049* (US). **San Marcos**: San Sebastian, along road between San Sebastian at km 21 and km 8, 8–18 mi NW of San Marcos, 4 km from San Sebastián, NW of San Marcos, *J.A. Steyermark 35598* (MO). **Zinacantán:** near Paraje Nachij, *D.E. Breedlove & G. Davidse 53877* (CAS, MO). Mexico. **Chiapas: Chamula:** large sphagnum bog at Paraje Muk'in ha, *D.E. Breedlove & B. Bartholomew 55504* (SLPM, CAS, MO). **Chenalhó:** edge of pasture 1 mile south of Chenalho Center, *D.E. Breedlove & P.H. Raven 8254* (DS). **Huixtán:** Chilil, SE de San Cristóbal de Las Casas, *M. González et al. 405* (SLPM); 10.5 mi SE of San Cristobal de las Casas, *P.M. Peterson & C.R. Annable 4723* (GH, MO, NY, US, WS).

37. *Muhlenbergia versicolor* Swallen, Contr. U.S. Natl. Herb. 29(4): 412. 1950. Fig. 10A–F

Type. México, Oaxaca, 170 km N of Oaxaca, 13 Dec 1945, *E. Hernandez-Xolocotzi & J.A. Jenkins X-810* (holotype: US-1961991!).

Description. Caespitose ***perennials***. ***Culms*** (80–)100–150 cm tall, erect, with 3 or 4 nodes, strigulose below the nodes; ***internodes*** mostly glabrous. ***Leaf sheaths*** longer than the internodes, basal sheaths compressed but not strongly keeled, the old sheaths brown becoming fibrillose with age, lower sheaths short pilose; ***sheath auricles*** 3–10 mm long, hyaline, wide, becoming frayed at the apex when mature; ***ligules*** (4–)7–22 mm long, hyaline above and firm and brown below; ***blades*** 25–40 cm long, 3–5 mm wide, blades arising near the middle of the culm 12–27 cm long, often shorter than those below, conduplicate or flat, finely scaberulous to scabrous, prominently veined on the upper surface. ***Panicles*** 20–50 cm long, 1.5–6 cm wide, erect, dark green to plumbeous, sometimes tinged in purple; ***primary branches*** 4–12 cm long, ascending or spreading up to 30° from the rachis; ***pedicels*** 1–2.5 mm long. ***Spikelets*** (2.5–)3–3.5 mm long; ***glumes*** (2.5)3–3.5 mm long, subequal, unveined or faintly 1-veined, apex erose-toothed, scabrous, unawned or awned; ***upper glumes*** mostly awned, the awn 1–1.2 mm long; ***lemmas*** 2.5–3(–3.5) mm long, villous on the lower ½ to 2/3, mostly pilose along the margins near the base, the awns 10–15(–25) mm long, flexuous; ***callus*** long-pilose; ***paleas*** equal to the lemmas, moderate to densely pilose between the keels; ***anthers*** up to 1.5 mm long, purple. ***Caryopses*** 1.5 mm long, 0.3 mm wide, fusiform, reddish-brown.

Distribution. *Muhlenbergia versicolor* ranges from Central México (Colima, Ciudad de México, Guanajuato, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Veracruz) to el Salvador, Guatemala, and Honduras (Sanchez-Ken 2018).

Ecology. This species is mainly found in oak forests, less frequent in pine-oak woodlands, rain forests, and grasslands on slopes and disturbed roadsides associated with *Alnus*, *Salvia*, *Rubus*, and *Thalictrum*; 900–2850 m.

Comments. Morphologically, *Muhlenbergia versicolor* resembles *M. distichophylla* but differs in having longer lemmas 2.5–3(–3.5) mm long (1.4–2.7 mm long in *M. distichophylla*) and shorter sheath auricles 3–10 mm long (versus 4–26 mm long).

Muhlenbergia versicolor is a member of *M.* subg. *Trichochloa* and is found in the clade with *M. breviligula*, *M. maxima*, *M. articulata* Scribn., *M. lehmanniana*, and M. *longiglumis* Vasey (Fig. 1; Peterson et al. 2021).

Specimens examined. El Salvador. **Santa Ana**: *P. Galán et al. 3920* (LAGU); *R. A. Carballo et al. 965* (LAGU, MO). Guatemala. **Huehuetenango**: San Lorenzo, 7 km S. of San Lorenzo, *W.E. Harmon & J.A. Fuentes 4786* (MO); Aguacatan road, 10 km east of Huehuetenango, *P.C. Standley 82073* (US); Barranco “Palo Negro” about 10 km W of Aguacatan, *L.O. Williams et al. 21850* (US). **Sololá**: Lago Atitlan, *M. De Koninck 146* (US). Honduras. **El Paraíso**: In forest on Mt. Yuscaran, *A. Molina R. 605* (US). **Francisco Morazán**: San Antonio de Oriente, Guayabillas, pine forest of Guayabillas on road to Ojo de Agua, *A.R. Molina 25899* (MO); Distrito Central, Tegucigalpa, alrededores de la Universidad Nacional Autonoma de Honduras, *K.J. Cantarero 48* (MO, TEFH); vicinity of Suyapa, hills above Suyapa, *J.R. Swallen 11277* (US). Mexico. **Chiapas**: **Cintalapa:** Slope, near La Cienega de

León 30 km N of Las Cruces, *D.E. Breedlove & F. Almeda 48070* (CAS, MO). **Ixtapa:** Ixtapa, at Escopetazo, *D.E. Breedlove & G. Davidse 53960* (SLPM, CAS, MO); near Ixtapa, *D.E. Breedlove & G. Davidse 54364* (CAS, MO), *D.E. Breedlove & G. Davidse 54363* (CAS, MO). **Motozintla:** SW side of Cerro Mozotal, 11 km NW of the junction of the road to Motozintla along the road to El Porvenir and Siltepec, *D.E. Breedlove & B.M. Bartholomew 55785* (CAS, MO). La Trinitaria, 12 km al S de la Trinitaria, camino a Cd. Cuauhtemoc, *E. Martínez-Salas 23905* (MEXU). *D.E. Breedlove & G. Davidse 54631* (CAS) citada en Flora Mesoamericana. **Teopisca:** Marsh near Teopisca, *D.E. Breedlove & G. Davidse 54813* (CAS, MO); slopes at W edge of Teopisca, *D.E. Breedlove & J.L. Strother 46378* (CAS, MO). **Villa Corzo:** Above Colonia Vincente Guerrero on road to Finca Cuxtepec, *D.E. Breedlove & G. Davidse 54642* (CAS, MO), *D.E. Breedlove & G. Davidse 54631* (CAS, MO).

38. ***Muhlenbergia xanthodas*** **Soderst., Contr. U.S. Natl. Herb. 34: 173. 1967.**
Fig. 2F–H

Type. México, Chiapas, collected on rock on Mt. Ovando, 2300 m, 14–18 Nov 1939, *E. Matuda 4003* (holotype: US-1817864!; isotypes: F-64101, F-64108!, GH-00024052 [image!], NY-00381481 [image!], NY-00381482 [image!], US-2075810!).

Description. Densely caespitose ***perennials***. ***Culms*** 50–100 cm tall, glabrous. ***Leaf sheaths*** compressed-keeled, glabrous, minutely scabrillose near the collar; ***sheath auricles*** absent; ***ligules*** (3–) 6–13 mm long, delicate, hyaline, frayed with age, scarcely decurrent, becoming somewhat firm at base; ***blades*** 30–50(–70) cm long, 2–4 mm wide, conduplicate, becoming involute towards the apex, scabrous, apically long attenuate, the margins scabrous. ***Panicles*** 20–45(–55) cm long, 2–3(–4) cm wide, erect, golden yellow to yellowish-brown; ***primary branches*** 4–6 (–7) cm long, tightly appressed with spikelets to the base; ***pedicels*** shorter than the spikelets, thin, usually straight, scaberulous and often with a few hairs near the apex. ***Spikelets*** 2–3 mm long; ***glumes*** 2–2.5(–3) mm long, about equal in length, mostly smooth, somewhat lustrous and shining, translucent, unveined, apex acute; ***lemmas*** (2–)2.5–2.9 mm long, as long as the glumes or shorter, mostly glabrous or with a few appressed and very short trichomes at the base of the central vein, the awns (5–)6–20 mm long, golden; ***callus*** short-pilose; ***paleas*** as long as the lemma or a little longer, glabrous; ***anthers*** 1.5–2 mm long. ***Caryopses*** not seen.

Distribution. *Muhlenbergia xanthodas* is known from Guatemala and Chiapas, México (Sanchez-Ken 2018).

Ecology. This species is found on rocky limestone slopes in deciduous tropical forests; 1500–2300 m.

Comments. Morphologically, *M. xanthodas* is similar to *M. aurea* but differs in having longer spikelets 2–3 mm long (1.7–2.2 mm long in *M. aurea*) and veinless glumes (1-veined in *M. aurea*) with the upper mucronate.

Specimens examined. Guatemala. **Huehuetenango.** Clearings and mixed forest in mountains near El Reposo, about 8 km from Mexican frontier, *L.O. Williams et al.41241* (MEXU); Canyon of Río Seligua, in "El Tapón" near Monos bridge, 40 km, NW of Huehuetenango, *L.O. Williams et al.41263* (MEXU). Mexico. **Chiapas. Altamirano**: 15 km Norte a colonia Puebla Nueva, *A. Pérez M. 221*

(MEXU); **Ixtapa**: Intersection of the Tuxtla Gutiérrez-San Cristóbal de las Casas and the Villahermosa highways, *G. Davidse et al. 30101* (MEXU); **San Fernando**: Parque Nacional del Sumidero, 222 km NW of Tuxtla Gutiérrez, along the road to the canyon outlook, *G. Davidse et al. 29764* (MEXU); **Tenejapa**: Ojo del Río Yash zanal, *Alush Méndez Ton 5322* (MEXU); **Tuxtla Gutiérrez**: 18 km NE de Tuxtla Gutiérrez, carr al cañón del Sumidero, *A.J. Zenón*, *Ruíz y Valle # 2* (CIIDIR); Between Escuiplas and Cañada Honda, *Hernández X. & Sharp X-311* (US).

Infrageneric classification of the species of *Muhlenbergia* in Central America

***Muhlenbergia* subg. *Ramulosae* P.M. Peterson, subgen. nov. – Type: *Vilfa ramulosa* Kunth, Nov. gen. sp. 1: 137. 1815 ≡ *Agrostis ramulosa* (Kunth) Roem. & Schult. ≡ *Sporobolus ramulosus* (Kunth) Kunth ≡ *Muhlenbergia ramulosa* (Kunth) Swallen.**
urn:lsid:ipni.org:names:77324812-1

Description. Delicate ***annuals***. ***Culms*** (3–)5–25 cm tall, erect or spreading, not rooting at the lower nodes. ***Leaf sheaths*** 3–30 cm long, usually shorter than the internodes; ***ligules*** 0.2–0.5 mm long, hyaline, apex truncate; ***blades*** 0.5–3.0 cm long, 0.8–1.2 mm wide, involute or flat. ***Panicles*** (1–)2–9 cm long, 0.6–2.7 mm wide, exserted, ovoid or deltoid, **branches** loosely contracted, ascending or spreading. ***Spikelets*** 1-flowered; ***glumes*** 0.4–0.7 mm long, shorter than the lemma, 1-veined, glabrous, apex obtuse to subacute; ***lemmas*** 0.8–1.3 mm long, oval, plump, 3-veined, awnless, mottled with greenish-black and greenish-white areas, apex acute. ***Stamens*** 3; ***anthers*** 0.2–0.3 mm long. ***Caryopses*** 0.5–1 mm long, ellipsoid.

Species included (monotypic): *M. ramulosa* (Kunth) Swallen.

Muhlenbergia subg. *Bealia* (Scribn.) P.M. Peterson: *M. ligularis*, *M. minutissima*.
Muhlenbergia subg. *Clomena* (P. Beauv.) Hack.: *M. flabellata*, *M. montana*, *M. peruviana*, *M. quadridentata*.
Muhlenbergia subg. *Muhlenbergia: M. cenchroides*, *M. ciliata*, *M. diandra*, *M. diversiglumis*, *M. microsperma*, *M. pereilema*, *M. plumiseta*, *M. setarioides*, *M. spiciformis*, *M. tenella*, *M. uniseta*.
Muhlenbergia subg. *Pseudosporobolus* (Parodi) P.M. Peterson: *M. implicata*, *M. phalaroides*, *M. repens*, *M. tenuissima*, *M. utilis*.
Muhlenbergia subg. *Ramulosae* P.M. Peterson: *M. ramulosa*.
Muhlenbergia subg. *Trichochloa* (P. Beauv.) A. Gray: *M. aurea*, *M. breviligula*, *M. capillaris*, *M. distichophylla*, *M. lehmanniana*, *M. macroura*, *M. mucronata*, *M. mutica*, *M. nigra*, *M. rígida*, *M. robusta*, *M. versicolor*, *M. xanthodas*.
Unplaced: *M. orophila*, *M. plumbea*.

Excluded names

Muhlenbergia beyrichiana is not known to occur in Chiapas or Central America and was reported in error (see comments under *M. diandra*) [Dávila et al. 2018], We believe *M. beyrichiana* occurs in Brazil, Ecuador, and Peru. Earlier, it was reported in México and Central America but these are in error (Espejo Serna et al. 2000; Lægaard and Peterson 2001; Peterson et al. 2001, 2018).

Muhlenbergia emersleyi Vasey is not known to occur in Chiapas or Central America but was reported in Dávila et al. (2018) as occurring in Chiapas. We have not seen any specimens of this species from Central America or Chiapas.

Muhlenbergia fragilis Swallen is not known to occur in Chiapas or Central America but was reported in Dávila et al. (2018) and Sanchez-Ken (2018).

Muhlenbergia grandis Vasey has been reported for Tabasco by Sanchez-Ken (2018) but we have not seen any specimens of this species from there, and since its distribution is primarily restricted to the Pacific slope of Sonora, Durango, Nayarit, Jalisco, Michoacán, and Queretero at elevations of 800–1600m, it seems unlikely to occur in Tabasco (Soderstrom 1967; Sanchez-Ken 2018). Additionally, *M. grandis* was not treated in Flora Mesoamericana by Reeder (1994).

Muhlenbergia repens (J Presl) Hitchc. is not known to occur in Chiapas or Central America but was reported in Dávila et al. (2018) and Sanchez-Ken (2018).

Muhlenbergia sinuosa Swallen is not known to occur in Chiapas or Central America but was reported in Sanchez-Ken (2018).

Muhlenbergia tarahumara P.M. Peterson & Columbus is not known to occur in Chiapas or Central America but was reported in Dávila et al. (2018).

Muhlenbergia tenuifolia (Kunth) Kunth is not known to occur in Chiapas or Central America but was reported in Dávila et al. (2018) and Sanchez-Ken (2018).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Peterson wrote manuscript, descriptions, key, and contributed to Specimens cited; Herrera Arrieta contributed to descriptions, key, and specimens examined; Lobo Cabezas contributed specimens examined; Romaschenko provided the molecular DNA tree and performed the DNA analysis.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Brown W (1977) The Kranz syndrome and its subtypes in grass systematics. Memoirs of the Torrey Botanical Club 23: 1–97.

Columbus JT, Smith JP (2010) Nomenclatural changes for some grasses in California and the *Muhlenbergia* clade (Poaceae). Aliso 28(1): 65–67. https://doi.org/10.5642/aliso.20102801.07

Columbus JT, Peterson PM, Refulio Rodríguez NF, Cerros Tlatilpa R, Kinney MS (2010) Phylogenetics of Muhlenbergiinae (Poaceae, Chloridoideae, Cynodonteae) based on ITS and *trnL-F* DNA sequences. In: Seberg O, Petersen G, Barfod AS, Davis JI (Eds) Diversity, phylogeny, and evolution in the monocotyledons. Aarhus University Press, Aarhus, Denmark, 477–495.

Davidse G (1994) 88. *Lycurus* Kunth. In: Davidse G, Sousa SM, Chater AO (Eds) Flora Mesoamericana, volume 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Instituto de Biología, México, D.F., 286 pp.

Davidse G, Pohl RW (1992) New taxa and nomenclatural combinations of Mesoamerican grasses (Poaceae). Novon 2(2): 81–110. https://doi.org/10.2307/3391667

Davidse G, Pohl RW (1994) 262. Poaceae. In: Davidse, G, Sousa S M, Chater AO (Eds) Flora Mesoamericana, Volume 6 Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Missouri Botanical Garden, The Natural History Museum (London), México, D.F.

Dávila P, Mejia-Saulés MT, Soriano-Martínez AM, Herrera-Arrieta Y (2018) Conocimiento taxonómico de la familia Poaceae en México. Botanical Sciences 96(3): 462–514. https://doi.org/10.17129/botsci.1894

Dengler NG, Dengler RE, Hattersley PW (1986) Comparative bundle sheath and mesophyll differentiation in the leaves of C_4 grasses *Panicum effusum* and *P. bulbosum*. American Journal of Botany 73(10): 1431–1442. https://doi.org/10.1002/j.1537-2197.1986.tb10889.x

Espejo Serna A, Lopez-Ferrari AR, Valdés-Reyna J (2000) Poaceae Barnhart. In: Espejo Serna A, Lopez-Ferrari AR (Eds) Las Monocotyledóneas mexicanas: Una sinopsis floristica, partes 9–11. Consejo Nacional de la Flora de México, A.C., Universidad Autónoma Metropolitana-Izpalapa and Comision Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F.

Giraldo-Cañas D, Peterson P (2009) El género *Muhlenbergia* (Poaceae: Chloridoideae: Cynodonteae: Muhlenbergiinae) en Colombia. Caldasia 31: 269–302. https://repository.si.edu/handle/10088/8913

Gutierrez M, Gracen VE, Edwards GE (1974) Biochemical and cytological relationships in C_4 plants. Planta 119(4): 279–300. https://doi.org/10.1007/BF00388331

Hattersley PW, Watson L (1976) C4 grasses: An anatomical criterion for distinguishing between NADP-malic enzyne species and PCK or NAD-malic enzyme species. Australian Journal of Botany 24(2): 297–308. https://doi.org/10.1071/BT9760297

Hattersley PW, Watson L (1992) Diversification of photosynthesis. In: Chapman GP (Ed.) Grass evolution and domestication. Cambridge University Press, Great Britain, 38–116.

Herrera Arrieta Y (1998) A revision of the *Muhlenbergia montana* (Nutt.) Hitchc. complex (Poaceae: Chloridoideae). Brittonia 50(1): 23–50. https://doi.org/10.2307/2807714

Herrera Arrieta Y, Peterson PM (2007) *Muhlenbergia* (Poaceae) de Chihuahua, México. Sida. Botanical Miscellany 29: 1–109.

Herrera Arrieta Y, Peterson PM (2017) Subfamily Chloridoideae, Parte 1 (Muhlenbergia). Flora del Bajío y de Regiones Adyacentes 199: 1–130. https://repository.si.edu/handle/10088/8913

Herrera Arrieta Y, Peterson PM (2018) Grasses of Chihuahua, México. Smithsonian Contributions to Botany 107: 1–380. https://doi.org/10.5479/si.1938-2812.107

Herrera Arrieta Y, Peterson PM, Cortés Ortiz A (2010) Gramíneas de Zacatecas, México. Sida. Botanical Miscellany 32: 1–239.

Hitchcock AS (1935) Manual of the grasses of the United State. Government Printing Office, Washington, DC, 1–1040. https://doi.org/10.5962/bhl.title.19358

Lægaard S, Peterson PM (2001) 214(2). Gramineae (part 2) Subfam. Chloridoideae. In: Harling G, Andersson L (Eds) Flora of Ecuador 68, Botanical Institute, University of Göteborg, Göteborg, 1–131.

McVaugh R (1983) Volume 14 Gramineae. In: Anderson WR (Ed.) Flora Novo-Galiciana, A descriptive account of the vascular plants of western México. University of Michigan press, Ann Arbor, 1–436.

Menjívar Cruz JE, Baldini RM, Davidse G, Peterson PM (2021) El Salvador grasses: An updated catalogue and nomenclator. Phytoneuron 2021-22: 1–131. https://www.phytoneuron.net/2021Phytoneuron/22PhytoN-ElSalvadorGrasses.pdf

Morales JF (2003) Poaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de plantas de Costa Rica, Vol. III Monocotyledóneas (Orchidadeae–Zingiberaceae). Missouri Botanical Garden Press, St. Louis, 598–821.

Morden CW, Hatch SL (1984) Cleistogamy in *Muhlenbergia cuspidata* (Poaceae). Sida 10: 254–255.

Peterson PM (2000) Systematics of the Muhlenbergiinae (Chloridoideae: Eragrostideae). In: Jacobs SWL, Everett J (Eds) Grasses: Systematics and Evolution. CSIRO, Melbourne, 195–212.

Peterson PM (2003) 17.33 *Muhlenbergia* Schreb. In: Barkworth ME, Capels KM, Long S, Piep MB (Eds) Magnoliophyta: Commelinidae (in part): Poaceae, part 2 Flora of North America North of México, Vol 25. Oxford University Press, New York, 145–201.

Peterson PM, Annable CR (1991) Systematics of the annual species of *Muhlenbergia* (Poaceae-Eragrostideae). Systematic Botany Monographs 31: 1–109. https://doi.org/10.2307/25027794

Peterson PM, Giraldo-Cañas D (2011) Las especies de *Muhlenbergia* (Poaceae: Chloridoideae) de Argentina. Caldasia 33: 21–54.

Peterson PM, Giraldo-Cañas D (2012) *Muhlenbergia* Schreb. In: Zuloaga FO, Rugolo ZE, Anton AMR (Eds) Flora Argentina, Flora Vascular de la Republica Argentina, Vol. 3, Tomo 1, Monocotyledoneae, Poaceae: Aristidoideae a Pharoideae. IBODA-IMBIV, CONICET, Buenos Aires, Argentina, 140–154.

Peterson PM, Herrera Arrieta Y (2001) A leaf blade anatomical survey of *Muhlenbergia* (Poaceae: Muhlenbergiinae). Sida 19: 469–506.

Peterson PM, Morrone O (1997) Allelic variation in the amphitropical disjunct *Lycurus setosus* (Poaceae: Muhlenbergiinae). Madrono 44: 334–346.

Peterson PM, Webster RD, Valdés-Reyna J (1995) Subtribal classification of the New World Eragrostideae (Poaceae: Chloridoideae). Sida 16: 529–544. https://doi.org/10.5962/bhl.part.3478

Peterson PM, Webster RD, Valdes Reyna J (1997) Genera of New World Eragrostideae (Poaceae: Chloridoideae). Smithsonian Contributions to Botany 87(87): 1–50. https://doi.org/10.5479/si.0081024X.87

Peterson PM, Soreng RJ, Davidse G, Filgueiras TS, Zuloaga FO, Judziewicz EJ (2001) Catalogue of New World grasses (Poaceae): II. subfamily Chloridoideae. Contributions from the United States National Herbarium 41: 1–255.

Peterson PM, Columbus JT, Pennington SJ (2007a) Classification and biogeography of New World grasses: Chloridoideae. Aliso 23(1): 580–594. https://doi.org/10.5642/aliso.20072301.43

Peterson P, Valdés-Reyna J, Herrera Arrieta Y (2007b) Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae): from northeastern México. Journal of the Botanical Research Institute of Texas 1(2): 933–1000.

Peterson PM, Romaschenko K, Johnson G (2010a) A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Molecular Phylogenetics and Evolution 55(2): 580–598. https://doi.org/10.1016/j.ympev.2010.01.018

Peterson PM, Romaschenko K, Johnson G (2010b) A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. American Journal of Botany 97(9): 1532–1554. https://doi.org/10.3732/ajb.0900359

Peterson PM, Romaschenko K, Herrera Arrieta Y (2016) A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaqiqahinae; and a subgeneric classification of *Distichlis*. Taxon 65(6): 1263–1287. https://doi.org/10.12705/656.4

Peterson PM, Sánchez Vega I, Romaschenko K, Giraldo-Cañas D, Refulio Rodriguez NF (2018) Revision of *Muhlenbergia* (Poaceae, Chloridoideae, Cynodonteae, Muhlenbergiinae) in Peru: Classification, phylogeny, and a new species, *M. romaschenkoi*. PhytoKeys 114: 123–206. https://doi.org/10.3897/phytokeys.114.28799

Peterson PM, Roquet C, Romaschenko K, Herrera Arrieta Y, Susanna A (2021) A biogeographical analysis of *Muhlenbergia* (Poaceae: Chloridoideae: Cynodonteae: Muhlenbergiinae). Journal of Systematics and Evolution 60(3): 621–629. https://doi.org/10.1111/jse.12805

Pohl RW (1980) Family #15, Gramineae. In: Burger W (Ed.) Flora Costaricensis. Fieldiana Botany, New Series 4: 1–608. https://doi.org/10.5962/bhl.title.2650

Pohl RW (1994a) 104. *Aegopogon* Humb. & Bonpl. ex Willd. In: Davidse G, Sousa SM, Chater AO (Eds) Flora Mesoamericana, Volume 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Instituto de Biología, México, D.F., 296–297.

Pohl RW (1994b) 89. *Pereilema* J.S. Presl. In: Davidse G, Sousa SM, Chater AO (Eds) Flora Mesoamericana, volume 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Instituto de Biología, México, D.F., 286–287.

Pohl RW, Davidse G (1971) Chromosome numbers of Costa Rican grasses. Brittonia 23(3): 293–324. https://doi.org/10.2307/2805632

Reeder JR (1967) Notes on Mexican grasses VI. Miscellaneous chromosome numbers. Bulletin of the Torrey Botanical Club 94(1): 1–17. https://doi.org/10.2307/2483595

Reeder JR (1968) Notes on Mexican grasses VIII. Miscellaneous chromosome numbers–2. Bulletin of the Torrey Botanical Club 95(1): 69–86. https://doi.org/10.2307/2483808

Reeder CG (1985) The genus *Lycurus* (Gramineae) in North America. Phytologia 57: 283–291.

Reeder CG (1994) 87. *Muhlenbergia* Schreber. In: Davidse G, Sousa SM, Chater AO (Eds) Flora Mesoamericana, volume 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Instituto de Biología, México, D.F., 276–286.

Reeder CG, Reeder JR (1995) The resurrection of a species: *Muhlenbergia straminea* (Gramineae). Phytologia 78: 417–427. https://doi.org/10.5962/bhl.part.29684

Renvoize SA (1998) Gramineas de Bolivia. The Royal Botanic Gardens, Kew, 1–644.

Sánchez E, Rúgolo de Agrasar ZE (1986) Estudio taxonómica sobre el genero *Lycurus* (Gramineae). Parodiana 4: 267–310.

Sanchez-Ken JG (2018) Riqueza de especies, clasificación y listado de las gramíneas (Poaceae) de México. Acta Botánica Mexicana 126(126): 1–115. https://doi.org/10.21829/abm126.2019.1379

Soderstrom TR (1967) Taxonomic study of subgenus *Podosemum* and section *Epicampes* of *Muhlenbergia* (Gramineae). Contributions from the United States National Herbarium 34: 75–189.

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O (2015) A worldwide phylogenetic classification of the Poaceae (Gramineae). Journal of Systematics and Evolution 53(2): 117–137. https://doi.org/10.1111/jse.12150

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Teisher JK, Clark LG, Barberá P, Gillespie LJ, Zuloaga FO (2017) A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution 55(4): 259–290. https://doi.org/10.1111/jse.12262

Soreng RJ, Peterson PM, Zuloaga FO, Romaschenko K, Clark LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA, De-Zhu L, Davidse G (2022) A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. Journal of Systematics and Evolution 60(3): 476–521. https://doi.org/10.1111/jse.12847

Swallen JR (1950) New grasses from México, Central America, and Surinam. Contributions from the United States National Herbarium 29(9): 395–428.

Thiers B (2023) Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/ih/

Tiwari S, Tiwari S, Prasad D, Jaiswal S, Yadav R, Sharma S, Agnihotri P (2023) Typification and taxonomic notes on species of *Muhlenbergia* Schreb. (Poaceae, Muhlenbergiinae) in India. Plant Science Today 10(2): 69–73. https://doi.org/10.14719/pst.1971

Tovar Ó (1993) Las Gramíneas (Poaceae) del Perú. Ruizia 13: 1–480.

Villaseñor Ríos JL (2016) Checklist of the native vascular plants of México. Catálogo de las plantas vasculares nativas de México. Revista Mexicana de Biodiversidad 87(3): 559–902. https://doi.org/10.1016/j.rmb.2016.06.017

Wu ZL, Peterson PM (2006) 140. *Muhlenbergia*. In: Wu Z, Raven PH, Hong DY (Eds) Flora of China: Poaceae, volume *22*. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 486–487.

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Research Article

Primula medogensis, a new species of Primulaceae from Tibet of China

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Abstract

We present a description of a newly discovered species, *Primula medogensis*, found in southern Xizang, China. Additionally, we explore distinctive morphological characteristics that aid in its taxonomy. The new species belongs to sect. *Cordifoliae* and exhibits morphological similarities to *P. baileyana* and *P. rotundifolia*. However, it can be distinguished by its densely grayish-haired roots, petioles that are 3–7 times longer than the leaf blades, a short stock surrounded by straight and withered petioles, reniform leaf blades with revolute margins, scapes shorter than or equal to leave and both at flowering and in fruiting, flowers solitary on the scapes.

Key words: Morphological characters, *Primula* sect. *Cordifoliae*, taxonomy

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Introduction

The genus *Primula* L. is known for its remarkable complexity within the realm of angiosperm taxonomy. Comprising approximately 500 herbaceous plant species, it predominantly thrives in moderate and cold regions of the Northern Hemisphere; individual species can be found in the mountains of South America and Africa, as well as tropical Asia (Hu 1990, 1994; Hu and Kelso 1996; APG 2016). In China, more than 300 species of the genus are distributed (Richards 2003).

Section *Cordifoliae*, established by Pax (1889), consists of seven species primarily found in the Eastern Himalayas. These species typically inhabit alpine rocky areas beyond the tree-line on the southern side of the Eastern Himalayas (Richards 2003). The distinguishing characteristics of this section include withered leaves and bud scales at the base, long and slender discrete petioles, and predominantly round leaves with a cordate base.

During botanical explorations in Motuo County, Xizang Province, located in southwest China, we collected a remarkable species of *Primula* that thrives among mosses, often in crevices on wet cliffs and among boulders. After subsequent examination of herbarium specimens available at CDBI, and careful consultation of literature (Pax 1889; Pax and Knuth 1905; Smith and Forrest 1928; Smith and Fletcher 1943; Hara 1966, 1971; Ohashi 1975; Fenderson 1986;

Hu 1986, 1990; Naithani 1990; Fang 1994, 2003; Hu and Kelso 1996; Grierson and Long 1999; Wu 1999; Bista et al. 2001; Sun and Zhou 2002; Kress et al. 2003; Richards 2003; Basak et al. 2014; Xu et al. 2014; Rajbhandari et al. 2021; Li et al. 2023), we identified that this population represents a new species of *Primula* sect. *Cordifoliae* by its morphological characters, which is similar to *Primula baileyana* Kingdon-Ward and *P. gambeliana* Watt. In this study, we provide a detailed description of this new species based on observations of living plants in the field and pressed specimens in the herbarium.

Materials and methods

The descriptions and photographs provided in this study were derived from an extensive analysis of the habits and characteristics observed in wild populations during field surveys. Specimens of the new species were collected from the designated type locality and have been stored at CDBI. To supplement our examination, we also accessed digital specimens available online through various platforms, including the Chinese Virtual Herbarium (http://www.cvh.ac.cn/), the JSTOR Global Plants (https://plants.jstor.org/), the Global Biodiversity Information Facility (https://www.gbif.org/), and the Europeana (https://www.europeana.eu), especially type specimens from A, BM, E, K, P, US.

Taxonomic treatment

***Primula medogensis* W.B.Ju, Bo Xu & X.F.Gao, sp. nov.**
urn:lsid:ipni.org:names:77324820-1

Diagnosis. This new species is similar to *P. baileyana* and *P. rotundifolia*, but it differs from them in having roots with hairs, straight petiole remaining from the previous year, leaf blade reniform and revolute at the margin, petiole more than 3 times the length of the leaf blade, scape equal to or shorter than the leave, flower solitary at the apex of the scape, capsule shorter than the calyx.

Type. China. Xizang: Motuo City, Duoxiongla, growing in moist rock crevices covered with moss. 31°04'N, 103°11'E, elevation ca. 3607 m, 18 May 2021, *W. B. Ju & X. Li* YLZB07293 (holotype CDBI!; isotypes KUN!, PE!).

Description. A perennial plant with a short stock, or up to 2.0 × 1.0 cm, usually girt at the base by the straight and withered petioles. ***Roots*** reddish, tuft of wiry, woody on maturity, covered with grayish hairs. Bud scales usually girt at the base by imbricate ovate-oblong to ovate with pale-yellow farinose on the abaxially surface. ***Leaves*** including the petiole 1.2–12.5 cm long; leaf blade reniform or suborbicular, but mostly reniform, 0.3–1.5 × 0.4–2.3 cm, firm papery or subleathery, glabrous and with potentially farinose glands above, copious pale-yellow farina on the lower surface, margin dentate revolute on the lower surface, with a deeply cordate to occasionally truncate base, lateral veins 3–4 pairs; petioles 0.9–11.0 cm long, reddish brown, glabrous, slightly broadened and membranous towards the base. ***Scape*** 1, sparsely short-stalked glandular, 3.0–10.5 cm tall, erect, hardened in fruiting, usually with a single flower; bracts linear-lanceolate, 0.2–0.5 cm long; pedicels 0.2–1.2 cm long, sparsely short-stalked glandular, not extended in fruit. ***Flowers*** heterostylous. Calyx campanulate, 5–8 mm long, glabrous outside, green, inside of pale-yellow farinose, parted nearly to base; lobes lanceolate, margin entire, apex acute, veins 3 with not prominent. Corolla pinkish-purple with a golden-yellow eye, annulate; limb 15–25 mm across, funnelform; lobes spreading, 6–11 × 5–10 mm, broadly obovate, deeply emarginate. ***Thrum flower***: corolla tubes 10–15 mm in length, 2–3 mm in diameter, 2 times the length of calyx, widely ampliated above insertion of stamens; stamens situated at the near apex of the corolla tube; style 3–4 mm. ***Pin flower***: corolla tubes 9–13 mm in length, 2–3 mm in diameter, 2 times the length of calyx; stamens inserted at the middle of corolla tube, style as long as tube. ***Capsule*** broad-ovoid to globose, shorter than calyx, dehiscence by apical valves. ***Seeds*** numerous, free within capsule at maturity, irregularly ovoid-quadrate or pyriform, ca. 0.5–0.8 mm, brown, testa reticulate.

Phenology. Flowering occurs in May to June; fruiting at the end of June.

Etymology. The specific epithet refers to the administrative county name of the type locality viz Motuo (Medog) county in southeast Xizang Autonomous Region, China.

Distribution and habitat. The new species is currently known only from its type locality in Lage, Motuo (Medog) county, Xizang Autonomous Region. It grows in the cracks of steep wet cliffs covered with moss, at elevations of 3550–3700 m.

Additional specimens examined (Paratypes). China, Xizang Autonomous Region, Motuo County, Duoxiongla, it grows in the cracks of steep wet cliffs covered with moss, at elevations of 3626 m, 31 May 2015, *Bo Xu & X.M.Zhou* YLZB01705 (CDBI!).

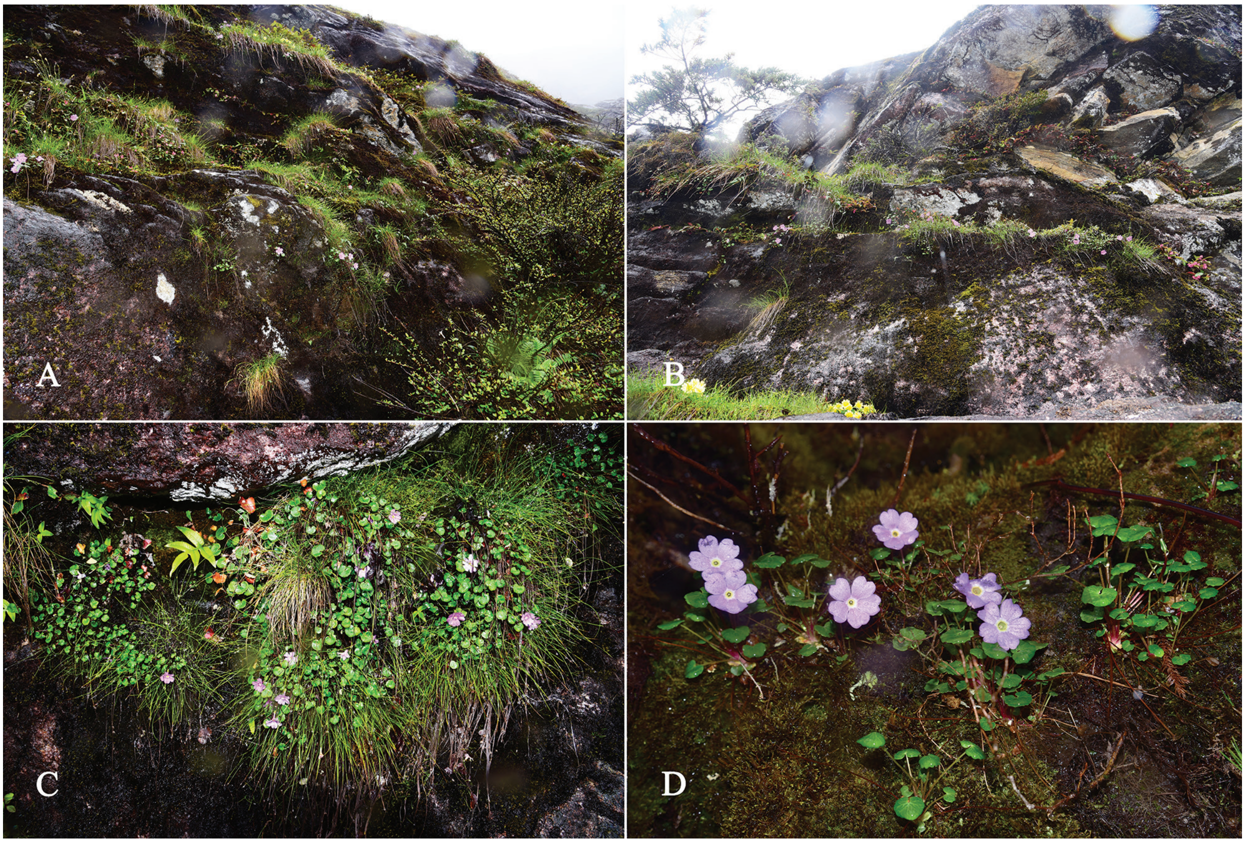

Figure 1. Habitat of the *Primula medogensis* sp. nov. (**A–D**)

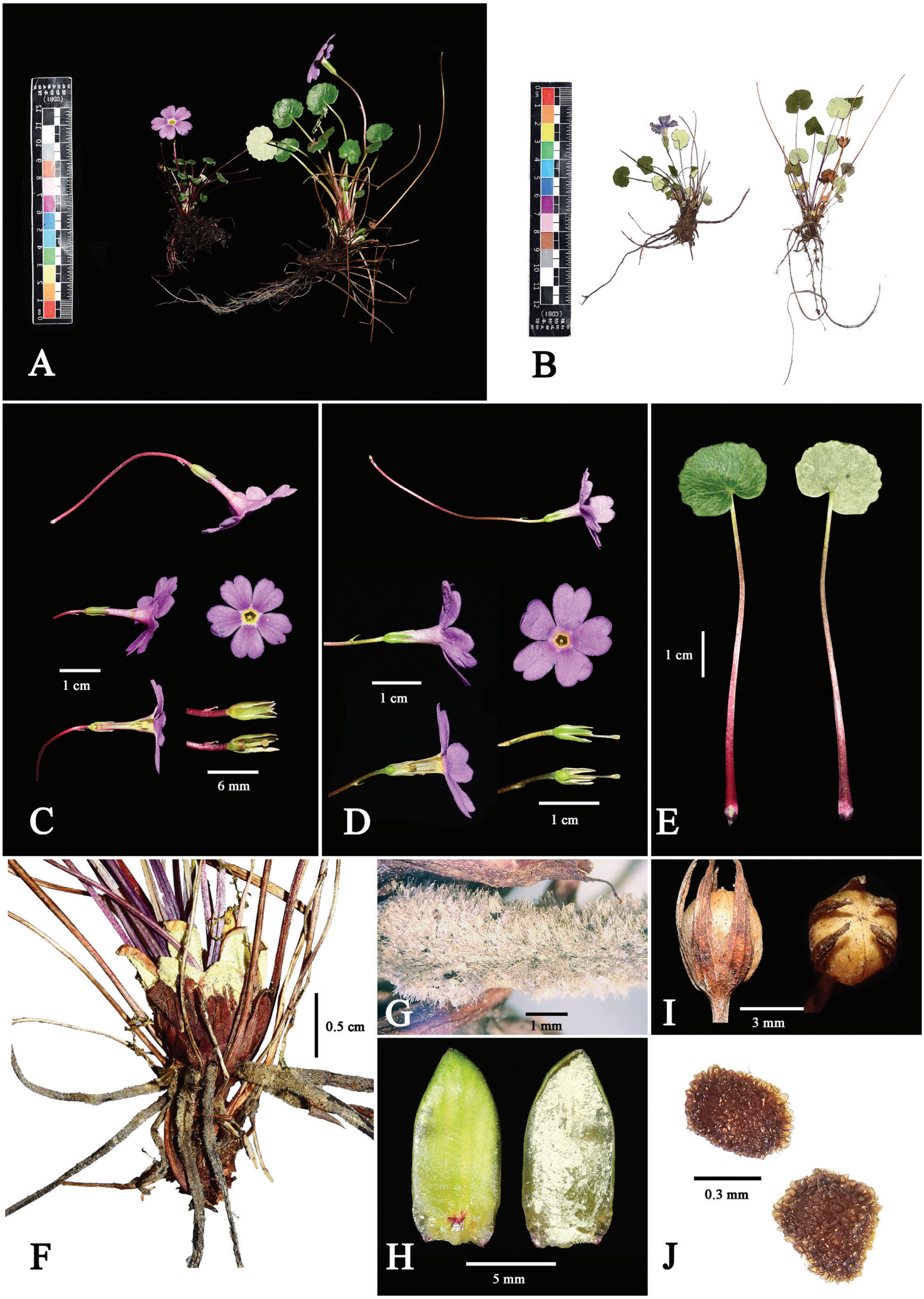

Figure 2. *Primula medogensis* sp. nov. **A** fresh plants **B** pressed specimen **C** thrum flower **D** pin flower **E** leaves **F** plants base, showing roots, bud scales and petioles **G** roots covered with greyish hairs **H** bud scales **I** capsule **J** seed.

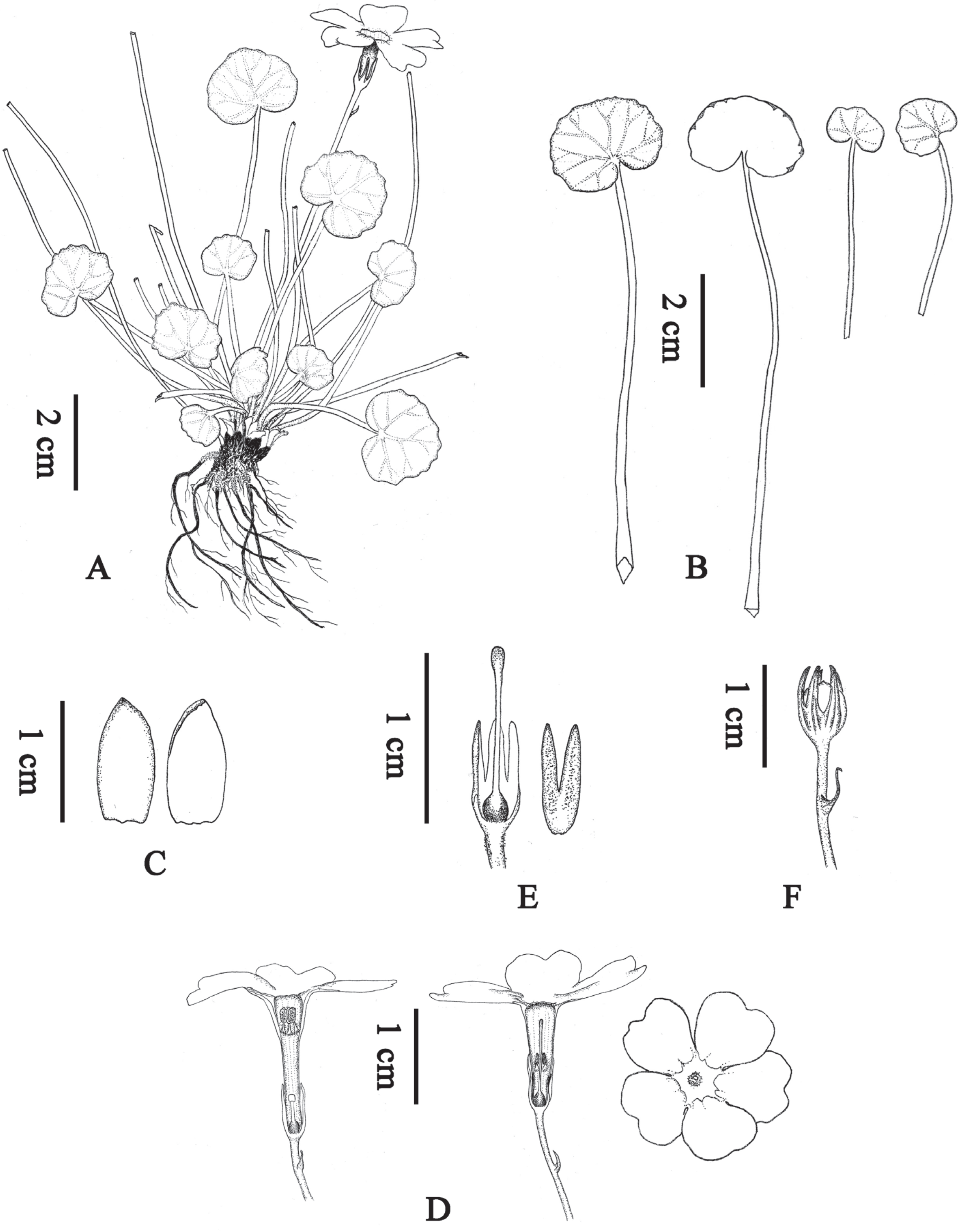

Figure 3. *Primula medogensis* sp. nov. **A** habit **B** leaves **C** bud scales **D** flowers: thrum flower, pin flower, and front of the flower **E** calyx and ovary **F** capsule.

Conservation status. Currently, only one population have been found. The size of the Lage population remains unknown. According to the IUCN red list criteria (IUCN 2019), the conservation status of the new species should be better categorized as 'Data Deficient (DD)'. Further explorations in the adjacent mountainous tracts are necessary for an adequate assessment.

Discussion. Section *Cordifoliae* is a small group within the genus *Primula* that has undergone multiple revisions. Currently, it includes several species such as *P. baileyana* Kingdon-Ward, *P. caveana* W.W.Smith, *P. gambeliana* Watt, *P. macklinae* A.J.Richards (not validly published), *P. littledalei* I.B.Balfour & Watt, *P. ramzanae* Smith & Fletcher and *P. rotundifolia* Wallich (Richards 2003). These species primarily inhabit the tree-line on mountain rocks of the southern slopes of the Himalayas, at altitudes ranging from 3300 to 6000 meters. The most western species, *P. ramzanae*, is exclusively found in Phoksumdo Lake in western Nepal. The most eastern species in this section is one incompletely known species *P. macklinae*, found in northern Myanmar. *P. littledalei* extends from the southern slopes to Lhasa in the Xizang Autonomous Region, and together with *P. baileyana* is only found in China. The species represented by *P. rotundifolia*, *P. gambeliana*, *P. caveana* are from central Nepal through Sikkim to Bhutan and Tibet. The distribution area of the new species overlaps with *P. baileyana* and *P. littledalei* of this section, which is the lowest elevation distribution except *P. macklinae*.

Morphologically, *P. medogensis* shares certain similarities with *P. baileyana* and *P. rotundifolia*, both of which also belong to *P.* sect. *Cordifoliae*. These similarities include mealy, deciduous plants arising from substantial resting buds, the base of the leaf cluster often has many withered petioles, leaf blades are usually reniform or suborbicular, base cordate, with a conspicuous petiole, corolla pinkish-purple, calyx campanulate, with splitting to below middle, capsule horny (Figs 1–3). However, this new species has a series of morphological characters unique to the section that consists of straight old petioles at the base, petioles 3–7 times longer than the leaf blades, leaf blades mostly reniform with revolute margins, single flowers, and scape shorter than or equal to the leaves. In addition to the unique features described above, *P. medogensis* clearly differs from *P. baileyana* by roots clothed in dense grayish hairs, pale- yellow farinose, smaller leaf blades, calyx lobes with 3 veins, and capsules shorter than the calyx; and it differs from *P. rotundifolia* by its smaller leaf blades, corolla lobes deeply emarginate, the capsule broad-ovoid to globose and shorter than the calyx. For a comprehensive overview of the contrasting characteristics between *P. medogensis*, *P. baileyana*, and *P. rotundifolia*, please refer to Table 1.

Table 1. Comparison of morphological characters among *Primula medogensis*, *P. baileyana* and *P. rotundifolia*.

Characters	*Primula medogensis*	*P. baileyana*	*P. rotundifolia*
Root	dense grayish hairs	Glabrous	Glabrous
Stem	straight old petioles at the base	twisted old leaves at the base	twisted old petioles at the base
Petiole	3–7 times as long as the leaf blade	1–3 times as long as the leaf blade	1–3 times as long as the leaf blade
Leaf blade	0.4–2.3 cm wide	0.5–4.0 cm wide	4–12 cm wide
	mostly reniform	mostly suborbicular	Suborbicular
	abaxially pale-yellow farinose	abaxially white farinose	abaxially yellow farinose
	margin revolute	margin not revolute	margin not revolute
Scape	one flower	umbel 1–7 flowered	umbel 2–16 flowered
	shorter than or equal to leaves	2–3 times as long as leaves	1.5–2 times as long as leaves
Calyx	pale- yellow farinose inside, veins 3	white farinose inside, veins 5	yellow farinose inside, veins 3
Corolla	lobes deeply emarginate	lobes deeply emarginate	lobes margin entire to obscurely crenulate
Capsule	broad-ovoid to globose, shorter than calyx	ovoid to oblong, ca. as long as calyx	oblong, longer than calyx

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

APG [Angiosperm Phylogeny Group] (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181(1): 1–20. https://doi.org/10.1111/boj.12385

Basak SK, Maiti G, Hajra PK (2014) The Genus *Primula* L. in India: A Taxonomic Revision. Bishen Singh Mahendra Pal Singh, Dehra Dun, 1–668.

Bista MS, Adhikari MK, Rajbhandari KR (2001) Flowering plants of Nepal (Phanerograms). Department of Plant Resources, Kathmandu, Nepal, 1–399.

Fang RZ (1994) Primulaceae. In: Wang WT, Wu SG (Eds) Vascular Plants of the Hengduan Mountains. Science Press, Beijing, 1477–1524.

Fang RZ (2003) Primulaceae. In: Institutum Botanicum Kunmingense Academiae Sinicae (Org.) Flora of Yunnanica, Vol. 15. Science Press, Beijing, 326–514.

Fenderson GK (1986) A synoptic guide to the genus *Primula*. Allen press, Lawrence, Kansas, 1–213.

Grierson AJC, Long DG (1999) *Primula*. In: Long DG (Ed.) Flora of Bhutan, Vol. 2(2). Royal Botanic Garden Edinburgh and Royal Government of Bhutan, 516–554.

Hara H (1966) The flora of Eastern Himalaya. University of Tokyo Press, Tokyo, 1–754.

Hara H (1971) Flora of Eastern Himalaya: Second Report. University of Tokyo Press, Tokyo, 1–393. https://doi.org/10.2307/1219257

Hu CM (1986) Primulaceae. In: Wu ZY (Ed.) Flora Xizangica, Vol. 3. Science Press, Beijing, 745–847.

Hu CM (1990) *Primula*. In: Chen FH, Hu CM (Eds) Flora Reipublicae Popularis Sinicae, Vol. 59(2). Science Press, Beijing, 1–277.

Hu CM (1994) On the geographical distribution of the Primulaceae. Journal of Tropical and Subtropical Botany 2(4): 1–14. http://jtsb.ijournals.cn/jtsb_cn/article/abstract/199404001?st=article_issue

Hu CM, Kelso S (1996) Primulaceae. In: Wu ZY, Raven PH (Eds) Flora of China, Vol. 15. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 99–185. http://www.iplant.cn/info/Primulaceae?t=foc

IUCN (2019) Guidelines for Using the IUCN Red List Categories and Criteria, prepared by the Standards and Petitions Committee, version 14. https://www.iucnredlist.org/resources/redlistguidelines

Kress WJ, DeFilipps RA, Farr E, Kyi DYY (2003) A Checklist of the Trees, Shrubs, Herbs, and Climbers of Myanmar. United States National Herbarium, Washington, DC: Smithsonian Institution, 1–590.

Li X, Cheng YH, Lin HQ, Chen C, Gao XF, Deng HN, Feng Y, Andlka PM, Ju WB, Xu B (2023) *Primula wolongensis* (Primulaceae), a new species of the primrose from Sichuan, China. PhytoKeys 218: 47–57. https://doi.org/10.3897/phytokeys.218.91161

Naithani HB (1990) Flowering Plants of India, Nepal & Bhutan (not recorded in Sir J.D.Hooker's Flora of British India). Surya Publications, Dehradun, 1–711.

Ohashi H (1975) The Flora of Eastern Himalaya: Third Report. University of Tokyo Press, Tokyo, 1–458.

Pax FA (1889) Monographische Übersicht über die Arten der Gattung *Primula*. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 10(3): 75–241.

Pax FA, Knuth R (1905) Primulaceae. Das Pflanzenreich: regni vegetablilis conspectus 22: 1–363.

Rajbhandari KR, Rai SK, Chhetri R (2021) A Handbook of the Flowering Plants of Nepal 3. Department of Plant Resources, Thapathali, Kathmandu, Nepal, 331 pp.

Richards J (2003) *Primula*. Timber Press, Portland, Oregon, 1–346.

Smith WW, Fletcher HR (1943) The Genus *Primula*: Section *Rotundifolia* Balf. Fil. Transactions of the Botanical Society of Edinburgh 33(4): 473–487. https://doi.org/10.1080/13594864309441399

Smith WW, Forrest G (1928) The Sections of the Genus *Primula*. Notes from the Royal Botanic Garden Edinburgh 16(76): 1–47.

Sun H, Zhou ZK (2002) Seed plants of the big bend gorge of Yalu Tsangpo in SE Tibet, Himalayas. Yunnan Science and Technology Press, Kunming, 1–425.

Wu YT (1999) Flora Sichuanica, vol. 13. Sichuan Science and Technology Press, Chengdu, 1–288.

Xu B, Li ZM, Sun H (2014) Seed plants of the alpine subnival belt from the Hengduan Mountains SW China. Science Press, Beijing, 1–409.

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Research Article

Ixeridium sagittarioides (Asteraceae-Cichorieae) revisited: range extension and molecular evidence for its systematic position in the *Lactuca* alliance

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Abstract

Our first record of the rare and scatteredly distributed *Ixeridium sagittarioides* for Guizhou, China, triggered a study to assess its systematic position. The species was placed in four different genera in the course of its taxonomic history and was recently treated with doubts as a member of *Ixeridium* in the Flora of China. Comparative morphological investigation and phylogenetic analyses based on the nuclear ribosomal DNA internal transcribed spacer (nrITS) and five non-coding plastid DNA regions (*petD* region, *psbA-trnH*, *trnL-trnF*, *rpl32-trnL*(UAG) and *5´rps16-trnQ*(UUG) spacers) provided evidence that the species is not a member of *Ixeridium* and the Crepidinae but has evolved by ancient hybridisation of members of the *Lactuca* alliance (Lactucinae). It is reinstated as *Lactuca sagittarioides* and a comprehensive morphological description is provided, based on material from its entire range of distribution.

Key words: Asteraceae, Cichorieae, Crepidinae, Lactucinae, *Lactuca sagittarioides*, reticulate evolution, systematic position, taxonomy

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Introduction

A perennial herb with very conspicuous, usually long-petiolate sagittiform rosette leaves and a scattered distribution along the Himalayan mountain chain from N Pakistan and NW India across Nepal, Bhutan, N Myanmar and N Thailand to Yunnan (China), was originally described as *Lactuca sagittarioides* C.B.Clarke (Clarke 1876) based on material from NW India, Nepal and Burma (Shi and Kilian in Shi et al. 2011). Later, Stebbins (1937a) removed it from *Lactuca* and placed it in *Ixeris* as *I. sagittarioides* (C.B.Clarke) Stebbins, Pak and Kawano (1992) moved it then to *Ixeridium* as *I. sagittarioides* (C.B.Clarke) Pak & Kawano, whereas Sennikov (1997) placed it in *Mycelis* as *M. sagittarioides* (C.B.Clarke) Sennikov. Today, we know from molecular phylogenetic analyses that *Lactuca* and *Mycelis* are members of the subtribe Lactucinae, while *Ixeris* and *Ixeridium* are a sister group in the subtribe

Crepidinae (Kilian et al. 2009a, 2017; Wang et al. 2013; Nakamura et al. 2014; Wang et al. 2020; Güzel et al. 2021). Both subtribes were only recently separated (Bremer 1994), lack exclusive morphological synapomorphies (Bremer 1994; Kilian et al. 2017), and disentangling them even resulted in the splitting of genera (e.g. Zhang et al. 2011a, b). Shi and Kilian (in Shi et al. 2011) expressed doubts at the placement of the species in *Ixeridium* and the Crepidinae but left the problem unsolved and up for further studies. However, *Ixeridium sagittarioides* so far has not been included in any phylogenetic study and its systematic position has not been addressed. A first record of the species from SW Guizhou made by us in 2018 (Fig. 1) then triggered a study of *I. sagittarioides*, and this contribution has the aim to reconsider its systematic position based on morphological and molecular phylogenetic investigations.

Materials and methods

Plant material

The study was based on the gathering of herbarium and tissue material for DNA isolation of *Ixeridium sagittarioides* from Guizhou, deposited in KUN, additional herbarium samples of this species from the herbaria of E, IMDY, K, KUN and PE, and further herbarium material of other species for morphological comparison from the herbaria of B, KUN, M and MSB (herbarium codes according to Index Herbariorum, http://sweetgum.nybg.org/science/ih/). In addition, digital images of specimens at BM and L were consulted through GBIF (https://www.gbif.org/species/3100771). To avoid wrong conclusions due to misidentification, occurrence records not substantiated by physical or digital specimens were not taken into account.

DNA extraction, amplification and sequencing

Extraction of DNA and amplification of markers for the accession of *Ixeridium sagittarioides* followed the protocols by Wang et al. (2013) and, as in that study, the nrITS region and five non-coding plastid DNA markers, the *petD* region and the spacers *psbA-trnH*, *trnL-trnF*, *rpl32-trnL*(UAG), *5'rps16-trnQ*(UUG), were used. PCR products were purified with a QIAquick PCR Purification Kit (BioTeke, Beijing, China) and sequenced using an ABI 3730XL automated DNA sequencer (Applied Bio-systems, Foster City, California, U.S.A.). The sequences were deposited through GenBank (Table 1).

Table 1. INSDC (International Nucleotide Sequence Database Collaboration) accession numbers of newly generated nrITS and plastid DNA sequences with specimen data of the sample used.

Sample	Specimen	Locality	Date	Marker: accession no.
Lactuca sagittarioides_ ZJW1091	*J. W. Zhang 1091* (KUN)	China, Guizhou, Wangmo, 25.18°N, 106.12°E, 700 m	13 Apr 2018	nrITS: OR196839; *petD*: OR221191; *psbA-trnH*: OR221192; *trnL-trnF*: OR221190; *rpl32-trnL*(*UAG*): OR221193; *5'rps16-trnQ*(*UUG*): OR221194.

Figure 1. *Lactuca sagittarioides* – specimen collected in Guizhou at Wangmo, 25.18°N, 106.12°E, 13 Apr 2018, *J.W. Zhang 1091* (KUN).

Sampling and sequence alignment

The *Ixeridium sagittarioides* sequences were initially included in the separate nrITS and plastid DNA matrices built by Kilian et al. (2017), aligned with MAFFT v.7 using default parameters (Katoh et al. 2017) and adjusted manually using PhyDE v.0.9971 (Müller et al. 2010). Indels were coded as binary characters using simple indel coding (Simmons and Ochoterena 2000) implemented in SeqState v.1.40 (Müller 2005); inversions were re-inverted. The nrITS matrix was subdivided into the four partitions ITS1, 5.8S, ITS2, indels. The plastid DNA matrix was subdivided into six partitions, one for each of the markers and a binary partition for the coded indels. Length-variable mononucleotide portions and hypervariable sections were excluded because of homology uncertainty. After an initial tree calculation with MP (see below) to infer the subtribal systematic position of *I. sagittarioides* based on either matrix, the sampling in the two original matrices was strongly condensed with a focus on the next related taxa in the initial reconstruction, and the nrITS matrix was supplemented by an accession of *Lactuca adenophora* from Güzel et al. (2021). Voucher data and INSDC (International Nucleotide Sequence Database Collaboration, including GenBank/EMBL/DDBJ) accession numbers of the published sequences are given in Kilian et al. (2017: appendix 1) and Güzel et al. (2021: Online Resource 1).

Phylogenetic reconstructions

Phylogenetic relationships were inferred using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). The last two were run on the high-performance computing system of the Freie Universität Berlin (Bennett et al. 2020). MP was performed with the parsimony ratchet using PRAP v.2.0 (Müller 2004) with 10 additional random cycles and default parameters in combination with PAUP v.4.0b10 (Swofford 2003); Jackknife (JK) support values were calculated in PAUP with 10,000 replicates using the TBR branch swapping algorithm with 36.788% of characters deleted and one tree held during each replicate. ML analyses were done with the MPI version of RAxML-NG 0.9.0 (Kozlov et al. 2019). The best-fit evolutionary models were searched with ModelTest-NG (Darriba et al. 2019) and selected according to the Bayesian Information Criterion: SYM+G4 for ITS1, TrNef+I+G4 for 5.8S, TIM3ef+G4 for ITS2; TPM1uf+G4 for the *petD*-region and the *trnL-F* spacer and TVM+G4 for the *psbA-trnH*, *trnQ-rps16* and *rpl32-trnL* spacers; the binary indel partitions were not included due to software restrictions. The tree space was explored with 50 tree searches using 25 random and 25 parsimony-based starting trees. Standard bootstrapping was done employing the bootstopping test with a bootstrap convergence requirement of 3% default cut-off; the support values were mapped onto the best-scoring tree. The BI analyses were performed with the MPI version of MrBayes (Ronquist et al. 2012). The best-fit evolutionary models were sampled across the general time reversible (GTR) model space in the Bayesian MCMC analysis (Huelsenbeck et al. 2004) and two simultaneous runs of four parallel chains each were performed for 3×10^7 generations with a sample frequency of 1 tree per 2000 generations and a conservative burn-in of 20%. Convergence of the runs was ensured by having the post-burn-in average standard deviation of split frequencies below 0.01 and an effective sampling size (ESS) of some 1000s in either run for all parameters. TreeGraph v.2 (Stöver and Müller 2010) was used to visualize the trees with statistical node support.

Results

Phylogenetic analysis

The aligned nrITS region of 76 samples had a length of 687 characters; together with the coded indels the matrix included a total of 778 characters, of which 298 were parsimony-informative. The MP analysis resulted in 1532 most parsimonious trees (L = 1391, CI = 0.479, RI = 0.674, RC = 0.323, HI = 0.521), largely congruent in topology with the trees of the BI and ML analyses. Fig. 2 shows the BI majority consensus phylogram with the BI posterior probabilities (PP) and ML bootstrap (BS) support values (bootstrapping converged after 1400 replicates) below the branches and the MP jackknife (JK) support values above the branches.

The final aligned concatenated plastid DNA markers of 74 samples had a length of 5827 characters; together with the coded indels the matrix included a total of 6207 characters, of which 504 were parsimony-informative. The MP analysis resulted in 1720 most parsimonious trees (L = 1627, CI = 0.770, RI = 0.814, RC = 0.627, HI = 0.230), largely congruent in topology with the trees of the BI and ML analyses. Fig. 3 shows the BI majority consensus phylogram with the BI posterior probabilities (PP) and ML bootstrap (BS) support values (bootstrapping converged after 300 replicates below the branches and the MP jackknife (JK) support values above the branches.

Ixeridium sagittarioides is deeply nested in the subtribe Lactucinae both in the nrITS (Fig. 2) and the plastid DNA phylogeny (Fig. 3), but at different positions. In the nrITS phylogeny, the species is nested in the *Lactuca* clade (PP 1, BS 79, JK 75) and resolved as sister to the strongly supported *Lactuca racemosa-L. macrophylla* clade with very weak support (PP 0.88, JK 56) in the Bayesian and MP analyses, and only moderate support (BS 77) in the ML analysis. In contrast, in the plastid DNA phylogeny, the species is nested in the earlier diverging *Notoseris-Paraprenanthes* clade and resolved as sister to *Paraprenanthes alatipes* (Collett & Hemsl.) Z.Wei & S.X.Zhu = *Lactuca parishii* Craib with strong support (PP 1) in the Bayesian, moderate support (BS 77) in the ML and weak support (JK 62) in the MP analysis.

Morphology

For the comparison of *Lactuca sagittarioides* with *Ixeridium* on the one hand and its sister clades in the subtribe Lactucinae inferred from the molecular phylogenetic analyses of the nrITS and the plastid DNA matrices on the other hand, diagnostic morphological characters, in particular of the achenes (Fig. 4), were used. The results are summarised in Table 2 and show that, in contrast to superficial resemblance through capitulum shape and corolla colour, the species also differs from *Ixeridium* in achenes morphology. Congruence is highest with *Paraprenanthes*, apart from the different capitulum shape and corolla colour, whereas also achene and pappus morphology of the *Lactuca racemosa-L. macrophylla* clade does not well match with that of *L. sagittarioides*.

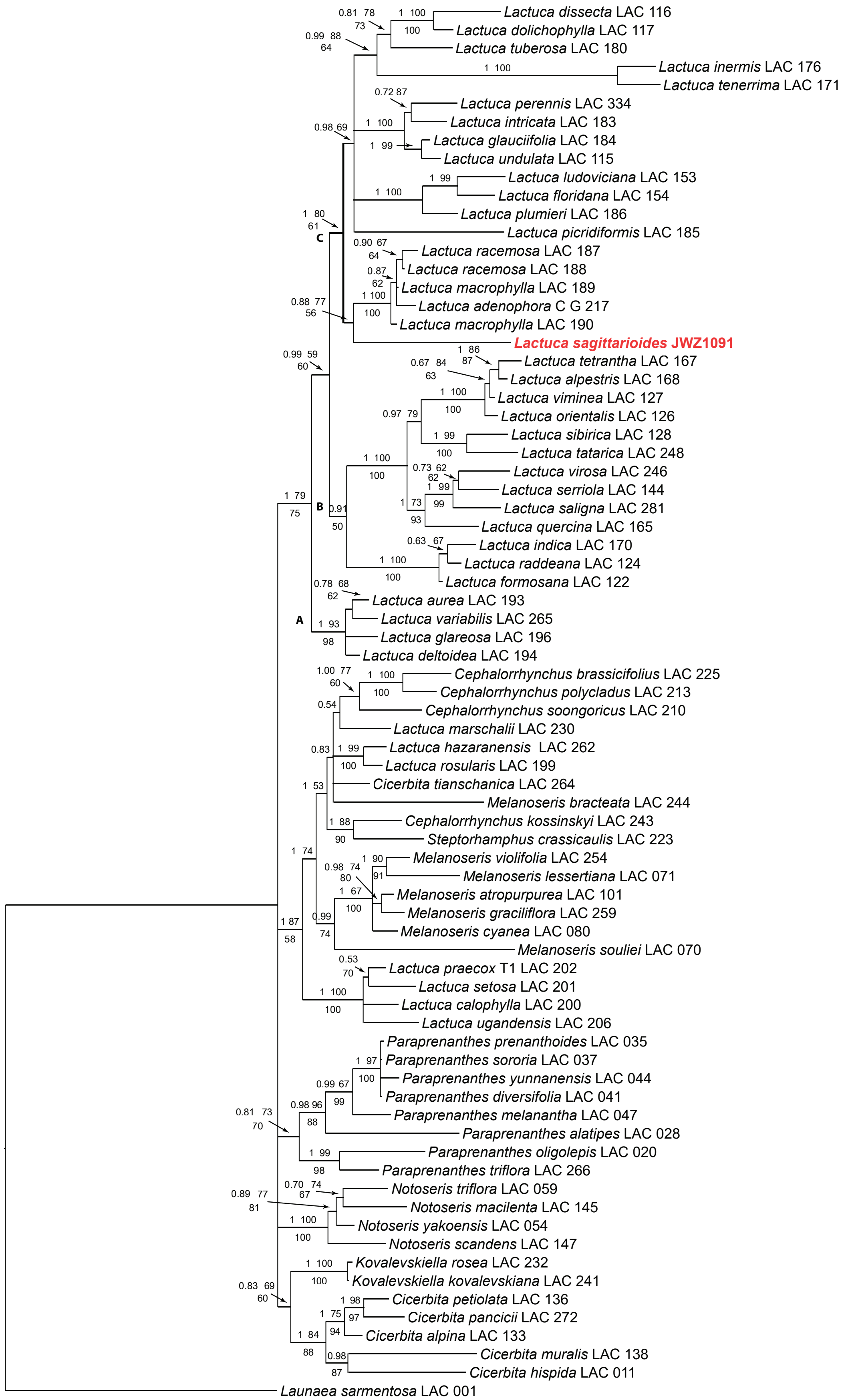

Figure 2. Majority consensus phylogram of the Lactucinae from Bayesian analysis (support values: first line Bayesian posterior probability / maximum likelihood bootstrap; second line maximum parsimony jackknife) based on the nrITS region.

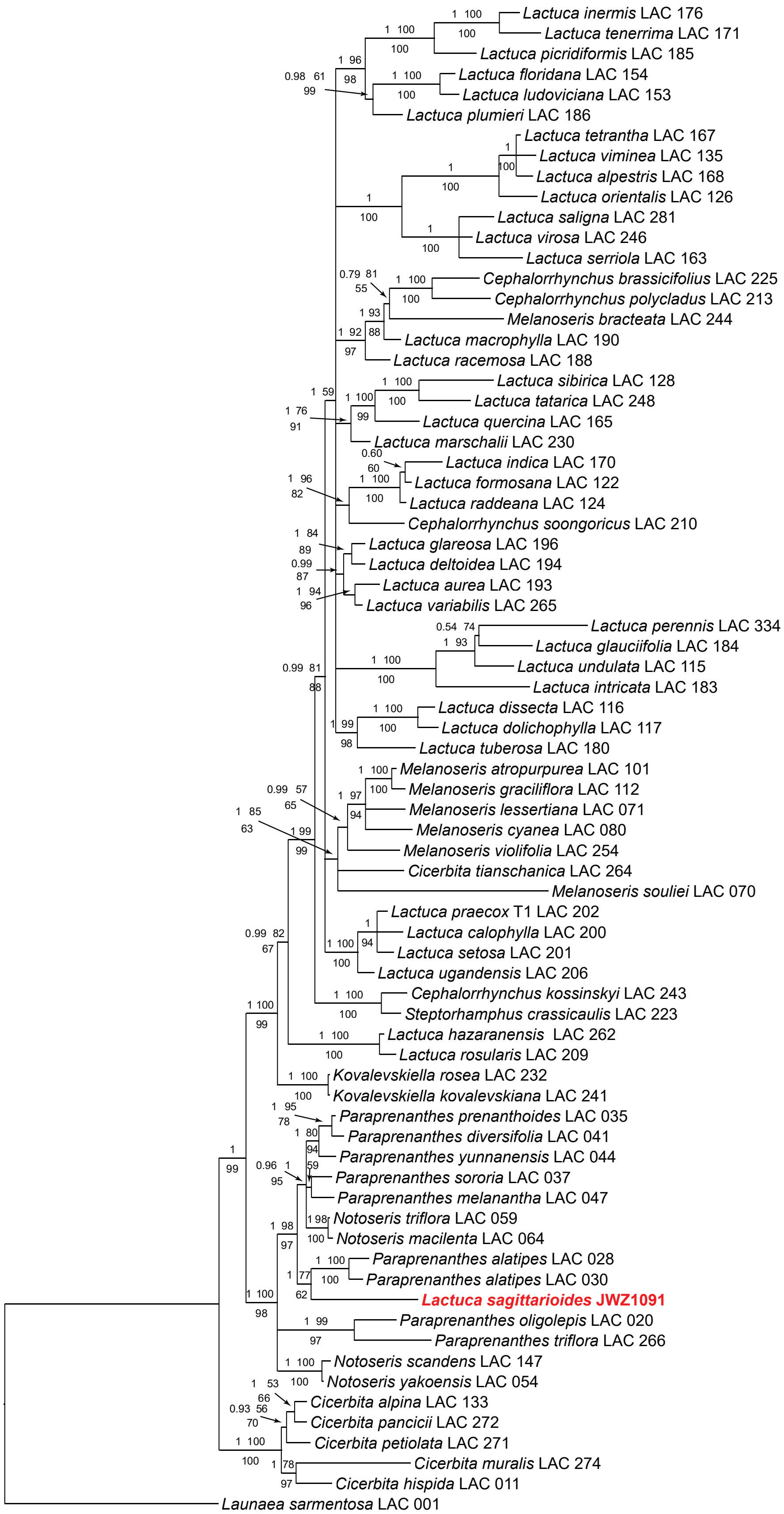

Figure 3. Majority consensus phylogram of the Lactucinae from Bayesian analysis (support values: first line Bayesian posterior probability / maximum likelihood bootstrap; second line maximum parsimony jackknife) based on the five non-coding plastid DNA regions.

Table 2. Diagnostic morphological features of *Lactuca sagittarioides* in comparison with the genus *Ixeridium* and the related Lactucinae members inferred from the molecular phylogenetic analyses of the nrITS and the plastid DNA matrices, respectively.

Diagnostic features	*Lactuca sagittarioides*	*Ixeridium*	*Lactuca racemosa-L. macrophylla* clade	*Paraprenanthes*
Capitula	moderately narrowly cylindrical	moderately narrowly cylindrical	moderately narrowly to broadly cylindrical	narrowly cylindrical
Corolla, colour	yellow	yellow	cyanic	cyanic
Achenes, ribbing pattern	5 main ribs each accompanied by 2 secondary ribs; lateral ribs not enlarged	10 equal ribs, none winged	usually 4 main ribs each accompanied by 2 secondary ribs, lateral ribs winglike enlarged	5 main ribs each accompanied by 2 secondary ribs; lateral ribs not enlarged
Achenes, ornamentation	muricate	± smooth	faintly muricate	muricate
Achenes, carpopodium	callose, uninterrupted annular	± callose, uninterrupted tubular	callose, uninterrupted annular	callose, uninterrupted annular
Pappus, composition	one series of bristles	one series of bristles	one series of bristles and outer row of minute hairs	one series of bristles
Pappus, colour	white	yellowish or straw-coloured	white	white

Discussion

Systematic position of *Ixeridium sagittarioides*

Molecular phylogenetics

Our molecular phylogenetic analyses resolved *Ixeridium sagittarioides* unanimously as a member of subtribe Lactucinae and therefore deprive the basis for the placement in *Ixeridium* and the Crepidinae. Otherwise, the analyses revealed a surprising cytonuclear discordance (Lee-Yaw et al. 2018). All three phylogenetic reconstructions based on the nrITS matrix placed the species deeply in the *Lactuca* clade. There, it is resolved in a sister group relationship to the *L. racemosa*-*L. macrophylla* clade, but with very weak (BI and MP) or moderate (ML) support and at a comparatively long branch, indicating genetic distance (Fig. 2). Hence whereas the placement in *Lactuca* must be considered well supported, the indicated relationship to the *L. racemosa*-*L. macrophylla* clade should be taken with caution, in view of the dissimilarities in achene morphology, and may be even suspected as a result of long branch attraction (Bergsten 2005). The plastid DNA analyses, resolved the species in a very well supported clade including the E Asian genera *Notoseris* and *Paraprenanthes*. This clade is known from the previous analyses based on plastid DNA by Wang et al. (2013) and Kilian et al. (2017). Within the *Notoseris-Paraprenanthes* clade, the species forms a sister group relationship with *Paraprenanthes alatipes*. However, the altogether moderate statistical support and the comparatively long branch (Fig. 3) speak against a very close relationship.

Morphology

The achenes of *Lactuca sagittarioides* (Fig. 4A) are slightly compressed and have 5 main ribs accompanied by usually 2 secondary ribs (best seen in the middle third), thus altogether usually have 15 ribs, sometimes a single secondary rib

Figure 4. Achenes **A** *Lactuca sagittarioides*; specimen: China, Yunnan, Forrest 29519 (E 00489230) **B** *Paraprenanthes triflora*; specimen: Nepal, Pokahara region, between Tikhedhunga and Ghorepani. 19 Sep 2008, A. Suchorukow N-15 (B) **C** *Lactuca macrophylla*; specimen: Turkey Artvin, Şavşat, Pınarlı Köyü, Balıkgölü girişi, kalıntı bitkiler arası, 2035 m, 13 Sep 2014, Coşkunçelebi & Güzel 339 (KTUB). Scale bars: 0.5 mm (**A, B**); 1 mm (**C**); photographs by Murat Güzel.

may be (partly) missing. Of the five main ribs two are in lateral position, one in the middle of the adaxial face and two are about equally spaced on the abaxial face. This ribbing pattern is considered plesiomorphic for the tribe (Kilian et al. 2009a) and is also present in both the Lactucinae and Crepidinae. In the Lactucinae, reductions in the number of main ribs as well as of the number of secondary ribs are frequent (Stebbins 1937b, 1940; Kilian et al. 2009a). In the Crepidinae, in contrast, both increases (Stebbins 1940) and reductions in the number of the secondary ribs have evolved, whereas the number of the main ribs is assumed to have been unchanged. Shape and prominence of main and secondary ribs have become equal in several groups. Achenes with only 10 ribs, by fusion of the adjacent secondary ribs, characterise *Askellia* (Pak 1993 sub *Crepis* sect. *Ixeridopsis*), *Ixeris* and *Ixeridium* (Pak and Kawano 1990 sub *Ixeris* s.l.), and are a synapomorphy of the *Askellia-Ixeris-Ixeridium* clade (see the phylogenetic backbone of the Crepidinae based on nrITS by Wang et al. 2020). Apparently, the ribbing pattern of the achenes of *L. sagittarioides* is clearly different from that of *Ixeridium*. The achenes of *L. sagittarioides*, moreover, have a callose non-interrupted annular carpopodium (Haque and Godward 1984), which is characteristic for members of the subtribe Lactucinae (Kilian et al. 2009a), whereas in the Crepidinae interrupted callose carpopodia predominate. *Ixeris* and *Ixeridium*, however, are exceptions and have uninterrupted, somewhat tubular carpopodia, which may have contributed to their former placement along with *Lactuca* by Bentham (in Bentham and Hooker 1873). Hence, the systematically relevant achene morphology provides further evidence against a placement of *L. sagittarioides* in *Ixeridium* and the Crepidinae, and corroborates its placement in the Lactucinae. Also with respect to pappus colour, *L. sagittarioides* disagrees with *Ixeridium*, because all species clearly known to belong to *Ixeridium* have a straw-coloured or yellowish pappus, a feature which also distinguishes the genus from its sister group *Ixeris*.

Within the Lactucinae, the weakly supported sister group relationship with the *Lactuca racemosa*-*L. macrophylla* clade in the nrITS phylogeny does not agree well with achene morphology (Fig. 4C): the members of this clade are characterised by distinctly compressed achenes with four main ribs, narrowly winged lateral ribs, usually rather weak or inconspicuous secondary ribs, a faintly muricate surface and a pappus with an outer row of minute hairs; hence markedly different to the achenes of *L. sagittarioides*. The yellow flower colour of *L. sagittarioides* also disagrees with the cyanic flower colour of the three members of that clade. Achenes of the plesiomorphic constitution with five main ribs, well developed secondary ribs and a less strongly compressed corpus are, however, still present in most other terminal clades of *Lactuca*, including the larger clade C (Fig. 2), to which the *Lactuca racemosa*-*L. macrophylla* clade belongs. This also holds for the yellow flower colour, which, moreover, is not only known to vary within clades but sometimes also within a species, examples being *L. tuberosa* Jacq. and *L. inermis* Forssk.

The sister group relationship with *Paraprenanthes alatipes* of the *Notoseris*-*Paraprenanthes* clade revealed in the plastid DNA marker phylogeny, in contrast, shows a better agreement with achene morphology: shape, ribbing pattern, surface ornamentation and also pappus structure of *L. sagittarioides* and *Paraprenanthes* principally match (Fig. 4A, B). However, in view of this more widespread, plesiomorphic constitution, the resemblance with *L. sagittarioides* is not very conclusive for a closer phylogenetic relationship. Other morphological features, such as the exclusively cyanic or purple flower colour and predominantly few-flowered, slender capitula in the *Notoseris*-*Paraprenanthes* clade even speak against a very close relationship.

Lactuca sagittarioides is distributed along the lower escarpments of the Himalaya belt and extends into the mountain ranges adjacent to the east in Yunnan and Guizhou. The new record from central northern Guizhou makes its presence also in the province of Sichuan rather likely. The *Lactuca* lineage (in the sense of Kilian et al. 2017 and Jones et al. 2018) is distributed chiefly from the Mediterranean Basin and Europe along the Alpine-Himalayan belt (Storetvedt 1990) across SW to E Asia, and also in North America. Its region of origin is the E Mediterranean-SW Asian area according to Kilian et al. (2017), where also the *Lactuca racemosa*-*L. macrophylla* clade is present, being restricted to the Caucasus, Ural Mts., Turkey and N Iran (Güzel et al. 2021). *Paraprenanthes alatipes*, in contrast, is distributed in a rather small area at the easternmost edge of the Alpine-Himalayan belt in SW Yunnan, N Myanmar, N Thailand and N Vietnam. A plausible scenario according to the molecular phylogenetic findings would be that *Lactuca sagittarioides* originates from the hybridisation of a *Lactuca* ancestor on its eastward migration from SW Asia along the Alpine-Himalayan belt with a *Paraprenanthes* ancestor extending its area of distribution westwards.

The context of the subtribe lends further support to such a scenario when we consider the numerous reticulation events at various depths of the species tree to be concluded from previous studies (Liu et al. 2013; Wang et al. 2013; Kilian et al. 2017; Jones et al. 2018; Güzel et al. 2021; Yin et al. 2022). *L. sagittarioides*, however, is the first case with evidence for a putative reticulation event between ancestors of the *Lactuca* lineage and the *Notoseris*-*Paraprenanthes* lineage(s). Low statistical support for, and morphological discrepancies of

L. sagittarioides with the sister groups resolved in the nrITS tree and the plastid tree, make it likely that both parental ancestors are extinct.

Taxa supposed to have evolved from ancient intergeneric reticulation events would, for consistency, be treated in a phylogeny-based classification as nothogenera. The relationships of the Lactucinae lineages tentatively classified at generic rank (Kilian et al. 2017) are, however, incompletely resolved. For any revised classification the relationships of these lineages are essential. The inferred relative frequency of ancient reticulation events in the Lactucinae show that the barriers between different lineages were rather weak at times and that may also have added to the shallow morphological differentiation between the different lineages treated as genera. In particular, the separation of *Lactuca* and *Melanoseris* is strongly questionable (Güzel et al. 2021). For the time being, creating nothogenera seems therefore premature and a classification of ancient hybridogenous lineages according to the nuclear tree the preferable interim solution, considering the essential weight of the nuclear genome or the nature of the taxon.

Taxonomy

We treat the taxon in accordance with the findings of the nuclear ribosomal ITS phylogeny as a member of *Lactuca*.

***Lactuca sagittarioides* C.B.Clarke, Compos. Ind.: 265. 1876.**

≡ *Ixeris sagittarioides* (C.B.Clarke) Stebbins in J. Bot. 75: 51. 1937.
≡ *Ixeridium sagittarioides* (C.B.Clarke) Pak & Kawano in Mem. Fac. Sci. Kyoto Univ., Ser. Biol. 15: 48. 1992.
≡ *Mycelis sagittarioides* (C.B.Clarke) Sennikov in Bot. Zhurn. 82(5): 112. 1997.

Syntypes. “Himalaya boreali-occidentali”, 6000’, *T. Thomson* (K); [India, Uttarakhand, Kumaon Hills] “Nynee Tal” [= Nainital], *T. Thomson* (K); [India, Himachal Pradesh, Punjab] “Dhurmsala” [= Dharamshala], *C.B. Clarke* (K); Nepal, 3.1821, *Wallich Cat. 3270* (K001118954, digit. image!; BM 000035537, digit. image!); Burma, ad Moyen, 1200’, *J. Anderson* (K).

Description. Perennial rosette herb, (15–)20–65 cm tall; caudex small, often branched and plant with a two or a few rosettes. Taproot cylindric to narrowly turniplike, to c. 1 cm in diam.; lateral roots perhaps also shoot-bearing. Stem usually one per rosette, erect, branched from basal half or higher up, leafless or with few leaves in proximal portion, sparsely hairy. Rosette leaves conspicuously sagittiform and usually long-petiolate; petiole 2–22 cm, narrowly winged, margin entire or distantly sinuate-dentate; lamina triangular in outline, 2–8 × 1.5–10 cm, usually with a basal pair of acute to acuminate triangular lateral lobes and an acute triangular terminal lobe; the lateral lobes narrow or broad, sometimes much reduced to missing, directed downwards, outwards or upwards; sometimes lamina with an additional rudimentary pair of lobes above the basal one and then pentagonal; margin shallowly sinuate-dentate and often also denticulate. Stem leaves few, the lower ones similar to basal leaves but smaller and less lobed, upper leaves lanceolate to linear-lanceolate, entire, narrowed into short petiolate portion. Synflorescence paniculiform-corymbiform, with some to many capitula. Capitula with c. 12–25 florets; peduncle wiry, mostly 1–2 cm long. Involucre narrowly cylindric, 7–8 mm at anthesis to 8–10 mm at fruiting; outer phyllaries narrowly ovate to lanceolate, apex acute, outermost c. 2 mm, innermost up to 2/3 of the length of the inner (rarely longer); inner phyllaries c. 8(–10), linear-lanceolate, acute. Florets with [orange-, according to collector] yellow corolla, c. 12–14 mm; ligulae c. 6–8 mm; anther tube yellow, fertile portion c. 2.2 mm, apical appendages 0.2 mm, basal appendages 0.4–0.5 mm; style yellow. Achenes 4–4.5 mm long, slightly compressed, subfusiform with largest diameter in middle third, apically attenuate into a beak, basally less strongly attenuate into an annular carpophore; corpus with 5 main ribs, each with ±2 secondary ribs; scabrid of antrorse triangular apical projections of achene epidermis cells, brown to purplish brown; beak 0.6–1.2(–2) mm, pale. Pappus 4–6 mm, persistent, of scabrid, white bristles.

Variation. Although the leaves are always distinctly sagittiform, their shape and size underlie considerable variation. The shape variation given in the description is believed to circumscribe its full extent, but we are uncertain whether the size variation is fully covered in the description. A sterile specimen from NW Himalaya (Chamba state, Kuntha Forest, Aug 1898, J.H. Lace 14C (E00360966) only including a leaf rosette may belong to *Lactuca sagittarioides*; its leaves approach 40 cm in length, with a petiole of up to 30 cm, and a lamina of up to 10 × 20 cm. The beak length of the achenes usually ranges between 0.6–1.2 mm, but Gamble 23483 from NWP has a beak of c. 2 mm; its innermost outer phyllaries are unusually long, approaching the inner in length.

Specimens seen. India. Uttarakhand: Kumaon, Lohba, 5500’ Apr 1848, R. Strachey & J.B. Winterbottom (K); Kumaon, Gungoli, 5300’, R. Stratchey & J.S. Winterbottom (BM 011024277, digit. image). – Uttar Pradesh, [“North western Province, Jannsar[?] District, 3000’, May 1892, J.S. Gamble (K).

Bhutan. Khine Lhakang, 6000’, 15 Apr 1949, F. Ludlow et al. 20135 (BM 000035434, digit. image)

Burma. Shan hills Matean[?] near Wankou[?], 5000’, Mar 1888, H. Collett 471 (K); Mundat, 4800’, 29 Apr 1956, F. Kingdon-Ward 22171 (BM 11024278, digit. image).

Thailand. Chiengmai, Doi Sutep, open *Quercus* forest, 1250 m, 18 Apr 1958, T. Sørensen et al. 2876 (C, digit. image)

China. Yunnan: Salween valley, 25°6'N, 98°50'E, slopes, dry grassy banks, Apr 1931 G. Forrest 29519 (E 00489230, PE); Jengyueh, 25°N, 98°36'E, 5000–7000’, hills, dry clay pasture, Aug 1924, G. Forrest 24794 (E00489233); Jengyueh, 25°N, 98°36'E, 5000–7000’, hills, open pasture, Mar 1924 G. Forrest 24004 (E00489232); Jengyueh, 25°N, 98°36'E, 7000’, hills, open stony clay pasture, Apr 1925, G. Forrest 26308 (E 00489231; K, PE); [...], S.W. grass mts, 5000’, A. Henry 12998 (K); Jingdong, San Cha Ho, 24°36'56"N, 100°42'35"E, 1600 m, 13 Mar 1940, M.G. Li 1884 (KUN); Shuangjiang, 23°28'24.6"N, 99°49'39.72"E, 1068 m, Apr 1936, C.W. Wang 72957 (KUN, PE); Xingping, Pingdian, 24°01'21"N, 101°52'20"E, 1326 m, 1 Jun 2012, Xingping survey team 5304270356 (IMDY); Menghai, Meng’e, 22°13'30"N, 100°17'49"E, 1195 m, Menghai survey team 5328220572 (IMDY); Jinghong, Caiyang River, 22°09'23.51"N, 101°11'59.28"E, 1250 m, Jinghong survey team 5328010664 (IMDY). – Guizhou: Wangmo, 25.18°N, 106.12°E, 700 m, 13 Apr 2018, *J.W. Zhang 1091* (KUN).

Distribution. *Lactuca sagittarioides* is distributed along the Himalayan chain from N Pakistan across NW India, Nepal, Bhutan, N Myanmar and N Thailand to SW China (for references see Kilian et al. 2009b). It is found on open, often grassy slopes, at altitudes mostly between 1500 and 2000 m, but down to 700 m in Guizhou and up to somewhat above 2000 m in Yunnan. The occurrence of the species seems altogether very scattered and it does not seem to be frequent anywhere.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Jianwen Zhang and Norbert Kilian conceptualised the paper and worte the draft of the manuscript, and did, together with Jiang-Hua Huang and Hang Sun, the investigation. All authors reviewed and revised the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Bennett L, Melchers B, Proppe B (2020) Curta: a general-purpose high-performance computer at ZEDAT, Freie Universität Berlin. Refubium, Dokumente FU. http://dx.doi.org/10.17169/refubium-26754 [Accessed 15 March 2021]

Bentham G, Hooker JD (1873) Genera plantarum, vol. 2(1). Londini [London], Lovell Reeve & Co. https://doi.org/10.5962/bhl.title.747

Bergsten J (2005) A review of long-branch attraction. Cladistics 21(2): 163–193. https://doi.org/10.1111/j.1096-0031.2005.00059.x

Bremer K (1994) Asteraceae. Cladistics and classification. Portland, Timber.
Clarke CB (1876) Compositae indicae descriptae et secus genera *Benthamii* ordinatae. Calcutta, Thacker, Spink and Company. https://doi.org/10.5962/bhl.title.49202
Darriba D, Posada D, Kozlov AM, Stamatakis A, Morel B, Flouri T (2019) ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. Molecular Biology and Evolution 37(1): 291–294. https://doi.org/10.1093/molbev/msz189
Güzel ME, Coşkunçelebi K, Kilian N, Makbul S, Gültepe M (2021) Phylogeny and systematics of the Lactucinae (Asteraceae) focusing on their SW Asian centre of diversity. Plant Systematics and Evolution 307(1): 1–14. https://doi.org/10.1007/s00606-020-01719-y
Haque MZ, Godward MBE (1984) New records of the carpopodium in Compositae and its taxonomic use. Botanical Journal of the Linnean Society 89(4): 321–340. https://doi.org/10.1111/j.1095-8339.1984.tb02564.x
Huelsenbeck JP, Larget B, Alfaro ME (2004) Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. Molecular Biology and Evolution 21(6): 1123–1133. https://doi.org/10.1093/molbev/msh123
Jones KE, Schilling EE, Dias EF, Kilian N (2018) Northern Hemisphere disjunctions in *Lactuca* (Cichorieae, Asteraceae): Independent Eurasia to North America migrations and allopolyploidization. Willdenowia 48(2): 259–284. https://doi.org/10.3372/wi.48.48206
Katoh K, Rozewicki J, Yamada KD (2017) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20(4): 1160–1166. https://doi.org/10.1093/bib/bbx108
Kilian N, Gemeinholzer B, Lack HW (2009a) Tribe Cichorieae. In: Funk VA, Susanna A, Stuessy T, Bayer R (Eds) Systematics, evolution, and biogeography of the Compositae. IAPT, Vienna, 343–383.
Kilian N, Hand R, von Raab-Straube E [Eds] (2009b[+]) Cichorieae Systematics Portal. http://cichorieae.e-taxonomy.net/portal/
Kilian N, Sennikov A, Wang Z-H, Gemeinholzer B, Zhang J-W (2017) Sub-Paratethyan origin and Middle to Late Miocene principal diversification of the Lactucinae (Compositae: Cichorieae) inferred from molecular phylogenetics, divergence-dating and biogeographic analysis. Taxon 66(3): 675–703. https://doi.org/10.12705/663.9
Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A (2019) RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics (Oxford, England) 35(21): 4453–4455. https://doi.org/10.1093/bioinformatics/btz305
Lee-Yaw JA, Grassa CJ, Joly S, Andrew RL, Rieseberg LH (2018) An evaluation of alternative explanations for widespread cytonuclear discordance in annual sunflowers (*Helianthus*). The New Phytologist 221(1): 515–526. https://doi.org/10.1111/nph.15386
Liu Y, Chen Y-S, Yang Q-E (2013) Generic status, circumscription, and allopolyploid origin of *Faberia* (Asteraceae: Cichorieae) as revealed by ITS and chloroplast DNA sequence data. Taxon 62(6): 1235–1247. https://doi.org/10.12705/626.14
Müller K (2004) PRAP— Computation of Bremer support for large data sets. Molecular Biology and Evolution 31: 780–782. https://doi.org/10.1016/j.ympev.2003.12.006
Müller K (2005) SeqState: Primer design and sequence statistics for phylogenetic DNA datasets. Applied Bioinformatics 4: 65–69. https://doi.org/10.2165/00822942-200504010-00008
Müller K, Müller J, Quandt D (2010) PhyDE: Phylogenetic Data Editor, version 0.9971. http://www.phyde.de/index.html

Nakamura K, Chung S-W, Kono Y, Ho M-J, Hsu T-C, Peng C-I (2014) *Ixeridium calcicola* (Compositae), a new limestone endemic from Taiwan, with notes on its atypical basic chromosome number, phylogenetic affinities, and a limestone refugium hypothesis. PLoS ONE 9(10): e109797. https://doi.org/10.1371/journal.pone.0109797

Pak J-H (1993) Taxonomic implications of fruit wall anatomy and karyology of *Crepis* sect. *Ixeridopsis* (Compositae, Lactuceae). Korean Journal of Plant Taxonomy 23: 1–11. https://doi.org/10.11110/kjpt.1993.23.1.011

Pak J-H, Kawano S (1990) Biosystematic studies on the genus *Ixeris* and its allied genera (Compositae-Lactuceae) I. Fruit wall anatomy and its taxonomic implications. Acta Phytotaxonomica et Geobotanica 41: 43–60.

Pak J-H, Kawano S (1992) Biosystematics studies on the genus *Ixeris* and its allied genera (Compositae-Lactuceae) IV. Taxonomic treatments and nomenclature. Memoirs of the Faculty of Science Kyoto University 15: 29–61. [Series of Biology]

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhn S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sennikov AN (1997) Critical notes on the species of the subtribes Lactucinae and Crepidiinae (Asteraceae, Lactuceae) from Mongolia, China and Vietnam. Botanicheskii Zhurnal (St Petersburg) 82: 110–117.

Shi Z, Ge X, Kilian N, Kirschner J, Štěpánek J, Sukhorukov AP, Mavrodiev EV, Gottschlich G (2011) Cichorieae. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China Volume 20–21 (Asteraceae). Beijing, Science Press; St. Louis, Missouri Botanical Garden Press, 195–353.

Simmons MP, Ochoterena H (2000) Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49(2): 369–381. https://doi.org/10.1093/sysbio/49.2.369

Stebbins GL (1937a) Critical notes on the genus *Ixeris*. Le Journal de Botanique 75: 43–51.

Stebbins GL (1937b) Critical notes on *Lactuca* and related genera. Le Journal de Botanique 75: 12–18.

Stebbins GL (1940) Studies in Cichorieae: *Dubyaea* and *Soroseris*. Endemics of the Sino-Himalayan region. Memoirs of the Torrey Botanical Club 19: 1–76.

Storetvedt KM (1990) The Tethys Sea and the Alpine-Himalayan orogenic belt; mega-elements in a new global tectonic system. Physics of the Earth and Planetary Interiors 62(1–2): 141–184. https://doi.org/10.1016/0031-9201(90)90198-7

Stöver BC, Müller K (2010) TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11(1): 7. https://doi.org/10.1186/1471-2105-11-7

Swofford DL (2003) PAUP*: Phylogenetic Analysis Using Parsimony (*and other methods), version 4.0b 10. Sunderland, Sinauer Associates Inc. Publishers.

Wang Z-H, Peng H, Kilian N (2013) Molecular phylogeny of the *Lactuca* alliance (Cichorieae subtribe Lactucinae, Asteraceae) with focus on their Chinese centre of diversity detects potential events of reticulation and chloroplast capture. PLoS ONE 8(12): e82692. https://doi.org/10.1371/journal.pone.0082692

Wang Z-H, Kilian N, Chen Y-P, Peng H (2020) *Sinoseris* (Crepidinae, Cichorieae, Asteraceae), a new genus of three species endemic to China, one of them new to science. Willdenowia 50(1): 91–110. https://doi.org/10.3372/wi.50.50109

Yin Z-J, Wang Z-H, Kilian N, Liu Y, Peng H, Zhao MX (2022) *Mojiangia oreophila* (Crepidinae, Cichorieae, Asteraceae), a new species and genus from Mojiang County, SW

Yunnan, China, and putative successor of the maternal *Faberia* ancestor. Plant Diversity 44(1): 83–93. https://doi.org/10.1016/j.pld.2021.06.007

Zhang J-W, Boufford DE, Sun H (2011a) *Parasyncalathium* J.W. Zhang, Boufford & H. Sun (Asteraceae, Cichorieae): A new genus endemic to the Himalaya-Hengduan Mountains. Taxon 60(6): 1678–1684. https://doi.org/10.1002/tax.606012

Zhang JW, Nie ZL, Wen J, Sun H (2011b) Molecular phylogeny and biogeography of three closely related genera, *Soroseris*, *Stebbinsia*, and *Syncalathium* (Asteraceae, Cichorieae), endemic to the Tibetan Plateau, SW China. Taxon 60(1): 15–26. https://doi.org/10.1002/tax.601003

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Research Article

Neotypification for five names linked to *Arenaria* (Caryophyllaceae) for the endemic flora of Peru and Bolivia

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Abstract

The names *Arenaria mattfeldii*, *A. pallens*, *A. peruviana*, *A. pintaudii*, and *A. stuebelii* (Caryophyllaceae, Arenarieae) from Peru and Bolivia were studied and neotypified based on specimens preserved at B and P.

Key words: Arenarieae, Bolivia, nomenclatural type, Peru

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Introduction

Arenaria L. (Caryophyllaceae Juss.) is a genus comprising about 160–175 species of annual and perennial herbs mostly distributed in the northern temperate and subarctic regions, the Mediterranean, Mexico, and the Andes of South America (see Bittrich 1993; Hernández-Ledesma et al. 2015; POWO 2023) but other authors (Sadeghian et al. 2015) include 150–300 species in the genus. The molecular data by Greenberg and Donoghue (2011), Dillenberger and Kadereit (2014), and Sadeghian et al. (2015) showed that *Arenaria* is polyphyletic and several names were transferred to other genera (see e.g., Conti et al. 2014; Dillenberger and Kadereit 2014; Sadeghian et al. 2015; Iamonico 2016; De Luca et al. 2022). From a nomenclatural point of view, questions remaining to be addressed concern several names that are still untypified (see e.g., Iamonico 2013, 2014, 2016, 2019, 2022).

As part of ongoing studies on the systematics of Andean *Arenaria* (Montesinos-Tubée and Teillier 2022; Montesinos-Tubée and Iamonico 2023), here we present nomenclatural notes concerning some names in *Arenaria* described from the Andean region and included in section *Dicranilla* (Fenzl) F.N. Williams and sect. *Leiosperma* Williams.

Materials and methods

The first author went to the type localities described by Weberbauer in Muschler (1911) and Macbride (1937) during expeditions carried out between 2015–2022 in the Central Andes and made numerous collections of *Arenaria*.

The collections were deposited mostly at HSP and B. A subsequent exhaustive investigation of herbarium material at B (Herbarium Berolinense) revealed that some of the material appointed by Macbride (1937) was unfortunately not photographed prior to the destructions of large parts of the herbarium. Only an image of *Arenaria mattfeldii* is available at the Berlin Negatives Digitization Project (https://collections–botany.fieldmuseum.org/project/6454).

The present study is based on the analysis of relevant literature (protologues included) and examination (mainly by the first author) of specimens preserved at the herbaria B, F, GOET, LPZ, MO, and P (acronyms according to Index Herbariorum - Thiers 2023).

The International Code of Nomenclature articles cited throughout the text follow the Shenzhen Code (ICN; Turland et al. 2018).

Results and discussion

***Arenaria mattfeldii* Baehni, Publ. Field Mus. Nat. Hist., Bot. Ser. 13(2/2): 601. 1937.**

Neotype (designated here). Peru. La Libertad: Llautabamba, Huamachuco, 4650 m, 8 May 1954, *J. Infantes 4672* (B100747343!, Fig. 2).

Macbride (1937: 601) validly published *Arenaria mattfeldii* providing a detailed diagnosis accompanied by the following note: “Junín: Yauli, above the Hacienda Arapa, near the Lima–Oroya railroad, *Weberbauer 353* (type, in Herb. Deless.)”. “Herb. Deless.” means “Herbarium Delessert”. According to HUH–Index of Botanists (2013a), the surname “Delessert” refers to, at least, three different people, i.e. Adolphe Delessert (collector in India, Indonesia, Malaysia, Reunion), Henri Delessert (collector in Cuba), and Jules Paul Benjamin Delessert (collector in Brazil). Unfortunately, Macbride (1936: 9–81), in the Introduction of his *Flora of Peru*, did not mention “Delessert” and we did not find any other reference to an “Herb. Deless.” throughout the various volumes of the flora. However, based on the collector reported by Baehni in Macbride (1937: 601), i.e., Weberbauer, we tried to search original material at B, where Weberbauer’s collection is preserved (HUH–Index of Botanists 2013b). Unfortunately, no specimen could be traced (the section holding these collections at herbarium B was destroyed during the II World War). No other specimen useful for the purpose of lectotypification was found. We traced only a photograph (no. 29871) of the original Weberbauer’s collection no. 353 at F and MO (Fig. 1). However, this photograph, which was made after 1937, cannot be considered as part of the original material for *A. mattfeldii* under the Art. 9.4a of ICN; hence a neotypification is required under the Art. 9.8 of the ICN. We here designate as a neotype, a specimen collected in Peru and preserved at B (B100747308).

Observations. The species is considered narrowly endemic to Junín and designated as Critically Endangered by Cano and Sánchez (2006).

Description. Perennial herb, densely caespitose, matt-forming, 3–5 cm height, 10 cm wide; leaves 1.5–2.0 mm long, closely imbricate, shortly appressed, thick, lamina with deltate to broadly ovate, apex obtuse or rarely acute, base truncate; margins shortly revolute and ciliate, trichomes simple, 0.10–0.15 mm long and irregularly shaped, rarely straight, leaf lamina surface glabrous both on

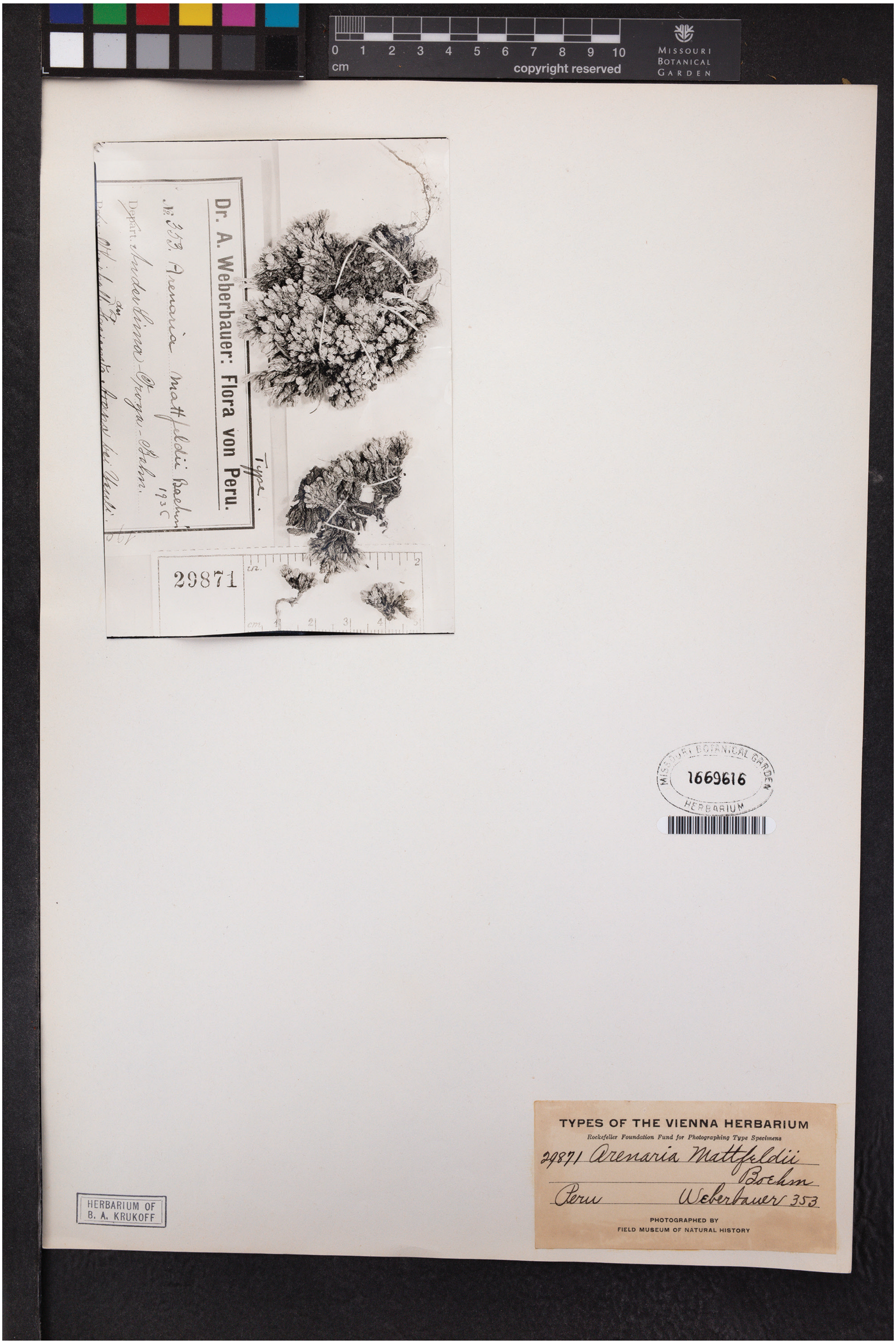

Figure 1. MO sheet of the type photograph of *Arenaria mattfeldii* [Weberbauer 353].

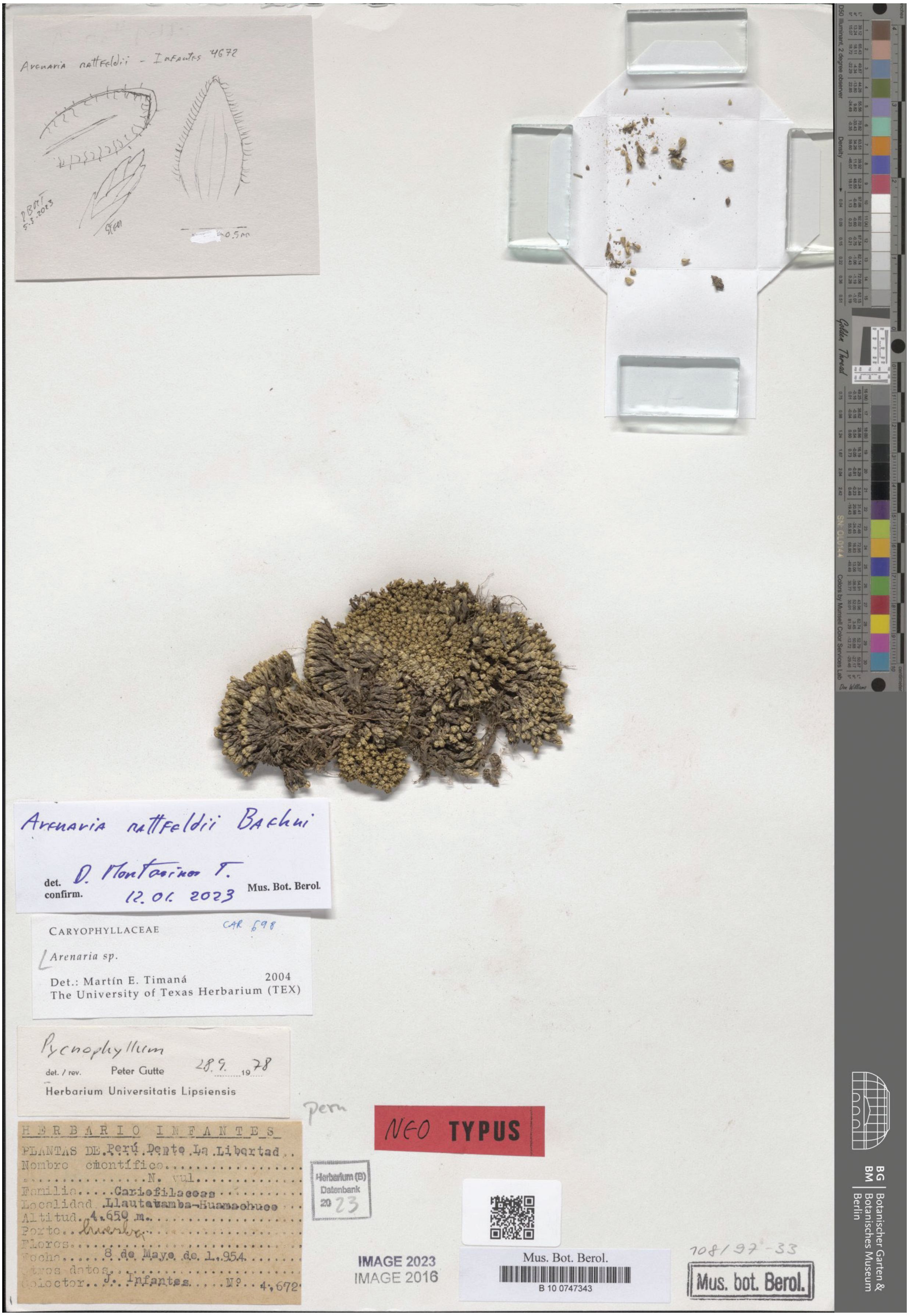

Figure 2. Neotype of *Arenaria mattfeldii* Baehni (*J. Infantes 4672*, B100747308).

the upperside and underside, and without a visible midrib; flowers apical, pedicels < 1 mm long, sepals 2 mm long, ovate-deltate, apex slightly curved downwards; petals reduced, ovate, translucid, ½ as long as sepals; stamens 10, ovary 0.75–1.00 mm long, glabrous, styles two; seeds about 8, with smooth surface.

Specimens examined. Peru. Junín: La Oroya, Morococha, Hacienda Pucará, 4700 m., 23 May 1974, *P. Gutte 2353b* (LPZ!).

***Arenaria pallens* Muschl., Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 45(4): 450–451. 1911.**

Neotype (designated here). Peru. Huánuco: Lauricocha, Jesús, Abra Tocana, 4195 m, 03 Aug 2016, *D. Montesinos 4902* (B–100766251!, Fig. 3).

Muschler (1911: 450–451) validly published the name *Arenaria pallens*, giving a detailed description, as well as the citation of a syntype (Art. 9.6 of ICN), i.e., "Peru: ad viam ferream inter oppida Lima et Oroya ad hacienda Arapa prope Yauli, ad rupes, in 4400 m altitudine" (Weberbauer 267). –Specimina florigera fructiferaque 18–27 Januarii 1902 – Herb. Berol. [Herbarium Berolinensis, B]". According to Hiepko (1987), the only known collection at B was destroyed. Consequently, lacking original material (Art. 9.3 of ICN), a neotypification is required. The analysis of two specimens stored at B revealed them as alternative material from near the type locality, which is here chosen as neotypes. Note that Muschler's taxon is a member of *Arenaria* sect. *Dicranilla* which has the characteristic ciliate leaf margins and bisexual flowers (see also Timaná, 2017) as typical for *A. pallens*. We here designate a collection made by one of the authors (DBMT) as the neotype of Muschler's *A. pallens*. The species is considered narrowly endemic and was designated as Critically Endangered by Cano and Sánchez (2006). The finding of the species in the Huánuco department expands its distribution and it can be considered to occur in the Pasco department as well and Junín department as first established by Cano and Sánchez (2006).

Further analysis needs to be made for three species described by Muschler (1911) which were not found at the explored localities, in addition to the lack of herbarium material, types destroyed and doubtful protologues. It is concluded that Muschler (1911) described the taxa with an apparent mixture of characters (Ryding 1939) as seem to occur in *Arenaria horizontalis* (Muschl.) Molinari (= *Pycnophyllum horizontale* Muschl.), due to impossible character symmetry as described on page 449, a fact that was not corrected by Molinari (2016).

Description. Diffuse herb, with branches of about 2–8 cm long, more or less angled and pubescent near the nodes but glabrous in mid-sections; internodes of about 6–10 mm long; leaves linear to linear-lanceolate, rarely ovate-lanceolate, thick or fleshy, with acuminate apex bearing a mucronate tip, base petiolate, lamina of about 5–10 mm long × 1.0–3.0(–3.5) mm width, bearing trichomes at the base, margins and apex; pedicels filiform, densely pubescent or rarely glabrous, less than 1 cm long, curved when fruiting; sepals ovate-oblong, carinate, apex acuminate, hirsute or puberulent along the margins, 3–4 mm long; petals tending to be shorter than the sepals, ovate-oblong and obtuse; anthers pale yellow; styles 3; capsule longer than the calyx; 8 seeds, shiny and smooth.

Specimens examined. Peru. Huánuco: Huamalies, Singa, W of Bellas Flores, 3601 m, 26 jul 2016, *D. Montesinos 4853* (B–1007613519!).

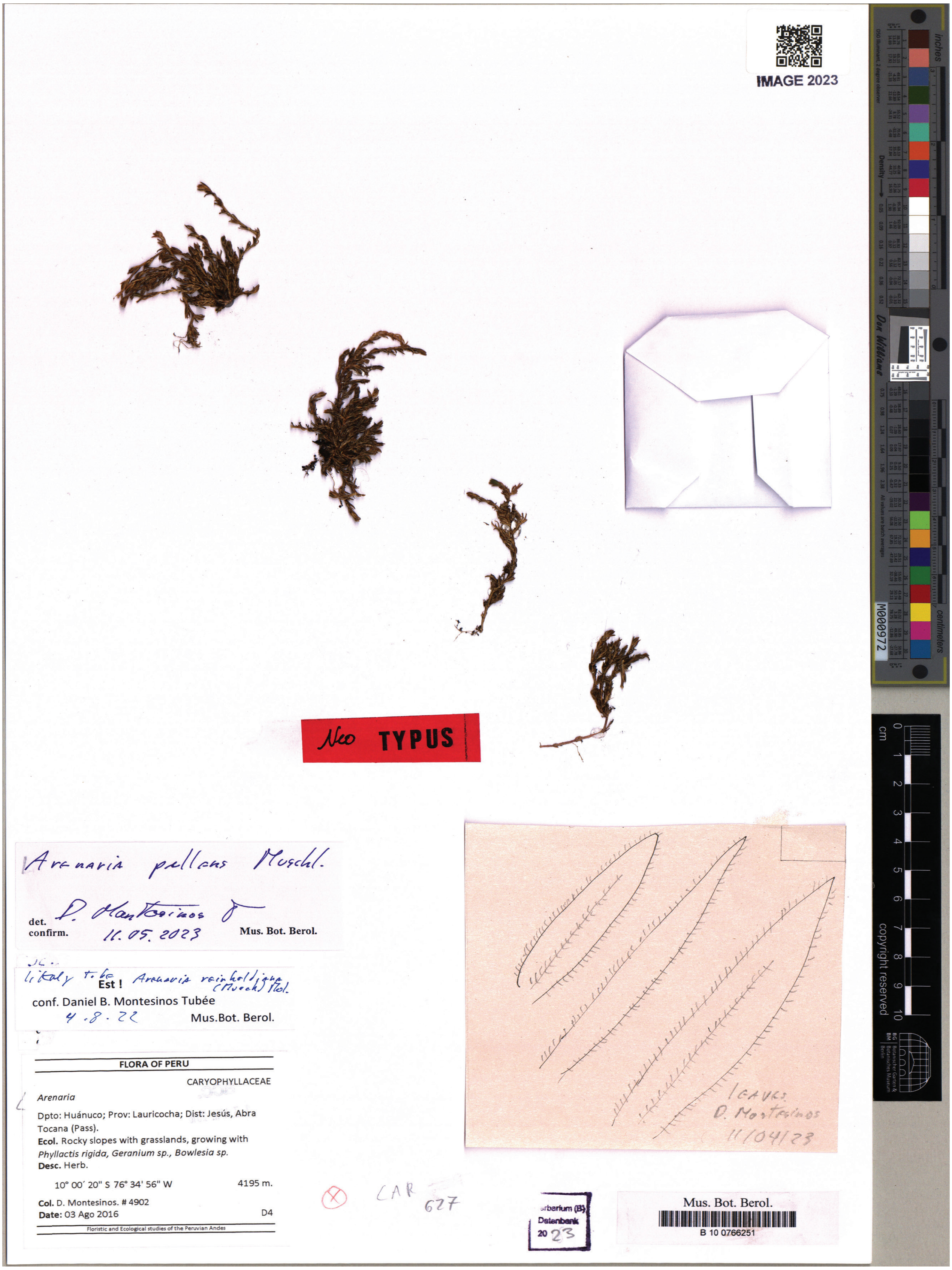

Figure 3. Neotype of *Arenaria pallens* Muschl. (*D. Montesinos 4902*, B100766251).

Arenaria peruviana (Muschl.) Molinari, Polish Bot. J. 61(2): 276. 2016

≡ *Pycnophyllum peruvianum* Muschl., Bot. Jahrb. Syst. 45(4): 457–458. 1911.

Neotype (designated here). Peru. Junín: Pacuy-Wila, 4250 m, 16 Jun 1960, *G.W.H. Kunkel 6211* (B100538376!, Fig. 4).

Muschler (1911: 276) validly published *Pycnophyllum peruvianum* with a detailed description; including the provenance and habitat reported as "Peru: Prope La Oroya in departamento Junin, in formation planti caespitosis ac pulviniaribus composite, 4300 m s. m.", as well as the collector and number of the original collection ("Weberbauer 2597") followed by "Specimina florigera fructiferaque Februario 1903. – Herb. Berol.". The only known collection of *Pycnophyllum peruvianum* by Weberbauer at B ("Herb. Berol." = Herbarium Berolinensis) was destroyed (see Hiepko 1987). The cited collection by Molinari (2016) at MOL (where additional material of Weberbauer is preserved; see HUH–Index of Botanists 2013b) is inexistent (pers. observ.; see also Timaná 2017). Lacking original material, a lectotype cannot be designated (Arts. 9.3 and 9.4 of ICN) and a neotypification is required (Art. 9.8 of ICN). Despite knowing this, Molinari (2016) published the new combination without observing or selecting a type specimen (Timaná 2017). We consider a collection made by Kunkel nearby the locus classicus as the neotype of the name *Pycnophyllum peruvianum*.

Observations. Muschler's taxon is a member of *Arenaria* sect. *Dicranilla* which has the characteristic of having ciliate leaves and bisexual flowers (see also Timaná, 2017). The species is considered as narrowly endemic and treated as Critically Endangered by Cano and Sánchez (2006).

Description (see also Muschler 1911 and Macbride 1937). perennial herb, densely caespitose, 3–5 cm long × 15 cm width; densely leaved, leaves 1.2–1.8 mm long, imbricate, shortly appressed, thick, lamina subtriangular in outline, rigid or fleshy, densely ciliate, apex acuminate; margins ciliate and shortly revolute, trichomes long and thin, shortly distant at the base, ca. 0.2 mm long; flowers with short pedicels, less than 0.5 mm long, sepals 2 mm long, linear to ovate-lanceolate, scarious and with an acute apex; petals absent; stamens 2–3 mm long, style slightly longer; seeds triangular and compressed, shiny.

Arenaria pintaudii **Molinari, Polish Bot. J. 61(2): 275. 2016, nom. nov. pro *Alsine rupestris* Muschl., Bot. Jahrb. Syst. 45(4): 448–449. 1911, non Fenzl (1833).**

Neotype (designated here). Peru. Puno: Puno, *J. Infantes 6922* (B–100747308, Fig. 5).

The name *Arenaria pintaudii* was validly published by Molinari (2016: 275) as a *nomen novum pro Alsine rupestris* Muschler. Muschler (1911: 448–449), although validly published *A. rupestris*, overlooked the previous legitimate name *S. rupestris* (Scop.) Fenzl. [published in 1883 and currently accepted as *Facchinia rupestris* (Scop.) Dillenb. & Kadereit]. Hence Muschler's *Alsine rupestris* is illegitimate (later homonym) according to the Art. 53.1 of ICN. According to Art. 7.4 of ICN, "A replacement name ... is typified by the type of the replaced synonym". Therefore, the typification of Molinari's *Arenaria pintaudii* must be made studying Muschler's *Alsine rupestris*. Muschler (1911) provided a detailed

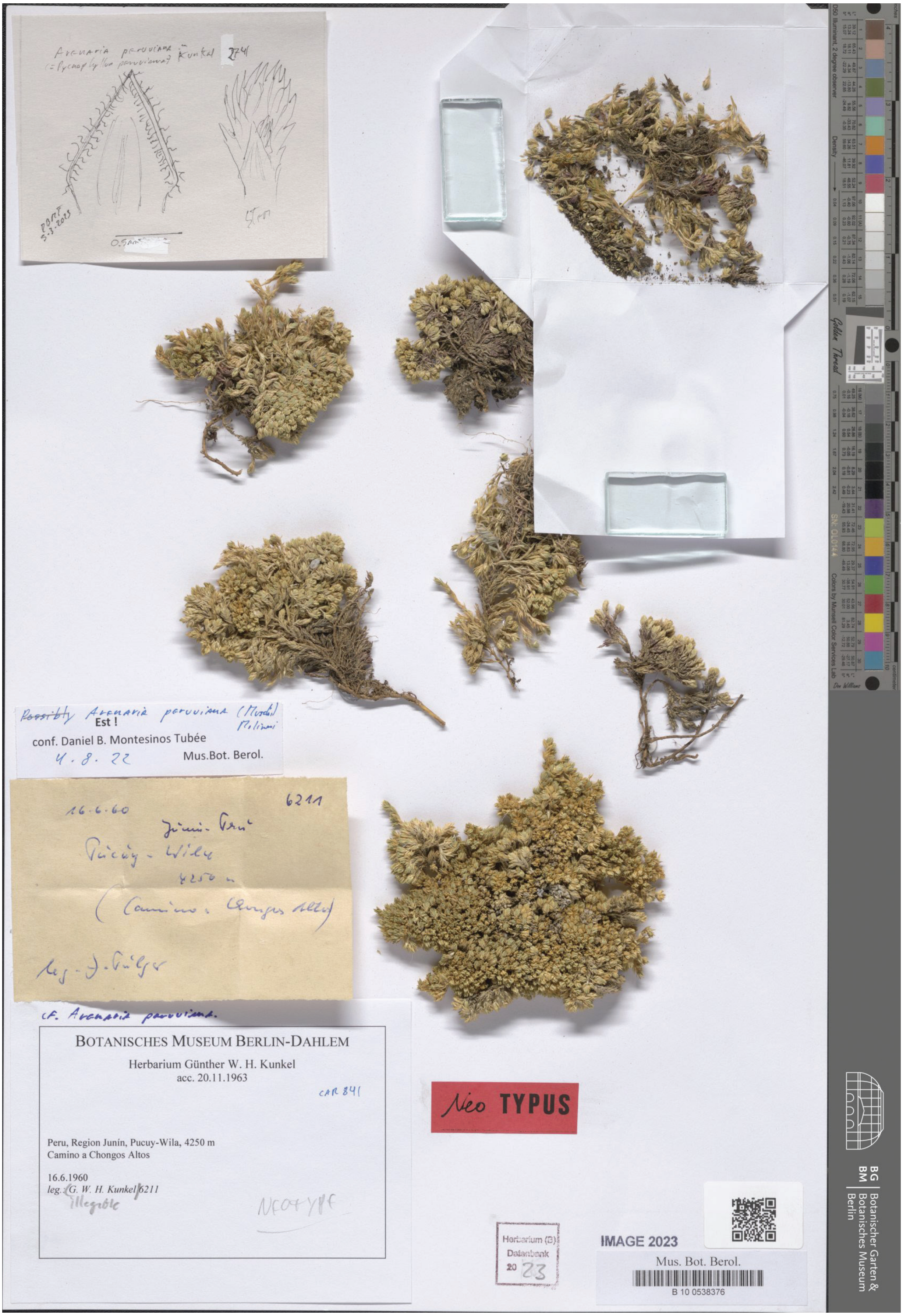

Figure 4. Neotype of *Arenaria peruviana* (Muschl.) Molinari (*G.W.H. Kunkel 6211*, B100538376).

description, the provenance and habitat ("Peruvia: supra Ananca, in Sandia provincial, rupiphus, 5100 ms.m."), collector and number of collection ("Weberbauer # 1042"); he also reported: "Specimina florigera fructiferaque 16 Mai 1902. – Herb. Berol. [Herbarium Berolinense, now B]". The only known collection of *Alsine rupestris* at B was destroyed according to Hiepko (1987) and no further original material could be found. It remains unclear how Molinari (2016) published the new name without observing or selecting a type specimen. Anyway, a neotypification is required under the Art. 9.8 of ICN.

Observations. The species is considered as Critically Endangered (Cano and Sánchez 2006) and it seems to have well-established populations in certain sectors of the altiplano in the department of Puno according to herbarium labels and personal observations. Moreover, few populations were observed north of the department of Moquegua from where one of the additional observations comes from.

Description. Pulvinate herb with several branches, 3–15 cm long, decumbent or procumbent, glabrous, internodes ca. 1 cm long; leaves lanceolate to ovate in outline, bearing an amplexicaul base and acute apex, 8–12 mm long × 2–3 mm wide, margins densely ciliated, rarely glabrous; pedicels up to 5 mm long, erect or curved, puberulent or glabrous; sepals oblong, 3.5–5.0 mm long; petals ovate-cuneate, ca. 4.5 mm long; seeds smooth, blackish.

Specimens examined. Peru. Puno: Santa Lucia, 3600 m, Nov 1939, *J.E. Sharpe 94* (K!); **Puno**: Santa Lucia, 3600 m, Nov 1939, *J.E. Sharpe 107* (K!); **Puno**: Puno, *J. Infantes 6922* (B100747308); **Puno**: Santa Lucia, 3600 m, 10 Nov 1939, *J.E. Sharpe 94* (K!); **Puno**: Azángaro, Arapa, 3820 m, 17 Feb 1948, *P. Aguilar 100* (USM–18587!); **Puno**: Cerro entre rocas, 3900 m, 11 Feb 1948, *P. Aguilar 148* (USM–18576!); **Moquegua**: Ichuña, Tolapampa, 4040 m, 14 Apr 2012, *D. Montesinos & F. Calizaya 3823a* (B–101156477!).

***Arenaria stuebelii* Hieron., Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 21(3): 307. 1895.**

Neotype (designated here). Bolivia. Hernando Siles: Azero, Nov–Dec 1845, *M.H. Weddell 3691* (P–05139758!, Fig. 6, http://mediaphoto.mnhn.fr/media/1441409343048mmKRKfSJcLXpH0CF).

Hieronymus (1895: 307) provided a detailed description of *Arenaria stuebelii*, citing the following syntype (Art. 9.6 of ICN): "Bolivia: crescit locis aridis Puna dictis supra Taca in valle Yungas, ubi floret mense dicembri (coll. boliv. n. 48d)". We have been unable to locate a specimen collected by M.A. Stüebel (the botanists who Hieronymus dedicated the species) and numbered as 48d at B (where Stüebel's herbarium and type are preserved; HUH–Index of Botanists 2013c), since they were mostly destroyed during the II World War. After an exhaustive investigation of different plant material collected near locus classicus, we here decide to designate a specimen from P (barcode P–05139758) as the neotype of the name *Arenaria stuebelii*.

Description. Herb with numerous stems branching from the taproot, 10–30 cm long, ascending and covered with minute trichomes varying from 0.1–0.2 mm long; leaves linear to narrowly linear-lanceolate, acute or acuminate, pubescent on the adaxial and abaxial sides, lamina ca. 8 mm × 1 mm; flowers

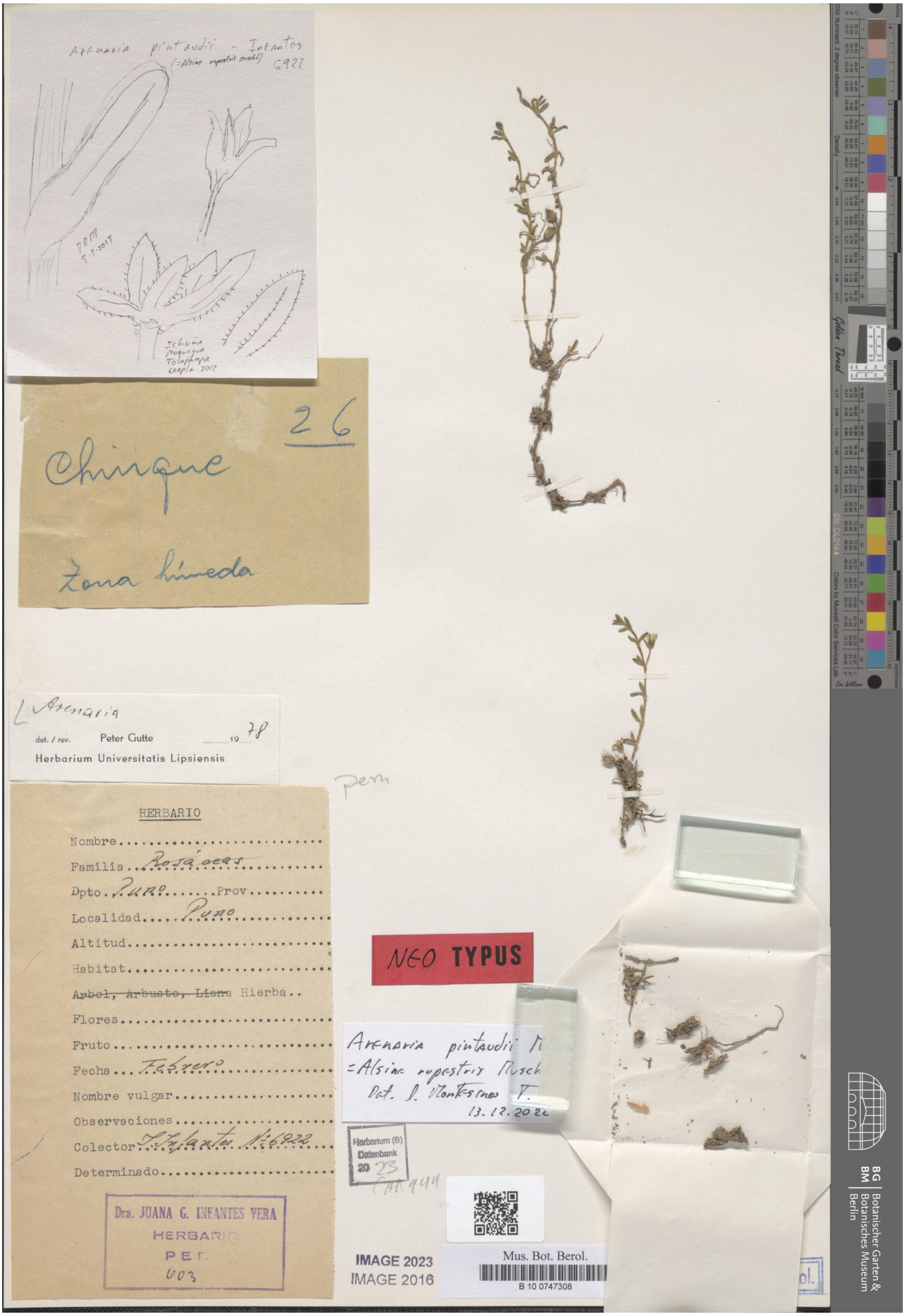

Figure 5. Neotype of *Arenaria pintaudii* Molinari (*J. Infantes 6922*, B100747343).

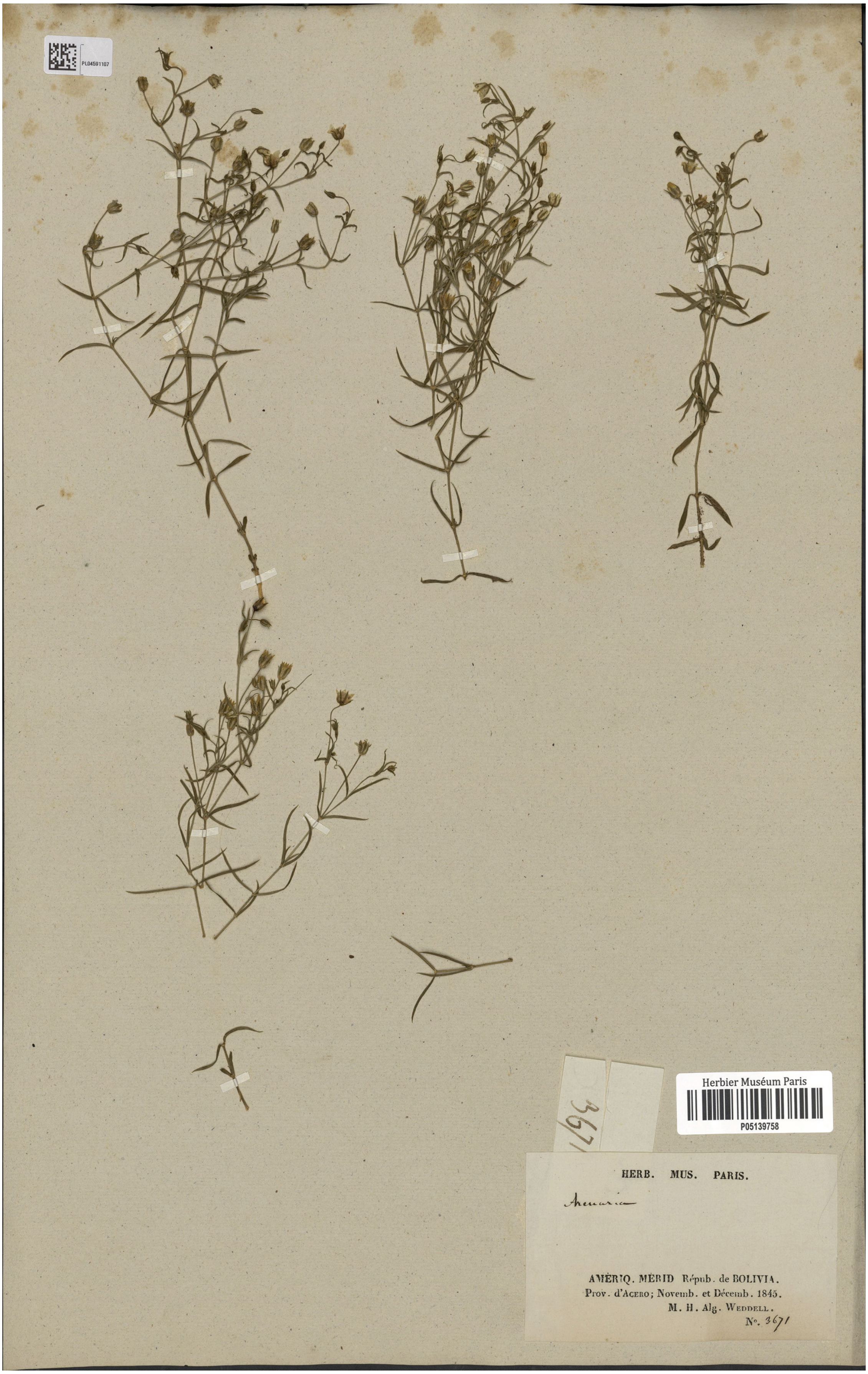

Figure 6. Neotype of *Arenaria stuebelii* Hieron. (*M.H. Weddell 3691*, P05139758).

with long pedicels, puberulent or scarious; sepals ovate, with scarious margins, 3–4 mm long × 2 mm wide; petals white, ovate-oblong, obtuse, 6–7 mm long × 3 mm wide; seeds globose, flattened, black, smooth and shiny.

Specimens examined. Bolivia. Tarija: Arce, Municipio Padcaya, Reserva Nacional de flora y fauna Tariquía, 2457 m, 27 Apr 2005, *M. Serrano et al. 6327* (MO–5956858!); **Franz Tamayo**: Parque Nacional Madidi, 2810 m., 23 Jun 2005, *A. Fuentes & E. Cuevas 8622* (MO–5956863!); **La Paz**: Sud Yungas, Chulumani, 1972 m, 27 jun 2007, *D. Ibañez & R. Hurtado 603* (B–100720358!); **La Paz**: Sud Yungas, Yanacachi a la Chojlla, 2100 m, 7 Sep 1987, *E. Vargas & R. Seidel 496* (B–100720356!).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

DBMT designed the study. IA assembled the taxonomic database. DBMT and IA jointly wrote the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Bittrich V (1993) Caryophyllaceae. In: Kubitzki K, Rohwer JG (Eds) The families and genera of vascular plants, Vol. 2. Springer, Berlin, 206–236. https://doi.org/10.1007/978-3-662-02899-5_21

Cano A, Sánchez I (2006) Caryophyllaceae endémicas del Perú. Revista Peruana de Biología 13(2): 246–252. https://doi.org/10.15381/rpb.v13i2.1835

Conti F, Bartolucci F, Iamonico D, Del Guacchio E (2014) A new combination in *Mcneillia* (Caryophyllaceae) for the Italian flora. Phytotaxa 170(2): 139–140. https://doi.org/10.11646/phytotaxa.170.2.8

De Luca D, Del Guacchio E, Conti F, Iamonico D, Caputo P (2022) Relationships within Mcneillia indicate a complex evolutionary history and reveal a new species of *Minuartiella* (Caryophyllaceae, Alsinoideae). Plants 11(16): 2118. https://doi.org/10.3390/plants11162118

Dillenberger MS, Kadereit JW (2014) Maximum polyphyly: Multiple origins and delimitation with plesiomorphic characters require a new circumscription of *Minuartia* (Caryophyllaceae). Taxon 63(1): 64–88. https://doi.org/10.12705/631.5

Fenzl E (1833) Versuch einer Darstellung der geographischen Verbreitungs– und Vertheilungs–Verhältnisse der natürlichen Familie der Alsineen in der Polarregion und eines Theiles der gemäſsigten Zone der alten Welt. Gedruckt bei Johan Baptist Wallishausser, Wien.

Greenberg AK, Donoghue MJ (2011) Molecular systematics and character evolution in Caryophyllaceae. Taxon 60(6): 1637–1652. https://doi.org/10.1002/tax.606009

Hernández-Ledesma P, Berendsohn WG, Borsch T, von Mering S, Akhani H, Arias S, Castañeda-Noa I, Eggli U, Eriksson R, Flores-Olvera H, Fuentes-Bazán S, Kadereit G, Klak C, Korotkova N, Nyffeler R, Ocampo G, Ochoterena H, Oxelman B, Rabeler RK, Sanchez A, Schlumpberger BO, Uotila P (2015) A taxonomic backbone for the global synthesis of species diversity in the angiosperm order Caryophyllales. Willdenowia 45(3): 281–383. https://doi.org/10.3372/wi.45.45301

Hiepko P (1987) The collections of the Botanical Museum Berlin-Dahlem (B) and their history. Englera 7: 219–252.

Hieronymus GHEW (1895) Plantae stuebelianae novae: Quas descripsit adjuvantibus aliis auctoribus. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 21(3): 307.

HUH–Index of Botanists (2013a) “Delessert”. https://kiki.huh.harvard.edu/databases/botanist_index.html [Accessed 12 July 2023]

HUH–Index of Botanists (2013b) Weberbauer, August. https://kiki.huh.harvard.edu/databases/botanist_search.php?mode=details&id=29914 [Accessed 12 July 2023]

HUH–Index of Botanists (2013c) Stübel, [Moritz] Alphons. https://kiki.huh.harvard.edu/databases/botanist_search.php?mode=details&id=29828 [Accessed 12 July 2023]

Iamonico D (2013) Taxonomical and chorological study on the Central Mediterranean Basin endemic *Arenaria bertolonii* Fiori & Paol. (Caryophyllaceae). Plant Biosystems 147(4): 923–930. https://doi.org/10.1080/11263504.2012.753956

Iamonico D (2014) *Arenaria tenuifolia* versus *Arenaria hybrida* (Caryophyllaceae): Nomenclatural study and taxonomic implications. Phytotaxa 173(3): 235–240. https://doi.org/10.11646/phytotaxa.173.3.6

Iamonico D (2016) Nomenclatural notes on four Linnaean names in *Arenaria* (Caryophyllaceae). Taxon 65(3): 610–616. https://doi.org/10.12705/653.13

Iamonico D (2019) Taxonomical, chorological and ecological notes on the Eastern Alps endemic *Arenaria huteri* (Caryophyllaceae-Alsinoideae). Phyton (Horn, Austria) 59(1): 11–19.

Iamonico D (2022) Notas nomenclaturales sobre el género *Arenaria* (Caryophyllaceae) en Chile. Darwiniana 10(1): 187–192. https://doi.org/10.14522/darwiniana.2022.101.967

Macbride JF (1936) Flora of Peru. Publications of the Field Museum of Natural History. Botanical series. Chicago, IL. https://doi.org/10.5962/bhl.title.7205

Macbride JF (1937) Caryophyllaceae, Flora of Peru. Publications of Field Museum of Natural History, Botanical Series 13(2/2): 578–638. https://doi.org/10.5962/bhl.title.2322

Molinari E (2016) Further nomenclatural changes regarding Peruvian endemics. Polish Botanical Journal 61: 275–277. http://10.1515/pbj–2016–0021

Montesinos-Tubée DB, Iamonico D (2023) Typifications of Andean *Arenaria* names (Caryophyllaceae), with a nomen novum. Phytotaxa 579(1): 54–60. https://doi.org/10.11646/phytotaxa.579.1.6

Montesinos-Tubée DB, Teillier S (2022) *Arenaria* L.(Caryophyllaceae) en Chile. Gayana. Botánica 79(2): 124–139. https://doi.org/10.4067/S0717-66432022000200124

Muschler R (1911) Caryophyllaceae andinae. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 45: 441–461.

POWO (2023) Plants of the World Online. *Arenaria* L. https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:329928–2 [Accessed 12 July 2023]

Ryding O (1939) Reno Muschler and the identity. In Biodiversity Research in the Horn of Africa Region: Proceedings of the Third International Symposium on the Flora of Ethiopia and Eritrea at the Carlsberg Academy, Copenhagen, August 25–27, 1999 (Vol. 54, p. 155). Ejnar Munksgaard.

Sadeghian S, Zarre S, Rabeler RK, Heubl G (2015) Molecular phylogenetic analysis of Arenaria (Caryophyllaceae: Tribe Arenarieae) and its allies inferred from nuclear DNA internal transcribed spacer and plastid DNA rps16 sequences. Botanical Journal of the Linnean Society 178(4): 648–669. https://doi.org/10.1111/boj.12293

Thiers B (2023 [continuously updated]) Index herbariorum. New York Botanical Garden. http://sweetgum.nybg.org/science/ih/ [Accessed 12 July 2023]

Timaná ME (2017) Nomenclatural notes on the Andean genera *Pycnophyllopsis* and *Pycnophyllum* (Caryophyllaceae). Lundellia 20(1): 4–24. https://doi.org/10.25224/1097-993X-20.1.4

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF [Eds] (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. Regnum Vegetabile 159: 1–254. https://doi.org/10.12705/Code.2018

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Research Article

Thrixspermum taeniophyllum (Orchidaceae, Epidendroideae), a new species from southwest China, based on molecular and morphological evidence

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Abstract

Thrixspermum taeniophyllum is described as a new orchid species from Wenchuan County, Sichuan Province of southwest China. It is morphologically similar to *T. japonicum*, but it differs from the latter in having branched stems, slightly fleshy strap-shaped leaves, longer inflorescences with 3–6 flowers and a capitate gynandrium with a lip-shaped mouth opening. Its species status is also supported by molecular phylogenetic analyses, based on nuclear ribosome internal transcribed spacer (nrITS) and three chloroplast DNA fragments (*mat*K, *psb*A-*trn*H and *trn*L-F), which showed distinct systematic boundaries from the most morphologically similar *T. japonicum* and their morphological relatives *T. saruwatarii* and *T. pygmaeum*.

Key words: Epiphytic orchid, flora of Sichuan, phylogeny, systematic position, taxonomy

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Introduction

Thrixspermum Lour. (1790) is a genus of mostly medium-sized epiphytes and lithophytes in the family Orchidaceae Juss. and it is known to include ca. 160 species widely distributed from tropical and subtropical Asia to the islands of the western Pacific islands (Chen et al. 2009; Chase et al. 2015; Kumar et al. 2017). This genus is characterised by the persistent floral bracts, a three-lobed labellum and the four waxy subglobose pollinia grouped into two unequal masses in appearance (Loureiro 1790; Chen et al. 2009). It is also a congregation of elusive orchids with limited floral materials for morphological comparison due to their rather short flowering period (Govaerts et al. 2016). From accounts of ca. 17 species distributed in southern China, only one species, *T. japonicum* (Miq.) Reichenbach fils (1878), has been recorded from Sichuan Province (Song et al. 2009; Kumar et al. 2017; Zhou et al. 2021).

* These authors contributed equally to this work.

As part of a continuous inventory of orchids from Sichuan, China, we have conducted continuous field explorations in the Wenchuan section of the Giant Panda National Park. During a field trip in March 2022, we encountered an interesting epiphytic orchid in Wolong National Nature Reserve (Wenchuan County, Sichuan Province, China), that we had initially identified it as *Thrixspermum japonicum*, based on its pendulous inflorescence, golden-yellow flowers and orange-red striped lateral lobes of the labellum. However, upon a critical morphological observation and comparison with available specimens including the type materials of two of the three [we were unsuccessful to trace the type specimen(s) of *T. pygmaeum* (King & Pantl.) Holttum (1960)] morphologically related species (Fig. 1A–I), for example, *T. japonicum* (*P. F. V. Siebold, s.n.*, L) and *T. saruwatarii* (Hayata) Schlechter (1919) (*T01201*, TI), we assumed it to be a new species of *Thrixspermum* that we are now describing hereafter.

Materials and methods

Morphological observations

Morphological information (including the colour, size and shape of the roots, stems, leaves, flowers and floral parts, details see Table 1) of this new species was obtained from observations and measurements of eight living plants in the field and four dried herbarium specimens (voucher information: *Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY144*; *Jun-Yi Zhang & Yue-Hong Cheng*

Table 1. Morphological comparison amongst *Thrixspermum taeniophyllum*, *T. japonicum*, *T. saruwatarii* and *T. pygmaeum*. Characters of the last three species are modified from the respective protologues (Miquel 1866; King and Pantling 1898; Hayata 1916) and Flora of China (Chen et al. 2009).

Character	*T. taeniophyllum*	*T. japonicum*	*T. saruwatarii*	*T. pygmaeum*
Stems	**4–8 cm long, often branched, internodes 5–8 mm**	3–13 cm long, unbranched, internodes 3–5 mm	shorter than 2 cm, unbranched, internodes ≤ 1 mm	shorter than 3 cm, unbranched, internodes ≤ 1 mm
Leaves	dichotomously alternate, **slightly fleshy**, **strap-shaped**, **5–7 × 0.5–1 cm**	dichotomously alternate, thinly leathery, oblong, 2–4 × 0.5–0.7 cm	nearly basal, narrowly oblong or linear-oblanceolate, 4–8 × 0.5–2 cm	nearly basal, elliptic to linear-oblong, rarely falcate, 2–8 × 0.7–1.5 cm
Inflorescences	**6–12 cm long, with 3–6 flowers**	3–5 cm long, with 2–3 flowers	longer than 8 cm, with 1–4 flowers	2–4 cm long, with 2–4 flowers
Floral bracts	broadly ovate-triangular, ca. 4 mm	broadly ovate-triangular, ca. 2.5 mm	ovate-triangular, 2–3 mm	ovate, 2–3 mm
Dorsal sepal	elliptic, 5–7 × 3.5–4.5 mm	oblong, 5–7 × 2.5–3 mm	oblong, 7–8 × 3–5 mm	elliptic, 6–8 × 4–5 mm
Lateral sepals	elliptic, 5–7 × 3.5–4.5 mm	ovate-lanceolate, 5–7 × 2.5–3 mm	slightly oblique, 7–8 × 3–5 mm	obliquely ovate, 6–7 × 4–5 mm
Petals	narrowly elliptic, 4.5–6 × 2–3 mm	narrowly oblong, 5–6 × 1.5–2 mm	linear, falcate, 5–6 × ca. 2 mm	oblong-spatulate, 6–7 × 2–3 mm
Lateral lobes of labellum	erect, nearly oblong, ca. 2.5 mm	narrowly ovate-oblong, ca. 2.5 mm	erect, falcate, ca. 3 mm	erect, oblong, falcate, 6–7 mm
Mid-lobe of labellum	fleshy, very small, teeth triangular	fleshy, very small, semi-orbicular	fleshy, very small, triangular	fleshy, small, semi-orbicular
Lip disc	without a callus, slightly depressed, with red purple or golden yellow hairs	with a callus, slightly depressed, densely tomentose	with a callus, where a tuft of brownish-yellowish hairs arises	without a callus, slightly depressed, with a tuft of purple hairs
Gynandrium	**Capitate, mouth opening lip-shaped**	conical, mouth opening triangular	cylindrical, mouth opening semi-lunar	cylindrical, mouth opening semi-lunar

Figure 1. Comparison of four species of *Thrixspermum*. Living plant of *T. taeniophyllum* (**A**), *T. japonicum* (**B**), *T. saruwatarii* (**C**) and *T. pygmaeum* (**D**); Detailed colour photos of *T. japonicum* (**E: a** habit **b** leaves **c** inflorescence **d, e** flower in front and back view **f1** dorsal sepal **f2–3** petals **f4–5** sepals **f6, h** labellum **g** gynandrium and ovary **i** anther cap); Type specimens of *T. taeniophyllum* (**F**: holotype at CDBI), *T. japonicum* (**G**: holotype at L) and *T. saruwatarii* (**H**: holotype at TI); and a representative specimen of *T. pygmaeum* (**I:** TI). [Images **A** and **E** photographed by Min Liao; image **B** photographed by Yue-Hong Cheng; image **C** cited from website (https://kevinyu589.blogspot.com/) image **D** cited from website (https://www.gbif.org/species/2846707); the image of the type specimen of *T. japonicum* was obtained from JSTOR and those of *T. saruwatarii* and *T. pygmaeum* were cited from available from Plants of Taiwan (https://tai2.ntu.edu.tw/search/2)].

ZJY189; *Jun-Yi Zhang & Yue-Hong Cheng ZJY191*; *Jun-Yi Zhang & Yue-Hong Cheng ZJY192*) deposited at CDBI (acronym of herbarium follows Thiers 2023). Voucher information for the four specimens used for morphological observations and their collection location are detailed in the taxonomic treatment. The terminology in Beentje (2012) was followed for the description.

DNA extraction and sequencing

The sequences of four individuals of this new species from two different areas (Wolong and Gengda towns) in Wenchuan County and two individuals of

T. japonicum (vouchers *Jun-Yi Zhang & Yue-Hong Cheng ZJY187* and *Jun-Yi Zhang & Yue-Hong Cheng ZJY188*, deposited at CDBI) were newly obtained in this study with the following protocols. Total DNA was extracted from silica-gel dried leaves via a Plant DNA Isolation Kit (Cat.No.DE-06111, Foregene, Chengdu, China). The sequences were amplified by means of the primers (Table 2) used in previous studies of *Thrixspermum* (Li et al. 2014; Zou et al. 2015). The PCR programme consisted of an initial 4 min preheating stage at 98 °C, followed by 35 cycles of 30 s at 98 °C (denaturation), 30 s at 48–56 °C (annealing) and 60–100 s at 68 °C (extension), followed by a final 8 min extension at 68 °C. The PCR products were sent to TSINGKE Biotech (Chengdu, China) for sequencing. The returned sequences were edited via Sequencher v.4.1.4 (Gene Codes, Ann Arbor, Michigan, USA) and checked manually and then deposited in the GenBank with the following accession numbers: nrITS (OP348891, OQ608783, OR054231, OR054232, OR054229, OR054230), *mat*K (OP373116, OQ626557, OR062235, OR062236, OR062233, OR062234), *psb*A-*trn*H (OP373121, OQ626556, OR062240, OR062241, OR062238, OR062239) and *trn*L-F (OR184926, OR184927, OR062245, OR062246, OR062243, OR062244), respectively.

Table 2. Information of DNA markers used in this study for *Thrixspermum*.

DNA markers	Length (bp)	Variable sites (bp)	Primer sequence (5'to3')	Origin
nrITS	675	239	ACGAATTCATGGTCCGGTGAAGTGTTCG	Sun et al. (1994)
			GAATTCCCCGGTTCGCTCGCCGTTAC	Sun et al. (1994)
*psb*A-*trn*H	748	44	GTTATGCATGAACGTAATGCTC	Sang et al. (1997)
			CGCGCATGGTGGATTCACAAATC	Sang et al. (1997)
*mat*K	881	122	CGATCTATTCATTCAATATTTC	Sun et al. (1994)
			TCTAGCACACGAAAGTCGA	Sun et al. (1994)
*trn*L-F	908	94	AAAATCGTGAGGGTTCAAGTC	Sang et al. (1997)
			GATTTGAACTGGTGACACGAG	Sang et al. (1997)

Phylogenetic analyses

A total of 54 accessions representing 44 taxa were incorporated in the phylogenetic analysis, including *Phalaenopsis marriottiana* (Rchb. f.) Kocyan & Schuiteman (2014) as outgroup. The ingroup includes 36 entities of *Thrixspermum* representing 26 species and 17 taxa belonging to six related genera in Aeridinae (Orchidaceae, Epidendroideae) following the two previous studies of Li et al. (2014) and Zou et al. (2015). The detailed information concerning the sampled taxa, voucher specimens and GenBank accession numbers (including the sequences retrieved from GenBank) used for the phylogenetic analyses are summarised in Appendix 1. The nrITS, *mat*K, *psb*A-*trn*H and *trn*L-F matrices contain 40, 22, 13 and 13 taxa, respectively (Appendix 1). All sequences were aligned using MAFFT v.7.475 (Katoh and Standley 2013) with default parameters. The incongruence length difference test (ILD) was used to quantify the conflicts between nuclear DNA (nrITS) and plastid DNA (*mat*K, *psb*A-*trn*H, *trn*L-F) data in PAUP v.4.0a169 (Darlu and Lecointre 2002; Swofford 2002). The ILD Test ($P = 0.11$) indicated that nrITS and plastid datasets were suitable for combined analysis in *Thrixspermum* and, thus, the results are based on the combined data of nrITS and three plastid markers. The nucleotide substitution models for these data matrices were estimated using the software jModelTest v.2.1.6 (Posada 2008) and the best fit models were selected using the corrected Akaike Information Criterion (AICc). Bayesian Inference (BI) and Maximum Likelihood (ML) analyses were performed to infer the phylogenetic relationships within the combined dataset. The BI analysis was conducted using MrBayes v.3.2.7a (Ronquist and Huelsenbeck 2003), with two separate Markov Chain Monte Carlo (MCMC) chains (1,000,000 generations and sampled every 1,000 generations). The first 25% of the trees were discarded as burn-in and the remaining trees were used to generate a majority-rule consensus tree. The ML analysis was performed using IQ-TREE v.1.4.2 (Nguyen et al. 2014) with branch support estimated using 2,000 replicates of both SH-like approximate likelihood-ratio test (SH-aLRT) (Guindon et al. 2010) and the ultrafast bootstrapping algorithm (UFboot) (Minh et al. 2013).

Results

The aligned nrITS matrix of 48 accessions (40 taxa) was 675 nucleotides in length with 239 variable sites and plastid matrix of 30 accessions (23 taxa) was 2537 nucleotides in length with 260 variable sites, of which 881 bp for *mat*K (29 accessions, 22 taxa, 122 variable sites), 748 bp for *psb*A-*trn*H (20 accessions, 13 taxa, 44 variable sites) and 908 bp for *trn*L-F (19 accessions, 13 taxa, 94 variable sites), respectively (Table 2). Phylogenetic analyses indicated that the 26 included taxa of *Thrixspermum* formed a well-supported monophyletic group (Fig. 2). Four individuals of the inferred new species from the two sites in Wenchuan County were resolved as a strongly-supported monophyletic lineage (Fig. 2; BI/ML = 1/100%), which further clustered with *T. japonicum*, *T. saruwatarii* and *T. pygmaeum* into a subclade (Fig. 2; BI/ML = 1/100%). These four species also showed certain morphological similarities (referring to Fig. 1 and Table 1). It is noted that *T. japonicum* is the most related species to the novelty by sharing with the new species pendulous inflorescence, inside brownish-striped lateral lobes and densely hairy small triangular mid-lobe of labellum (Fig. 1B, E). Besides, the following morphological diagnosis, their molecular boundary is clearly shown by the positions of their respective individuals as well (Fig. 2).

Taxonomic treatment

***Thrixspermum taeniophyllum* Jun Y.Zhang, H.He & Yue H.Cheng, sp. nov.**
urn:lsid:ipni.org:names:77324993-1
Figs 1A, 3

Type. China. Sichuan Province, Wenchuan County, Wolong Town, in coniferous and broadleaf mixed forest, on tree trunks, elev. ca. 1762 m, in flower, 30 March 2022, *Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY144* (holotype CDBI!).

Diagnosis. It is most similar to *Thrixspermum japonicum* in morphology, but it differs from the latter by its often-branched stems (vs. unbranched stems), slightly fleshy strap-shaped leaves 5–7 cm long (vs. thinly leathery oblong leaves 2–4 cm long), longer inflorescences with 3–6 flowers (vs. shorter

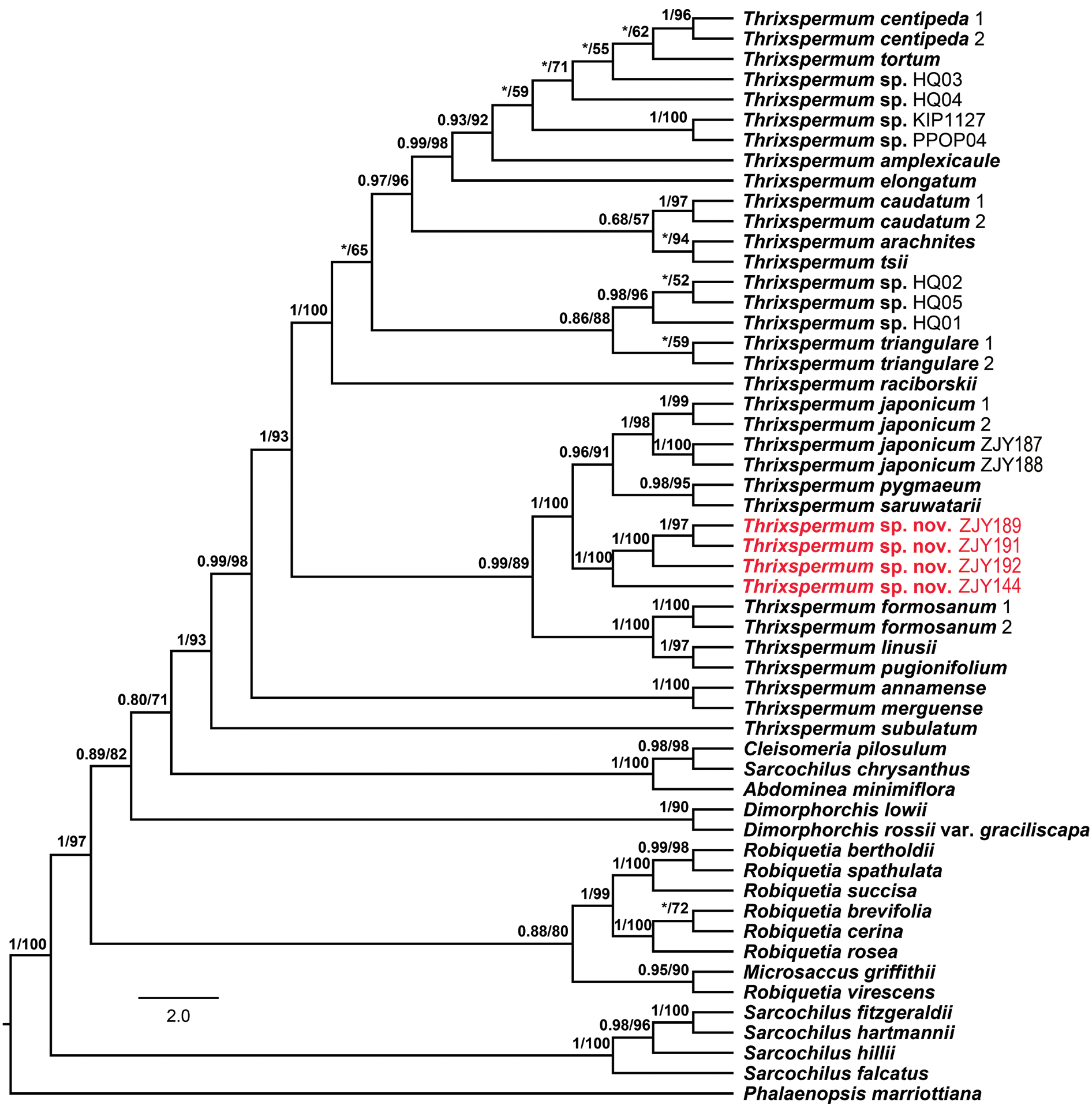

Figure 2. Maximum Likelihood tree of 36 entities of *Thrixspermum* reconstructed, based on combined nuclear and plastid dataset. Numbers before slash indicate Bayesian posterior probabilities and numbers after slash indicate ML bootstrap supports for major lineages. Asterisk (*) indicates that a node is not supported in the analysis. The four individuals of the inferred new species are highlighted in red.

inflorescences with 2–3 flowers) and its capitate gynandrium with a lip-shaped mouth opening (vs. conical gynandrium with a triangular mouth opening). It also resembles *T. saruwatarii* and *T. pygmaeum* and morphological comparison amongst the four species is visualised in Fig. 1 and summarised in Table 1.

Description. Epiphytic on tree trunks. **Roots** vermiform and slender. **Stems** ascending or pendulous especially when in flowering, 4–8 cm long, ca. 1.5 mm thick, often branched, internodes 5–8 mm apart. **Leaves** green, dichotomously alternate, slightly fleshy, strap-shaped, 5–7 × 0.5–1 cm, apex acute and bifid with two unequally mucronate tips. **Inflorescence** arising

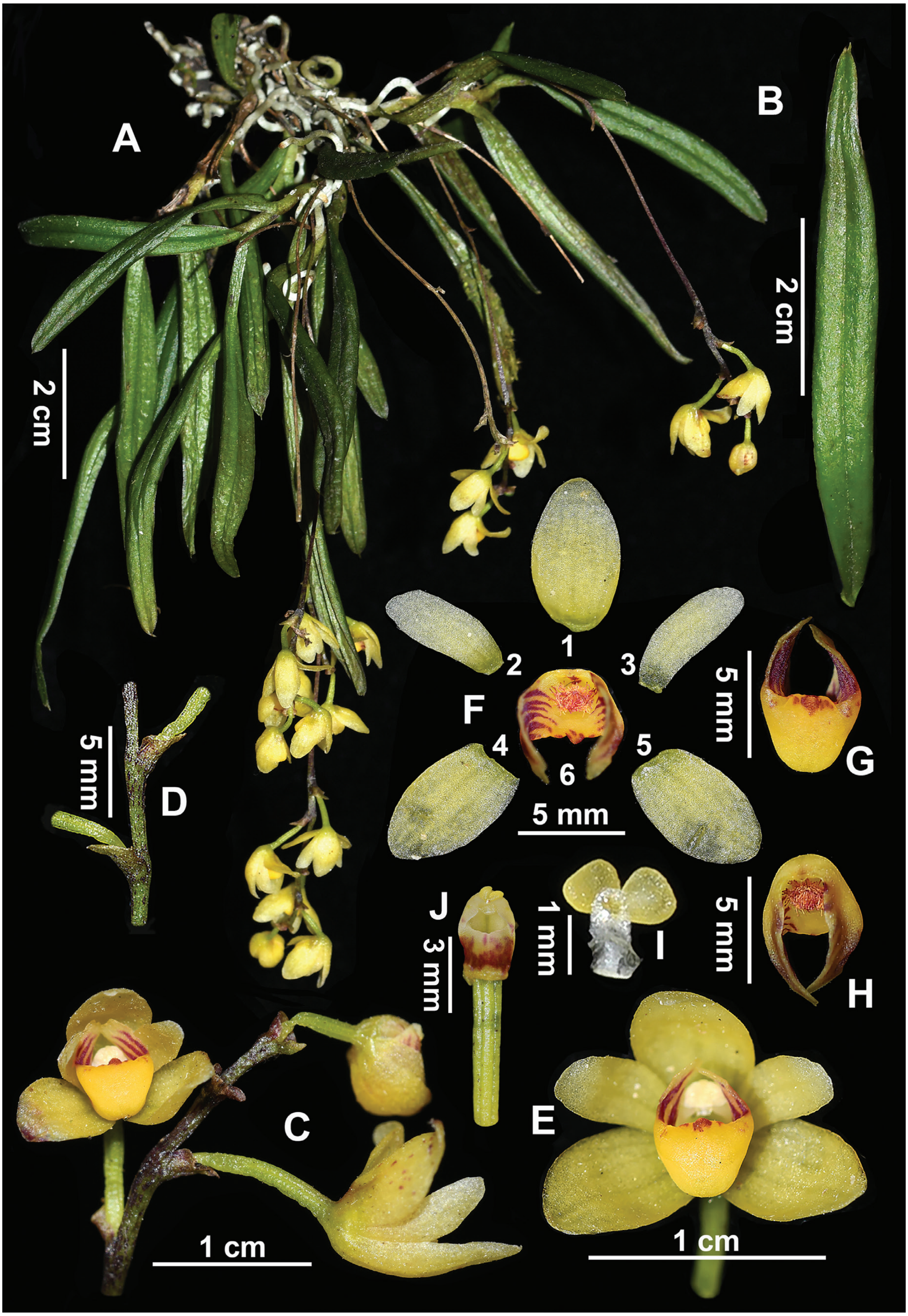

Figure 3. *Thrixspermum taeniophyllum* **A** flowering plant **B** leaves **C** inflorescence **D** part of the rachis showing persistent bracts **E** flower in front view **F** dissection of a flower **(**F1: dorsal sepal; F2–F3: petals; F4–F5: sepals; F6: labellum) **G, H** labellum **I** pollinia **J** gynandrium and ovary.

from basal stem laterally or opposite to leaves, usually pendulous, 6–12 cm long; rachis slightly flexuous and slightly thickened distally, 4–6 cm long, laxly 3–6 flowered; bracts spirally arranged, obliquely patent, ca. 3 mm long, broadly ovate-triangular, apex acute. **Flowers** initially white and later turning creamy yellow, blossoming almost simultaneously; dorsal and lateral sepals similar, elliptic, 5–7 × 3.5–4.5 mm, apex obtuse, with obscure 3 veins; petals narrowly elliptic, smaller than sepals, 4.5–6 × 2–3 mm, apex obtuse, with obscure 1 or 2 veins; labellum small, three-lobed, base shallowly saccate; lateral lobes erect, triangularly oblong, ca. 2.5 mm, apex rounded or ± notched, inner surface with many purplish-red stripes; mid-lobe fleshy, reddish-brown, very small, apex ended with triangular teeth; disc concave, inside base densely covered with red purple or golden yellow hairs; gynandrium capitate, with a lip-shaped mouth opening; ca. 2.5 mm high; column foot ca. 1.2 mm, with one joint at the junction with the labellum; pollinia 4 grouped into two nearly similar masses, ca. 0.8 × 0.7 mm, yellow, full and obovately spherical. **Fruits** unseen.

Distribution and habitat. *Thrixspermum taeniophyllum* was found in Wenchuan County, Sichuan Province, southwest China. It is epiphytic on trees in coniferous and broadleaf mixed forest at an elevational range between 1260 and 1770 m.

Phenology. Flowering in March and April.

Etymology. The specific epithet *taeniophyllum* is a compound adjective referring to the shape of leaves of this new species. A Chinese name, dai ye bai dian lan (带叶白点兰), is also suggested, based on the its leaf feature.

Additional specimens examined. China. Sichuan Province, Wenchuan County, Wolong Town, evergreen broad-leaved forest, on tree trunks, elev. ca. 1769 m, in flower, 1 May 2023, *Jun-Yi Zhang & Yue-Hong Cheng ZJY189* (CDBI!); Sichuan Province, Wenchuan County, Gengda Town, evergreen broad-leaved forest, on tree trunks, elev. ca. 1508 m, in flower, 2 May 2023, *Jun-Yi Zhang & Yue-Hong Cheng ZJY191* (CDBI!); Sichuan Province, Wenchuan County, Gengda Town, evergreen broad-leaved forest, on tree trunks, elev. ca. 1520 m, in flower, 2 May 2023, *Jun-Yi Zhang & Yue-Hong Cheng ZJY192* (CDBI!).

Examined specimens of Thrixspermum japonicum. Japan. *P. F. V. Siebold, s.n.* (holotype L; It is not clear whether duplicates exist); China. Sichuan, Emeishan, elev. ca. 990 m, 12 July 1980, *K. Y. Lang, B. C. Gao et al. 044* (PE); Baoxing, elev. ca. 1800 m, 2 April 1983, *D. Y. Peng 47469* (CDBI!); Beichuan, elev. ca. 1640 m, 1 August 1984, *C. L. Tang et al. 284* (CDBI!). Chongqing: Nanchuan, elev. ca. 900 m, 2 November 1983, *Z. Y. Liu 4669* (IMC); Nanchuan, elev. ca. 850 m, 30 May 1984, *Z. Y. Liu 5219* (PE).

Examined specimens of Thrixspermum saruwatarii. China. Taiwan, Alishan, 8 April 1916, *B. Hayata, s.n.* (holotype TI); Kaohsiung, 20 October 1934, *S. Sasaki, s.n.* (TAI). Yunnan, Gongshan, elev. ca. 1702 m, 20 May 2007, *X. H. Jin 9001* (PE). Hunan, Ningyuan, elev. ca. 340 m, 8 May 2011, *X. L. Yu 11050801* (CSFI). Guangdong, Dapu, elev. ca. 700 m, 9 June 1957, *L. Deng 4953* (IBSC).

Examined specimens of Thrixspermum pygmaeum. China. Taiwan, Taipingshan, 3 April 1940, *Y. Kobayashi, s.n.* (TI); Taitung, 22 March 1932, *S. Sasaki, s.n.* (TAI); Miaoli, 13 November 1972, *C. C. Hsu 12600* (TAI); Ilan, 10 March 2013, *C. C. Hsu, s.n.* (TAI).

Key to the four related species of *Thrixspermum*

1a Stems shorter than 3 cm, internodes ≤ 1 mm; leaves nearly basal **2**
2a Inflorescences longer than 8 cm; lip disc with a callus, where a tuft of brownish-yellowish hairs arises .... ***T. saruwatarii***
2b Inflorescences 2–4 cm long; lip disc without a callus, slightly depressed, with a tuft of purple hairs..***T. pygmaeum***
1b Stems longer than 3 cm, internodes ≥ 3 mm; leaves distichous alternate.. ....**3**
3a Stems branched; leaves strap-shaped, 5–7 × 0.5–1 cm; inflorescences 6–12 cm long with 3–6 flowers and a capitate gynandrium with a lip-shaped mouth opening .... ***T. taeniophyllum***
3b Stems unbranched; leaves oblong, 2–4 × 0.5–0.7 cm; inflorescences 3–5 cm long with 2–3 flowers and a conical gynandrium with a triangular mouth opening ....***T. japonicum***

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

JYZ, YHC, ML, GYL, PYY, HH and BX discovered and identified the species. YHC, GYL, and PYY assisted in extensive field investigation and samples collection. JYZ and ML performed the experiments and analyzed the data. JYZ wrote the manuscript. ML, HH and BX revised the manuscript. All authors read and approved last manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Appendix 1.

References

Beentje H (2012) The Kew Plant Glossary, an illustrated dictionary of plant terms. Kew Publishing, London, 164 pp.

Chase MW, Cameron KM, Freudenstein JV, Pridgeon AM, Salazar G, Berg CVD, Schuiteman A (2015) An updated classification of Orchidaceae. Botanical Journal of the Linnean Society 177(2): 151–174. https://doi.org/10.1111/boj.12234

Chen SC, Tsi ZH, Wood JJ (2009) *Thrixspermum* Lour. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China, vol. 19 (Orchidaceae). Missouri Botanical Garden Press, St. Louis and Science Press, Beijing, 336–342.

Darlu P, Lecointre G (2002) When does the incongruence length difference test fail? Molecular Biology and Evolution 19(4): 432–437. https://doi.org/10.1093/oxfordjournals.molbev.a004098

Govaerts R, Campacci MA, Baptista DH, Baptista PJ, George A, Kreutz K, Wood JJ (2016) World Checklist of Orchidaceae. The Board of Trustees of the Royal Botanic Gardens, Kew. http://apps.kew.org/wcsp/

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate Maximum-Likelihood phylogenies: Assessing the performance of PhyML 3.0. Systematic Biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

Hayata B (1916) Icones Plantarum Formosarum nec non et contributiones ad floram Formosanam, vol. 6. Governmnet of Formosa, Taihoku, 168 pp.

Holttum RE (1960) The genera *Sarcochilus* R. Br. and *Pteroceras* Hassk. (Orchidaceae) with notes on other genera which have been included in *Sarcochilus*. Kew Bulletin 14(2): 263–276. https://doi.org/10.2307/4114807

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

King G, Pantling R (1898) Orchids of the Sikkim-Himalaya. Annals of the Royal Botanic Garden, Calcutta 8: 207.

Kocyan A, Schuiteman A (2014) New combinations in Aeridinae (Orchidaceae). Phytotaxa 161(1): 61–85. https://doi.org/10.11646/phytotaxa.161.1.3

Kumar V, Verma D, Rao AN (2017) *Thrixspermum indicum* (Orchidaceae), a new species from Northeast India. Phytotaxa 292(1): 79–84. https://doi.org/10.11646/phytotaxa.292.1.8

Li MH, Zhang GQ, Liu ZJ, Lan SR (2014) Revision of *Hygrochilus* (Orchidaceae: Epidendroideae: Aeridinae) and a molecular phylogenetic analysis. Phytotaxa 159(4): 256–268. https://doi.org/10.11646/phytotaxa.159.4.2

Loureiro J (1790) Flora Cochinchinensis vols. 1–2. Typis et Expensis Academicis, Lisbon, 744 pp.

Minh BQ, Nguyen MAT, von-Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30(5): 1188–1195. https://doi.org/10.1093/molbev/mst024

Miquel FAW (1866) Prolusio florae laponicae. Annales Musei Botanici Lugduno-Batavi 2: 69–212, 257–300.

Nguyen LT, Schmidt HA, Von-Haeseler A, Minh BQ (2014) IQ-TREE: A fast and effective stochastic algorithm for estimating Maximum-Likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Posada D (2008) jModelTest: Phylogenetic model averaging. Molecular Biology and Evolution 25(7): 1253–1256. https://doi.org/10.1093/molbev/msn083

Reichenbach HG (1878) Ad Orchidographiam Japonicam Symbolae. Botanische Zeitung (Berlin) 36: 74–76.

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics (Oxford, England) 19(12): 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Sang T, Crawford D, Stuessy T (1997) Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). American Journal of Botany 84(8): 1120–1136. https://doi.org/10.2307/2446155

Schlechter FRR (1919) Orchideologiae Sino-Japonicae prodromus. Eine kritische Besprechtung der Orchideen Ost-Asien. Repertorium Specierum Novarum Regni Vegetabilis. Beihefte 4: 1–319.

Song XQ, Meng QW, Wing YT, Luo YB (2009) *Thrixspermum odoratum* (Orchidaceae), a new species from Hainan Island, China. Annales Botanici Fennici 46(6): 595–598. https://doi.org/10.5735/085.046.0617

Sun Y, Skinner D, Liang G, Hulbert S (1994) Phylogenetic analysis of *Sorghum* and related taxa using internal transcribed spacers of nuclear ribosomal DNA. Theoretical and Applied Genetics 89(1): 26–32. https://doi.org/10.1007/BF00226978

Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0 a169. Sinauer Associates, Sunderland.

Thiers B (2023) Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih

Zhou ZH, Shi RH, Zhang Y, Xing XK, Jin XH (2021) Orchid conservation in China from 2000 to 2020: Achievements and perspectives. Plant Diversity 43(5): 343–349. https://doi.org/10.1016/j.pld.2021.06.003

Zou YJ, Chen ZJ, Kondo K, Funamoto T, Wen J, Zhou SL (2015) A molecular phylogeny of Aeridinae (Orchidaceae: Epidendroideae) inferred from multiple nuclear and chloroplast regions. Molecular Phylogenetics and Evolution 85: 247–254. https://doi.org/10.1016/j.ympev.2015.02.014

Appendix 1

Table A1. The GenBank accession numbers for DNA sequences used in this study.

Taxa	Voucher	nrITS	*psb*A-*trn*H	*mat*K	*trn*L-F
Abdominea minimiflora	B200107222	AB217524	–	–	–
Cleisomeria pilosulum	TBG140482	AB217542	–	AB217718	–
Dimorphorchis lowii	TBG118871	AB217548	–	AB217724	–
Dimorphorchis rossii var. *graciliscapa*	Botanical Garden Heidelberg 122351	EF670358	–	EF655807	–
Microsaccus griffithii	KFBG2673	KY966620	–	–	–
Phalaenopsis marriottiana	Z. J. Liu 8743	KX579760	KX579764	KX579762	KX579766
Robiquetia bertholdii	Chase 17866	–	–	FR832824	–
Robiquetia brevifolia	WAMP_ORCH-13	MT505292	–	–	–
Robiquetia cerina	Carlsward 210 (SEL)	DQ091701	–	–	–
Robiquetia rosea	WAMP_ORCH-14	MT505293	–	–	–

Taxa	Voucher	nrITS	*psb*A-*trn*H	*mat*K	*trn*L-F
Robiquetia spathulata	Z. J. Liu 6691	—	KJ733523	KF421855	KJ733680
Robiquetia succisa	Z. J. Liu 5248	KJ733444	KJ733524	KJ733601	KJ733681
Robiquetia virescens	WAMP_ORCH-15	MT505294	—	—	—
Sarcochilus chrysanthus	TBG145831	AB217582	—	AB217757	—
Sarcochilus falcatus	A. Perkins 14	AF321600	—	—	—
Sarcochilus fitzgeraldii	Carlsward 231 (FLAS)	DQ091728	—	—	—
Sarcochilus hartmannii	TBG145793	AB217581	—	AB217758	—
Sarcochilus hillii	Perkins 15	AF321601	—	—	—
Thrixspermum amplexicaule	Z. J. Liu 4971	KF545882	KF545871	KF545892	KF545904
Thrixspermum annamense	Z. J. Liu 4972	KF545883	KF545872	KF545893	KF545905
Thrixspermum arachnites	Heidelberg BG 104401	—	—	EF065572	—
Thrixspermum caudatum 1	KIP0690	KX679330	—	—	—
Thrixspermum caudatum 2	KIP0352	KX679331	—	—	—
Thrixspermum centipeda 1	KIP06	KX679341	—	—	—
Thrixspermum centipeda 2	KFBG3306AL	KY966675	KJ733536	KJ733621	KJ733691
Thrixspermum elongatum	Carlsward 170 (SEL)	DQ091674	—	—	—
Thrixspermum formosanum 1	OT00257	—	KJ733540	KJ733620	KJ733695
Thrixspermum formosanum 2	Yue-Hong Cheng 321	OR054228	OR062237	OR062232	OR062242
Thrixspermum japonicum 1	PDBK2015-1270	—	KX871234	KX871234	KX871234
Thrixspermum japonicum 2	S. A. Choi 784	KT338782	KF262223	KF262105	—
Thrixspermum japonicum ZJY187	Jun-Yi Zhang & Yue-Hong Cheng ZJY187	OR054229	OR062238	OR062233	OR062243
Thrixspermum japonicum ZJY188	Jun-Yi Zhang & Yue-Hong Cheng ZJY188	OR054230	OR062239	OR062234	OR062244
Thrixspermum linusii	KIP1150	KX679333	—	—	—
Thrixspermum merguense	KIP1094	KX679334	—	—	—
Thrixspermum pugionifolium	WAMP_ORCH-17	MT505296	—	MT966905	—
Thrixspermum pygmaeum	OT00263	KJ733457	KJ733537	KJ733613	KJ733692
Thrixspermum raciborskii	AD7LN53	—	MF348752	MF349945	—
Thrixspermum saruwatarii	Z. J. Liu 3905	KJ733458	KJ733538	KJ733614	KJ733693
Thrixspermum sp. PPOP04	PPOP04	KX679342	—	—	—
Thrixspermum sp. HQ03	HQ03	KX679338	—	—	—
Thrixspermum sp. HQ04	HQ04	KX679339	—	—	—
Thrixspermum sp. KIP1127	KIP1127	KX679335	—	—	—
Thrixspermum sp. HQ02	HQ02	KX679337	—	—	—
Thrixspermum sp. HQ05	HQ05	KX679340	—	—	—
Thrixspermum sp. HQ01	HQ01	KX679336	—	—	—
Thrixspermum subulatum	TBG113211	AB217592	—	AB217768	—
Thrixspermum tortum	KIP0185	KX679347	—	—	—
Thrixspermum triangulare	HQ06	KX679348	—	—	—
Thrixspermum triangulare	980162 (L)	EF670367	—	—	EF670412
Thrixspermum tsii	Z. J. Liu 3264	KJ733459	KJ733539	KJ733615	KJ733694
Thrixspermum taeniophyllum ZJY144	Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY144	OP348891	OP373121	OP373116	OR184926
Thrixspermum taeniophyllum ZJY189	Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY189	OQ608783	OQ626556	OQ626557	OR184927
Thrixspermum taeniophyllum ZJY191	Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY191	OR054231	OR062240	OR062235	OR062245
Thrixspermum taeniophyllum ZJY192	Jun-Yi Zhang, Min Liao & Yue-Hong Cheng ZJY192	OR054232	OR062241	OR062236	OR062246

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Monograph

Revision of the genus *Agrostis* (Poaceae, Pooideae, Poeae) in Megamexico

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Abstract

Agrostis is one of the most diverse genera of the Poaceae, including ca. 198 species, principally distributed in cold and temperate regions of the world, but also found in the high mountains of the tropics. We present a revision based on morphoanatomical evidence, for the biogeographic region known as Megamexico 3 (i.e., Mexico including the desert areas of southern USA and the Central America territory, to northern Nicaragua). We include taxonomic descriptions and an identification key for the found taxa, maps with the known geographical distribution of the species, and figures with the morphoanatomical characteristics, elevation and phenology. *Agrostis* is represented in the study zone by 20 species, of which four are endemic and three are introduced. Most records of the genus are distributed in the mountains, above 1500 m a.s.l., in open areas of temperate forests, with conifers and *Quercus*. Specimens with spikelets occur year round, but most records occur during the wet season, in the months of July to October. We propose a preliminary conservation assessment for each species in the study zone, according to the International Union for Conservation of Nature categories: one with Deficient Data (DD), six as Endangered (EN), two as Vulnerable (VU), and 11 as Least Concern (LC).

Resumen

Agrostis es uno de los géneros más diversos de las Poaceae, con ca. 198 especies, principalmente distribuidas en regiones frías y templadas del mundo, aunque también se pueden encontrar en grandes elevaciones de los trópicos. En este trabajo se presenta una revisión basada en evidencia morfoanatómica para la región biogeográfica conocida como Megaméxico 3 (i.e., México incluyendo las áreas desérticas del sur de los EUA y el territorio de Centroamérica hasta el norte de Nicaragua). Se incluyen descripciones taxonómicas y una clave de identificación para los taxones encontrados, mapas con la distribución geográfica conocida de las especies, así como figuras con las características morfoanatómicas, elevación y fenología. *Agrostis* está representado en la zona de estudio por 20 especies, cuatro de las cuales son endémicas y tres son introducidas. La mayoría de los registros del género se distribuyen en regiones montañosas, por arriba de los 1500 de elevación, en áreas abiertas de bosques templados, con coníferas y

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Quercus. Es posible encontrar ejemplares con espiguillas durante todo el año, pero la mayoría de los registros ocurren durante la época lluviosa, durante los meses de julio a octubre. Se propone una evaluación preliminar de conservación para cada especie en la zona de estudio, de acuerdo con las categorías de la Union Internacional para la Conservación de la Naturaleza: una con Datos Deficientes (DD), seis como Amenzadas (EN), dos como Vulnerables (VU) y 11 de Preocupación Menor (LC).

Key words: Anatomy, distribution, Gramineae, grasses, identification, morphology, nomenclature, taxonomy

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Introduction

The genus *Agrostis* L. includes ca. 198 species (Soreng et al. 2022), principally distributed in cold and temperate regions of the world, but also found in the high mountains of the tropics. The genus belongs to the subfamily Pooideae Benth., tribe Poeae R. Br., and subtribe Agrostidinae Fr. (Soreng et al. 2022). *Agrostis* species are characterized by the usually fragile habit of the plants, synflorescences of the panicle type, spikelets one-flowered, floret notably shorter than the glumes, usually 1/3–3/4 the length of the glumes, rarely longer, lemma with usually five nerves, palea often reduced or absent, and rachilla prolongation absent. Some of the species are forage plants of regular to excellent quality (Mejía-Saulés and Dávila 1992), while others are agricultural weeds, and some are excellent lawn grasses in cool climates (Harvey 2007).

The systematics of *Agrostis* has been considered as challenging, since the limits between this and other genera remain poorly understood, and there are several species complexes where the limits between taxa are difficult to establish due to morphological variation. Attempts at infrageneric classifications have been made in the past, based on the habit of the plants, presence of awns in the glumes and lemmas, and the presence of transversal thickenings in the outer walls of the lemma epidemal cells (called the "*Trichodium* net"), but some authors indicate that the established groups are unnatural (e.g. Clayton and Renvoize 1986). Several authors recognize at least two subgenera, on the basis of the absence (*A.* subg. *Vilfa* (Adans.) Rouy) or presence of paleas (*A.* subg. *Agrostis*). Peterson et al. (2020) provide a molecular phylogeny of some European species of *Agrostis* and allied genera, where two clades that correspond with these two groups are recovered. Studies of the genus that incorporate several lines of evidence are scarce, but some outstanding works are the ones of Björkman (1960), Carlbom (1967), Widén (1971) and Romero-García et al. (1988). Recent studies based on molecular evidence include some species of *Agrostis*, showing that the sampled species form a well-supported clade, including species of *Bromidium* Nees & Meyen, *Chaetopogon* Janch, *Lachnagrostis* Trin., and *Polypogon* Desf. (Saarela et al. 2010, 2017; Tkach et al. 2020; Orton et al. 2021). Despite the existence of previous studies, the systematic knowledge of *Agrostis* has been far from ideal for decades, urging a worldwide revision of the genus (e.g., McVaugh 1983; Pohl and Davidse 1994).

Mexico is considered as a mega-diverse country, since 10–12% of the known species across the globe inhabit its territory (Llorente and Ocegueda 2008). In this country, ca. 23,314 native species of vascular plants have been reported, and a little more than half are endemic, which places Mexico in second position for endemism, after South Africa (Villaseñor 2016). Rzedowski (1991), based on the geographic affinities and endemism of the phanerogamic flora of Mexico, proposed three phytogeographic areas, which extend beyond the political limits of the country as follows: 1) Megamexico 1, which includes the Sonoran, Chihuahuan and Tamaulipan desert areas of the southern USA; 2) Megamexico 2, which includes the Centroamerican territory up to northern Nicaragua; 3) Megamexico 3, which includes the latter two (Fig. 1). This region has been recognized as a biodiversity hotspot and unique in its complex geology, orography, and its climatic heterogeneity (Rzedowski 1991; Ferrusquía-Villafranca 1993; García 2004).

One of the first taxonomic studies of *Agrostis* in Megamexico 3 was the work of Fournier (1886), where several species that are still accepted were described. Another pioneering work was from Hitchcock (1905), who studied the taxonomy of North American species of *Agrostis*. Years later, the same author provided a synopsis of the Mexican species of the genus (Hitchcock 1913). As part of North American Flora, Hitchcock (1937) updated and expanded his 1905 work. Several decades later, Beetle et al. (1983) provided a taxonomic revision of the Mexican species, but this work contains some errors and omissions (see Vigosa-Mercado 2022b), and since its publication, several of the included species have been transferred to other genera and new records have been made.

Other relevant works for *Agrostis* in Megamexico 3 are the catalogs of Mexican Poaceae species by Espejo-Serna et al. (2000), Dávila et al. (2006, 2018), Villaseñor (2016) and Sánchez-Ken (2019). The genus has also been studied in state catalogs and regional floras, including the states of Chihuahua (Herrera-Arrieta and Peterson 2018), Coahuila (Valdés-Reyna 2015), Durango (Herrera-Arrieta 2001), Morelos (Sánchez-Ken and Cerros-Tlatilpa 2016), Oaxaca (Pacheco et al. 2012), and Zacatecas (Herrera-Arrieta et al. 2010), as well as the regions of the Bajío (Vigosa-Mercado and Ruiz-Sánchez 2020), Nueva Galicia (McVaugh 1983), Valley of Mexico (Acosta 2001) and the Valley of Tehuacán-Cuicatlán (Vigosa-Mercado 2017). Other works that partially cover Megamexico 3 are those of Harvey (2007), which is part of the Flora of North America North of Mexico, and Pohl and Davidse (1994), as part of the Flora Mesoamericana. In this study, we provide an updated review of the morphoanatomy, taxonomy, distribution, and conservation of *Agrostis* in Megamexico 3.

Materials and methods

Taxonomic study

Herbarium specimens of *Agrostis* and related genera from the following collections were examined on both physical and digital repositories: ASU, CHAPA, CIIDIR, ENCB, F, FCME, HUMO, IBUG, IEB, INEGI, MEXU, MO, NY, SD, TEX, UAMIZ, US and XAL (abbreviations according to Thiers 2022). Digitalized specimens of the following repositories were also examined: Consortium of California Herbaria (CCH2 Portal 2022), SEINet (2022), Texas Oklahoma Regional Consortium of Herbaria (TORCH 2022), and the Portal de Biodiversidad de Guatemala [Biodiversity Portal of Guatemala] (2022). Available protologues and type specimens were examined.

The analysis of the specimens consisted of: 1) verification of their correct identification, 2) correction of erroneous determinations, 3) updating of the names in synonymy, 4) identification of unnamed specimens, 5) taking measurements of vegetative and reproductive structures for descriptions, and 6) integration of information of the specimens in a database. The synonyms of some of the species are too extensive, whereby only the names with types collected in the study zone, or names widely used in the literature, are cited in the main text. A list of other heterotypic synonyms is provided in Suppl. material 1. Descriptions are based on the examined specimens from the study zone, but measurements reported in the literature from other regions (e.g., Harvey 2007), are included as comments, below the species descriptions. The descriptions of species with few herbarium specimens were complemented with information from the literature. Below the description of each species, one to three representative specimens per state are cited. A list of additional examined specimens is provided in Suppl. materials 2, 3.

Anatomical and micromorphological study

Samples of mature leaves and florets were taken from herbarium specimens, with prior authorization, except for species of which no physical herbarium specimens were seen, as *A. idahoensis* Nash. For each species, a variable number of specimens was studied according to the availability of material. Specimens studied for leaf anatomy are marked with one asterisk (*), and specimens studied for floret micromorphology are marked with two asterisks (**) in the lists of examined specimens.

Leaf blade samples were rehydrated with hot water for 1–5 minutes. The abaxial epidermis was isolated by removing the adaxial epidermis and underlying tissues with a razor blade. Hand transversal sections were taken with a razor blade from the upper third of the leaf blades. The isolated epidermis and transversal sections were treated with 6% sodium hypochlorite solution to clarify and soften the tissues, then washed with water. Only the transversal sections were stained with 1% safranin, and washed again. Both kinds of preparations were mounted with glycerin gelatin. For the description of the anatomical characteristics, the terminology proposed by Ellis (1976, 1979) was used with some modifications.

Floret samples were mounted in aluminum sample holders with conductive carbon tape, exposing the abaxial surface of the lemma, and covered with a layer of gold. The observation and taking of digital photographs were carried out in a Hitachi SU1510 scanning electron microscope.

Elevation and phenology histograms

Histograms of elevation and phenology were drawn in Microsoft Excel (Microsoft Corporation 2022), using the date of collection of the herbarium specimens, excluding duplicates. Phenology histograms represent both the presence of flowers and fruits, since spikelets in a synflorescence contain both kind of structures during the reproductive season. The Y axis in the graphs represents the proportion of the occurrences.

Distribution maps and conservation assessment.

Maps of known geographic distribution of *Agrostis* species, are based on the herbarium specimen data. Herbarium specimens examined were georeferenced by using either Google Earth online or Mapa digital de Mexico V.6 [Digital Map of Mexico] (INEGI 2022). Maps were drawn using QGIS 3.22 (QGIS.org 2022). In the lists of examined specimens, coordinates georeferenced for the purposes of this work appear in square brackets. Records of distribution of *Agrostis* species in the study zone that we were unable to confirm, are discussed under each species description. These records were taken from several references (e.g., Villaseñor 2016; Dávila et al. 2018; Sánchez-Ken 2019), where no examined specimens are cited.

A preliminary conservation assessment in the study zone was proposed for each species, according to the International Union for Conservation of Nature categories and criteria B (IUCN 2012), as well as other sources of information, such as the size of populations indicated in the specimen labels, number of collections, and the presence of records in protected areas. The Extent of Occurrence (EOO), defined as the area contained within the shortest continuous imaginary boundary, which can be drawn to encompass all the known sites of present occurrence of a taxon, and the Area of Occupancy (AOO), defined as the area within the extent of occurrence which is occupied by a taxon (IUCN 2012), were calculated in km^2, using the data from localities, in the R package ConR (Dauby 2020), assuming cells of 2 km per side.

Species concept and delimitation

In this work, the cohesive species concept (Templeton 1989) was followed as an explanatory hypothesis to recognize species and infraspecific categories. This concept has a population genetics framework, but does not discard other cohesive factors to explain species or infraspecific taxa recognition, such as the expression of morphology (phenotypic variability constraints on individuals in the group) and habitat distinctiveness (geographic distribution and ecological constraints). Evolutionary processes act on these cohesive factors to maintain populations or generate new taxa. Species recognized here are characterized by a combination of characters, evaluated in most cases in a broad study of herbarium specimens and the individuals in the field, as well as the known distribution of the organism.

Results

Diversity, elevation, habitat, and phenology

The genus *Agrostis* is represented in Megamexico 3 by 20 species (Table 1), of which four are endemic and three are introduced. We include a list of 16 excluded names of *Agrostis*, previously reported in the study zone, at the end of the work. The found species are distributed mainly in the mountains of southwestern USA, Mexico and Central America, between 14–4,520 m a.s.l. (Fig. 9A). The mean elevation of the records is 2,544.5 m, and the median is 2,592 m. The species grow in a wide range of habitats, such as grasslands, shrublands, stream edges, and temperate forests. Most records of native species of *Agrostis* are distributed above 1,500 m a.s.l. (Fig. 9B), usually in open areas of temperate forests, with conifers and *Quercus*. Some species, such as *Agrostis microphylla* (Fig. 9N), *A. pallens* (Fig. 9O), as well as the populations in the southwestern USA of *A. exarata* (Fig. 9H), *A. hyemalis* (Fig. 9K), *A. perennans* (Fig. 27A), and *A. scabra* (Fig. 27B), are distributed at lower elevations, often in drier environments. Introduced species are distributed between 651–3300 m a.s.l. (Fig. 9C) and seem to prefer disturbed habitats. They are found mainly in moist soils of ditches, marshy habitats, and stream edges. Specimens with flowers and fruits occur all year round, but most records are during the wet season (Fig. 10A), between the months of July to October. Records of native species of *Agrostis* show the same pattern (Fig. 10B), while specimens of introduced species are found during the months of June to December and no specimens of introduced species were found from January to May (Fig. 10C). Elevation, habitat, and phenology for each species are discussed under each species description.

Distribution

Distribution of most found species extend beyond the study zone, and there are several main patterns of the native species: 1) species widely distributed in the Americas (*A. hyemalis*, *A. perennans*, *A. scabra*); 2) species widely distributed in North America, with a southern distribution limit in southwestern USA (*A. elliottiana*, *A. idahoensis*); 3) species distributed from Alaska to central Mexico (*A. exarata*); 4) species distributed from Canada to Baja California peninsula (*A. microphylla*, *A. pallens*, *A. variabilis*); 5) species distributed from northern Mexico to South America (*A. tolucensis*); 6) species distributed from central or southern Mexico to Central America (*A. ghiesbreghtii*, *A. laxissima*, *A. subpatens*, *A. turrialbae*); and 7) species distributed in central Mexico (*A. bourgaei*, *A. calderoniae*). *Agrostis subrepens* is an outlier by its disjunct distribution in Chihuahua, Mexico, and South America. Table 1 shows the distribution of the species in Megamexico 3. Distribution for each species is discussed under each species description.

Taxonomy

The two subgenera of *Agrostis* are represented in the study zone. The three introduced species belong to subgenus *Vilfa* (*A. capillaris*, *A. gigantea*, *A. stolonifera*), characterized by the stoloniferous or rhizomatous habit of the plants, spikelets with a usually well-developed palea, reaching (1/5–)1/3–3/4 of the lemma length, and epidermal cells of the lemmas without transversal thickenings. The remaining species belong to subgenus *Agrostis*, characterized by the usually caespitose habit of the plants, spikelets with usually reduced palea, less than 1/5 of the lemma length, and epidermal cells of the lemmas with transversal thickenings.

In the subgenus *Agrostis*, there are several informal groups of morphologically similar species, where the taxonomy is often complex, since the differences between the species are often subtle and intermediate forms are common. However, through a combination of characters, a reasonably good separation can be made. These groups are: 1) species with usually open panicles and usually awnless lemmas (*A. bourgaei*, *A. calderoniae*, *A. ghiesbreghtii*, *A. hyemalis*, *A. laxissima*, *A. idahoensis*, *A. perennans* sensu lato, *A. scabra*, *A. subrepens*, *A. turrialbae*); 2) species with usually narrow and dense panicles, and often acuminate to awned glumes (*A. exarata*, *A. microphylla*, this group is called the *A. exarata complex* by Carlbom (1967)); 3) species with mostly basal leaves, usually conduplicated to convolute leaf blades, and usually narrow and dense panicles (*A. subpatens*, *A. tolucensis*, *A. variabilis*). Particularly challenging is the taxonomy of *Agrostis perennans* sensu lato (see Sylvester et al. 2020a), where numerous entities have been identified under this name. There is still much work to do on the taxonomy of *Agrostis*, and molecular evidence may help in the systematics of the group (Vigosa-Mercado in prep.).

Conservation status

We propose a preliminary conservation assessment for each species in the study zone (Table 1), according to the International Union for Conservation of Nature categories: one with Deficient Data (DD), six as Endangered (EN), two as Vulnerable (VU), and 11 as Least Concern (LC). Values of EOO and AOO for each species are presented at Table 1. The mean for the EOO is 459,760 km^2, and for the AOO is 279 km^2. Endangered species are reported as scarce, with few plants per population, and usually are known only from one or two localities in the study zone. Vulnerable species are known from a greater number of localities. Species assessed as Least Concern are widespread, and often are reported as abundant in the populations. Introduced species often are weedy and are included in this latter category. The conservation status for each species is discussed under each species description.

Table 1. Distribution of the species of *Agrostis* in Megamexico 3 and conservation status.

Species	Distribution in the study zone	Elevation (m a.s.l.)	EOO (km^2)	AOO (km^2)	Conservation status
A. bourgaei E. Fourn.	Endemic of central Mexico	1800–3800	45,765	1,476	LC
A. calderoniae Acosta	Endemic of central Mexico	3500–3800	–	–	EN
A. capillaris L.	Introduced to Mexico and Honduras	2000–2830	–	–	LC
A. elliottiana Schult.	Southwestern USA (Arizona, New Mexico)	1189–1676	1,078	16	EN
A. exarata Trin.	Southern USA to central Mexico	350–2900	1,402,821	188	LC
A. ghiesbreghtii E. Fourn.	Endemic. Central Mexico to Guatemala	1110–3700	240,863	176	LC
A. gigantea Roth	Introduced to USA and Mexico	651–3300	–	–	LC
A. hyemalis (Walter) Britton, Sterns & Poggenb.	Southern USA to central Mexico	14–2710	1,491,700	248	LC
A. *idahoensis* Nash	Southwestern USA (Arizona, California)	3084–3121	–	–	DD
A. laxissima Swallen	Endemic. Southern Mexico to Guatemala	2250–3800	2,615	44	VU
A. microphylla Steud.	Baja California peninsula	37–315	897	12	EN
A. pallens Trin.	California to Baja California	40–1635	10,902	48	VU
A. perennans (Walter) Tuck.	Northern Mexico to Honduras	622–3847	992,915	700	LC
A. scabra Willd.	Southern USA to Guatemala	630–3500	2,076,712	712	LC
A. stolonifera L.	Introduced to Mexico	1800–2100	–	–	LC
A. subpatens Hitchc.	Southern Mexico to Guatemala	2900–3790	5,589	20	EN
A. subrepens (Hitchc.) Hitchc.	Mexico (Chihuahua)	2000–2168	74	12	EN
A. tolucensis Kunth	Northern Mexico to Guatemala	1330–4520	439,417	432	LC
A. turrialbae Mez	Central Mexico to Guatemala	1600–4240	183,426	84	LC
A. variabilis Rydb.	California to Baja California	2400–2639	1,621	16	EN

Morphoanatomy

A general morphoanatomical characterization of the species found in the study zone is presented below. Description of the morphology and anatomy of each species is presented in the taxonomic treatment.

Habit. All the species of *Agrostis* in the study zone are herbaceous plants, usually perennial, but some annual species occur (*A. elliottiana*, *A. microphylla*). Most species are caespitose, with the culms growing densely in tufts, some species develop stolons (*A. stolonifera*, Fig. 33A; rarely *A. capillaris* and *A. gigantea*), rhizomes (*A. capillaris*, *A. capillaris*, *A. gigantea*, *A. tolucensis*, rarely *A. exarata*), or pseudostolons that have the appearance of rhizomes on herbarium specimens (*A. perennans* sensu lato, *A. subrepens*, Fig. 35B). Usually, the species in the study zone develop extravaginal tillers that are covered with cataphylls. While the type of tillering has been considered as a character of taxonomic importance (Philipson 1937; Widén 1971), this character is difficult to observe on herbarium specimens.

Roots. They are fibrous, and the presence of arbuscular mycorrhiza has been reported in *Agrostis capillaris* (Gollotte et al. 2004).

Culms. They are unbranched, hollow, and usually erect, but sometimes are decumbent in the lower portion. The length of the culms is variable, from a few centimeters to 1.2 meters in some species (*A. gigantea*). The number of nodes is variable, from one to several.

Leaves. They are formed by the sheath, leaf blade and ligule. They could be basal (Fig. 38A), cauline (Fig. 24A), or both, as in most species of Megamexico 3.

Sheaths. They are tubular. Their margins are free and clasp the culms. In the species of the study zone, the sheaths range from shorter to longer than the internodes, and their abaxial surface are glabrous or scaberulous.

Ligules. The length and form of the ligules have been recognized as a valuable taxonomic character (Philipson 1937; Widén 1971; Romero-García et al. 1988). In the species of the study zone, the ligules are variable, but in most cases no significant differences were found between the species. The ligules range from longer or shorter than wide, their abaxial surfaces are usually scaberulous, and the apices are acute, erose or truncate. In several species of Megamexico 3, the old ligules are often lacerate (e.g., *A. bourgaei*, Fig. 3B).

Leaf blades. In the species of the study zone, leaf blades are filiform (e.g., *A. subpatens*, Fig. 34A) to linear (e.g., *A. perennans* sensu lato, Fig. 25A), and their consistency is usually chartaceous.

Leaf blade abaxial epidermis. Among the species in the study zone, the abaxial epidermis is quite homogeneous and thus its taxonomic value is poor, as previously noted by Romero-García et al. (1988).

The abaxial epidermis presents two differentiated regions, the intercostal and costal zones (Fig. 2A). The intercostal zone is made up of elongated cells of constant shape and size, their walls are straight, the sidewalls are angled outwards, and end walls are vertical or angled (Fig. 2B). In the intercostal zone there are one or two rows of stomata (Fig. 2A), with guard cells parallel-sided or low dome-shaped. No short cells were seen in the intercostal zone of the studied species. The costal zone presents elongated cells similar to the intercostal zone, but sometimes their walls are slightly thickened, with short cells (Fig. 2B), and silica bodies. Prickle hairs are present on both zones (Fig. 2A). They are medium sized, with a short and raised barb. No micro or macrohairs were seen in the abaxial epidermis of the studied species.

Leaf blade transversal section anatomy. The leaf blades of *Agrostis* species display a no-Kranz anatomy (C3 photosynthesis). The anatomical features of the leaf blade have been considered of taxonomic importance, particularly the patterns of sclerenchyma distribution (Romero-García et al. 1988). In the studied species, leaf blade anatomy is a useful character for distinguishing some species, but several species share similar attributes.

The leaf blade could be flat (Fig. 6A), convolute (15D), or v-shaped, (37A) in transversal section. Adaxial furrows of variable depth and width are present between all vascular bundles (Figs 6, 15, 22, 31, 37). Adaxial ribs of variable shape are present over all vascular bundles (Figs 6, 15, 22, 31, 37). No abaxial furrows and ribs were seen in the studied species.

A keel with several vascular bundles and parenchyma was found only in some individuals of *A. exarata* (Fig. 15A). There are one to three vascular bundles of second order between the bundles of first order, where all of them are at the same level, closer to the abaxial surface (Figs 6, 15, 22, 31, 37), and their shape is circular (Fig. 6B) to slightly elliptical (Fig. 31B). Sometimes there are third order vascular bundles, between the first and second order bundles, or near the leaf blade margins (Figs 6D, 22F). There are two sheaths surrounding the vascular bundles, an outer parenchymatous sheath that is interrupted abaxially (Fig. 15B), or sometimes also adaxially (Fig. 31E), and an inner sclerenchymatous complete sheath (Fig. 15J). Sclerenchyma is found associated with vascular bundles of first and second order, in abaxial or adaxial strands or girders (Figs 6, 15, 22, 31, 37). There are small caps of sclerenchyma in leaf margins (Fig. 22F). In some species, abaxial strands of sclerenchyma between the vascular bundles are found (Fig. 6E), and only in some individuals of *A. ghiesbreghtii* a hypodermal abaxial layer of sclerenchyma is detected (Fig. 15D, E).

The mesophyll is non-radiate, with regular small cells, isodiametric, and tightly packed (Fig. 6G). Colorless cells were found associated with the outer bundle sheath, only in some individuals of *A. exarata* (Fig. 15A). In all species, there are fan-shaped groups of small, bulliform cells in the base of adaxial furrows (Fig. 6E), but sometimes in dried specimens they could be collapsed. In all species, there are prickle hairs in adaxial and abaxial epidermis.

Synflorescences. They are made up of spikelets disposed in panicles, contracted (e.g., *A. microphylla*, Fig. 23A) to open (e.g., *A. perennans* sensu lato, Fig. 25A). The shape of the panicles could be linear (e.g., *A. variabilis*, Fig. 40A), or lanceolate (e.g., *A. exarata*, Fig.14A) to ovate (e.g., *A. ghiesbreghtii*, 16A). The branches are disposed in verticils and could be appressed (e.g. *A. stolonifera*, Fig. 33A) to divergent (e.g., *A. scabra*, Fig. 29A), with or without spikelets from the base, or sometimes the spikelets are clustered at branch tips (e.g., *A. hyemalis*, Fig. 19C).

Spikelets. They are small, no more than 4.5 mm long. They are made up of two basal bracts called glumes and a single floret (Fig. 3C). The florets consist of a lower bract called the lemma, an upper bract called the palea, and a bisexual flower (Fig. 3E). The base of the floret is slightly hardened (callus), usually with two tufts of hairs (Figs 5, 30).

Glumes. They are longer than the floret, equal to unequal in size between them and keeled on the back. Their apices are usually acute to acuminate (Fig. 14C), or sometimes awned (*A. microphylla*, Fig. 23C; sometimes *A. exarata*).

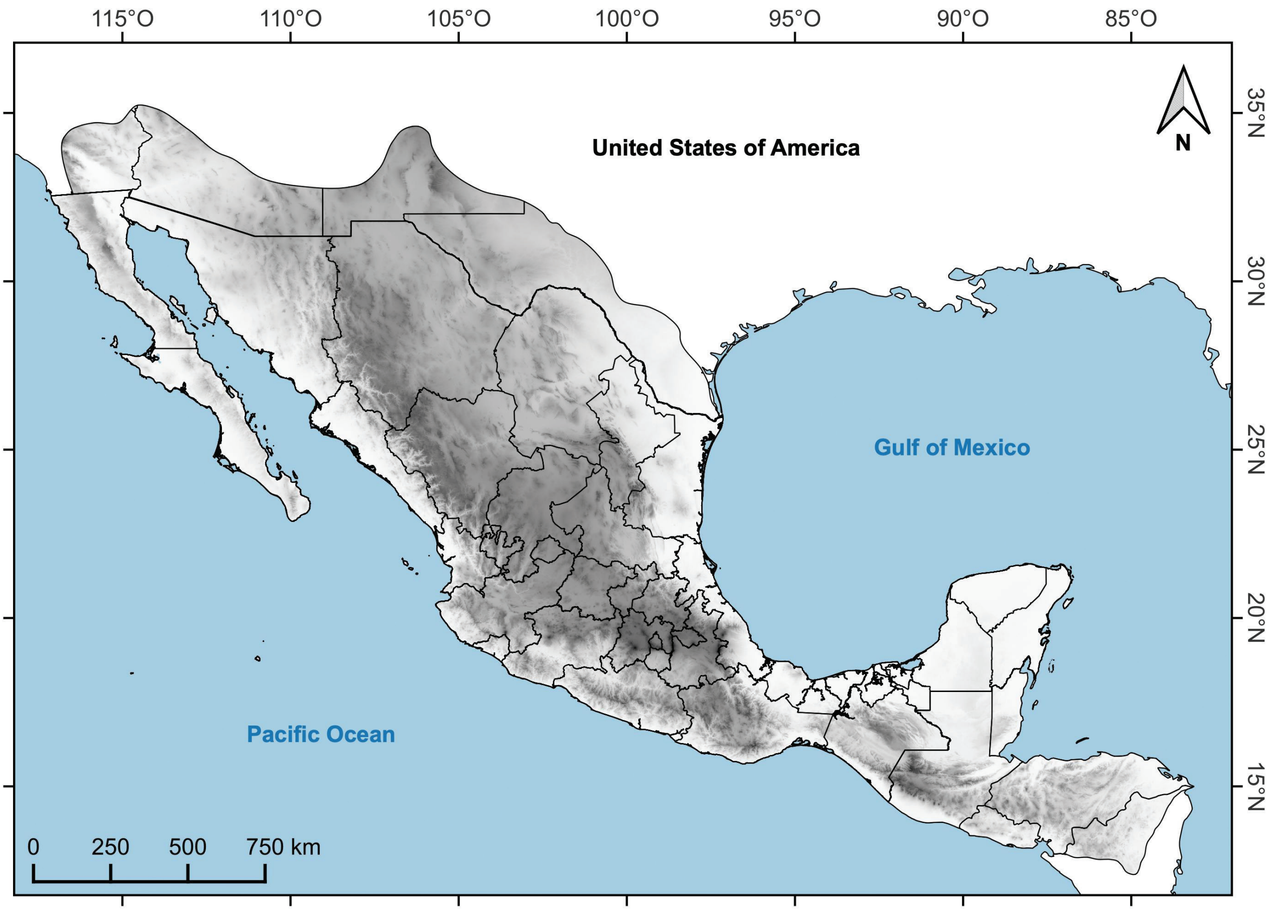

Figure 1. Area of Megamexico 3.

Their consistency is membranous, with a single vein, and are scaberulous on the keel (Fig. 19D), and sometimes in the rest of the body. It has been considered that the glumes do not have characters of taxonomic value (Widén 1971).

Lemmas. They have several characters of taxonomic importance (Widén 1971; Romero-García et al. 1988). The lemmas are elliptical to oblong, rounded on the back, and their apices could be acute (e.g., *A. gigantea*, Fig. 4G), truncate to obtuse (e.g., *A. hyemalis*, 4H), toothed (e.g., *A. tolucensiss*, Fig. 4Q), or sometimes the lateral veins are shortly excurrent (e.g., *A. capillaris*, Fig. 4C). Their consistency is membranous, usually with five veins that are prominent on the back, or inconspicuous. They are often awned on the back, with the awn inserted near the base (e.g., *A. ghiesbreghtii*, Fig. 4F), or near the apex, and could be straight to geniculate (e.g., *A. laxissima*, Fig. 21D).

Lemma micromorphology. Transversal thickenings in the outer walls of the abaxial epidermis cells, especially the ones of the lower half portion, could form a pattern that has been called the *Trichodium* net. It has been noted that this character is useful to form broad groups, and it has been proposed that it is an important character for the infrageneric classification of the genus (Björkman 1960; Widén 1971; Romero-García et al. 1988).

Widén (1971) has recognized seven types of net, based on the width of the transversal thickenings. In the studied species of *Agrostis*, taxa with absent or reduced paleas have a conspicuous net, while the species with paleate spikelets usually lack, or have fragmentary nets (Figs 7, 32), as noted in previous

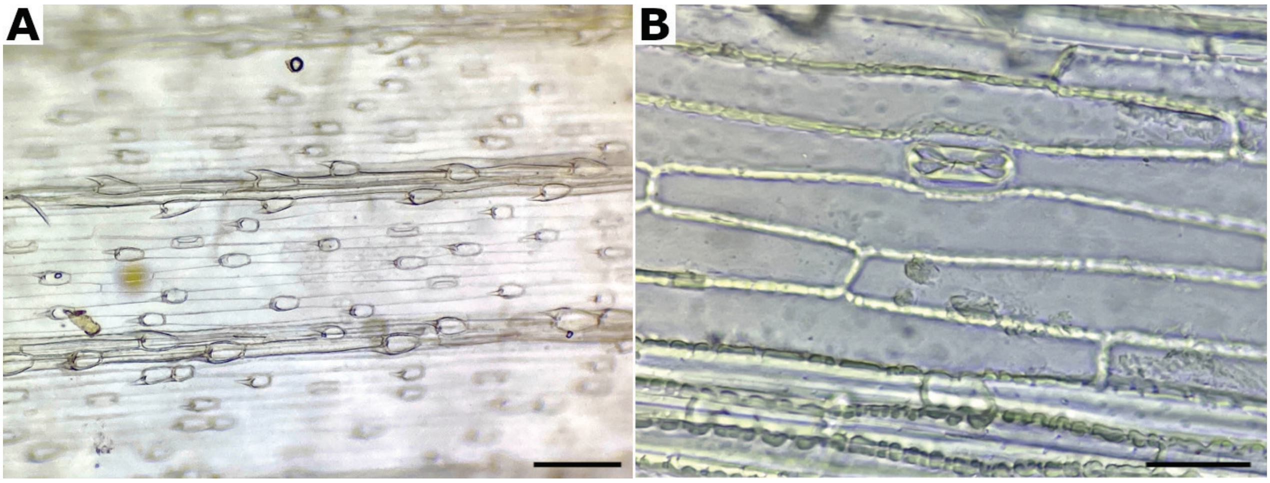

Figure 2. Abaxial epidermis of *Agrostis* species **A** *A. bourgaei* **B** *A. exarata*. Scale bars: 100 µm (**A**); 50 µm (**B**).

studies (Björkman 1960; Widén 1971; Romero-García et al. 1988). In the species of *Agrostis* present in Megamexico 3, it has also been found that this character is useful for distinguishing some morphologically similar species that are often confused (e.g., *A. bourgaei* and *A. gigantea*).

Paleas. They are usually minute, membranous, veinless, and often are missing. In some species, the paleas are well-developed, reaching (1/5–)1/3–3 /4 of the lemma length, usually with two visible veins (e.g., *A. capillaris*, Fig. 12F).

Flowers. They consist of a perianth with two scales (lodicules), an androecium of three stamens (one in *A. elliottiana*), and a unilocular gynoecium with two styles and two plumose stigmas.

Fruits. They are of the caryopsis type, usually ellipsoidal, with the surface smooth, and have a punctiform hilum. The endosperm is liquid, soft, or solid. The embryo is small in relation to the fruit size.

Taxonomic treatment

***Agrostis* L., Sp. Pl. 1: 61. 1753, nom. et typ. cons.**

= *Vilfa* Adans., Fam. Pl. 2: 495. 1763. Type: *Agrostis. stolonifera* L. (lectotype designated by Hitchcock (1920: 127)).

= *Trichodium* Michx., Fl. Bor.-Amer. 1: 41. 1803. Type: *T. laxiflorum* Michx. (lectotype designated by Hitchcock (1920: 127)).

= *Agraulus* P. Beauv., Ess. Agrostogr. 5, t. 4. 1812. Type: *Agrostis canina* L. (lectotype designated by Hitchcock (1920: 127)).

= *Decandolia* Bastard, Essai Fl. Maine et Loire 15, 28. 1809, nom. illeg. superfl. Type: *Agrostis stolonifera* L. (lectotype designated by Hitchcock (1937: 515)).

= *Notonema* Raf., Bull. Bot. (Geneva) 1: 220. 1830. Type: *Agrostis arachnoides* Elliott (=*A. elliotiana* Schult.).

= *Bromidium* Nees & Meyen, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, suppl. 1: 154. 1843. Type: *Agrostis hygrometrica* Nees (lectotype designted by Rúgolo 1982: 196)).

= *Anomalotis* Steud., Syn. Pl. Glumac. 1: 198. 1854. Type: *A. quinqueseta* Steud.

= *Didymochaeta* Steud., Syn. Pl. Glumac. 1: 185. 1854. Type: *D. chilensis* Steud. (lectotype designated by Clayton and Renvoize (1986: 134)).

= *Chaetopogon* Janch., Eur. Gatt. Farn. Bl.-Pfl. (ed. 2) 33. 1913. Type: not designated.
= *Neoschischkinia* Tzvelev, Bot. Zhurn. (Moscow & Leningrad) 53: 309. 1968. Type: *Trichodium elegans* Thore.
= *Linkagrostis* Romero Garcia & C. Morales, Candollea 42(1): 383. 1987. Type: *Agrostis juressi* Link.*

Type. *Agrostis canina* L. (lectotype designated by Widén (1971: 13), see also Philipson (1937), Jarvis (1992) and commentary below).

Description. Plants herbaceous, annuals or perennials, up to 1.2 m, caespitose, rhizomatous or stoloniferous, sometimes developing pseudoestolons. ***Tillers*** extravaginal and/or intravaginal. ***Culms*** decumbent to erect, usually slender, unbranched, internodes hollow. ***Leaves*** basal or cauline; sheaths open; auricles absent; ligules membranous, entire to lacerate, usually scabridulous dorsally; blades filiform to linear, flat, conduplicate, convolute, or involute. ***Synflorescence*** a panicle, usually terminal, contracted to open; branches usually in whorls. ***Spikelets*** up to 4.5 mm long, 1-flowered, pedicellate, laterally compressed; rachilla not prolonged beyond the base of the floret; disarticulation above the glumes; glumes as long as the spikelet, equal to unequal, keeled, membranous, usually 1-nerved, rarely awned; floret bisexual, shorter than the glumes, usually 1/3–3/4 the length of the glumes, rarely longer; callus rounded, glabrous to pubescent; lemmas rounded dorsally, apices entire, erose or toothed, membranous, (3)5-nerved, veins inconspicuous or prominent, unawned or awned dorsally, awn straight to geniculate; paleas often absent or diminute, sometimes well-developed and reaching (1/5–)1/3–3/4 of the lemma length; lodicules 2; anthers (1)3; ovary glabrous, styles 2, free to the base. ***Fruit*** a caryopsis; endosperm liquid, soft or solid. x= 7.

Commentaries. The name *Agrostis* was first described in the work of Linnaeus, Genera Plantarum (Linnaeus 1737: 19), with a Latin diagnosis. According to the International Code of Nomenclature for Algae, Fungi and Plants (Art. 13.1) (Turland et al. 2018), the beginning of effective publication dates for generic names is 1st May 1753, with the publication of Species Plantarum (Linnaeus 1753). In this latter work, Linnaeus described 12 names, classified in two groups: 1) Aristatae (*A. spica-venti* L., *A. miliacea* L., *A. arundinacea* L., *A. rubra* L., *A. canin*a L., *A. paradoxa* L.); and 2) Muticae (*A. stolonifera* L., *A. capillaris* L., *A. alba* L., *A. minima* L., *A. virginica* L., *A. indica* L.). No type species was designated by Linnaeus.

Hitchcock (1905) designated *A. alba* as the type, but the original material of this name is a *Poa* L. species (Widén, 1971), and the adoption of this name as lectotype would result in *Agrostis* becoming a synonym of *Poa* (McNeill et al. 1987). Years later, Hitchcock (1920), proposed *A. stolonifera* as lectotype, but this name conflicts with the original description of the genus, since it mentions that the lemmas are awned (Linnaeus 1737), and the original description of *A. stolonifera* mentions that the lemmas are unawned (Linnaeus 1753).

Philipson (1937) was the first to propose as lectotype the name *A. canina*. Widén (1971) agreed with that choice, and formally designated this name, since it is the one that keeps better the usage of the generic name. Jarvis (1992) proposed the conservation of the name *Agrostis*, with a conserved type.

* See Suppl. material 1 for other heterotypic synonyms.

The species of this genus are often confused with other genera found in the study zone, with one-flowered spikelets, such as *Lachnagrostis* Trin., *Muhlenbergia* Scherb., *Podagrostis* (Griseb.) Scribn. & Merr., *Polypogon* Desf., *Sporobolus* R. Br., and some species of *Peyritschia* E. Fourn., but it is distinguished from them by the following combination of characters: spikelets disarticulating above the glumes, florets shorter than the glumes, usually 1/3–3/4 the length of the glumes, rarely longer, lemmas with usually five veins, dorsal awns often present, palea often reduced or absent (sometimes reaching up to 3/4 of the lemma length), and rachilla not prolonged. See the work of Sylvester et al. (2020b) for a key to differentiate *Agrostis* from morphologically similar genera.

Identification key for the species of *Agrostis* of Megamexico 3

1	Paleas present, 0.5 mm or longer ((1/5–)1/3–3/4 of the lemma length)	**2**
–	Paleas absent or diminute, up to 0.2(–0.4) mm long (usually less than 1/5 of the lemma length)	**8**
2(1)	Panicles 0.4–3 cm wide, contracted, dense, often spiciform, branches appressed to ascending	**3**
–	Panicles (2–)3.5–20 cm wide, open, dense to lax, not spiciform, branches ascending to spreading	**4**
3(2)	Plants caespitose, rarely shortly rhizomatous; paleas up to 0.8 mm long, veinless; anthers 0.3–0.7 mm long	***A. exarata*** **Trin.**
–	Plants stoloniferous; paleas 0.7–1.4 mm long, 2-veined; anthers 0.9–1.5 mm long	***A. stolonifera*** **L.**
4(2)	Plants caespitose	**5**
–	Plants rhizomatous or stoloniferous	**6**
5(4)	Spikelets 2–2.7 mm long; lemmas 1.5–1.8 mm long, anthers (0.3–)0.5–0.7 mm long; leaves basal and cauline, blades flat	***A. bourgaei*** **E. Fourn.**
–	Spikelets 2.5–3.5 mm long; lemmas 2–2.5 mm long; anthers 0.7–1 mm long; leaves mostly basal, conduplicate to convolute	***A. calderoniae*** **Acosta**
6(4)	Ligules of the basal blades 0.2–1.5 mm long, the upper ones up to 2 mm long, usually shorter than wide, rarely longer than wide	***A. capillaris*** **L.**
–	Ligules 1–7 mm long, longer than wide	**7**
7(6)	Plants rhizomatous, rarely stoloniferous; culms up to 1.2 m long; panicles (9–)13–40 cm long, 4–16 cm wide, open; blades 1–8 mm wide, usually at least some blades larger than 5 mm wide	***A. gigantea*** **Roth**
–	Plants stoloniferous, stolons usually long; culms up to 0.6 m long; panicles 4–20 cm long, 0.5–3 cm wide, open at anthesis, becoming contracted after flowering; blades (1–)2–6 mm wide	***A. stolonifera*** **L.**
8(1)	Panicles 0.2–3 cm wide, contracted, usually dense, spiciform, branches appressed to ascending	**9**
–	Panicles 0.5–30 cm wide, usually open and lax, if narrow never spiciform, branches ascending to spreading	**15**

9(8) Plants annual; glumes with apices long acuminate or awned; lemma awned, awn 3.5–6 mm long .... ***A. microphylla* Trin.**

– Plants perennial; glumes usually with apices acute or shortly acuminate (sometimes awned in *A. exarata*); lemmas unawned or with an awn up to 3.5 mm long **10**

10(9) Plants rhizomatous, rhizomes up to 10 cm long; leaves mostly cauline; plants known in the study zone from inland San Diego and Baja California... ***A. pallens* Trin.**

– Plants caespitose, or shortly rhizomatous, rhizomes if present inconspicuous, or up to 2 cm long; leaves mostly basal or basal and cauline **11**

11(10) Leaf blades 0.5–4(–8) mm wide, linear, flat... **12**

– Leaf blades 0.4–1 mm wide, filiform, conduplicate or convolute (flat when young in *A. variabilis*) **13**

12(10) Lemmas unawned or awned about mid-length, awn up to 3 mm long; paleas absent or 0.3–0.8 mm long................................. ***A. exarata* Trin.**

– Lemmas usually awned near the base, sometimes above mid-length, rarely awnless, awn 1.5–3.5 mm long; paleas absent............................. .... ***A. tolucensis* Kunth**

13(10) Lemmas with apices entire, acute, usually unawned, rarely awned above mid-length, awn up to 1 mm long, straight, not reaching the lemma apices; plants known in the study zone from Baja California .... ***A. variabilis* Rydb.**

– Lemmas with apices toothed, usually awned near the base (sometimes above mid-length or rarely awnless in *A. tolucensis*), awn 1.5–3.5 mm long, geniculate, reaching the lemma apices **14**

14(13) Panicles somewhat lax; most pedicels longer than the spikelets; plants known in the study zone from Chiapas and Guatemala.......................... .... ***A. subpatens* Hitchc.**

– Panicles dense; most pedicels shorter than the spikelets...................... .... ***A. tolucensis* Kunth**

15(8) Plants rhizomatous or developing conspicuous pseudostolons......... **16**

– Plants caespitose (pseudostolons sometimes present in *A. perennans* sensu lato) **17**

16(15) Panicles 0.4–3 cm wide, open to contracted, branches appressed to ascending; leaf blades 1–4 mm wide; plants known in the study zone from inland San Diego and Baja California...................... ***A. pallens* Trin.**

– Panicles 5–10 cm wide, open, branches spreading; leaf blades 1–1.5 mm wide; plants known in the study zone from Chihuahua......... .... ***A. subrepens* (Hitchc.) Hitchc.**

17(15) Lemmas awned, awn 2–10 mm long, inserted near the base (inserted in the upper third in *A. elliottiana*) **18**

– Lemmas unawned, rarely with an awn up to 2.5 mm long, inserted above mid-length... **21**

18(17) Plants annual; awn of the lemma 3–10 mm long, inserted in the upper third, flexuous; anther 1 .... ***A. elliottiana* Schult.**

– Plants perennial; awn of the lemma 2.3–5 mm long, inserted near the base, geniculate; anthers 3... **19**

19(18) Culms with 1–2 nodes; leaves mostly basal, blades 0.4–0.8 mm wide, filiform..***A. subpatens* Hitchc.**
– Culms with 2–6 nodes; leaves basal and cauline, blades 1–4(–5) mm wide, linear...**20**
20(19) Leaf blades stiff, convolute, the upper ones sometimes flat; spikelets (2.5–)3–4 mm long... ***A. ghiesbreghtii* E. Fourn.**
– Leaf blades lax, flat; spikelets 1.7–3 mm long....... ***A. laxissima* Swallen**
21(17) Leaves basal and cauline (the basal ones often drying before anthesis in mature individuals of *A. perennans* sensu lato) **22**
– Leaves mostly basal **24**
22(21) Branches of the panicle rebranching about mid-length; spikelets not clustered; leaf blades 1–6 mm wide, usually at least some blades larger than 2 mm wide......................... ***A. perennans* (Walter) Tuck. sensu lato**
– Branches of the panicle rebranching in the upper third; spikelets clustered at the branch tips; leaf blades (0.3–)0.5–2(–3) mm wide..........**23**
23(22) Spikelets 1–2(–2.5) mm long; anthers 0.2–0.5 mm long .... ***A. hyemalis* (Walter) Britton, Sterns & Poggenb.**
– Spikelets 2–3(–3.4) mm long, less clustered at the branch tips; anthers 0.5–1.4 mm long..***A. scabra* Willd.**
24(21) Panicles (4–)8–30 cm long, (2.2–)4–20(–26) cm wide, branches rebranching in the upper third; spikelets 2–3(–3.4) mm long, usually somewhat clustered at the branch tips; leaf blades 2–14 cm long ....***A. scabra* Willd.**
– Panicles 3–13 cm long, 1–6(–8) cm wide, branches rebranching about or slightly above mid-length; spikelets 1.5–2.5 mm long, not clustered; leaf blades 1–9 cm long **25**
25(24) Leaf blades 0.5–2 mm wide, linear, flat, becoming involute when drying; plants known in the study zone from southern Arizona and California .. .. ***A. idahoensis* Nash**
– Leaf blades 0.2–0.5 mm wide, filiform, conduplicate to involute, rarely flat in the upper leaves; plants known in the study zone from central Mexico to Guatemala...***A. turrialbae* Mez**

1. *Agrostis bourgaei* E. Fourn., Mexic. Pl. 2: 95. 1886.
Figs 3, 4A, 5A

Agrostis bourgaei E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 550. 1885, nom. nud.
= *Agrostis thyrsigera* Mez, Repert. Spec. Nov. Regni Veg. 17(19): 301. 1921. Type: Mexico. State of México: wet banks, Sierra de las Cruces, 12 Aug 1893, C.G. Pringle 4485 (lectotype, designated by Vigosa-Mercado (2022a: 1): BR (BR0000006863616 [image!]); isolectoypes: BR (BR0000006864217 [image!]), K (K000308369 [image!]), KFTA (KFTA0002213 [image!]), MSC (MSC0129859 [image!]), NDG (NDG07467 [image!]), NY (NY00688876 [image!], NY00688877 [image!]), S (S12-16472 [image!]), W (W18940003052 [image!])).

Type. Mexico. Mexico City: pedrégal près Tizapan, vallée de Mexico, 2 Aug 1865, E. Bourgeau 682 (holotype: P (P00740531 [image!]); isotype: US [fragm. ex P] (US00156379)).

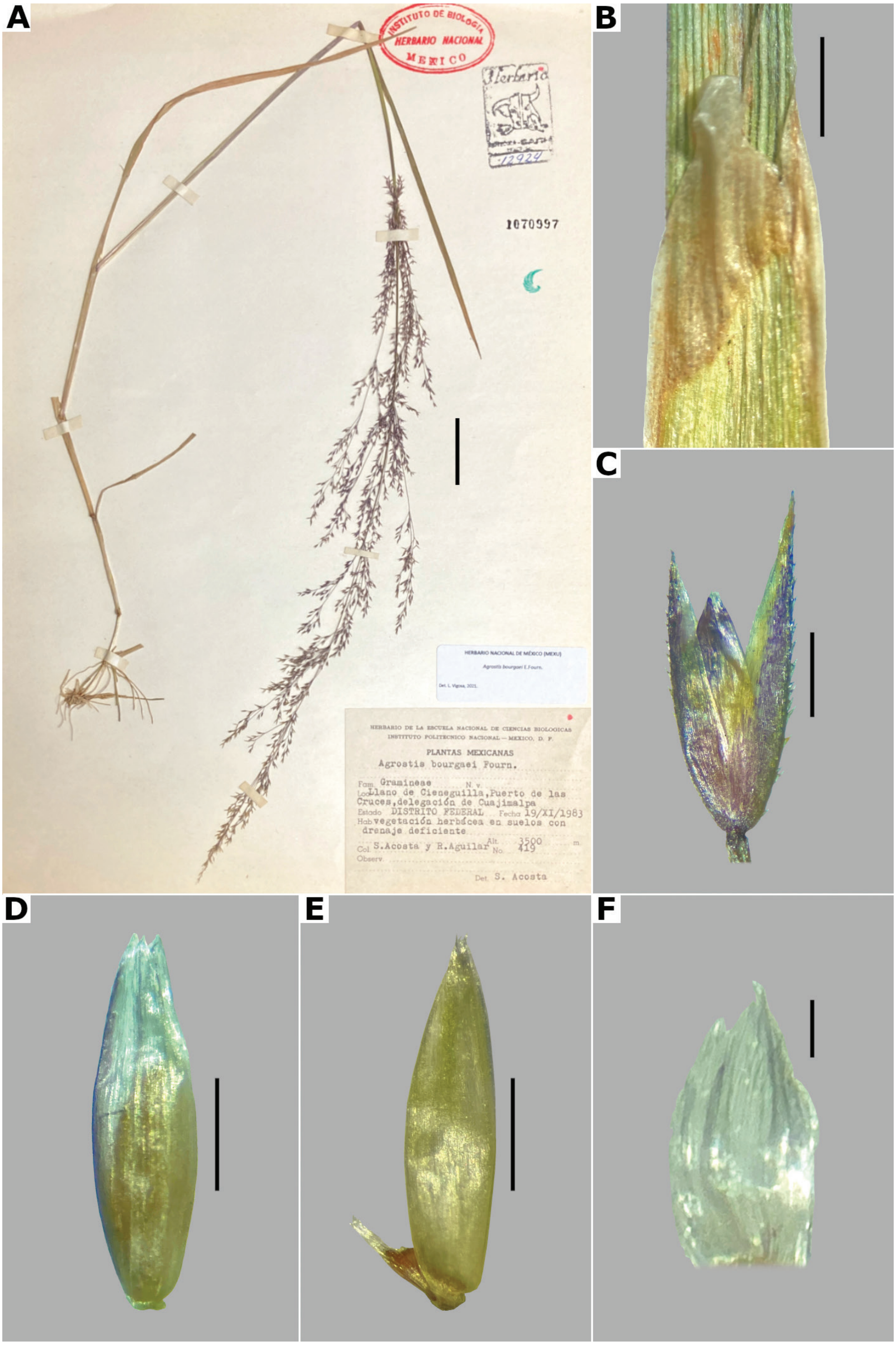

Figure 3. *Agrostis bourgaei* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view, **E** floret, lateral view showing the lemma and the palea **F** palea. Based on Acosta 419 (MEXU). Scale bars: 3 cm (**A**); 2 mm (**B**); 0.5 mm (**C–E**); 0.1 mm (**F**).

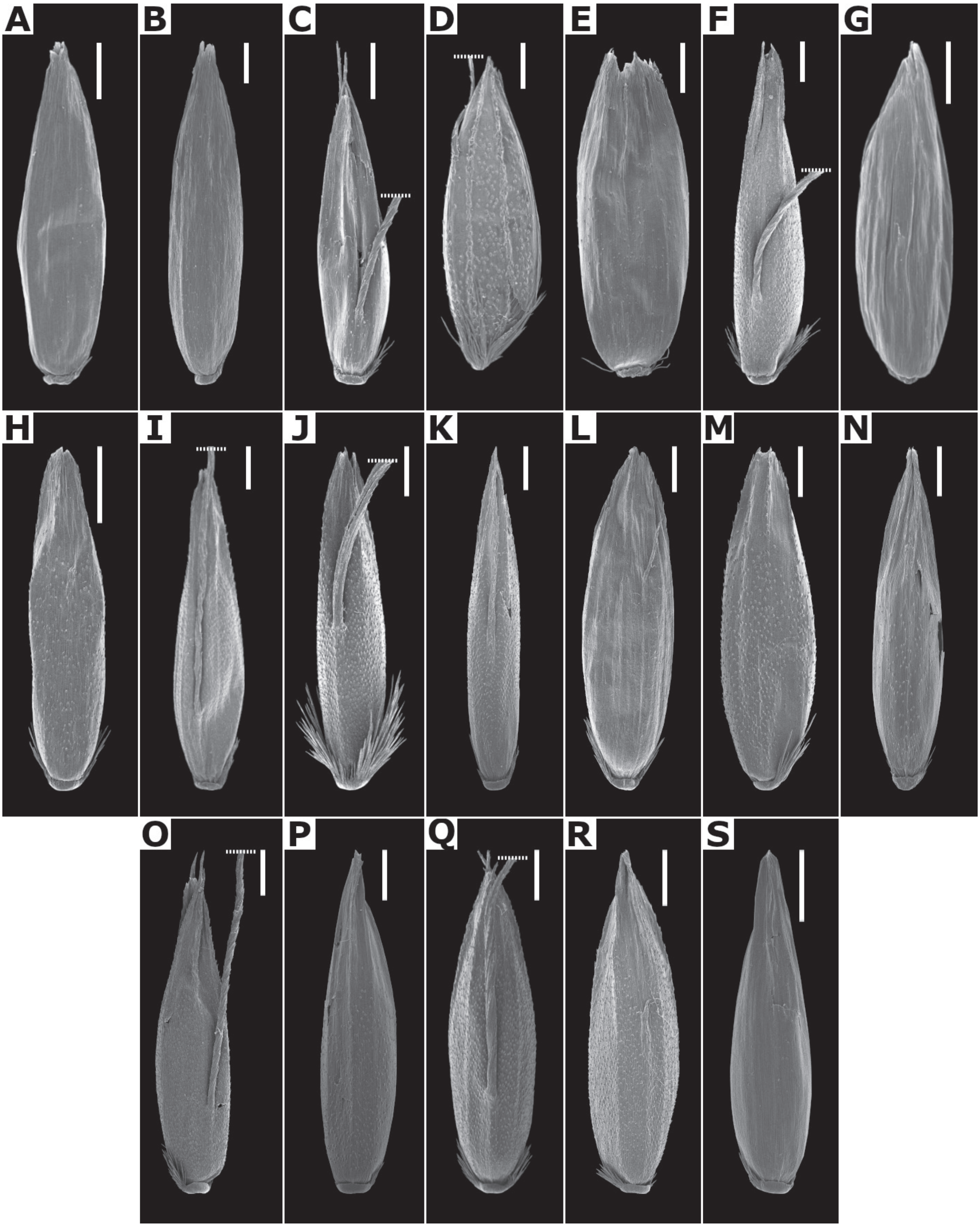

Figure 4. Florets of *Agrostis* species observed with SEM **A** *A. bourgaei* **B** *A. calderoniae* **C** *A. capillaris* **D** *A. elliottiana* **E** *A. exarata* **F** *A. ghiesbreghtii* **G** *A. gigantea* **H** *A. hyemalis* **I** *A. laxissima* **J** *A. microphylla* **K** *A. pallens* **L** *A. perennans* **M** *A. scabra* **N** *A. stolonifera* **O** *A. subpatens* **P** *A. subrepens* **Q** *A. tolucensis* **R** *A. turrialbae* **S** *A. variabilis*. Scale bars: 0.3 mm.

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 0.1–1.2 m long, erect, sometimes shortly decumbent at the base, nodes 2–4, glabrous, internodes glabrous, or sometimes scaberulous

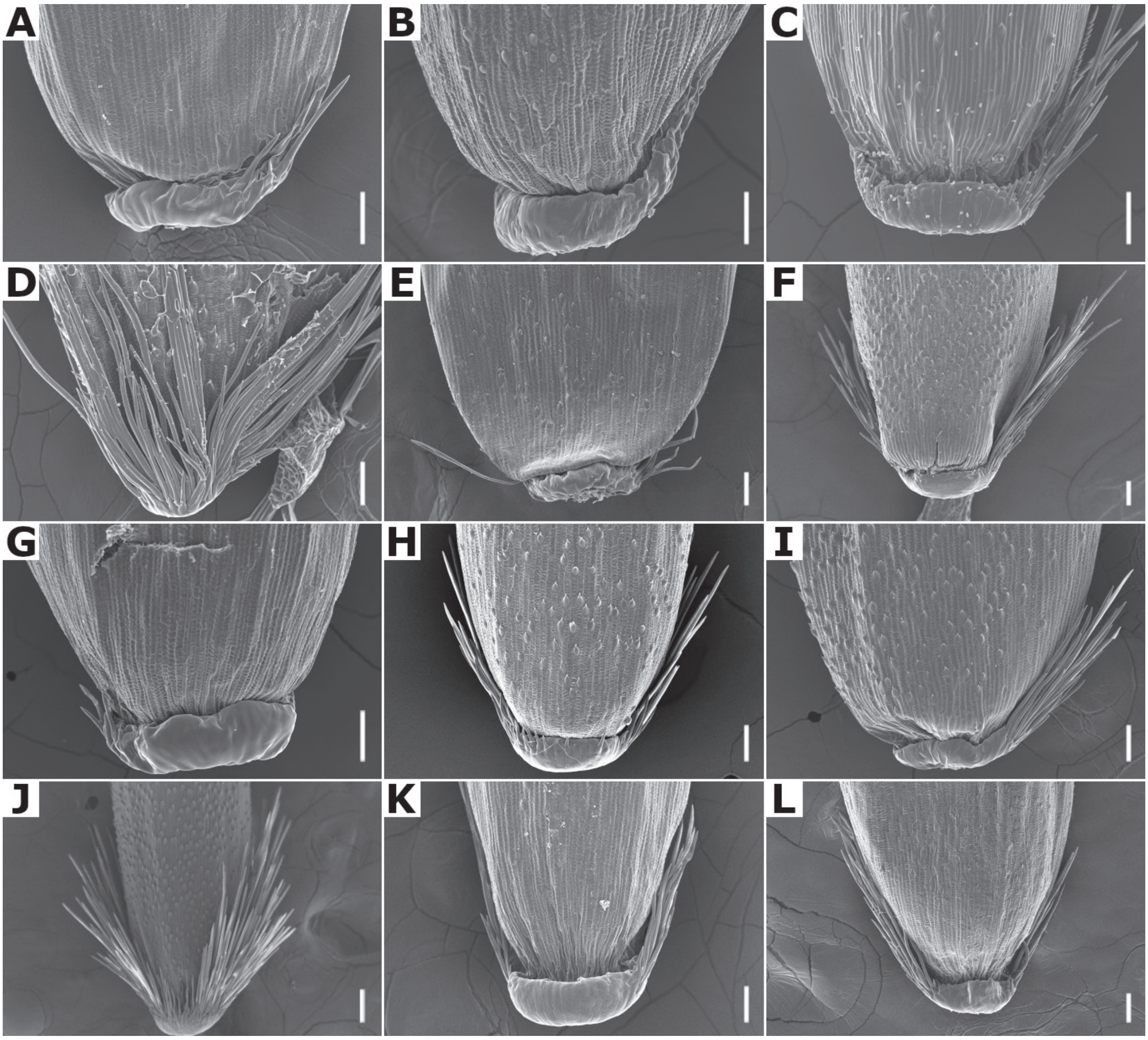

Figure 5. Calluses of *Agrostis* species observed with SEM **A** *A. bourgaei* **B** *A. calderoniae* **C** *A. capillaris* **D** *A. elliottiana* **E** *A. exarata* **F** *A. ghiesbreghtii* **G** *A. gigantea* **H** *A. hyemalis* **I** *A. laxissima* **J** *A. microphylla* **K** *A. pallens* **L** *A. perennans*. Scale bars: 50 μm.

below the nodes and panicle. ***Leaves*** basal and cauline; sheaths 3–18 cm long, usually shorter than the internodes, glabrous or scaberulous; ligules 1–7 mm long, longer than wide, dorsally scaberulous, apices acute, often lacerate; blades 3–15(–30) cm long, (0.5–)1–6 mm wide, linear, flat, scaberulous on both surfaces. ***Panicles*** (2–)9–25(–30) cm long, (0.8–)3–7(–10) cm wide, open, lax, lanceolate, usually long-exserted from the upper sheaths; branches ascending to spreading, rebranching from about or above midlength, scaberulous, without spikelets near their base, inferior branches (1–)2–10 cm long; pedicels 0.5–3 mm long, ascending to spreading, scaberulous. ***Spikelets*** 2–2.7 mm long, usually purplish; glumes subequal to equal, lanceolate, apices shortly acuminate, 1-veined, scaberulous on the keel, lower glume 2–2.7 mm long, upper glume 1.8–2.5 mm long; callus puberulous, with 2 bunches of short trichomes, often inconspicuous; lemmas 1.5–1.8 mm long, elliptic, apices entire, acute or toothed, 5-nerved, veins inconspicuous,

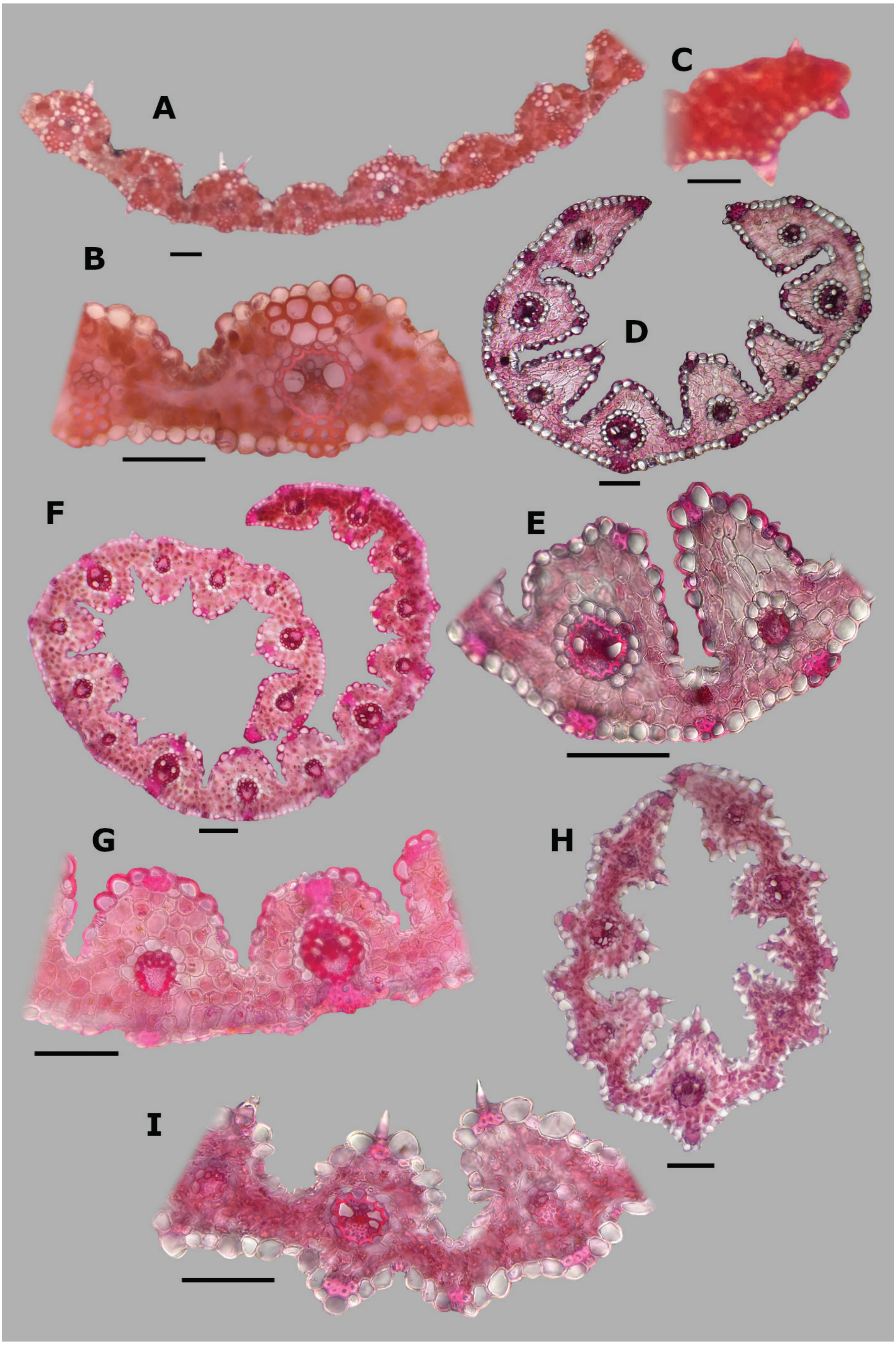

Figure 6. Leaf blade anatomy in transversal section of *Agrostis* species, in general view, and details of lateral bundles. **A**–**C** *A. bourgaei* **D**–**E** *A. calderoniae* **F**–**G** *A. capillaris* **H**–**I** *A. elliottiana*. Scale bars: 0.1 mm.

unawned; paleas present, (0.4–)0.5–0.7(–1) mm long, veinless, glabrous; anthers 3, (0.3–)0.5–0.7 mm long. ***Caryopsis*** 1.2–1.5 mm long, ellipsoid; endosperm soft. 2n= unknown.

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows medium-sized, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in girders, narrowing towards the bundle, adaxial sclerenchyma in strands or t-shaped girders; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 6A–C). Lemmas with transversal thickenings polygonal, wider than the unthickened portions of the wall; prickle hairs scarce (Fig. 7A).

Distribution and habitat. Endemic. Herbarium specimens of *A. bourgaei* have been collected in Mexico City and the Mexican states of Hidalgo, México, Michoacán, Morelos, Puebla, and Oaxaca (Fig. 8A). The species has also been reported for Durango, Guanajuato, Querétaro, Tlaxcala, and Veracruz (Villaseñor 2016; Dávila et al. 2018; Sánchez-Ken 2019), but no specimens from these states were seen. *Agrostis bourgaei* is mainly found on edges of streams and moist soils, in open areas of conifer forests of the Trans-Mexican Volcanic Belt, between 1800–3800 m a.s.l., with some outliers in Morelos found lower, at 725 m a.s.l. (Fig. 9D).

Phenology. Specimens with spikelets have been collected from June to February, but most of the records are from August (Fig. 10D).

Commentaries. *Agrostis bourgaei* is similar to *A. gigantea*, and both are often confused. They share very similar leaf anatomy and paleate spikelets, but *A. bourgaei* is distinguished from the latter in the much more fragile aspect of the plants, caespitose habit, lateral branches of the panicle without spikelets near their base, lemmas with prickle hairs, transversal thickenings, and shorter paleas of up to 0.7(–1) mm long (vs. robust plants, usually rhizomatous habit, often some inferior branches with spikelets near their base, lemmas glabrous, without transversal thickenings, paleas up to 1.2 mm long in *A. gigantea*). The specimen García-Mendoza 1116 (MEXU) from Oaxaca lacks vegetative parts that may allow a more acceptable identification, but is included tentatively in this species for its paleate spikelets.

Conservation status. *Agrostis bourgaei* is an abundant and widespread species in Central Mexico. It is represented by 61 collections, with several populations occurring in 13 protected areas. The EOO is 45,765 km^2 and the AOO is 1,476 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Mexico. Hidalgo: **Municipio Epazoyucan**, Peñas Largas, [20.1°N, 98.6°W], 2850 m alt., 22 Dec 1983 J. Rzedowski 38373a (IEB, MEXU, XAL). **México: Municipio Lerma**, 5 km al W de La Marquesa, en la desviación a Salazar, [19.304403°N, 99.39047°W], 2800 m alt., 1 Aug 1981, R. Guzmán 3966 (IBUG, MEXU). **Municipio Ocuilan**, Laguna de Zempoala, [19.05034984°N, 99.31696647°W], 2800 m alt., 1 Aug 1987, J. Castañeda 327 (MEXU [*]). **Mexico City: Alcaldía Cuajimalpa,** Llano de la Cieneguilla, Puerto de las Cruces, [19.24694444°N, 99.33444444°W], 3500 m alt., 19 Sep 1983, S. Acosta and R. Aguilar 417 (CIIDIR, IEB, MEXU), 418 (CIIDIR,

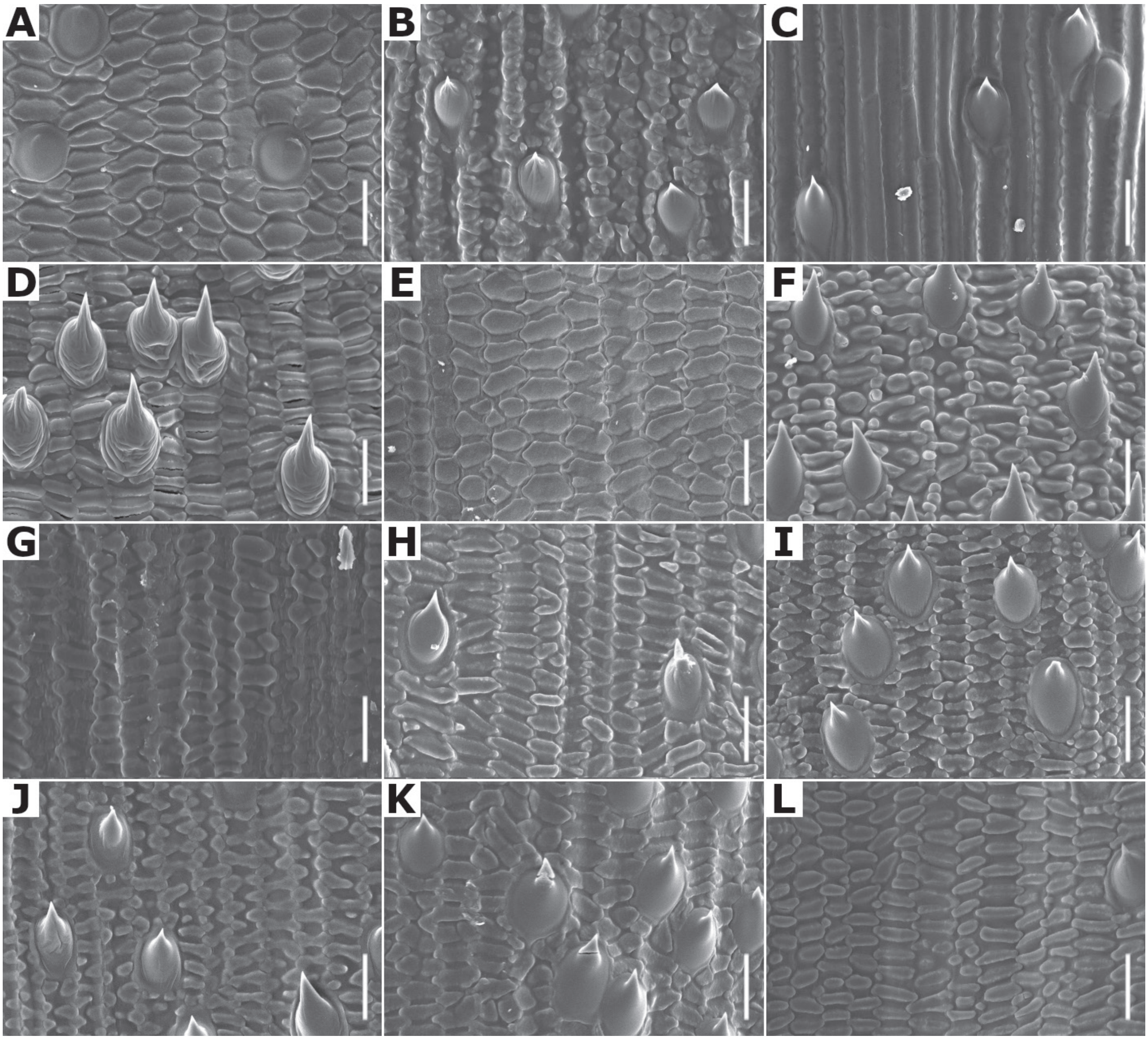

Figure 7. Lemma surface of *Agrostis* observed with SEM **A** *A. bourgaei* **B** *A. calderoniae* **C** *A. capillaris* **D** *A. elliottiana* **E** *A. exarata* **F** *A. ghiesbreghtii* **G** *A. gigantea* **H** *A. hyemalis* **I** *A. laxissima* **J** *A. microphylla* **K** *A. pallens* **L** *A. perennans*. Scale bars: 15 µm.

IEB, MEXU [*,**]), 419 (CIIDIR, IBUG, MEXU), 420 (CIIDIR, IBUG, IEB, MEXU); Parque Nacional Desierto de los Leones, 2 km a pie de La Venta por la brecha que va a Santa Rosa, 19.321112°N, 99.306817°W, 2881 m alt., 22 Aug 2021, L. Vigosa and A. Mercado 112 (MEXU [*,**]). **Michoacán: Municipio Angangueo**, Estación Chincua, Reserva de la Biósfera Mariposa Monarca, [19.65618889°N, 100.2717278°W], 3030 m alt., 5 Aug 2000, M.G. Cornejo et al. 67 (IEB, MEXU [*]). **Municipio Maravatío**, km 6 carretera Maravatío-Ciudad Hidalgo al S del poblado de Casa Blanca, [19.85705°N, 100.4516389°W], 2000 m alt., J.E. Morales and A. Pastor 56 (IEB, MEXU [**]). **Morelos: Municipio Huitzilac**, Lagunas de Zempoala, [19.05320158°N, 99.31276612°W, 2800 m alt.], 19 Sep 1938, E. Lyonnet 2518 (FCME [*], MEXU, UAMIZ, US); **Municipio Tlaquiltenango**, Huaxtla 18.37444444°N, 99.07222222°W, 725 m alt., 23 Feb 2015, G. Rendón et al. s.n. (HUMO). **Oaxaca: Municipio San Andrés Lagunas**, Laguna Grande, 1 km al N de San Isidro Lagunas, [17.62219847°N, 97.5414394°W], 2200 m alt., 5 Aug 1982,

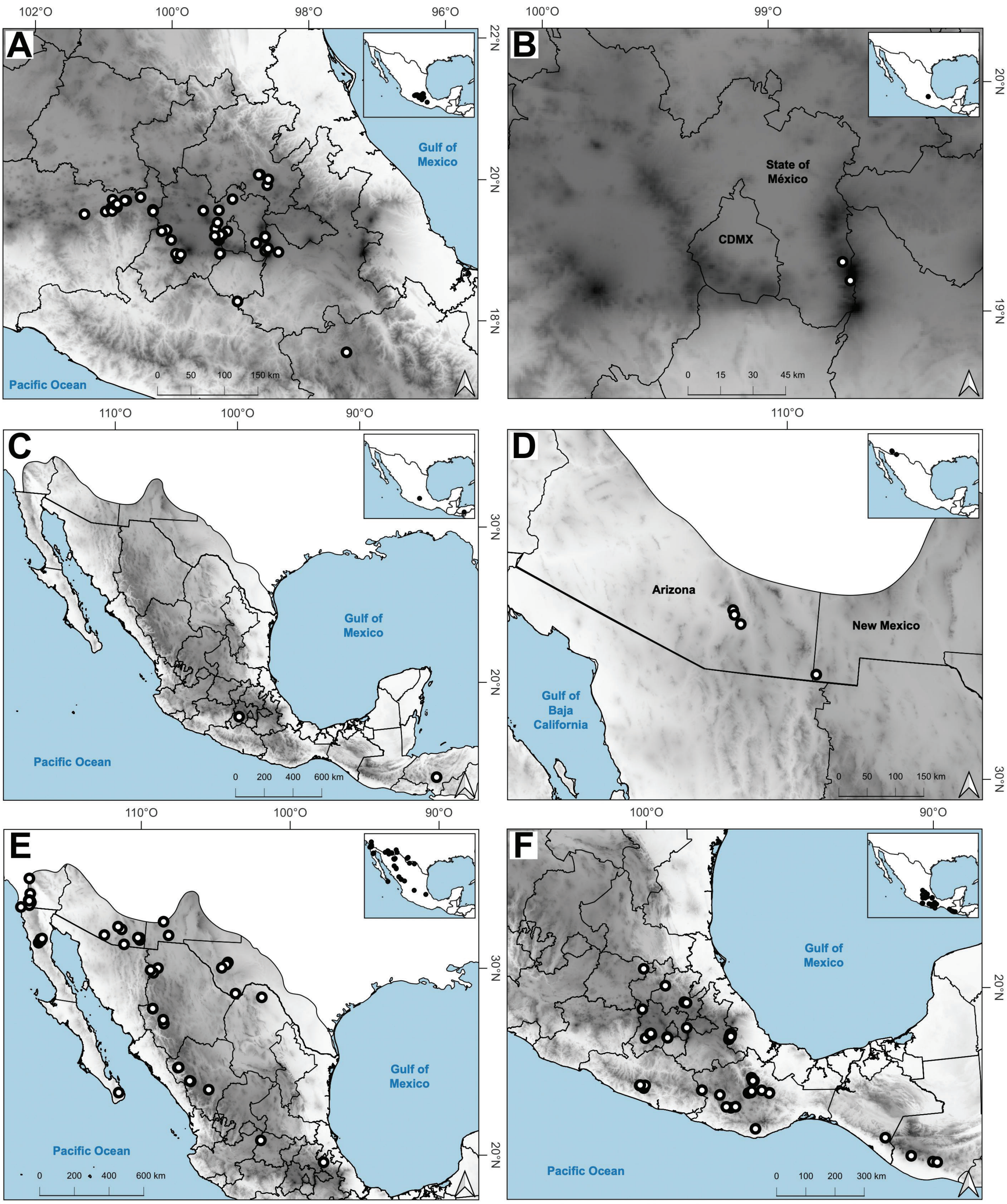

Figure 8. Map of known geographic distribution of *Agrostis* species, based on herbarium specimen data **A** *A. bourgaei* **B** *A. calderoniae* **C** *A. capillaris* **D** *A. elliottiana* **E** *A. exarata* **F** *A.ghiesbreghtii*.

A. García-Mendoza 1116 (MEXU). **Puebla: Municipio San Nicolás de los Ranchos**, Paso de Cortés, 3 km al S de la carretera a Amecameca, sobre la brecha al Volcán Iztaccíhuatl, 13 km al E de Amecameca, [19.12°N, 98.63°W], 3760 m alt., 1 Nov 1976, S.D. Koch 76237 (CHAPA, US). See Suppl. materials 2, 3 for additional examined specimens.

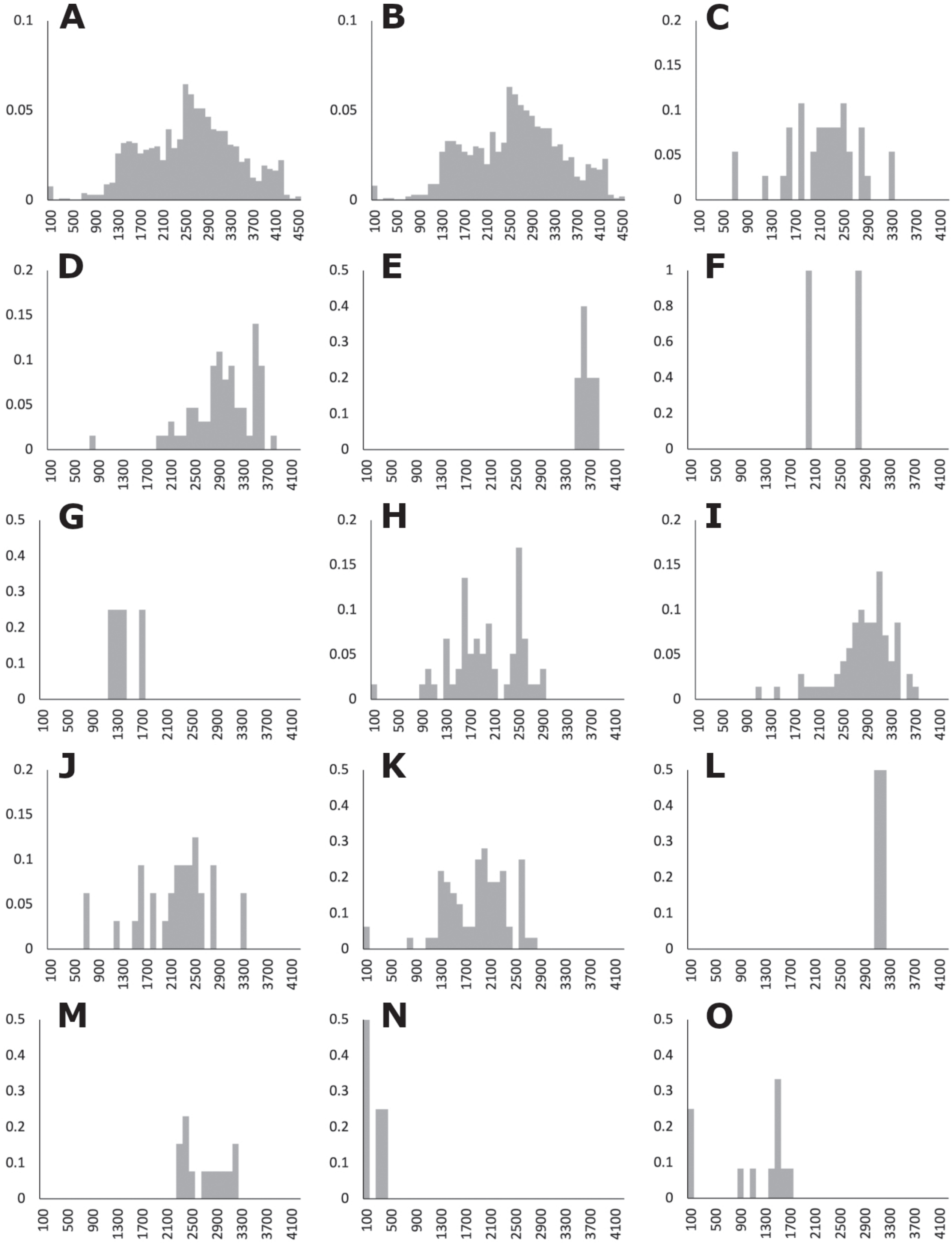

Figure 9. Elevation histograms of *Agrostis* species **A** all records **B** native species **C** introduced species **D** *A. bourgaei* **E** *A. calderoniae* **F** *A capillaris* **G** *A. elliottiana* **H** *A. exarata* **I** *A. ghiesbreghtii* **J** *A. gigantea* **K** *A. hyemalis* **L** *A. idahoensis* **M** *A. laxissima* **N** *A. microphylla* **O** *A. pallens*.

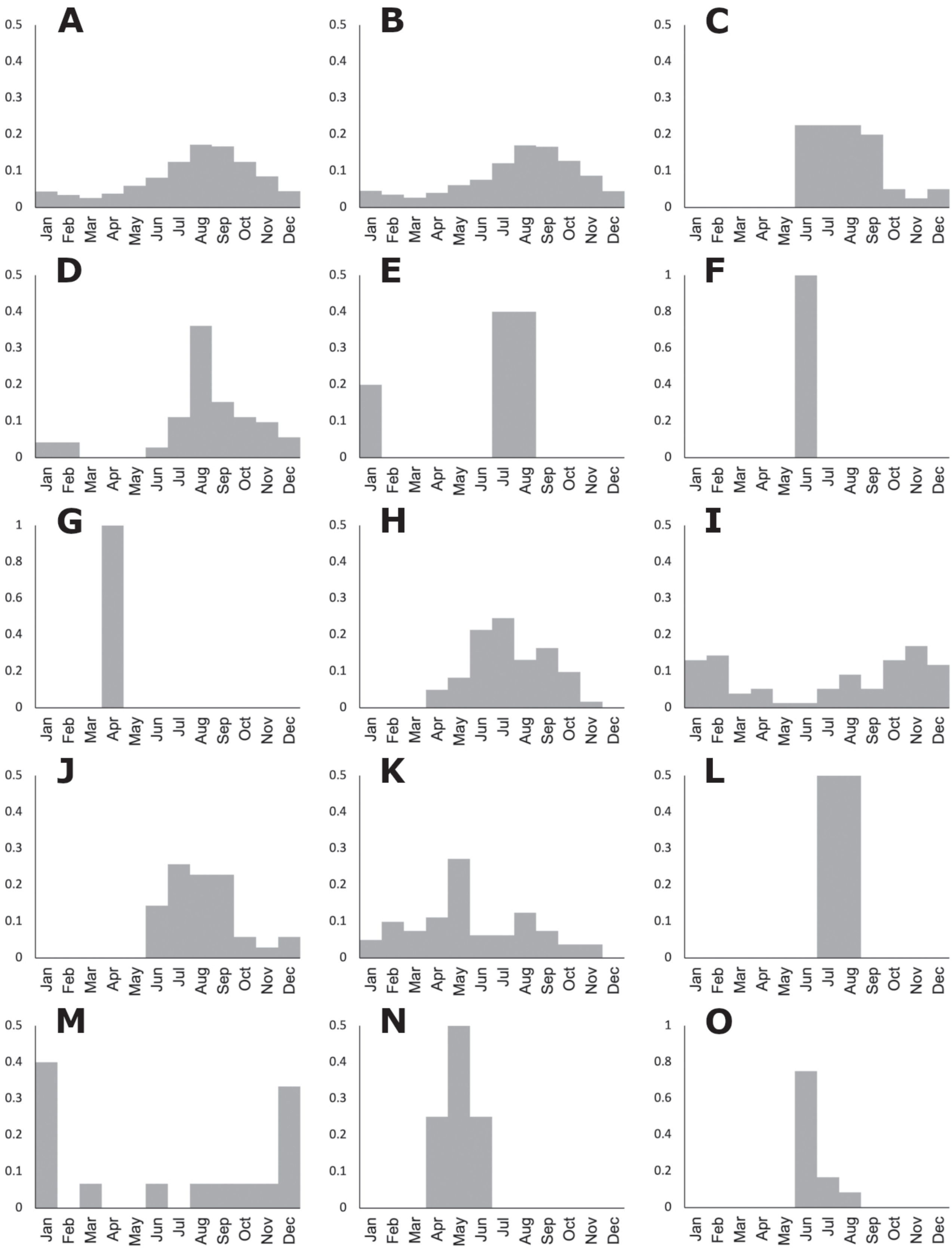

Figure 10. Phenology histograms of *Agrostis* species **A** all records **B** native species **C** introduced species **D** *A. bourgaei* **E** *A. calderoniae* **F** *A capillaris* **G** *A. elliottiana* **H** *A. exarata* **I** *A. ghiesbreghtii* **J** *A. gigantea* **K** *A. hyemalis* **L** *A. idahoensis* **M** *A. laxissima* **N** *A. microphylla* **O** *A. pallens*.

2. *Agrostis calderoniae* Acosta, Phytologia 62(6): 449, Fig. 1. 1987.
Figs 4B, 5B, 11

Type. Mexico. State of México: Municipio Tlalmanalco, La Ciénega, región de Peñas Cuatas, ladera NW del Iztaccíhuatl, 3600 m alt., 19 Aug 1984, S. Acosta 687 (holotype: ENCB! (ENCB003243 [image!]); isotypes: MEXU! (MEXU00436130 [image!]), CHAPA! (CHAPA0000037 [image!]), IEB, TEX).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 10–40 cm long, erect, nodes 1–2, glabrous, internodes glabrous. ***Leaves*** mostly basal; sheaths 3–10 cm long, usually longer than the internodes, glabrous; ligules 1.5–4 mm long, longer than wide, glabrous, apices acute, often lacerate; blades (1–)2–10 cm long, up to 2 mm wide, linear, conduplicate to convolute, scaberulous on both surfaces. ***Panicles*** 5–13 cm long, 2–10 cm wide, open, lax, lanceolate to ovate, long-exserted from the upper sheaths; branches ascending to spreading, rebranching about or above mid-length, scaberulous, without spikelets near their base, inferior branches 2–7 cm long; pedicels 1–3 mm long, ascending to spreading, scaberulous. ***Spikelets*** 2.5–3.5 mm long, purplish; glumes subequal to equal, lanceolate, apices shortly acuminate, 1-veined, scaberulous on the keel, lower glume 2.5–3.5 mm long, upper glume 2.2–3.5 mm long; callus glabrous; lemmas 2–2.5 mm long, elliptic, apices irregularly toothed, 5-nerved, veins inconspicuous, unawned; paleas present, 0.5–1 mm long, veinless, glabrous; anthers 3, 0.7–1 mm long. ***Caryopsis*** not seen. 2n= unknown.

Anatomy and micromorphology. Leaf blades convolute or v-shaped in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded to triangular; keel absent; first order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in strands or girders in the central bundle, narrowing towards the bundle, adaxial sclerenchyma in strands; second order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 6D, E). Lemmas with transversal thickenings irregular, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 7B).

Distribution and habitat. Endemic. *Agrostis calderoniae* has only been collected in the western slope of the Iztaccíhuatl volcano, in the state of México (Fig. 8B). This species grows in moist soils near the edge of streams, in open areas of temperate forests with *Pinus*, between 3500–3800 m a.s.l. (Fig. 9E).

Phenology. Specimens with spikelets have been collected in January, July, and August (Fig. 10E).

Commentaries. This species is similar to *A. bourgaei*, in the caespitose habit and paleate spikelets, but it is distinguished in the mostly basal leaves, leaf blades conduplicate or convolute, with deep adaxial furrows, abaxial intercostal sclerenchyma, longer spikelets of 2.5–3.5 mm long, and lemmas with transversal thickenings of irregular shape (vs. basal and cauline leaves, leaf blades flat, with medium-sized adaxial furrows, without intercostal sclerenchyma, spikelets of 2–2.7 mm long, lemmas with polygonal transversal thickenings in *A. bourgaei*).

Conservation status. *Agrostis calderoniae* only has been collected in two localities of the Iztaccíhuatl-Popocatéptl National Park, where it is reported as scarce in the labels of the herbarium specimens. The EOO and AOO cannot be calculated, but by the scarcity and size of the populations of this species, the category of Endangered (EN) is suggested.

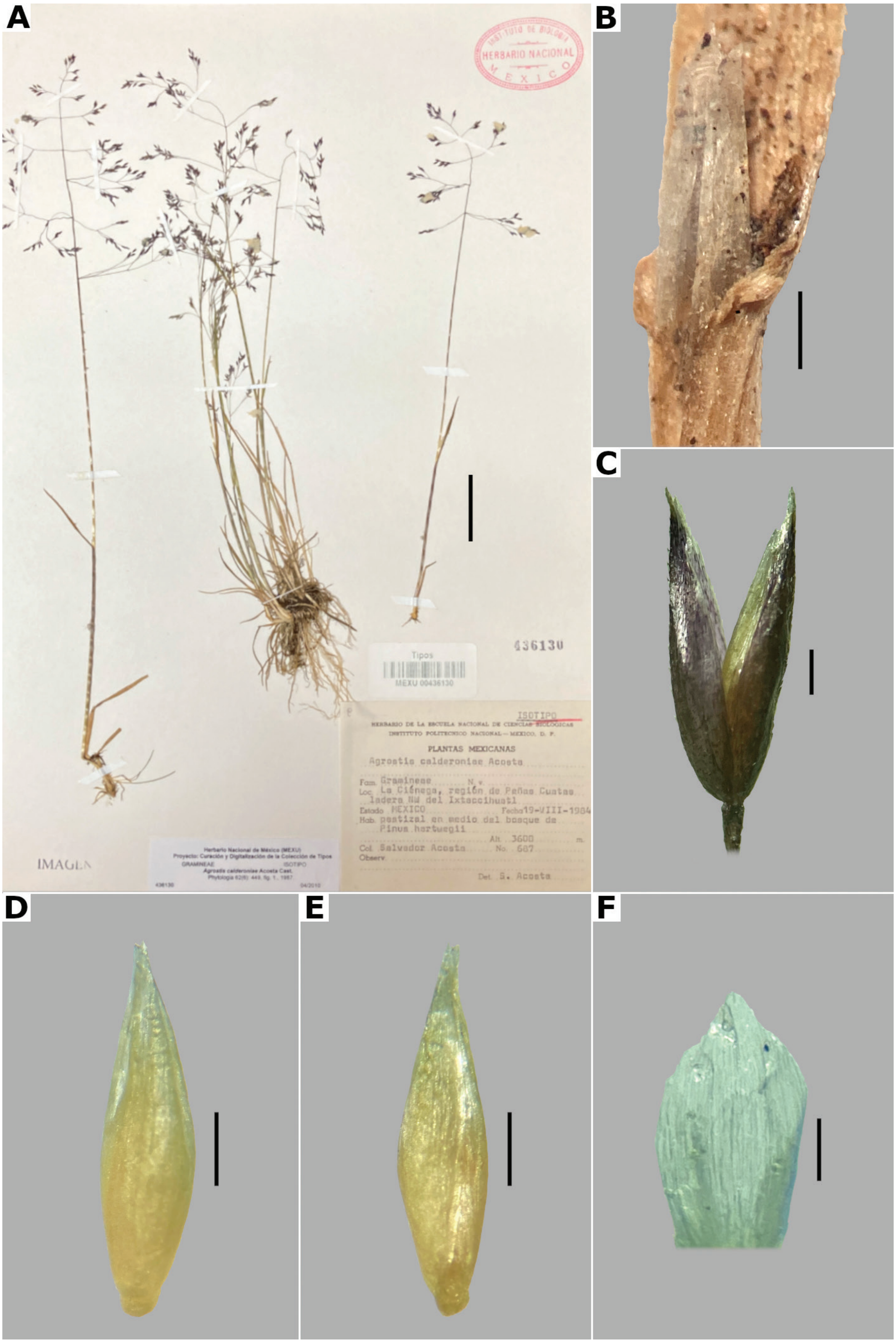

Figure 11. *Agrostis calderoniae* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view **E** floret, adaxial view **F** palea. A based on Acosta 687 (isotype, MEXU), B–F based on Acosta 692 (IEB). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C–E**); 0.2 mm (**F**).

Specimens examined. Mexico. México: Municipio Amecameca, vertiente SW del Iztaccíhuatl, 4 km al N de la estación retransmisora de TV, [19.14308652°N, 98.64774789°W], 3800 alt., 15 Jul 1965, J. Rzedowski 20161 (ENCB). **Municipio Tlalmanalco**, vertiente NW del Iztaccíhuatl, en la región de Peñas Cuatas, La Ciénega, [19.225278°N, 98.680833°W], 3650 m alt., 6 Jan 1966, J. Rzedowski 21798 (ENCB); La Ciénega, región de la cabeza del Iztacccíhuatl, [19.225278°N, 98.680833°W], 19 Aug 1984, S. Acosta 692 (IEB [*,**]); 3600 m alt., 18 Jul 1982, J. Rzedowski 37855 (ENCB).

3. *Agrostis capillaris* L., Sp. Pl. 1: 62. 1753.
Figs 4C, 5C, 12

= *Agrostis capillaris* Huds., Fl. Angl. 27. 1762, nom. illeg. hom., non L., 1753. *Agrostis tenuis* Sibth., Fl. Oxon. 36. 1794. *Agrostis alba* L. var. *tenuis* (Sibth.) Fiori, Nuov. Fl. Italia 1: 97. 1923. Type: England. Habitat in pratis et pascuis ubique (not located).
Agrostis polymorpha Huds. var. *capillaris* (L.) Huds., Fl. Angl. 1: 31. 1778.
Vilfa capillaris (L.) P. Beauv., Ess. Agrostogr. 147. 1812.
Trichodium capillaris (L.) Roth, Nov. Pl. Sp. 41. 1821.*

Type. Herb. A. Van Royen s.n. (lectotype, designated by Widén (1971: 65): L [left hand specimen] (L (L0052645 [image!])).

Description. ***Plants*** perennial, short rhizomatous, rarely stoloniferous. ***Tillers*** extravaginal, with cataphylls. ***Rhizomes*** up to 5 cm long. ***Culms*** 10–80 cm long, erect, decumbent at the base, nodes up to 7, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 1–13 cm long, longer or shorter than the internodes, glabrous; ligules of the basal blades 0.2–1.5 mm long, the upper ones up to 2 mm long, usually shorter than wide, rarely longer than wide, dorsally scaberulous, apices rounded to truncate, erose, sometimes lacerate; blades 3–15 cm long, 1–5 mm wide, linear, flat, sometimes becoming convolute when drying, scaberulous on both surfaces. ***Panicles*** (3–)10–20 cm long, (1–)2–12 cm wide, open, lax, oblong to ovate, usually long-exserted from the upper sheaths; branches ascending to spreading, rebranching about or above mid-length, scaberulous, without spikelets near their base, inferior branches up to 7 cm long; pedicels 0.4–3.3 mm long, usually spreading, scaberulous. ***Spikelets*** (1.7–)2–3(–3.5) mm long, greenish to purplish; glumes subequal, lanceolate, apices shortly acuminate, 1-veined, scaberulous on the keel, lower glume 2.5–3.5 mm long, upper glume 2.2–3.3 mm long; callus glabrous or with a few trichomes, inconspicuous; lemmas 1–2.5 mm long, elliptic, apices entire, acute to obtuse, sometimes truncate, 3(5)-veined, veins usually prominent, sometimes two veins excurrent ca. 0.5 mm, unawned, rarely awned near mid-length, awn up to 2 mm, geniculate or straight; paleas present, 0.6–1.2(–1.4) mm long, 2-veined, glabrous; anthers 3, 0.8–1.4 mm long. ***Caryopsis*** 0.8–1.5, elliptic; endosperm solid. 2n= 28 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat to convolute in transversal section; adaxial furrows medium-sized, narrow; adaxial ribs rounded to triangular; keel absent; first order bundles circular to slightly elliptical in outline,

* See Suppl. material 1 for other heterotypic synonyms.

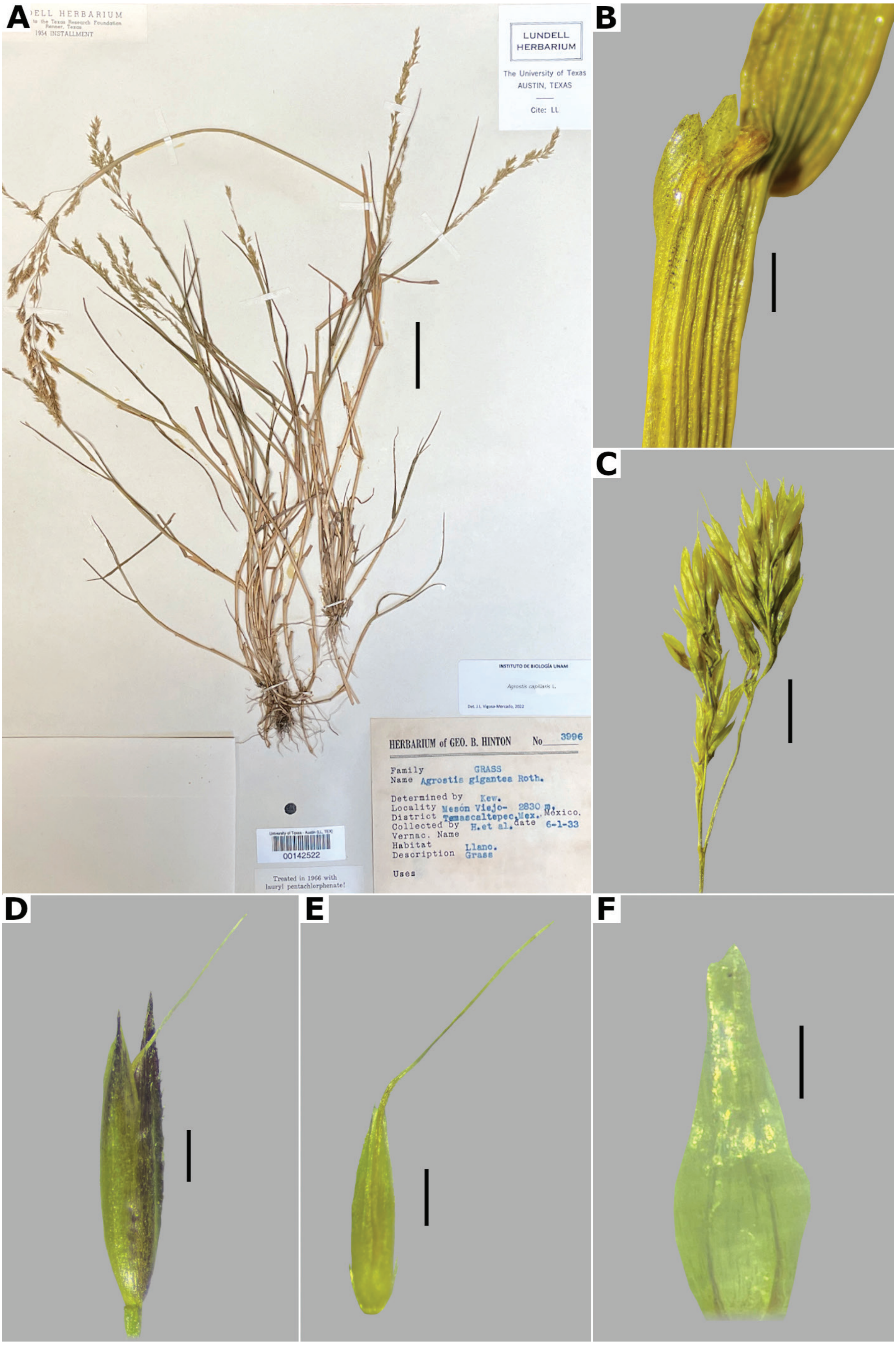

Figure 12. *Agrostis capillaris* **A** whole plant **B** ligular area **C** branch of the panicle **D** spikelet **E** floret, abaxial view **F** palea. Based on Hinton 3996 (TEX). Scale bars: 3 cm (**A**); 1 mm (**B**); 4 mm (**C**); 0.5 mm (**D, E**); 0.2 mm (**F**).

sheath interrupted abaxially or also adaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 6F, G). Lemmas without transversal thickenings; prickle hairs abundant (Fig. 7C).

Distribution and habitat. Introduced. *Agrostis capillaris* is native to Europe. This species has been collected in Francisco Morazán, Honduras, and in the state of México, Mexico (Fig. 8C). It grows in cloud forests and *Pinus* forests, at 2000–2830 m a.s.l. (Fig. 9F).

Phenology. Specimens with spikelets have been collected in June (Fig. 10F).

Commentaries. This species is often confused with *A. castellana* (see notes under excluded species). Some individuals of *A. capillaris* can develop ligules of the flowering culms longer than wide.

Conservation status. Since *Agrostis capillaris* is an introduced species in the study zone, its conservation status is considered as Least Concern (LC).

Specimens examined. HONDURAS. Francisco Morazán: Distrito Central, bosque denso, húmedo y nebuloso de Montaña La Tigra, al SO de San Juancito, [14.2°N, 87.1°W], 2000 m alt., 11 Jun 1963, A. Molina 12706 (MICH, US). **MEXICO. México: Municipio Temascaltepec**, Mesón Viejo, [19.16666667°N, 99.88333333°W], 2830 m alt., 1 Jun 1933, G.B. Hinton 3996 (MO, TEX [*, **], US).

4. ***Agrostis elliottiana*** Schult., Mant. 2: 202. 1824.

Figs 4D, 5D, 13

Agrostis arachnoides Elliott, Sketch Bot. S. Carolina 1(2): 134. 1816, nom. illeg. hom., non Poir., 1810. Type: USA. South Carolina near Orangeburgh, I.S. Bennet s.n. (holotype: CHARL (CHARL-BY3758 [image!])).

Notonema arachnoides Raf., Neogenyton 4. 1825.

= *Agrostis exigua* Thurb., Bot. California 2: 275. 1880. Type: USA. California: foothills of the Sierras, H.N. Bolander s.*n*. (holotype: GH (GH00022956 [image!]); isotypes: MO (MO-123096 [image!]), US (US00156423[image!])).

Notonema arachnoides Raf. ex B.D. Jacks., Index Kew. 2: 319. 1894, nom. inval., pro syn.

= *Agrostis elliottiana* Schult. fo. *molesta* Shinners, Rhodora 56(662): 28. 1954. Type: USA. Texas: Wood County, sandy upland pine woods 2.7 miles east of Mineaola, 23 Apr 1953, L.H. Shinners 14372 (holotype: BRIT (BRIT408703 [image!])).

Type. Based on *Agrostis arachnoides* Elliott.

Description. ***Plants*** annual, caespitose. ***Tillers*** absent. ***Culms*** 5–45 cm long, erect, sometimes geniculate at the base, nodes (3–)4–9, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 1–5 cm long, longer or shorter than the internodes, glabrous or scaberulous; ligules (0.7–)1.5–3.5(–5) mm long, longer than wide, dorsally scaberulous, apices rounded to truncate, lacerate; blades 0.5–4(–7) cm long, 0.5–1 mm wide, linear, flat, sometimes becoming conduplicated, scaberulous on both surfaces. ***Panicles*** (3–)5–20 cm long, (0.5–)2–12 cm wide, open, lax, linear to ovate, usually exserted from the

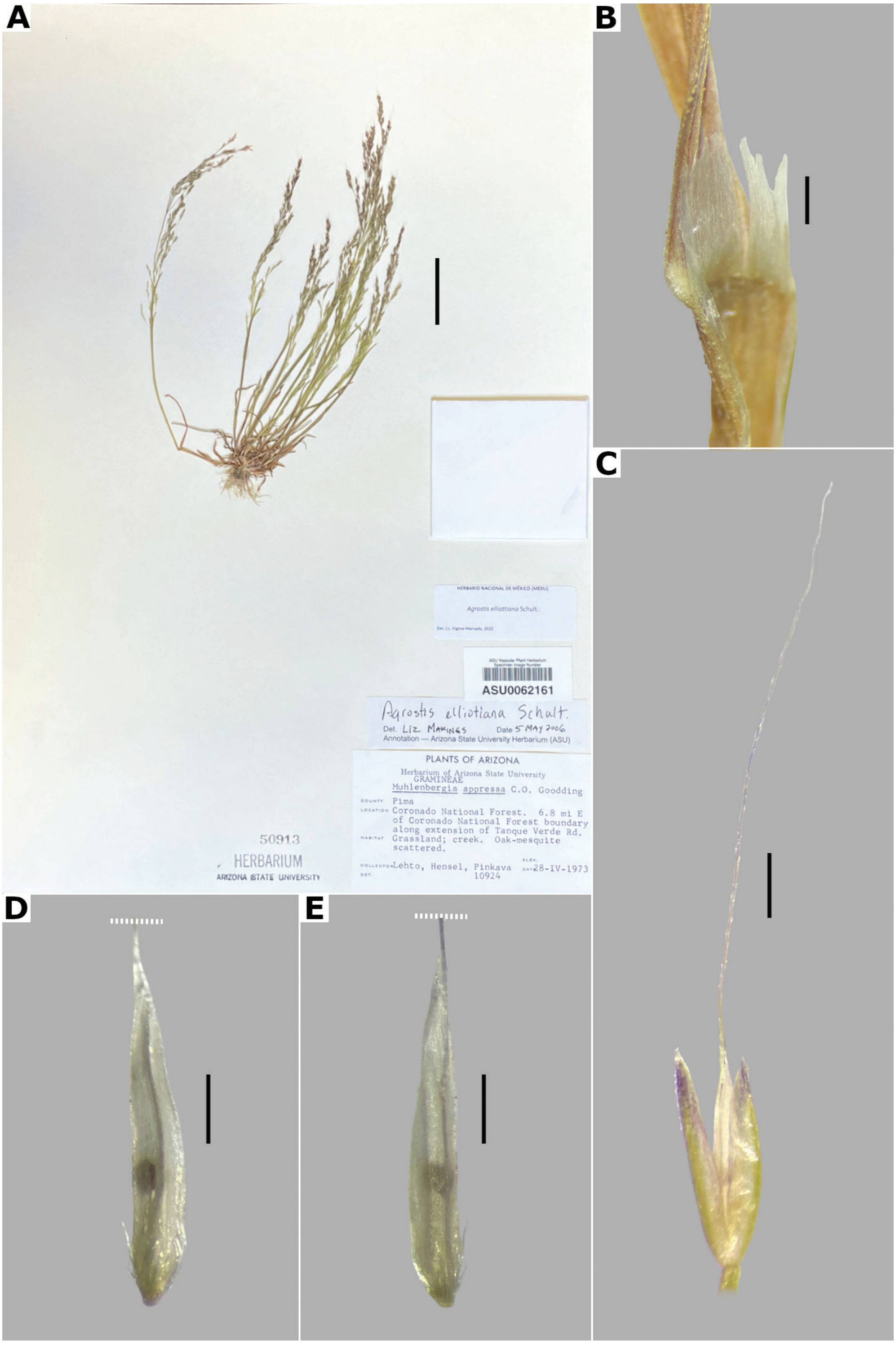

Figure 13. *Agrostis elliottiana* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view **F** floret, adaxial view. Based on Lehto et al. 10924 (ASU). Scale bars: 3 cm (**A**); 5 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**).

upper sheaths, the whole panicle detaching after maturity; branches ascending to spreading, rebranching about or above mid-length, scaberulous, without spikelets near their base, inferior branches 2–8 cm long; pedicels 0.3–7.5 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.5–2.2 mm long, purplish; glumes equal to subequal, lanceolate, apices acute, 1-veined, scaberulous on the keel, sometimes margins distally scaberulous, lower glume 1.5–2.2 mm long, upper glume 1.3–2 mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1–2 mm long, elliptic, apices entire, acute or toothed, 5-nerved, veins prominent, awned in the upper third, awn 3–10 mm, flexuous, deciduous; paleas absent, or up to 0.2 mm long, veinless, glabrous; anther 1, 0.1–0.2 mm long. ***Caryopsis*** 1–1.4 mm long, elliptic; endosperm liquid. 2n= 28 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat to v-shaped in transversal section; adaxial furrows deep, narrow; adaxial ribs triangular; keel absent; first order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 6H, I). Lemmas with transversal thickenings oblong, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 7D).

Distribution and habitat. *Agrostis elliottiana* is native to North America, distributed on the East Coast of USA, from Pennsylvania to Florida, and from northern California to Texas (Harvey 2007). Herbarium specimens from the study zone of this species have been collected in southern Arizona and New Mexico, USA (Fig. 8D). *Agrostis elliottiana* has also been reported from the Mexican state of Yucatán (Beetle et al. 1983), but herbarium specimens associated with this record have not been found. This species grows in the edges of streams, in the middle of scrublands, with *Arctostaphylos* and *Juniperus*, between 1189–1676 m a.s.l. (Fig. 9G). There are more records of this species in the study zone, on databases (GBIF 2023a), but not all of them have images, and thus we were unable to confirm their identity.

Phenology. Specimens with spikelets have been collected in April (Fig. 10G).

Commentaries. *Agrostis elliottiana* is often confused with *A. hyemalis* but differs from it in the annual habit of the plants, leaf blades sometimes conduplicated, with triangular adaxial ribs and abaxial intercostal sclerenchyma, spikelets not clustered, lemmas with a flexuous awn, and only one anther (vs. perennial plants, leaf blades flat, with rounded abaxial ribs, without intercostal sclerenchyma, spikelets clustered at branch tips, lemmas unawned, three anthers in *A. hyemalis*).

Conservation status. *Agrostis elliottiana* apparently is a rare species in the study zone. It is only represented by four collections, occurring in the Coronado National Forest. The EOO is 1,078 km^2 and the AOO is 16 km^2. Following the IUCN criteria, the preliminary assessment category is Endangered (EN).

Specimens examined. USA. Arizona: Pima County, Arizona National Scenic Trail, Santa Catalina Mountains, Coronado National Forest, along 4WD road west of Bellota Ranch, 32.324417°N, 110.6547°W, 1189 m alt., 28 Apr 2005, W.C. Hodgson et al. 20220 (DES); Coronado National Forest, 6.8 mi E of Coronado National Forest boundary, along extension of Tanque Verde Road, [32.2516°N, 110.62°W], 1300 m alt., 28 Apr 1973, E. Lehto et al. 10924 (ASU [*, **]); E edge of Rincon Mountains, 4 km N of Pima-Cochise County line along USFS-35 (Mescal Road), [32.116667°N, 110.483333°W], 1330 m alt., 16 Apr 1986, J.R. Reeder 842 (MICH). **New Mexico: Hidalgo County**, Peloncillo Mountains, Cloverdale Creek Canyon about 1.3 road mi NW of the Pendleton Ranch House, [31.448973°N, 108.986951°W], 1676 m alt., 20 Apr 1986, R.D. Worthington 14015 (COLO, DES, NY, UNM).

5. *Agrostis exarata* Trin., Gram. Unifl. Sesquifl. 207. 1824.
Figs 4E, 5E, 14

= *Polypogon monspeliensis* (L.) Desf. var. *monolepis* Torr., Pacif. Railr. Rep. 5(2): 366. 1858. *Agrostis exarata* Trin. var. *monolepis* (Torr.) Hitchc., Amer. J. Bot. 21(3): 136. 1934. *Agrostis ampla* Hitchc. fo. *monolepis* (Torr.) Beetle, Bull. Torrey Bot. Club 72: 544. 1945. Type. USA. California: Pose Creek, Walkers Pass, Aug 1853, Blake s.n. (holotype: NY (NY431434 [image!]); isotype: US [fragm. ex NY] (US04019109 [image!]).

= *Agrostis durangensis* Mez, Repert. Spec. Nov. Regni Veg. 17(19–30): 301. 1921. Type: MEXICO. Durango: collected at the city of Durango and vicinity, 1896, E. Palmer 190 (lectotype, designated by Vigosa-Mercado (2022a: 1): MO (MO-128909 [image!]; isolectotypes F (F0046563F [image!]), FCME! [fragm. ex US], GH (GH00022993 [image!]), NY (NY00327644 [image!]), US (US00151844 [image!], US00151845 [image!], US00151846 [image!], US00156413 [image!], US00486604 [image!])).*

Type. USA. Alaska: Unalaska, 1829, J.F. Eschscholtz s.n. (holotype: LE (LE00009316 [image!]); isotype: LE).

Description. ***Plants*** perennial, caespitose, rarely shortly rhizomatous. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 10–90 cm long, erect or decumbent at the base, nodes 2–4, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 3–10 cm long, usually shorter than the internodes, glabrous; ligules 2.5–5 mm long, longer than wide, dorsally scaberulous, apices acute, often lacerate; blades 3–15 cm long, 1.5–4(–8) mm wide, linear, flat, scaberulous on both surfaces. ***Panicles*** (2–)4–20(–30) cm long, 0.4–2(–3) cm wide, contracted, usually dense and spiciform, lanceolate to oblong, sometimes interrupted at the base, sometimes partially included in the upper sheaths; branches appressed to ascending, rebranching about or below mid-length, scaberulous, usually with spikelets almost to the base, inferior branches 1–5 cm long; pedicels 0.5–3 mm long, appressed, scaberulous. ***Spikelets*** 2–2.5 mm long, greenish to stramineous; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, sometimes also on the body, sometimes awned, awn ca. 1 mm long, lower glume 2–2.5 mm long, upper glume 1.5–2.3 mm long; callus glabrous or with 2 bunches of few, short trichomes, often inconspicuous; lemmas 1.2–2 mm long, elliptic, apices acute or shortly toothed, 5-nerved, veins prominent distally or inconspicuous throughout, usually unawned, sometimes awned about mid-length, awn up to 3 mm

* See Suppl. material 1 for other heterotypic synonyms.

long, geniculate or straight; paleas absent or 0.3–0.8 mm long, veinless, glabrous; anthers 3, 0.3–0.7 mm long. ***Caryopsis*** 1–1.5 mm long, elliptic; endosperm soft or solid. 2n= 28, 42, 56 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded; keel sometimes present, with three vascular bundles; first order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in girders, narrowing towards the bundle, adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells present, associated with first and second order vascular bundles (Fig. 15A–C). Lemmas with transversal thickenings polygonal, wider than the unthickened portions of the wall; prickle hairs absent or scarce (Fig. 7E).

Distribution and habitat. *Agrostis exarata* is distributed from Alaska to central Mexico, and is also found in Kamchatka and the Kuril Islands (Harvey 2007). In the study zone, this species has been collected in the USA states of Arizona, California, New Mexico and Texas, and in the Mexican states of Baja California, Baja California Sur, Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo and Sonora (Fig. 8E). It has also been reported from Mexico City and the Mexican states of México and Puebla (Villaseñor 2016; Sánchez-Ken 2019), but no specimens from these states were seen. It grows in moist soils of stream edges and lake margins, in open areas of temperate forests with *Pinus* or *Quercus*, and shrublands, between 350–2900 m a.s.l. (Fig. 9H). The USA and Baja California populations of this species grow in lower elevations than the southern ones.

Phenology. Specimens with spikelets have been collected from April to November (Fig. 10H).

Commentaries. For other regions it has been reported that the panicles can reach 4 cm wide, and paleas up to 0.5 mm long (Harvey 2007).

Agrostis exarata is a variable species. Several specific names or infraspecific taxa have been proposed, but none of them are recognized in this work. Mexican populations of this species have been called *A. durangensis*, and are characterized by the unawned lemmas, and the presence of a short, veinless palea, but these characters overlap with populations of other regions. *Agrostis exarata* is often confused with several *Polypogon* species, which are often sympatric, but differs from them in the spikelets disarticulating above the glumes (vs. disarticulation below the glumes, with a pedicel fragment). Mexican populations of *A. exarata* are sometimes confused with some individuals of *A. tolucensis* with wide leaf blades, but differ from it in the spikelets often with a palea, and lemma usually unawned (vs. spikelets without a palea, lemma awned in *A. tolucensis*). This species is also confused with *A. blasdalei* and *A. densiflora* (see the notes in excluded species).

Conservation status. *Agrostis exarata* is a widespread species in the study zone. It is represented by 61 collections, with several populations occurring in 13 protected areas. The EOO is 1,402,821 km^2 and the AOO is 188 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Mexico. Baja California. Municipio Ensenada, Sierra San Pedro Mártir, head of arroyo Copal, steep canyon on E sidelong crest of range, 1.5 km N of cerro Observatorio, [31.04418346°N,

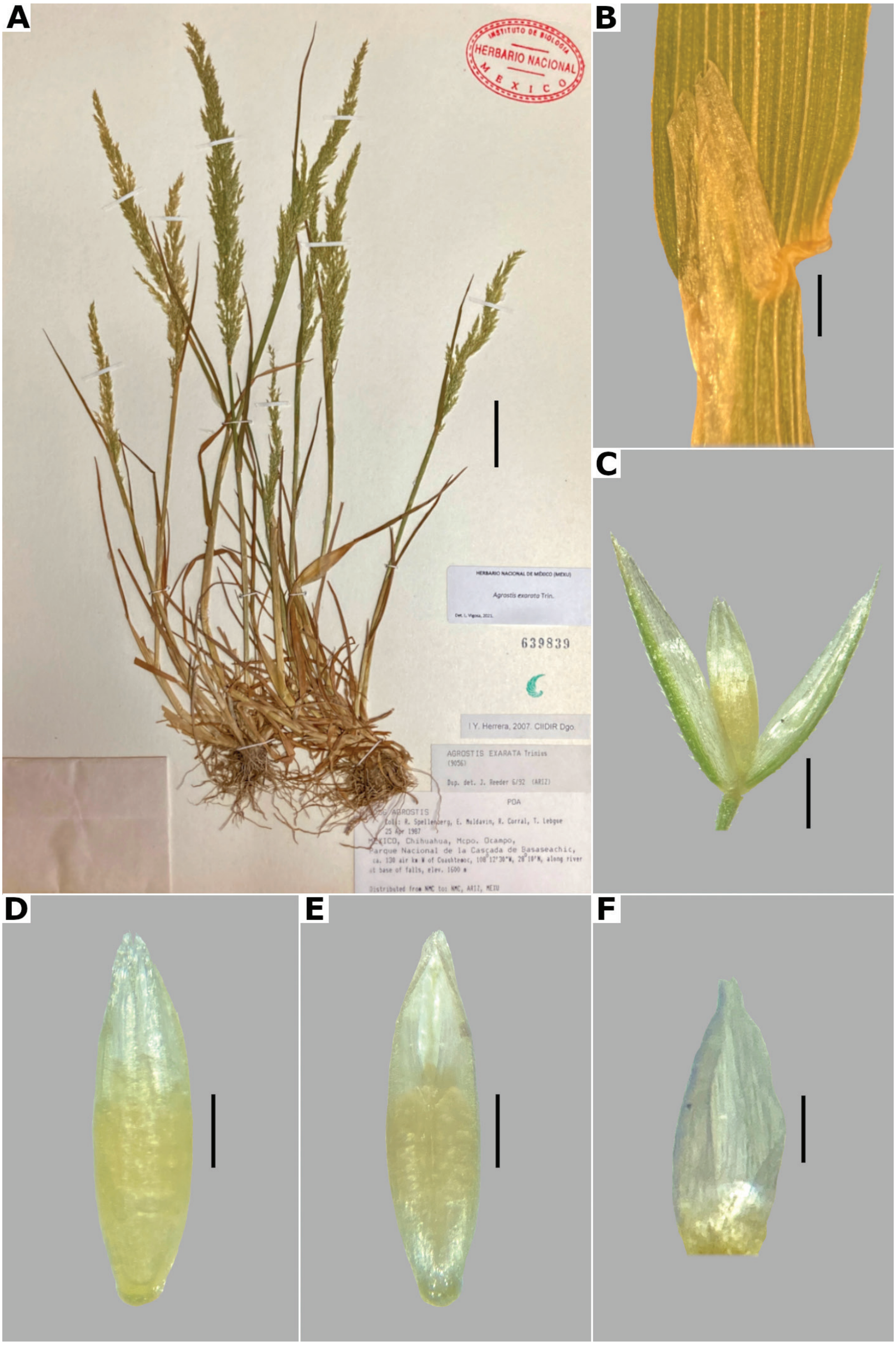

Figure 14. *Agrostis exarata* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view, **E** floret, adaxial view **F** palea. Based on Spellenberg et al. 9056 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**); 0.2 mm (**F**).

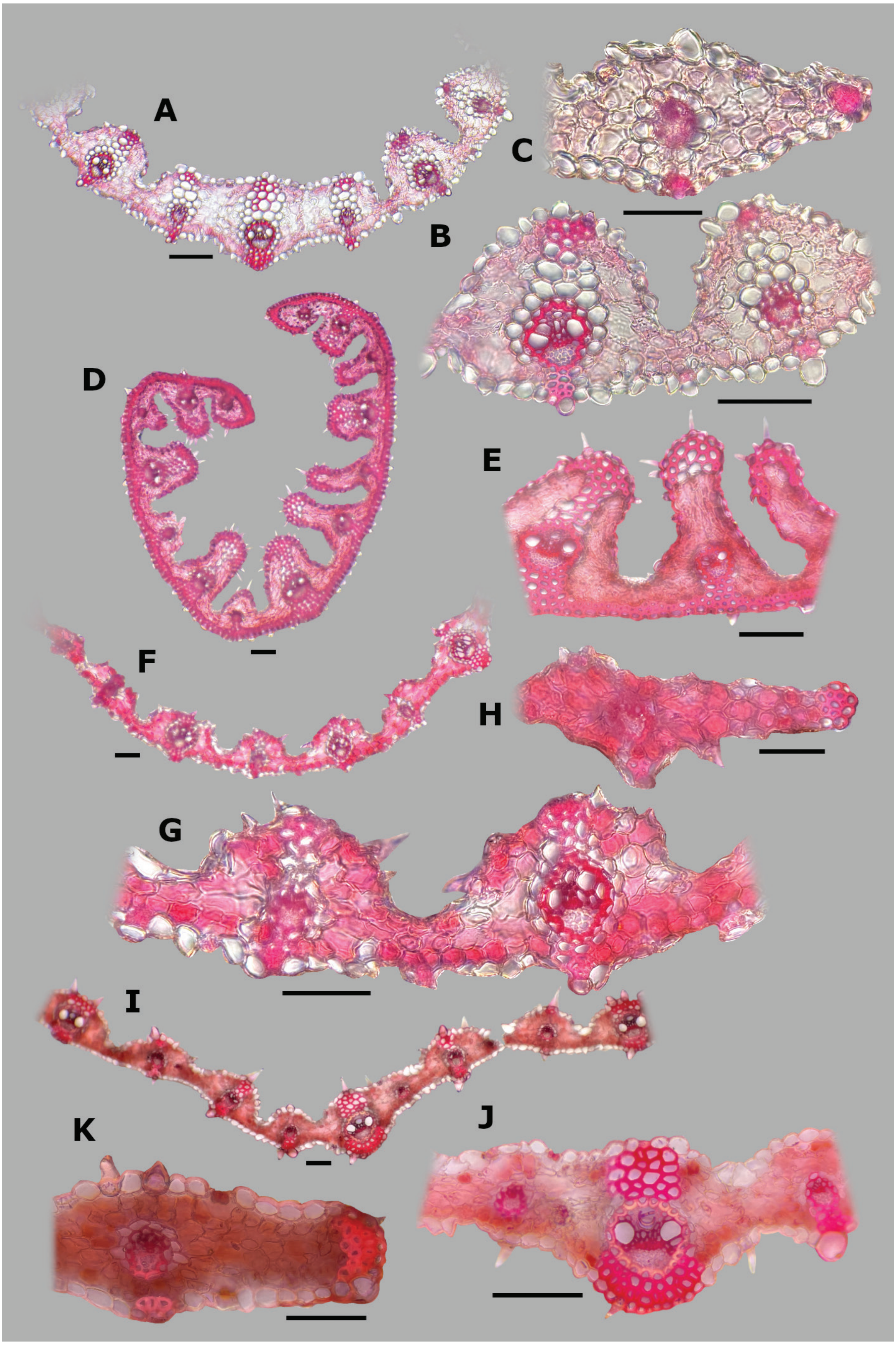

Figure 15. Leaf blade anatomy in transversal section of *Agrostis* species, in general view, and details of lateral bundles **A**–**C** *A. exarata* **D**–**E** *A. ghiesbreghtii* **F**–**H** *A. gigantea* **I**–**K** *A. hyemalis*. Scale bars: 0.1 mm.

115.463326°W, 2800 m alt.], 16 Jul 1988, S. Boyd and T. Ross 2544 (F, MEXU [*], NY). **Baja California Sur: Municipio Comondú**, along small dry streambed, on open rolling ridge tops, La Chuparosa, [26.22975°N, 111.97158°W, 350 m alt.], 12 Apr 1955, A. Carter and R.S. Ferris s.n. (SD). **Chihuahua: Municipio Ocampo**, Parque Nacional de la Cascada de Basaseachi, [28.16666667°N, 108.2083333°W], 1600 m alt., 26 Apr 1985, R. Spellenberg et al. (MEXU), 9056 (MEXU). **Without municipality**, by springs, Sierra Madre, 2900 m alt., 3 Oct 1887, C.G. Pringle 1421 (F, MEXU). **Coahuila**: **Municipio Zaragoza**, Sierra del Carmen, Canyon de Sentenela [Centinela] on Hacienda Piedra Blanca, [29.11021676°N, 101.7054129°W, 860 m alt.], 6 Jul 1936, F.L. Wynf and C.H. Muller 547 (MSC). **Durango: Municipio San Dimas:** Vencedores, camino a las cabañas, 24.44944444°N, 105.7758333°W, 2355 m alt., 25 Aug 2013, S. Heynes 587 (MEXU [*,**]); **Guanajuato: Municipio San Felipe**, Vergel de la Sierra, [21.38504722°N, 101.6354389°W], 2440 m alt., 3 Sep 1981, R. Guzmán 4543 (MEXU [*,**]), R. Santillán 154-R (MEXU). **Hidalgo: Municipio Acaxochitlán**, San Francisco, [20.1897756°N, 98.14532383°W], 2000 m alt., 30 May 1985, A. Villa 186 (MEXU). **Sonora:** Sonora, 24 Jun 1855, A. Schott s.n. (F). **USA. Arizona: Cochise County**, Rucker Canyon, [31.757451°N, 109.360505°W], 2495 m alt., 28 May 1952, E.R. Blakley 1301 (DES). **California: San Diego County**, Cuyamaca Rancho State Park, 0.4 mile NE of intersection of state highway 79 and Stonewall Mine road, ca. 100 m NE of Los Caballos equestrian campground and 20 m south of Stonewall Mine road in north-treading drainage, 32.9728°N, 116.5714°W, 1440 alt., 26 Jun 2005, L. Hendrickson 1093 (BSCA, SD [*,**]). **New Mexico: Grant County**, Mimbres River, [32.858382°N, 107.977694°W], 1676 m alt., 1 Jul 1904, O.B. Metcalfe 1073 (F, NY). **Texas: Brewster County**, Lower Oak Creek, Chisos Mountains, [29.266025°N, 103.301199°W, 1700 m alt.], 6 Jul 1937, B.H. Warnock 20153 (TEX). See Suppl. materials 2, 3 for additional examined specimens.

6. *Agrostis ghiesbreghtii* E. Fourn., Mexic. Pl. 2: 97. 1886.

Figs 4F, 5F, 16

Agrostis ghiesbreghtii E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 551. 1885, nom. nud.

= *Agrostis setifolia* E. Fourn., Mexic. Pl. 2: 97. 1886, nom. illeg. hom., non Brot., 1804. *Agrostis setifolia* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 551. 1885, nom. nud. Type. México. Veracruz: pic d'Orizaba, F.M. Liebmann 712 (holotype: C (C10016729 [image!])).

Type. Mexico. Oaxaca: Province d'Oaxaca, 1842, A. Ghiesbreght s.n. (holotype: P (P00740574 [image!]); isotype: US [fragm. ex P] (US00156357 [image!])).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 30–90 cm long, erect, rarely shortly decumbent at the base, nodes 2–5, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 4–10 cm long, the lower ones shorter than the internodes, the upper ones longer, glabrous; ligules 1.5–6(–12) mm long, longer than wide, dorsally scaberulous, apices acute, often lacerate; blades 3.5–27 cm long, 1–3.5(–5) mm wide, stiff, linear, convolute or involute, the upper ones sometimes flat, scaberulous on both surfaces. ***Panicles*** 8–30 cm long, 5–19 cm wide, open, lax, ovate, usually long-exserted from the upper sheaths; branches spreading, rebranching about or above mid-length, scaberulous, without spikelets near their base, inferior branches 1.5–10 cm long; pedicels 2.5–5(–10) mm long, ascending to spreading, scaberulous. ***Spikelets*** (2.5–)3–4 mm long, usually purplish; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume (2.5–)3–4 mm long, upper glume (2.2–)2.7–3.9 mm long; callus pubescent, with 2 bunches of trichomes; lemmas (1.5–)1.8–2.5 mm long, elliptic, apices irregularly toothed, 5-nerved, veins prominent, awned from near the base, awn 2.3–5 mm long, geniculate; paleas absent, or up to 0.2 mm long, veinless, glabrous; anthers 3, 1–1.5 mm long. ***Caryopsis*** 1.2–1.5 mm long, elliptic; endosperm soft. 2n= unknown.

***Leaf anatomy*.** Leaf blades convolute, rarely flat in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders; second order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in girders, narrowing towards the bundle, adaxial sclerenchyma in strands; intercostal sclerenchyma usually present, a hypodermal band, sometimes absent; leaf margins with sclerenchyma continuous with the hypodermal band; colorless cells absent (Fig. 15D, E). Lemmas with transversal thickenings oblong, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 7F).

Distribution and habitat. Endemic. *Agrostis ghiesbreghtii* is distributed from central Mexico to Guatemala. In Mexico, it has been collected in Mexico City and the states of Chiapas, Guanajuato, Guerrero, Hidalgo, México, Michoacán, Morelos, Oaxaca, Puebla and Veracruz (Fig. 8F). It is also reported from Chihuahua and Durango (Sánchez-Ken 2019), but no specimens from these states were seen. In Guatemala, it has been collected in the departments of Quetzaltenango and Sacatepéquez. This species grows in open areas of temperate forests, with *Abies*, *Pinus*, *Quercus*, and alpine grasslands, between 1110–3700 m a.s.l. (Fig. 9I).

Phenology. Flowering and fruiting specimens have been collected year round, but most of them between the months of August and February (Fig. 10I).

Commentaries. This species is similar to *A. laxissima* in the open panicles, awned lemmas and lemma micromorphological features, but it is distinguished in the leaf blades stiffer, usually convolute or involute, with deep adaxial furrows and usually with a hypodermal bland of abaxial sclerenchyma, and usually larger spikelets of (2.5–)3–4 mm long (vs. leaf blades lax, flat, with medium-sized adaxial furrows, without intercostal sclerenchyma, spikelets of 1.7–3 mm long in *A. laxissima*). Some specimens with unusually wide and flat upper leaf blades have been collected in Guerrero and Chiapas, but the other characters are congruent with *A. ghiesbreghtii*. This species is also very similar to *A. mertensii*, and more studies are needed to define its taxonomic boundaries (see the notes in excluded species).

Conservation status. *Agrostis ghiesbreghtii* is a widespread species in the study zone. It is represented by 80 collections, with several populations occurring in 12 protected areas. The EOO is 240,863 km^2 and the AOO is 176 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

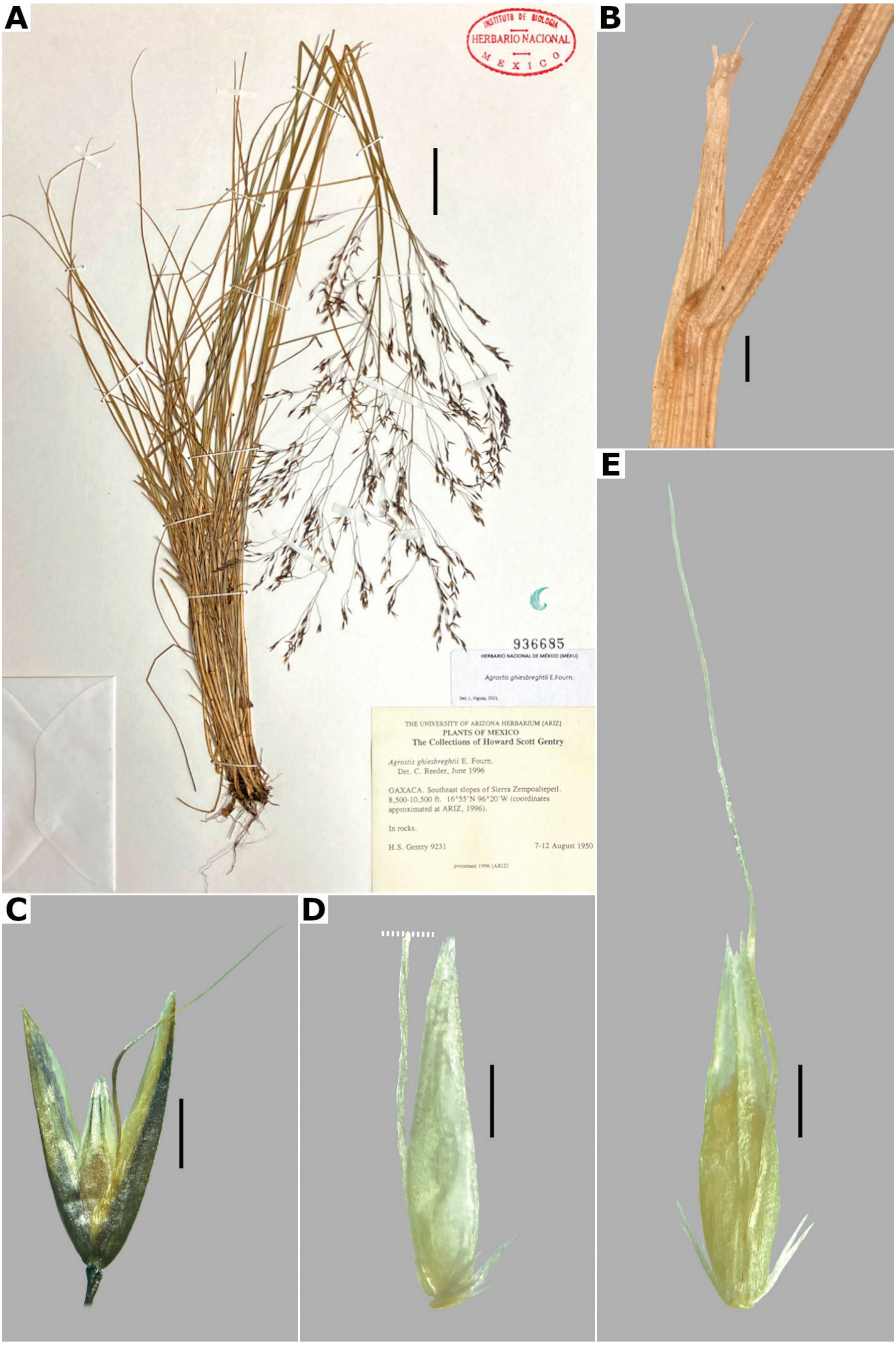

Figure 16. *Agrostis ghiesbreghtii* **A** whole plant **B** ligular area **C** spikelet **D** floret, lateral view, **E** floret, abaxial view. Based on Gentry 9231 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B**); 1 mm (**C**); 0.5 mm (**D, E**).

Representative specimens examined. Guatemala. Sacatepéquez: Distrito Alotenango, Volcán de Acatenango, [14.499453°N, 90.87175°W], 3700 m alt., 10 Apr 2000, M. Véliz et al. 8303 (MEXU), 8371 (MEXU). **Quetzaltenango: Distrito Quetzaltenango**, Volcán Santa María, upper NE facing slopes to summit of volcano, [14.7583°N, 91.5492°W], 3600 m alt., 13 Jan 1940, J.A. Steyermark 34160 (F). **Mexico. Chiapas: Municipio Motozintla**, near summit of cerro Mozotal, [15.42605394°N, 92.34362676°W], 2750 m alt., 24 Nov 1981, D.E. Breedlove 55885 (MICH, MEXU [*], TEX), 55893 (MEXU, MO). **Guanajuato: Municipio Xichú**, Sierra de Xichú, [21.28736944°N, 100.0888472°W], 1900 m alt., 19 Sep 1981, A. Mora 281-AMB (MEXU). **Guerrero: Municipio General Heliodoro Castillo**, Escalerilla, [17.47217778°N, 100.0386778°W], 2550 m alt., 1 Nov 1998, N. Diego 8296 (FCME [*], MEXU); cerro Teotepec, [17.46666667°N, 100.2166667°W], 3350 m alt., 11 Apr 1963, J. Rzedowski 18137 (ENCB, F, IEB, MICH). **Hidalgo: Municipio Mineral del Chico**, alrededores de Las Ventanas, 5 km al N de Pachuca, [20.19252776°N, 98.73954093°W], 2900 m alt., 2 Nov 1983, S Acosta et al. 416 (FCME, MEXU [*,**], UAMIZ, XAL). **Municipio Zimapán**, 11 km al S de La Luz, [20.733333°N, 99.366667°W], 1100 m alt., 10 Jan 1991, V.M. Huerta 1165 (CIB, IEB, XAL). **México: Municipio San Simón de Guerrero**, 3 km sobre la desviación de Simón de Guerrero, carretera hacia Sultepec, [19.01857206°N, 100.0280164°W], 2870 m alt., 7 Feb 1984, E. Manrique et al. 673 (MEXU). **Mexico City: Alcaldía Cuajimalpa**, loma La Vaquera (arroyo Agua de Leones), 3220 m alt., 16 Oct 1985, A. Miranda and P. Guerrero 136a (MEXU). **Michoacán: Municipio Contepec**, cerro Altamirano, Reserva de la Biósfera Mariposa Monarca, 19.96667°N, 100.13333°W, 3027 m alt., 6 Mar 2005, J. Martínez 1453 (IEB, MEXU [**]). **Morelos: Municipio Huitzilac,** Zempoala, [19.03333333°N, 99.3°W], 3000 m alt., 3 Nov 1951, E. Matuda 26005 (MEXU, US). **Oaxaca: Municipio Santa María Tlahuitoltepec**, SE slopes of Sierra Zempoaltepetl, [17.129956°N, 96.01353°W], 3300 m alt., 7 Aug 1950, H.S. Gentry 9231 (MEXU [*]). **Municipio San Martín Peras:** Santiago Juxtlahuaca, San Martín Peras, carretera Tecomaxtlahuaca-San Martín Peras, 2 km de la intersección a Coicoyán de las Flores, 17.2963333°N, 98.195528°W, 2570 m alt., 17 Oct 1994, J.L. Panero et al. 5117 (MEXU [*], TEX). **Puebla: Municipio Atzitzintla,** Teamalaquilla [Texmalaquilla], [18.943056°N, 97.2875°W], 3100 m alt., 29 Aug 1938, E.K. Balls 5393 (MICH, MSC, US). **Veracruz: Municipio Calcahualco**, barranca de San Miguel Tlacotiopa, [19.11192082°N, 97.20509861°W], 2700 m alt., 19 Jan 1989, P. Tenorio 15470 (CIIDIR, MEXU [*,**]). See the Suppl. material 2 for additional examined specimens.

7. *Agrostis gigantea* Roth, Tent. Fl. Germ. 1: 31. 1788.
Figs 4G, 5G, 17

Triticum giganteum (Roth) Roth, Catal. Bot. 3: 22. 1806.
Vilfa gigantea (Roth) P. Beauv., Ess. Agrostogr. 16: 147. 1812.
Agrostis alba L. var. *aristata* Spenn., Fl. Friburg. 1: 94. 1825.
Agrostis stolonifera L. subsp. *gigantea* (Roth) Schübl. & G. Martens, Fl. Würtemberg (ed. 1) 64. 1834.
Agrostis stolonifera L. var. *gigantea* (Roth) Bréb., Fl. Normandie 390. 1835.

Agrostis alba L. var. *gigantea* (Roth) G. Mey., Chloris Han. 655. 1836, non Spenner 1825.

Agrostis alba L. subsp. *gigantea* (Roth) Arcang., Comp. Fl. Ital. 768. 1882.

= *Agrostis virletii* E. Fourn., Mexic. Pl. 2: 96. 1886. *Agrostis virletii* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 552. 1885, nom. nud. Type. Mexico. San Luis Potosí: Prov. de San Luis, 1851, *M. Virlet d'Aoust 1345* (lectotype, designated by Vigosa-Mercado (2022a: 2): P (P00740442 [image!]); isolectotypes: P (P00740440 [image!], P00740441 [image!]), US [fragm. ex P] (US00156515 [image!])).

Agrostis stolonifera L. subsp. *gigantea* (Roth) Maire & Weiller, Fl. Afrique N. 2(XLV): 120. 1953.

Agrostis stolonifera L. subsp. *gigantea* (Roth) Beldie, Fl. Republ. Socialiste Romania 12: 152. 1972, nom. illeg. hom.*

Type. Germany. Herb. Albrecht de Haller, A.W. Roth s.n. (lectotype, designated by Widén (1971: 97): G (G00195254 [image!])).

Description. ***Plants*** perennial, rhizomatous. ***Tillers*** extravaginal, with cataphylls. ***Rhizomes*** up to 25 cm long. ***Culms*** 0.2–1.2 m long, erect, sometimes geniculate, nodes 3–7, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 4.5–13 cm long, usually shorter than the internodes, glabrous or scaberulous; ligules 1–7 mm long, longer than wide, dorsally scaberulous, apices rounded to truncate, erose to lacerate; blades (2–)3.5–20 cm long, 1–8 mm wide, usually at least some blades larger than 5 mm wide, linear, flat, scaberulous on both surfaces. ***Panicles*** (9–)13–40 cm long, 4–16 cm wide, open, dense to lax, lanceolate to ovate, exserted from the upper sheaths; branches ascending to spreading, rebranching about or above mid-length, scaberulous, without spikelets near their base or often some inferior branches with spikelets, inferior branches 2.5–15 cm long; pedicels 0.3–3 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.7–3 mm long, greenish to purplish; glumes subequal to unequal, lanceolate to ovate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume 1.7–3 mm long, upper glume 1.3–2.8 mm long; callus glabrous or with 2 bunches of few, very short trichomes, inconspicuous; lemmas 1.4–2 mm long, elliptic to oblong, apices entire, acute or sometimes truncate, 3–5-veined, veins inconspicuous or prominent distally, usually unawned; paleas present, 0.5–1.2 mm long, faintly 2-veined, glabrous; anthers 3, 0.7–1.2 mm long. ***Caryopsis*** 1–1.5 mm long, elliptic, endosperm solid. 2n= 42 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows medium-sized, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; intercostal sclerenchyma absent; leaf margins with small to well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 15F–H). Lemmas without transversal thickenings, or these poorly developed; prickle hairs absent or scarce (Fig. 7G).

* See Suppl. material 1 for other heterotypic synonyms.

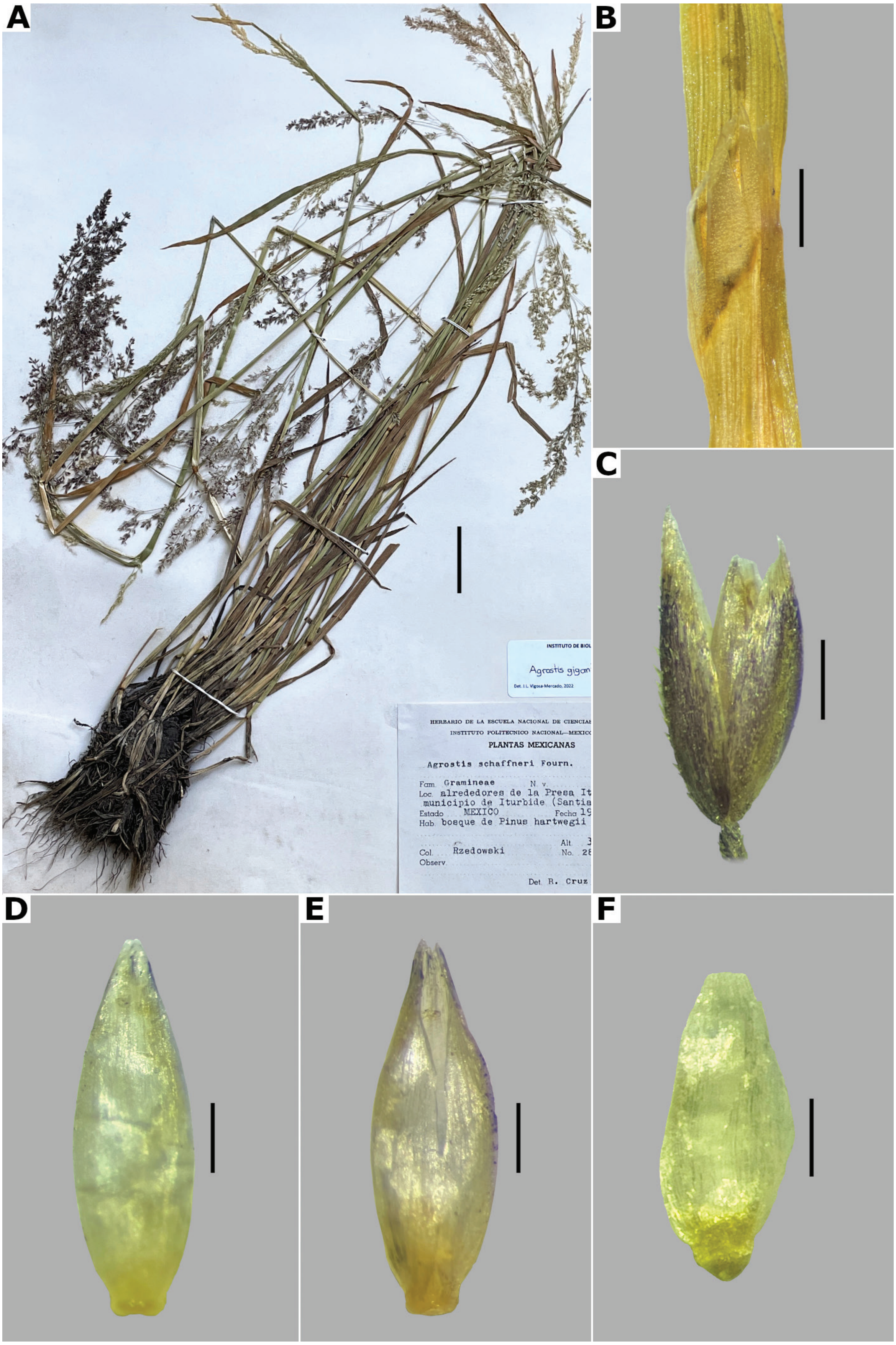

Figure 17. *Agrostis gigantea* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view, **E** floret, adaxial view **F** palea. Based on Rzedowski 28545 (IBUG). Scale bars: 3 cm (**A**); 2 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**); 0.2 mm (**F**).

Distribution and habitat. Introduced. *Agrostis gigantea* is native to Eurasia. In the study zone, it has been collected in the USA states of Arizona, California, New Mexico, Texas, and in Mexico City, and the Mexican states of Durango, México, Michoacán, San Luis Potosí, and Sonora (Fig. 18A). This species has also been reported from Guanajuato, Morelos, and Oaxaca (Sánchez-Ken 2019), but no specimens from these states were found. *Agrostis gigantea* grows in disturbed areas, mainly in moist soils of ditches, marshy places and stream edges, between 651–3300 m a.s.l. (Fig. 9J).

Phenology. Specimens with spikelets have been collected from June to December (Fig. 10J).

Commentaries. It has been reported for other regions that the blades can reach 12 mm wide, spikelets up to 3.2 mm long and lemmas up to 2.2 mm long (Harvey 2007). This species is often confused with *A. bourgaei* (see the note under the description of that species). *Agrostis gigantea* also is similar to *A. stolonifera* in the paleate spikelets, but differs from it in the rhizomatous habit of the plants and more open panicle (vs. stoloniferous plants, panicle usually contracted in *A. stolonifera*).

The rhizomatous plants of *Agrostis*, with paleate spikelets, were formerly known as *A. alba* L., a name that was described without a type designation (Linnaeus 1753). Hitchcock (1905) considered the specimen LINN 84.23 as the type, but this was received by Linnaeus long after 1753 (Jarvis 2007). Widén (1971) indicates that this name must be typified by a specimen at the Van Royen Herbarium (L0052692), since *A. alba* was based on the work of Royen (1740), but that specimen corresponds to *Poa nemoralis* L., so currently *A. alba* is a synonym of the latter.

Conservation status. Since *Agrostis gigantea* is an introduced species in the study zone, its conservation status is considered as Least Concern (LC).

Representative specimens examined. Mexico. Durango: Municipio Canelas, Las Cebollitas, [25.10273363°N, 106.4441947°W], 2460 m alt., 1 Aug 1990, A. Benítez 1725 (CIIDIR, MEXU, UAMIZ). **México: Municipio Amecameca**, km 15 carretera Amecameca-Tlamacas, [19.08516405°N, 98.68113865°W, 3288 m alt.], 2 Oct 1992, A. Miranda and G. Villegas 634 (MEXU [*]). **Municipio Isidro Fabela**, alrededores de la presa Iturbide, [19.52454734°N, 99.46880154°W], 3300 m alt., 19 Aug 1971, J. Rzedowski 28545 (IBUG [*, **]). **Municipio Jilotepec**, Jilotepec, [19.96787783N, 99.51665054], 2450 m alt., 27 June 1954, E. Matuda 30961 (MEXU [*, **]). **Mexico City: Alcaldía Cuajimalpa**, La Venta, Santa Rosa-Contreras, [19.33155°N, 99.31138889°W], 2600 m alt., 29 Jul 1951, E. Matuda 21271 (MEXU [*, **]). **Michoacán: Municipio Salvador Escalante**, Santa Clara del Cobre, [19.41071944°N, 101.6532583°W], 2150 m alt., E. Pérez 96 (IEB, MEXU). **Sonora: Municipio Yécora**, 5.2 km W of Yécora on Mex 16, 28.36184916N, 108.961472, 1720 m alt., 1 Jun 1999, A.L. Reina et al. 99–160 (TEX). **USA. Arizona: Graham County**, Hospital Flat, Pinaleno Mountains, 32.6651°N, 109.877°W, 700 m alt, 7 Sep 1980, C.E. Jenkins and G. Yatskievych 3120 (ASU). **California: San Diego County**, Cuyamaca Rancho State Park, Cuyamaca Peak, 1 mi E of highway 79, beside Fern Flat Fire Road (unpaved), 0.5 mi SE of intersection with Lookout Fire Road and 0.8 air mile ENE of summit, 32.9487°N, 116.5935°W, 1586 m alt., 18 Sep 2008, L. Hendrickson 3272 (SD). **New Mexico. Socorro County**, Bosque del Apache refuge, San Antonio, [33.917844°N, 106.865859°W], 651 m, 7 Dec 1940, L. Lee

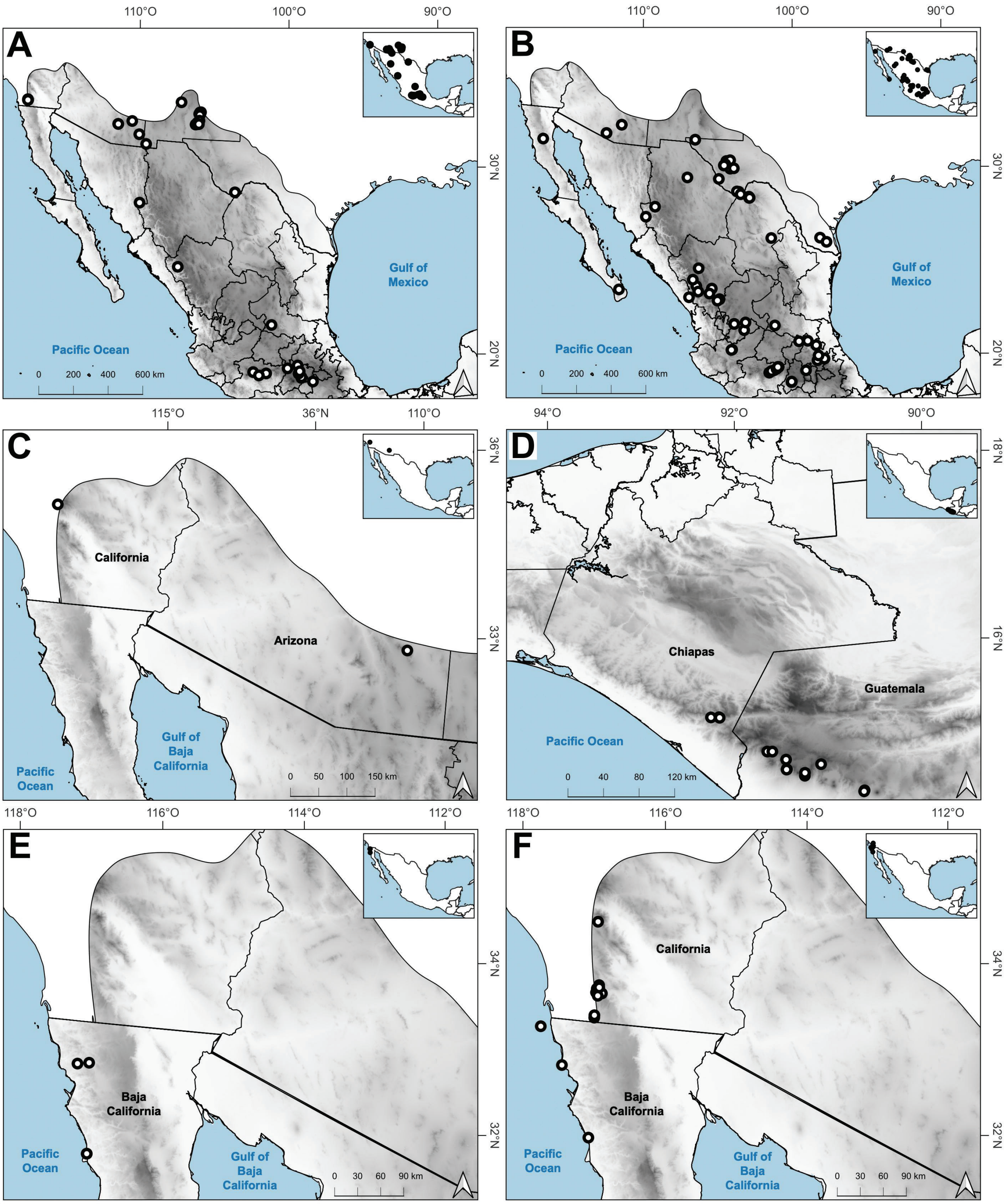

Figure 18. Map of known geographic distribution of *Agrostis* species, based on herbarium specimen data **A** *A. gigantea* **B** *A. hyemalis* **C** *A. idahoensis* **D** *A. laxissima* **E** *A. microphylla* **F** *A. pallens*.

s.n. (UNM). **Texas: Brewster County**, along creek from Boot Springs toward Boot, Chisos Mountains, [29.2724465°N, 103.2657998°W], 2065 m alt., 26 Aug 1937, B.H. Warnock 1039 (MICH). See Suppl. materials 2, 3 for additional examined specimens.

8. *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb., Prelim. Cat. 68. 1888. Figs 4H, 5H, 19

= *Cornucopiae hyemalis* Walter, Fl. Carol. 73. 1788. *Agrostis canina* L. var. *hyemalis* (Walter) Kuntze, Revis. Gen. Pl. 3(3): 338. 1898. *Agrestis hyemalis* (Walter) Lunell, Amer. Midl. Naturalist 4: 216. 1915. Type: USA. South Carolina: Charleston, sandy open ground near Navy Yard, 27 Apr 1912, B.L. Robinson 97 (neotype, designated by Ward (2007: 1099): GH (GH00247993 [image!]): isoneotypes: BH, US (US00955689 [image!])).*

Type. Based on *Cornucopiae hyemalis* Walter.

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 15–90 cm long, erect, sometimes shortly decumbent at the base, nodes (2–)3–7, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 5–11 cm long, usually shorter than the internodes, glabrous or scaberulous; ligules 1–7 mm long, longer than wide, dorsally scaberulous, apices rounded to truncate, erose, sometimes acute, often lacerate; blades 3–10(–15) cm long, 1–2(–3) mm wide, linear, flat, often becoming involute when dry, scaberulous on both surfaces. ***Panicles*** 10–30 cm long, (1.5–)4–25(–30) cm wide, open, lax, ovate, exserted from the upper sheaths, sometimes partially included; branches spreading, sometimes ascending, rebranching in the upper third, scaberulous, without spikelets near their base, spikelets clustered at the tips, inferior branches up to 15 cm long; pedicels (0.1–)0.5–2(–3.5) mm long, appressed, scaberulous. ***Spikelets*** 1–2(–2.5) mm long, greenish to purplish; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, sometimes also on the body, lower glume 1–2(–2.3) mm long, upper glume 0.8–1.9(–2.2) mm long; callus pubescent, with two bunches of trichomes; lemmas 0.8–1.3(–1.4) mm long, elliptic, apices entire, acute to obtuse, sometimes truncate, 5-nerved, veins inconspicuous or prominent, unawned; paleas absent or up to 0.2 mm long, veinless, glabrous; anthers 3, 0.2–0.5 mm long. ***Caryopsis*** 0.6–1.2 mm long, elliptic; endosperm soft. 2n= 28 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows medium-sized, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma absent or in girders, narrowing towards the bundle, adaxial sclerenchyma absent or in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 15I–K). Lemmas with transversal thickenings oblong, wider than the unthickened portions of the wall; prickle hairs abundant to scarce (Fig. 7H).

Distribution and habitat. *Agrostis hyemalis* is distributed from Ontario province in Canada to central Mexico, and is also present in the West Indies and Ecuador (Harvey 2007). The records of this species in western North America

* See Suppl. material 1 for other heterotypic synonyms.

could represent the confusion with *A. scabra* (see note below). It has also been reported from Perú (Soreng and Peterson 2003). In the study zone, this species has been collected in southern Arizona and Texas, USA, and in the Mexican states of Aguascalientes, Baja California, Baja California Sur, Chihuahua, Coahuila, Durango, Hidalgo, Jalisco, México, Michoacán, Puebla, Querétaro, San Luis Potosí and Sonora (Fig. 18B). It has also been reported from the Mexico City and the states of Colima, Guanajuato, Morelos, Nuevo Leon, Oaxaca, Sinaloa, Tlaxcala and Veracruz (Villaseñor 2016), but no specimens from these states were found. *Agrostis hyemalis* grows in open areas of temperate forests, with *Abies*, *Juniperus*, *Pinus* or *Quercus*, cloud forests, rocky areas of grasslands and stream edges, between 14–2710 m a.s.l. (Fig. 9K). The Texan populations of this species grow in lower elevations than the Mexican ones.

Phenology. Specimens with spikelets have been collected from January to November, but most of the records are from May (Fig. 10K).

Commentaries. It has been reported for other regions that the panicles can reach 36 cm long (Harvey 2007).

Agrostis hyemalis is often confused with *A. elliottiana* (see the note under the description of that species). It is also similar to *A. scabra*, in the panicle branches rebranching in the upper third and somewhat clustered spikelets, and also shares several leaf blade anatomy features. *Agrostis hyemalis* differs from the latter in the culms with usually more than three nodes, basal and cauline leaves, more clustered and shorter spikelets, of 1–2(–2.5) mm long, and smaller anthers of 0.2–0.5 mm long (vs. culms with usually 1–2(–3) nodes, usually mostly basal leaves, spikelets of 2–3(–3.4) mm long, anthers 0.5–1.4 mm long in *A. scabra*). The identification of these two species is especially difficult if the plants are not collected with the basal parts.

Conservation status. *Agrostis hyemalis* is a widespread species in the study zone. It is represented by 86 collections, with several populations occurring in 15 protected areas. The EOO is 1,491,700 km^2 and the AOO is 248 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Mexico. Aguascalientes: Municipio Calvillo, margen Presa Los Adobes, 21.805°N, 102.6886111°W, 1960 m alt., 29 Mar 2010, F. Macías 5 (FCME, IEB, INEGI, MEXU [*], UAMIZ). **Baja California: Municipio Ensenada**, Los Llanitos, [30.96666667°N, 115.4333333°W], 2550 m alt., 17 Aug 1967, R. Moran and R.F. Thorne 14267 (MEXU). **Baja California Sur**: **Municipio La Paz**, Sierra de la Laguna, arroyo la Boquilla, [23.53333°N, 109.9°W], 1850 m alt., 2 Jun 1995, M. Domínguez 1009 (SD [*]). **Chihuahua: Municipio Chihuahua**, rancho El Peñasco, km 150 carretera Chihuahua-Ciudad Juárez, [29.875°N, 106.375°W], 750 m alt., 9 Aug 1979, M.E. Siqueiros 340 (MEXU [*]). **Municipio Chínipas**, rancho Byerly, Sierra Charuco, [27.581389°N, 108.696111°W], 1767 m, Apr 1948, H.S. Gentry 8027 (MEXU, US). **Coahuila: Municipio Ocampo**, Madera del Carmen, 0.5 mi from Campo Uno, up the road towards the summit, 28.99611111°N, 102.6113889°W, 2355 m alt., 22 Sep 2007, P.M. Peterson et al. 21016 (CAN, MEXU [*, **], US); **Durango: Municipio Durango**, predio Las Bayas (UJED), arroyo San Rafael, 23.44416667°N, 105.8775°W, 2710 m alt., 8 Aug 1990, A. García and M. González 610 (CIIDIR). **Municipio Suchil**, arroyo El Toboso, potrero Jacales, San Juan de Michis, [23.432778°N, 104.132778°W], 2220 m alt., 3 Jan 1986, J. Alvarado 711 (CIIDIR, IBUG, IEB, MEXU [*], UAMIZ). **Hidalgo: Municipio Huasca de**

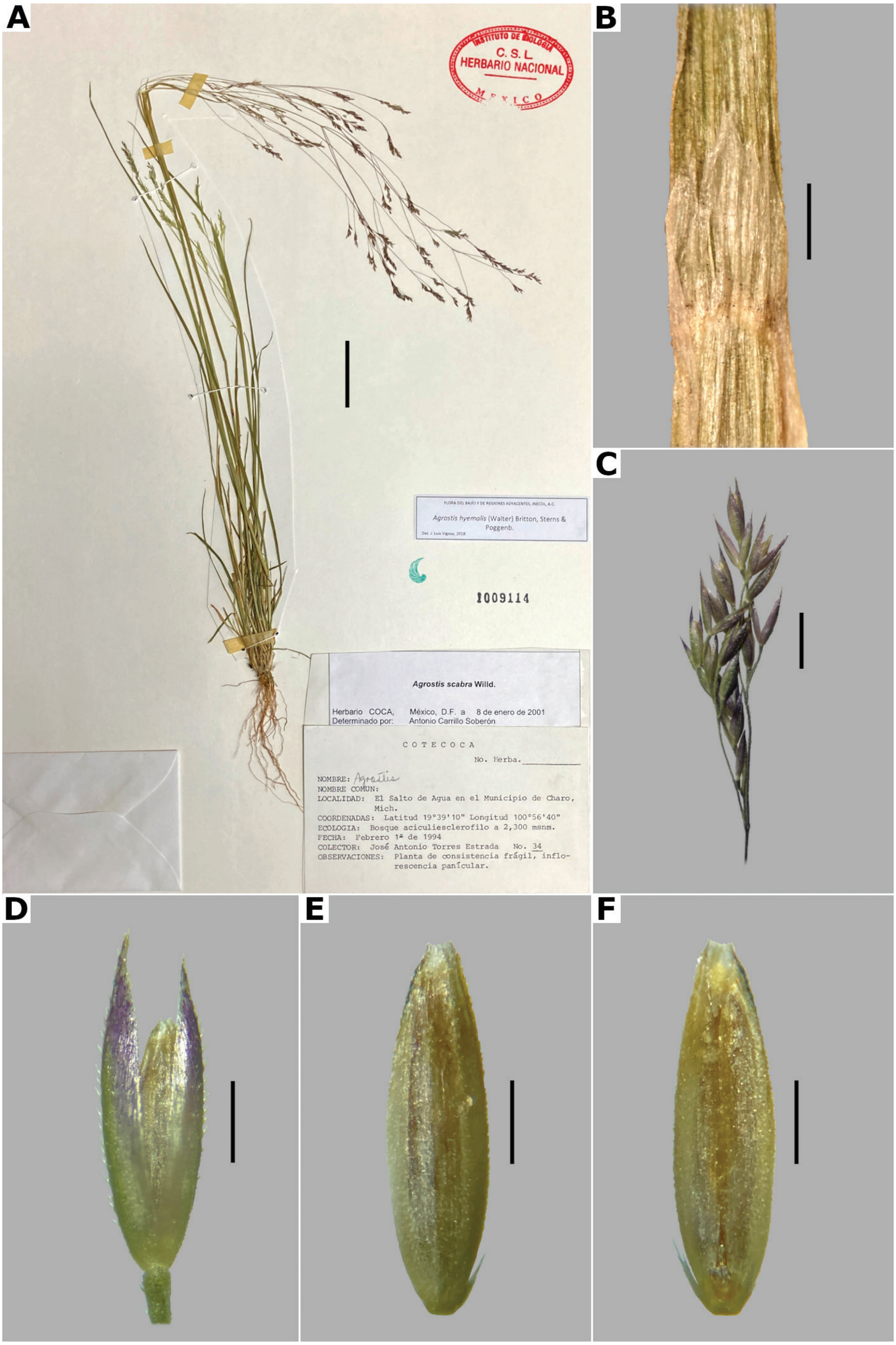

Figure 19. *Agrostis hyemalis* **A** whole plant **B** ligular area **C** detail of a terminal branch of the panicle **D** spikelet, **E** floret, abaxial view, **F** floret, adaxial view. Based on Torres 34 (MEXU). Scale bars: 3 cm (**A**); 2 mm (**B, C**); 0.5 mm (**D**); 0.3 mm (**E, F**).

Ocampo, 0.5 km al W de Bermúdez, sobre el camino de terracería que conduce de Bermúdez a Huasca de Ocampo, [20.1975°N, 98.58861111°W], 2230 m alt., 21 Jul 1994, M. Osorio 27 (MEXU). **Jalisco: Municipio Gudalajara**, periférico de Guadalajara, cercano al auditorio Benito Juárez, [20.72784467°N, 103.3330636°W], 1540 m alt., 13 Nov 1975, C. García 238 (IBUG). **México: Municipio Cuautitlán**, alrededores de Cuautitlán, [19.65834784°N, 99.22657358°W], 2250 m alt., 5 Jun 1982, J. Rzedowski 37841 (CIIDIR, IEB, INEGI, MEXU [*], XAL). **Municipio San Simón de Guerrero:** 3 km sobre la desviación a San Simón de Guerrero, por la carretera Temascaltepec-Tejupilco, [19.01841341°N, 100.0282873°W], 1974 m alt., 15 Mar 1983, E. Manrique et al. 207 (MEXU [*]). **Michoacán: Municipio Charo:** cerca de Pontezuela, 25 km al E de Morelia, sobre la carretera a Mil Cumbres, [19.65730833°N, 100.9891889°W], 2200 m alt., 29 Jan 1987, J. Rzedowski 42417 (CHAPA, CIIDIR, ENCB, FCME, IBUG, IEB, MEXU); El Salto de Agua, 2300 m alt., 1 Feb 1994, J.A. Torres 34 (MEXU [*,**]). **Puebla: Municipio Honey**, 1 km al E de Ocahuales, carretera a Pahuatlán, [20.28333333°N, 98.2°W], 1880 m alt., 4 May 1989, P. Tenorio 15742 (IEB, MEXU, NY, TEX). **Querétaro: Municipio Landa**, 5 km al S de El Lobo, sobre el camino a Agua Zarca, [21.26118889°N, 99.11667778°W], 1500 m alt., 21 Feb 1987, J. Rzedowski 42572 (IEB). **San Luis Potosí: Municipio San Luis Potosí**, Cañada de Lobos, Sierra de San Miguelito, 5 km al S de la ciudad de San Luis Potosí, [22.09433995°N, 100.9645498°W], 1900 m alt., 1968, F. Takaki 2170 (MEXU). **Sonora: without municipality**, Sonora, 24 Jun 1855, A. Schott s.n. (F). **Zacatecas: Municipio Guadalupe**, ladera N del cerro de la Virgen, 215 m, 10 Aug 1988, J. Balleza 1580 (CHAPA). **USA. Arizona: Pima County**, Forest Cabin, Baboquivari Mountains, [31.7897°N, 111.586°W], 2091 m alt., 14 May 1941, C. Goodding 105-41 (ASU). **Texas: Hidalgo County**, ca. 1.3 airmiles SW of junction of Hidalgo, Kennedy and Willacy Counties, Hunke Ranc, La Sal Vieja Quadrangle, 26.59958°N, 97.97172°W, 14 m alt., 16 Mar 2004, W.R. Carr and M. Pons 22785 (TEX). **Jeff Davis County**, NW flank of Mount Livermore, ca. 0.3 mi ESE of Madrea Tank, ca. 0.7 mi, NNW of summit of Baldy Peak, 30.64722°N, 104.17833°W, 1890 m alt., 11 Aug 2000, W.R. Carr 19093 (TEX [*]). See Suppl. materials 2, 3 for additional examined specimens.

9. *Agrostis idahoensis* Nash, Bull. Torrey Bot. Club 24(1): 42–43. 1897.
Fig. 20

= *Agrostis tenuis* Vasey, Bull. Torrey Bot. Club 10(2): 21. 1883, nom. illeg. hom., non Sibth., 1794. *Agrostis tenuiculmis* Nash, Mem. New York Bot. Gard. 1: 32. 1900. Type: USA. California: San Bernardino County, on the San Bernardino Mountains, Aug 1881 or 1882, S.B. Parish and W.F. Parish 1085 (holotype: US (US00131119 [image!]).
= *Agrostis filiculmis* M.E. Jones, Contr. W. Bot. 14: 13. 1912. Type: USA. Arizona: Little De Motte Park on the Kaibab in N Arizona, 19 Sep 1894, M.E. Jones 6056bb (holotype: RSA (RSA0000394 [image!]).*

Type. USA. Idaho: Nez Perce County, Forest, 1160 m alt., 1 Jul 1896, A.A. Heller and E.G. Heller 3431 (holotype: NY (NY00327633 [image!]); isotypes: BAA

* See the Suppl. material 1 for other heterotypic synonyms.

(BAA00001339 [image!]), CAS (CAS0000194 [image!]), DAO (DAO000465362 [image!]), ID (ID00157714 [image!]), JE (JE00020223[image!]), K (K000838198 [image!]), LE (LE00009307 [image!]), MO (MO-123094 [image!]), MIN (MIN1000077 [image!]), MSC (MSC0129856 [image!]), NDG (NDG07456 [image!]), NY (NY00327634 [image!]), P (P00740552 [image!], P00740553 [image!]), S (SG-259 [image!]), US (US00131762 [image!]).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 8–40 cm long, erect, nodes 2–5, glabrous, internodes glabrous. ***Leaves*** mostly basal; sheaths 5–11 cm long, the lower ones usually shorter larger than the internodes, glabrous or scaberulous; ligules (0.7–)1–2(–4) mm long, longer than wide, dorsally scaberulous, apices rounded to truncate, erose to lacerate; blades 1–7 cm long, 0.5–2 mm wide, linear, flat, often becoming involute when dry, scaberulous on both surfaces. ***Panicles*** 3–13 cm long, 1–6(–8) cm wide, open, lax, lanceolate to ovate, exserted from the upper sheaths; branches ascending, sometimes spreading, rebranching about or slightly above mid-length, scaberulous, without spikelets near their base, inferior branches 1–4 cm long; pedicels 0.5–6.5 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.5–2.5 mm long, purplish; glumes subequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume 1.5–2.5 mm long, upper glume 1.4–2.4 mm long, sometimes glabrous; callus puberulous; lemmas 1.2–2.2 mm long, elliptic, apices entire, acute to obtuse, 5-nerved, veins inconspicuous, unawned; paleas absent or up to 0.2 mm long, veinless, glabrous; anthers 3, 0.3–0.6 mm long. ***Caryopsis*** 1–1.3 mm long, elliptic; endosperm soft. 2n= 28 (Harvey 2007).

Anatomy and micromorphology. Not seen.

Distribution and habitat. *Agrostis idahoensis* is distributed from Alaska to California and New Mexico (Harvey 2007). It is also present in Chile and Argentina (Rúgolo and Molina 1997). In the study zone, this species has been collected in southern Arizona and California (Fig. 18C). It grows in stream edges of temperate forests, with *Abies*, *Arctostaphylos*, *Picea* or *Pinus*, between 3084–3121 m a.s.l. (Fig. 9L). There are more records of this species in the study zone, on databases (GBIF 2023b), but not all of them have images, and thus we were unable to confirm their identity.

Phenology. Specimens with spikelets have been collected in July and August (Fig. 10L).

Commentaries. *Agrostis idahoensis* is similar to *A. perennans* sensu lato. It differs from it in the mostly basal leaves, persistent, with leaf blades 0.5–2 mm wide (vs. basal and cauline leaves, the basal ones often drying before anthesis, with leaf blades often more than 2 mm wide in *A. perennans*). It is also similar to *A. scabra*, from which it differs in the branches of the panicle rebranching about or slightly above mid-length, and spikelets not clustered at the branch tips (vs. branches rebranching in the upper third, spikelets somewhat clustered in *A. scabra*). *Agrostis idahoensis* is scarcely different from *A. turrialbae*, distributed from central Mexico to Central America. The former differs in flatter and wider leaf blades, 0.5–2 mm wide (vs. conduplicate or involute leaf blades, 0.3–0.5 mm wide in *A. turrialbae*).

Conservation status. Herbarium specimens from only two localities in the United States were examined, whereby the EOO and AOO cannot be calculated. The category of Deficient Data (DD) is suggested.

Figure 20. Herbarium specimen of *Agrostis idahoensis*. Based on Bell and Chambers 9968 (RSA). Scale bar: 3 mm.

Specimens examined. USA. Arizona: Graham County, High Peak Cienega, Pinaleno Mountains, 32.693861°N, 109.867556°W, 3121 m alt., 9 Aug 2014, M. Licher 4524 (ASC). **California: San Bernardino County**, San Bernardino National Forest, San Gorgonio Wilderness area, High Meadow Springs in the upper watershed of Mill Creek, approximately 0.75 air miles west northwest of Dollar Lake, 34.12471°N, 116.86665°W, 3084 m alt., 21 Jul 2016, D.S. Bell and A. Chambers 9968 (RSA).

10. *Agrostis laxissima* Swallen, Contr. U.S. Natl. Herb. 29(9): 402. 1950.
Figs 4I, 5I, 21

= *Agrostis abietorum* Swallen, Contr. U.S. Natl. Herb. 29(9): 403. 1950. Type: Guatemala. San Marcos: dry banks in *Cupressus-Abies* forest, along road between San Sebastian at km 21 and km 8, 8–18 miles NW of San Marcos, 2700–3800 m alt., 15 Feb 1940, J.A. Steyermark 35652 (holotype: F (F0046562F [image!]); isotype: US [fragm. ex F] (US00156356)).

Type. Guatemala. San Marcos: dense *Abies-Cupressus* forest, along road between San Marcos and Serchil, 2700–3150 m alt., 30 Jan 1941, P.C. Standley 85379 (holotype: US (US00131078); isotypes: F (V0046566F [image!]), US (US00131079)).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 25–85 cm long, decumbent to erect, nodes 2–6, glabrous, internodes glabrous. ***Leaves*** basal and cauline; sheaths 4–15 cm, shorter than the internodes, scaberulous; ligules 2.5–6 mm long, longer than wide, dorsally scaberulous, apices acute, often lacerate; blades 4–15(–25) cm long, 1–4 mm wide, lax, flat, scaberulous on both surfaces. ***Panicles*** 7–18 cm long, 2–9 cm wide, open, lax, lanceolate to ovate, sometimes partially included in the upper sheaths; branches ascending to spreading, rebranching about or above midlength, scaberulous, without spikelets near their base, inferior branches 2–7 cm long; pedicels 1.5–6 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.7–3 mm long, greenish; glumes subequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume 1.7–3 mm long, upper glume 1.5–2.8 mm long; callus pubescent, with two bunches of trichomes; lemmas 1.3–2.2 mm long, elliptic, apices irregularly toothed, 5-nerved, veins inconspicuous, awned from near the base, awn 3–4 mm long, geniculate; paleas absent or up to 0.4 mm long, veinless, glabrous; anthers 3, 0.7–1 mm long. ***Caryopsis*** not seen. 2n= unknown.

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows medium-sized, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in girders, narrowing towards the bundle, adaxial sclerenchyma in strands; second order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in girders, narrowing towards the bundle, adaxial sclerenchyma in strands; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, extending along abaxial side of the leaf; colorless cells absent (Fig. 22A–C). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 7I).

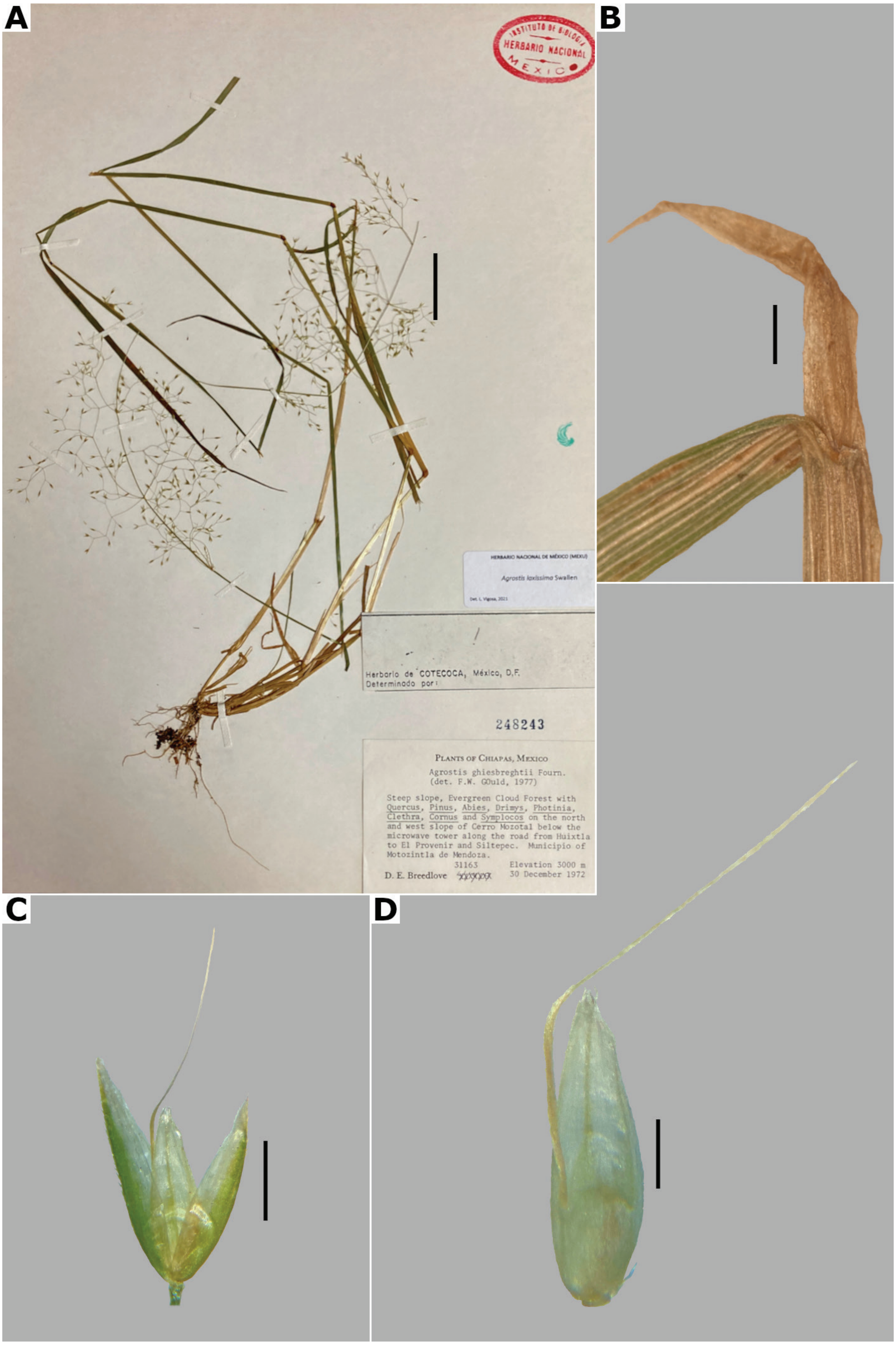

Figure 21. *Agrostis laxissima* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view. Based on Breedlove 31163 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B, C**); 0.5 mm (**D**).

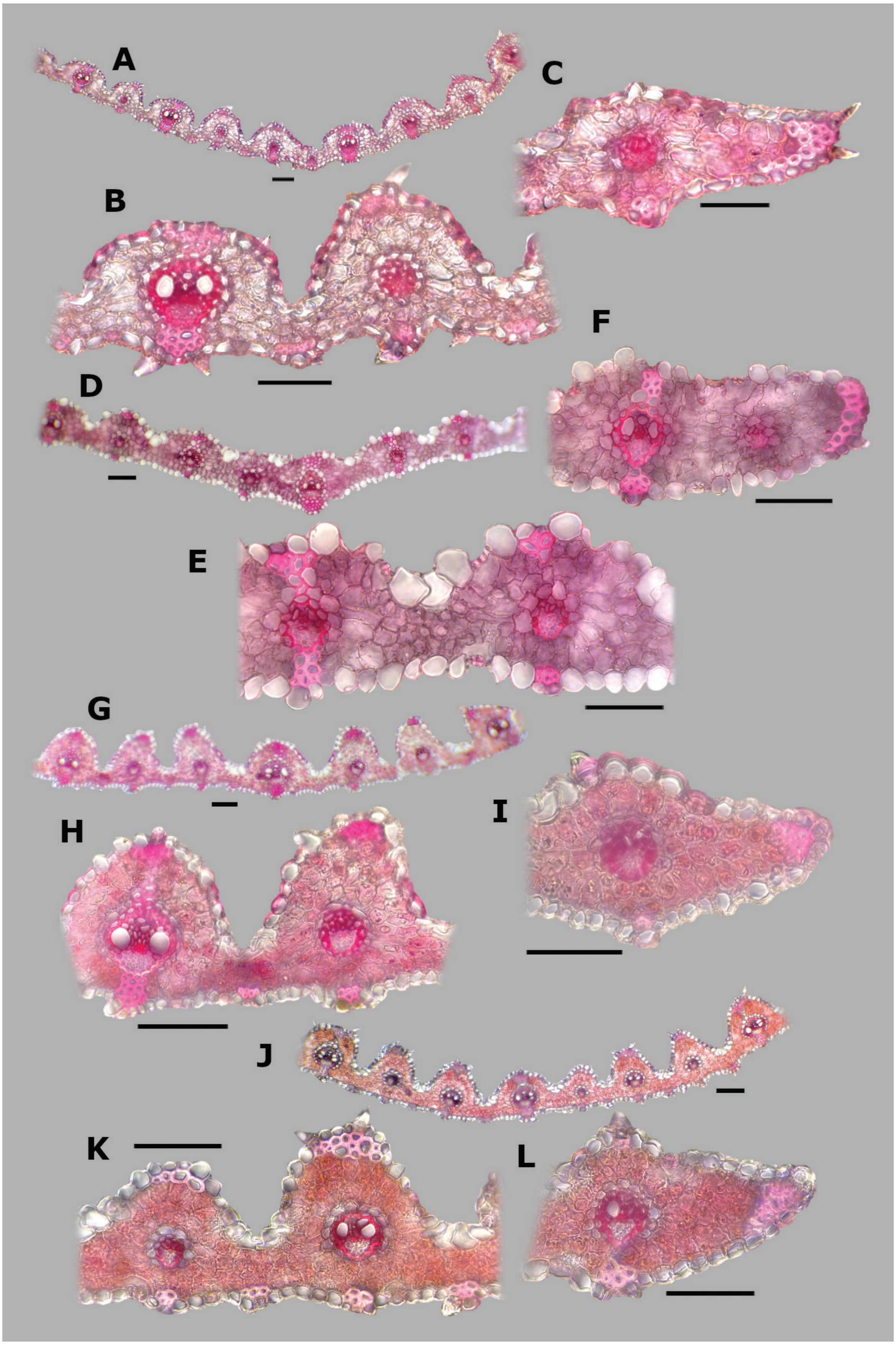

Figure 22. Leaf blade anatomy in transversal section of *Agrostis* species, in general view, and details of lateral bundles. **A**–**C** *A. laxissima* **D**–**F** *A. microphylla* **G**–**I** *A. pallens* **J**–**L** *A. perennans*. Scale bars: 0.1 mm.

Distribution and habitat. Endemic. *Agrostis laxissima* is distributed from Southern Mexico to Guatemala (Pohl and Davidse 1994). It has also been reported in Honduras (Soreng and Peterson 2003). This species has been collected from the Mexican state of Chiapas, and the departments of Quezaltenango, Sacatepéquez, San Marcos and Solola in Guatemala (Fig. 18D). *Agrostis laxissima* grows in temperate forests, with *Abies*, *Pinus*, or *Quercus*, in cloud forests and grasslands, between 2250–3200 m a.s.l. (Fig. 9M).

Phenology. Specimens with spikelets have been collected from June to March, but most of the records are from December and January (Fig. 10M).

Commentaries. *Agrostis laxissima* is often confused with *A. ghiesbreghtii* (see the note under the description of that species).

Conservation status. *Agrostis laxissima* is only known from a few localities of southern Mexico and Guatemala. It is represented by 17 collections, with several populations occurring in six protected areas. The EOO is 2,615 km^2 and the AOO is 44 km^2. Following the IUCN criteria, the preliminary assessment category is Vulnerable (VU).

Representative specimens examined. Guatemala. Quezaltenango: Municipio San Juan Ostuncalco, barranco Buena Vista, cuesta El Caracol, Sierra Madre Mountains, about 5 km. northwest of San Juan Ostuncalco, [14.90886385°N, 91.66847343°W], 2800–2900 m alt., 11 Dec 1962, O. Williams et al. 22792 (F, US). **Municipio San Martín Sacatepéquez**, cumbre de Tuilacán, SW of San Martín Chile Verde, [14.80612°N, 91.66872°W], 2400 m alt., 8 Mar 1939, P.C. Standley 67819 (F). **Sacatepéquez: Municipio Alotenango**, Volcán de Acatenango, [14.499453°N, 90.87175°W], 3200 m alt., 11 Sep 1993, I. Arias and M. Véliz 933265a (MEXU [*]), 18 Aug 2000, M. Véliz et al. 10263 (MEXU [*, **]). **Mexico: Chiapas: Municipio Motozintla**, NW slope of cerro Mozotlan, below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, [15.42605394°N, 92.34362676°W], 3000 m alt., 30 Dec 1972, D.E. Breedlove 31163 (MEXU [*, **]); 27 km al NO de Motozintla, camino a Coadesmech, torre de microondas, [15.43104735°N, 92.42724341°W], 3030 m alt., 21 Oct 1985, P. Dávila et al. 181 (MEXU [*]). See the Suppl. material 2 for additional examined specimens.

11. *Agrostis microphylla* Steud., Syn. Pl. Glumac. 1: 164. 1854.

Figs 4J, 5J, 23

Agraulus brevifolius Nees ex Torr., Pacif. Railr. Rep. 4: 154. 1857, nom. inval., pro syn.

Agrostis virescens Kunth var. *microphylla* (Steud.) Scribn., Circ. Div. Agrostol. U.S.D.A. 30: 2. 1901.

Agrostis exarata Trin. var. *microphylla* (Steud.) Hitchc., Amer. J. Bot. 2: 303. 1915.

= *Agrostis microphylla* Steud. var. *intermedia* Beetle, Bull. Torrey Bot. Club 72(6): 547. 1945. Type. USA. California: Lake County, 2.9 miles north of Middletown, 11 May 1943, J.T. Howell 18063 (holotype: AHUC (AHUC9939 [image!]); isotype: CAS (CAS0000198 [image!])).*

Type. America septentrionalis, D. Douglas s.n. (not located).

* See Suppl. material 1 for other heterotypic synonyms.

Description. ***Plants*** annual, caespitose. ***Tillers*** absent. ***Culms*** 4–25 cm long, erect, nodes 1–3, glabrous, internodes glabrous. ***Leaves*** usually mostly cauline; sheaths 1.5–8 cm long, longer or shorter than the internodes, glabrous; ligules 1–5 mm long, longer than wide, dorsally scaberulous, apices acute to truncate, erose, often lacerate; blades 1–8 cm long, 0.5–2.5 mm wide, flat, scaberulous on both surfaces. ***Panicles*** 1–9 cm long, 0.5–1.4 cm wide, contracted, dense, spiciform, linear to lanceolate, sometimes interrupted at the base, sometimes partially included in the upper sheaths; branches appressed, rebranching from below mid-length, scaberulous, with spikelets almost to the base, inferior branches 0.6–2.5 cm long; pedicels 0.3–2.5 mm long, appressed, scaberulous. ***Spikelets*** 3–4.5 mm long, greenish to stramineous; glumes unequal, lanceolate, apices long acuminate or awned, 1-veined, scaberulous on the keel, sometimes also on the body, lower glume 3–4.5 mm long including the awn, upper glume 2.5–4 mm long; callus pubescent, with two bunches of trichomes; lemmas 1.5–2 mm long, elliptic, apices 2(–4) toothed, 5-nerved, veins inconspicuous or prominent distally, awned about mid-length, awn 3.5–6 mm long, inserted 0.8–1 mm above the base, geniculate; paleas absent or up to 0.2 mm long, veinless, glabrous; anthers 3, 0.4–0.5 mm long. ***Caryopsis*** 1–1.5 mm long, elliptic; endosperm soft. 2n= 56 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows shallow, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with small sclerenchyma caps, rounded; colorless cells absent (Fig. 22D–F). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portions of the wall; prickle hairs scarce to abundant (Fig. 7J).

Distribution and habitat. *Agrostis microphylla* is distributed from British Columbia, Canada, to the northern peninsula of Baja California, Mexico (Harvey 2007). In the study zone, this species has been collected in the Mexican state of Baja California (Fig. 18E), where it grows in stream edges and vernal pools, between 37–315 m a.s.l. (Fig. 9N). It has also been reported from the state of Baja California Sur, but the database record linked to this report has no images (GBIF 2023c), and thus we were unable to confirm its identity.

Phenology. Specimens with spikelets have been collected from April to June (Fig. 10N).

Commentaries. It has been reported for other regions that the culms can reach 45 cm long, panicles up to 12 cm long, spikelets up to 5 mm, and awns up to 8 mm (Harvey 2007).

Agrostis microphylla is one of the few annual *Agrostis* species. It is often confused with the smaller forms of *A. exarata*, from which it differs in the annual habit, spikelets of 3–4.5 mm long and lemmas with an awn of 3.5–6 mm long (vs. perennial plants, spikelets of 2–2.5 mm, lemmas unawned or with an awn up to 3 mm long in *A. exarata*), as well as the leaf blade anatomy and lemma micromorphology.

Conservation status. *Agrostis microphylla* is apparently a rare species in the study zone. It is represented by only four collections, with no populations occurring in protected areas. The EOO is 897 km^2 and the AOO is 12 km^2. Following the IUCN criteria, the preliminary assessment category is Endangered (EN).

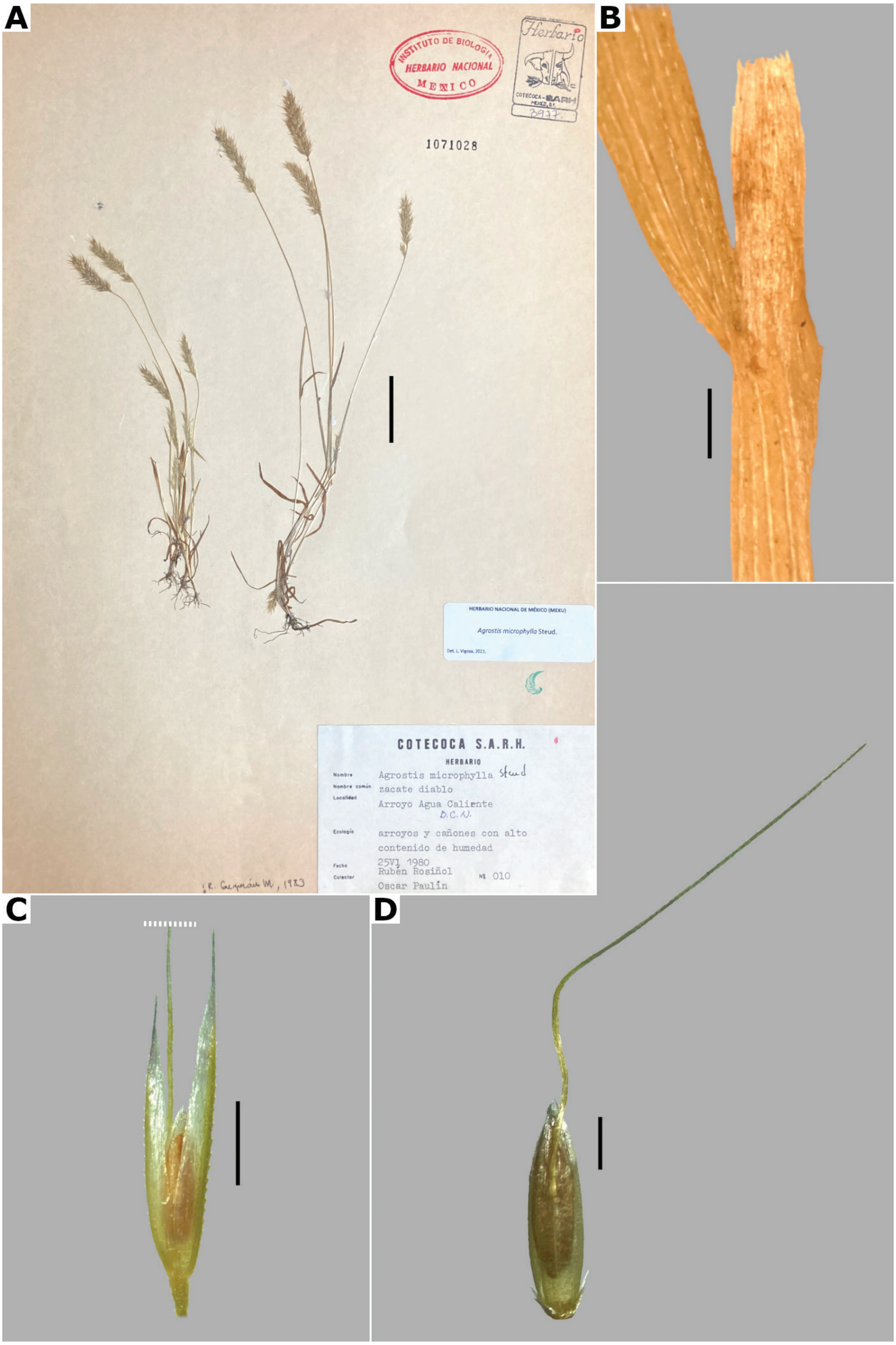

Figure 23. *Agrostis microphylla* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view. Based on Rosiñol 10 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B, C**); 0.5 mm (**D**).

Specimens examined. Mexico. Baja California: Municipio Ensenada, 5 km SSO of Johnson Ranch, N of Cabo Colonet, [31.05833°N, 116.29167°W], 37 m alt., 31 May 1980, R. Moran 28447 (SD), 28643 (MEXU [*,**], SD); Guadeloupe [Guadalupe] ranch, [32.0754°N, 116.6217°W, 315 m alt.], 6 Apr 1886, C.R. Orcutt s.n. (US); arroyo Agua Caliente, [32.11163081°N, 116.4650486°W], 300 m alt., 25 June 1980, R. Rosiñol 10 (MEXU [*, **]).

12. *Agrostis pallens* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 328. 1841.
Figs 4K, 5K, 24

= *Agrostis diegoensis* Vasey, Bull. Torrey Bot. Club 13: 55. 1886. *Agrostis multiculmis* Vasey ex Beal, Grass. N. Amer. 328. 1896, nom. inval., pro syn. Type: USA. California: San Diego, 1884, C. Orcutt s.n. (lectotype, designated by Vigosa-Mercado (2022a: 2): US (US00131740 [image!]); isolectotypes: GH (GH00022962 [image!]), K (K000838209 [image!]), NY (NY00327625 [image!]), OSC (OSC0001812 [image!]), W (W19160036561 [image!])).*

Type. America borealis, J.D. Hooker 243 (holotype: LE-TRIN (LE-TRIN-1634.01); isotype: US [fragm. ex LE-TRIN] (US00156470 [image!])).

Description. ***Plants*** perennial, rhizomatous. ***Tillers*** extravaginal, with cataphylls. ***Rhizomes*** up to 10 cm long. ***Culms*** 10–70 cm long, erect or decumbent at the base, nodes 2–7, glabrous, sometimes rooting at the lower nodes, internodes glabrous. ***Leaves*** mostly cauline; sheaths 2.5–13 cm long, longer or shorter than the internodes, glabrous or scaberulous; ligules 1–5 mm long, longer than wide, dorsally scaberulous, apices acute, lacerate; blades 2.5–14 cm long, 1–4 mm wide, flat, involute when drying, scaberulous on both surfaces. ***Panicles*** (4–)5–20 cm long, 0.4–3 cm wide, contracted to open, dense to lax, lanceolate to narrow ovate, sometimes spiciform, sometimes partially included in the upper sheaths; branches appressed to ascending, rebranching from about mid-length, scaberulous, without spikelets near their base, inferior branches 1.5–3 cm long; pedicels 0.5–4 mm long, appressed to ascending, scaberulous. ***Spikelets*** 2–3.5(–4) mm long, greenish to stramineous, sometimes tinged with purple; glumes equal to subequal, lanceolate, apices acute, 1-veined, scaberulous on the keel, sometimes also on the body, lower gluma 2–3.5(–4) mm long, upper glume 1.8–3.5(–4) mm long; callus pubescent, with two bunches of trichomes, sometimes short and inconspicuous; lemmas 1.5–2.5 mm long, elliptic, apices entire, acute, or toothed, 5-nerved, veins prominent throughout or only distally, unawned, sometimes awned subapically to about mid-length, awn 0.5–1.5(–2.5) mm long, straight; paleas absent or up to 0.2 mm, veinless, glabrous; anthers 3, 0.7–1.5 mm long. ***Caryopsis*** 1–1.5 mm long, elliptic; endosperm solid. 2n= 42, 56 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted adaxially and abaxially, abaxial sclerenchyma in strands or girders, narrowing towards the bundle, adaxial scleren-

* See Suppl. material 1 for other heterotypic synonyms.

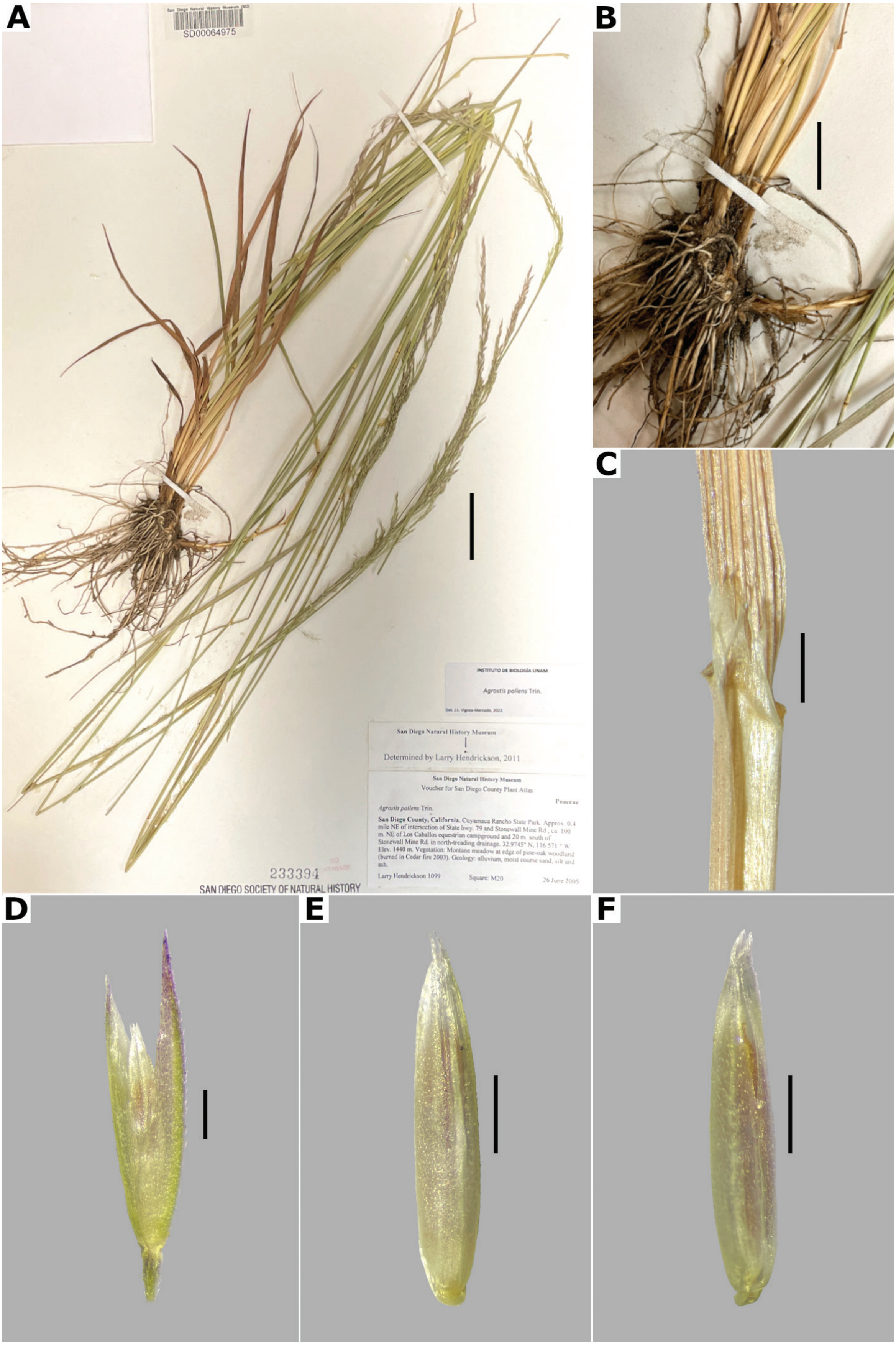

Figure 24. *Agrostis pallens* **A** whole plant **B** detail of the rhizome **C** ligular area **D** spikelet **E** floret, abaxial view **F** floret, adaxial view. Based on Hendrickson 1099 (SD). Scale bars: 3 cm (**A**); 2 cm (**B**); 2 mm (**C**); 0.5 mm (**D–F**).

chyma in strands or t-shaped girders; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 22G–I). Lemmas with transversal thickenings polygonal, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 7K).

Distribution and habitat. *Agrostis pallens* is distributed from British Columbia, Canada, to Baja California, Mexico, and is also present in Montana and Utah (Harvey 2007). In the study zone, this species has been collected in southern California and the Mexican state of Baja California (Fig. 18F). It grows in coastal sands, stream edges, temperate forests with *Pinus* or *Quercus*, and xeric shrublands, between 40–1635 m a.s.l. (Fig. 9O).

Phenology. Specimens with spikelets have been collected from June to August (Fig. 10O).

Commentaries. It has been reported for other regions that panicles can reach 6(–8) cm wide (Harvey 2007).

The Mexican populations of *A. pallens* have lemmas with longer awns, up to 2.5 mm long, than those of southern California, but the other characters are congruent with the previous descriptions of this species. The plants of lower elevations have more contracted panicles than those of higher elevations, as noted previously by Harvey (2007). Plants of lower elevations are often confused with *A. exarata*, from which they differ in the rhizomatous habit, mostly cauline leaves, and palea absent or up to 0.2 mm long (vs. usually caespitose habit, basal and cauline leaves, palea often present, up to 0.8 mm long in *A. exarata*).

Conservation status. *Agrostis pallens* is apparently a rare species in the study zone. It is represented by 12 collections, with several populations occurring in four protected areas. The EOO is 10,902 km^2 and the AOO is 48 km^2. Following the IUCN criteria, the preliminary assessment category is Vulnerable (VU).

Representative specimens examined. Mexico. Baja California: Municipio Ensenada, S bank of arroyo Jatay, 1.5 km from the mouth, [32.01673537°N, 116.8665199°W], 40 m alt., 11 Jun 1980, R. Moran 28770 (MEXU [*,**], SD). **USA. California: Riverside County**, at Idyllwild, in San Jacinto Mountains, [33.746537°N, 116.715288°W], 1635, m alt. 14 Aug 1971, P.C. Baker 7110 (LOB). **San Diego County**, Cuyamaca Rancho State Park, 0.4 mile NE of intersection of state highway 79 and Stonewall Mine Road, ca. 100 m NE of Los Caballos equestrian campground and 20 m south of Stonewall Mine Road, in north-treading drainage, 32.9745°N, 116.571°W, 1440 m alt., 26 Jun 2005, L. Hendrickson 1099 (SD [*, **]). See Suppl. materials 2, 3 for additional examined specimens.

13. ***Agrostis perennans*** **(Walter) Tuck., Amer. J. Sci. Arts 45: 44. 1843, sensu lato.**

Figs 4L, 5L, 25

Cornucopiae perennans Walter, Fl. Carol. 74. 1788. Type: USA. South Carolina: at the intersection of cut off road and Fire Break 49 on Ft. Jackson Military Reservation, 11 Jul 1995, K.B. Kelly and J.B. Nelson 254 (neotype, designated by Ward (2007: 1099): GH (GH00247994 [image!])).

Agrostis cornucopiae Sm., Gent. Mag. 59: 873. 1789, nom. illeg. superfl.

Agrostis elegans (Walter) Salisb., Prodr. Stirp. Chap. Allerton 25. 1796.
Agrostis anomala Willd., Sp. Pl., 1(1): 370. 1797, nom. illeg. superfl.
Trichodium perennans (Walter) Elliott, Sketch Bot. S. Carolina 1(2): 99. 1816.
= *Agrostis michauxii* Zuccagni var. *alpina* Rupr., Bull. Acad. Roy. Sci. Bruxelles 52: 228. 1842, nom. nud. Type. Mexico. Oaxaca. Cordillera, 1840, H.G. Galeotii 5767 (holotype: P (P00740583 [image!]).
Agrostis scabra Willd. var. *perennans* (Walter) Alph. Wood, Class Book Bot. (3 ed.) 774. 1861.
= *Agrostis schaffneri* E. Fourn., Mexic. Pl. 2: 94. 1886. *Agrostis schaffneri* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 551. 1885, nom. nud. Type. MEXICO. Mexico City: Tacubaya, J.G. Schaffner 308 (lectotype, designated by Vigosa-Mercado (2022a: 3): P (P00740418 [image!]).
= *Agrostis schaffneri* E. Fourn. var. *mutica* E. Fourn., Mexic. Pl. 2: 94. 1886. Type. MEXICO. Mexico City: Tacubaya: J.G. Schaffner 1 (holotype: P (P00740419 [image!]).
= *Agrostis tacubayensis* E. Fourn., Mexic. Pl. 2: 95. 1886. *Agrostis tacubayensis* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 551. 1885, nom. nud. Type. MEXICO. Mexico City: Tacubaya, J.G. Schaffner 97 (holotype: P (P00740425 [image!])).
= *Agrostis chinantlae* E. Fourn., Mexic. Pl. 2: 96. 1886. *Agrostis chinantlae* E. Fourn. ex Hemsl., Biol. Cent.-Amer., Bot. 3: 550. 1885, nom nud. Type. MEXICO. Veracruz: Chinantla, May 1841, F.M. Liebmann 709 (lectotype, designated by Vigosa-Mercado (2022a: 2): C (C10016725 [image!]); isolectotypes: C (C10016726 [image!]), K (K000308372 [image!]), US (US00131733).*

Type. Based on *Cornucopiae perennans* Walter.

Description. ***Plants*** perennial, caespitose, sometimes developing short pseudostolons. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 0.2–0.8(–1) m long, decumbent to erect, nodes 3–7(–10), glabrous, internodes glabrous, sometimes scaberulous. ***Leaves*** basal and cauline, the basal ones often drying at anthesis in mature individuals; sheaths 2–20 cm long, shorter or longer than the internodes, glabrous or scaberulous; ligules (0.5–)1.5–5(–7) mm long, longer than wide, dorsally scaberulous, rarely glabrous, apices acute to truncate, erose to lacerate, often ciliolate; blades 1–20 cm long, 1–6 mm wide, usually at least some blades larger than 2 mm wide, linear, usually flat, scaberulous on both surfaces. ***Panicles*** (3.5–)8–30(–40) cm long, (1–)2–20 cm wide, slightly contracted to open, dense to lax, lanceolate to ovate, long-exserted from the upper sheaths or partially included; branches ascending to spreading, rebranching slightly above mid-length, scaberulous, without spikelets near their base, inferior branches 4–12 cm long; pedicels 1–10 mm long, ascending to spreading, scaberulous. ***Spikelets*** (1.5–)1.8–3.2 mm long, greenish to purplish; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume (1.5–)1.8–3.2 mm long, upper glume 1.5–3.2 mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1.3–2.2 mm long, elliptic, apices acute, entire to irregularly toothed, 5-nerved, veins inconspicuous to prominent, unawned, rarely awned from above mid-length, awn up to 1.5(–2) mm long, inserted above mid-length, straight or weakly geniculate; paleas absent or up to 0.2(–0.5) mm long, veinless, glabrous; anthers 3, 0.4–1 mm long. ***Caryopsis*** 1–1.9 mm long, elliptic: endosperm liquid to soft. 2n= 42 (Harvey 2007).

* See Suppl. material 1 for other heterotypic synonyms.

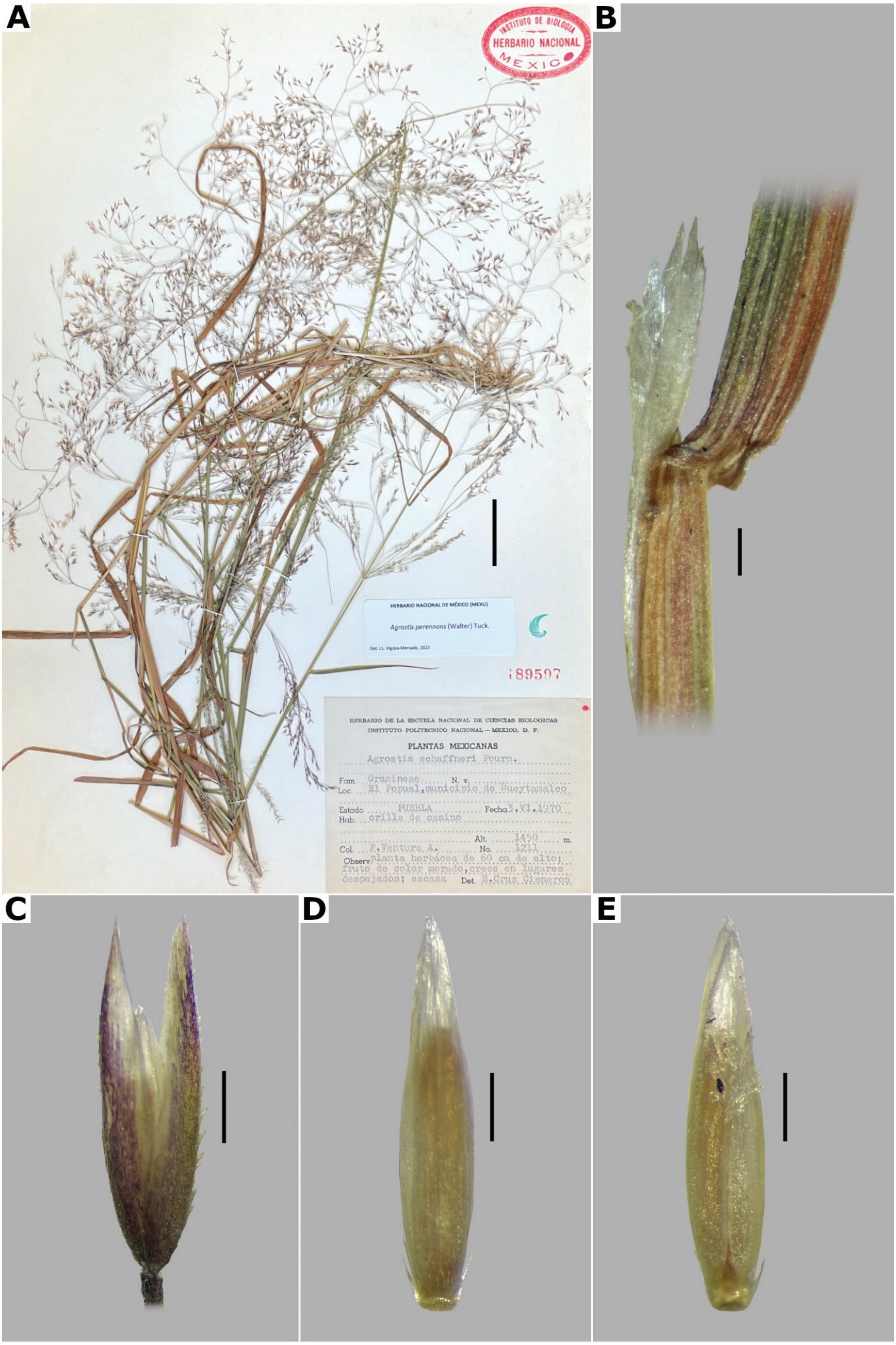

Figure 25. *Agrostis perennans* **A** whole plant **B** ligular area **C** spikelet **E** floret, abaxial view **F** floret, adaxial view. Based on Ventura 1211 (MEXU). Scale bars: 3 cm (**A**); 5 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows shallow to deep, wide; adaxial ribs rounded; keel absent; first order bundles circular in outline, sheath interrupted abaxially, sometimes also adaxially, abaxial and adaxial sclerenchyma in strands or girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, pointed to rounded; colorless cells absent (Fig. 22J–L). Lemmas with transversal thickenings oblong, wider than the unthickened portion of the wall; prickle hairs absent, or abundant to scarce (Fig. 7L).

Distribution and habitat. *Agrostis perennans* sensu lato is distributed from Alaska to Patagonia, in Argentina and Chile, and also in the West Indies (Sylvester et al. 2020a). In the study zone, this species has been collected in Mexico City and the Mexican states of Chiapas, Chihuahua, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, Tlaxcala, Veracruz, and Zacatecas; in the Guatemalan departments of Alta Verapaz, Baja Verapaz, Huehuetenango, Quetzaltenango, Quiché and San Marcos; in the Honduran state of Ocotepeque (Fig. 26A). It has also been reported from the Mexican states of Coahuila and San Luis Potosí (Dávila et al. 2018; Sánchez-Ken 2019), but no specimen from these states have been found. Records from the southern USA, in California, Arizona, New Mexico and Texas, appear to be misidentified specimens of *A. scabra* (Harvey 2007). This species grows in open areas of temperate forests, with conifers and *Quercus*, in cloud forests, stream edges, roadsides, and often in marshy places, between 622–3847 m a.s.l. (Fig. 27A).

Phenology. Specimens with spikelets have been collected year round, but most of them between the months of July and October (Fig. 28A).

Commentaries. *Agrostis perennans* is a widespread and variable species. It is considered a “dustbin” taxon (Sylvester et al. 2020a), which includes plants with basal and cauline leaves, usually flat leaf blades, more or less open panicles, usually unawned lemmas, and absent or minute paleas. More studies are necessary to clarify the relationships of the plants that have been included under this name, thus a wide circumscription of this species is adopted in this work.

Plants examined from the study zone fit well in *A. perennans* sensu lato, but at least three forms were observed: 1) fragile plants with open panicles; 2) more robust plants with open panicles; 3) robust plants with slightly contracted, denser panicles, and sometimes awned lemmas. The plants of the latter form have been called *A. schaffneri*, but despite the form of the panicles, no differences have been found in other characters, such as leaf anatomy and lemma micromorphology thus, this name is considered a synonym of *A. perennans* sensu lato.

Young plants of *A. perennans* sensu lato often have more conspicuous basal leaves and are confused with *A. scabra*, but differ from it in the leaf blades often greater than 2 mm wide, branches rebranching slightly above mid-length, and spikelets not clustered (vs. leaf blades up to 2(–3) mm wide, branches of the panicle usually rebranching in the upper third, with the spikelets usually clustered at the tips in *A. scabra*).

Agrostis perennans sensu lato is often confused with several species distributed in the study zone, which share several macromorphological, leaf blade

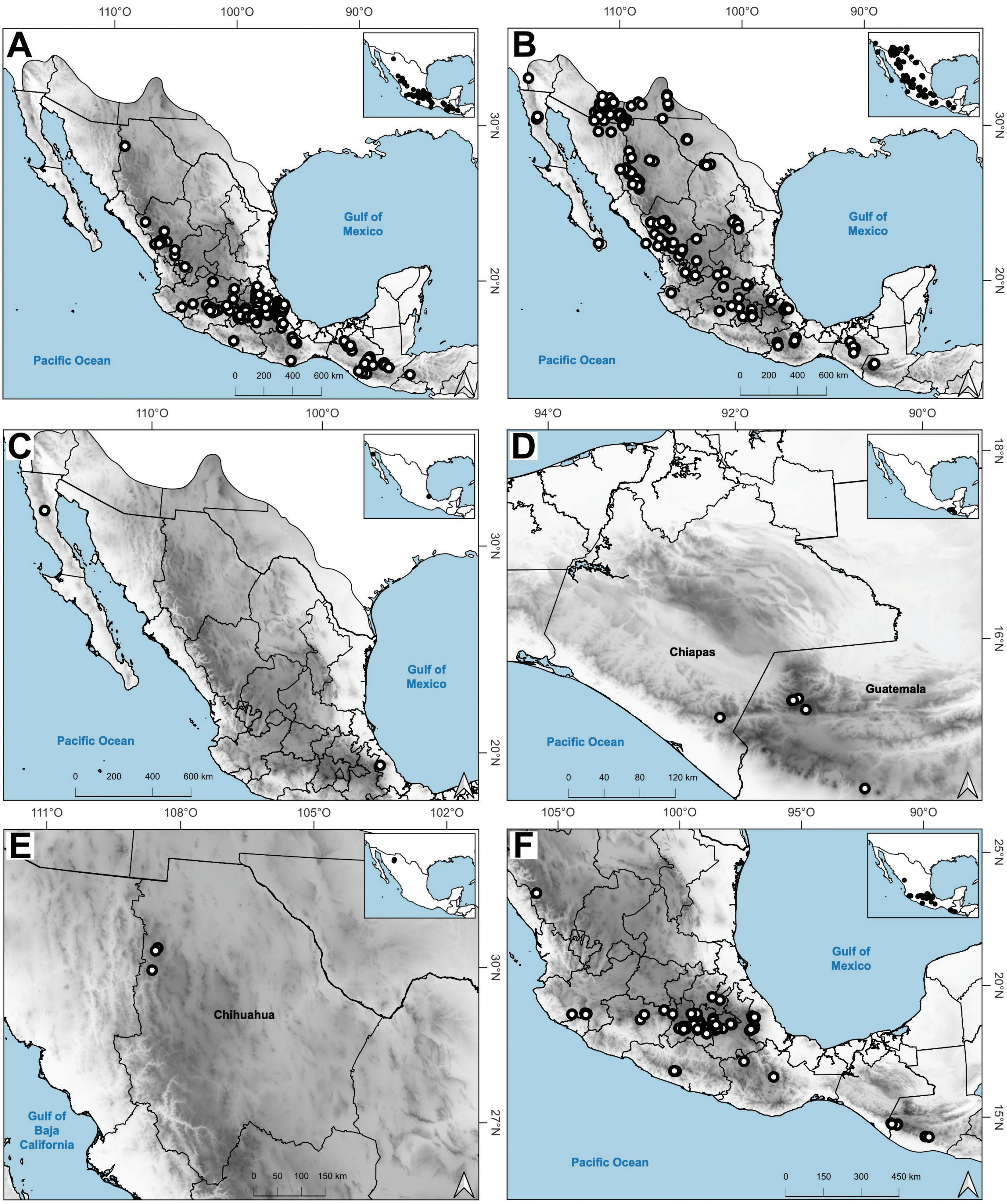

Figure 26. Map of known geographic distribution of *Agrostis* species, based on herbarium specimen data **A** *A. perennans* **B** *A. scabra* **C** *A. stolonifera* **D** *A. subpatens* **E** *A. subrepens* **F** *A. tolucensis*.

anatomy, and lemma micromorphology characters. These species are *A. bourgaei*, *A. calderoniae*, *A. ghiesbreghtii*, *A. hyemalis*, *A. laxissima*, *A. idahoensis*, *A. perennans*, *A. scabra*, *A. subrepens*, and *A. turrialbae*. In the identification key provided in this work, a reasonably good separation of the mentioned species was reached using a combination of characters.

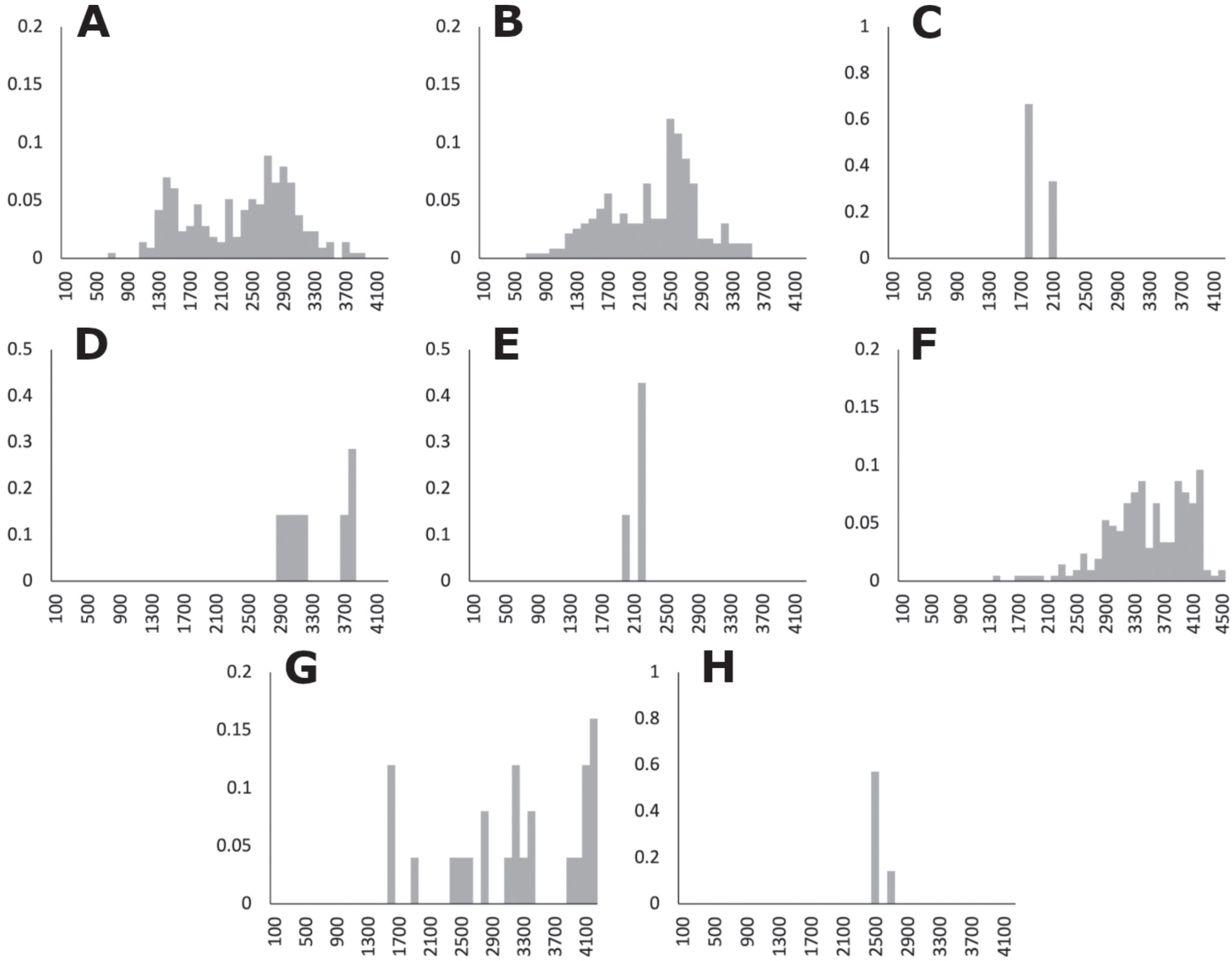

Figure 27. Elevation histograms of *Agrostis* species **A** *A. perennans* **B** *A. scabra* **C** *A. stolonifera* **D** *A. subpatens* **E** *A. subrepens* **F** *A. tolucensis* **G** *A. turrialbae* **H** *A. variabilis*.

Conservation status. *Agrostis perenanns* is a common and widespread species in the study zone. It is represented by 229 collections, with several populations occurring in 18 protected areas. The EOO is 992,915 km^2 and the AOO is 700 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Mexico. Guatemala. Alta Verapaz: Municipio Cobán, Chicu'sha, 8 km al SO de Cobán, [15.43333333°N, 90.45°W], 1400 m alt., 22 Jul 1988, P. Tenorio 14646 (CIIDIR, MEXU [*]). **Baja Verapaz: Municipio Salamá**, 6 km al SO de Chilascó, [15.13333333°N, 90.11666667°W], 1700 m alt., 24 Jul 1988, P. Tenorio 14842 (CIIDIR, MEXU [*], US). **Honduras. Ocotepeque: Municipio Belén de Gualcho**, cordillera de Celaque, Cruz Alta, 3 mi N of Belén Gualcho long road to Cucuyagua [14.50722222°N, 88.785°W], 1890 m alt., 23 Jun 1994, G. Davidse et al. 35319 (MEXU). **Mexico. Chiapas: Municipio Amatenango del Valle**, NE slope of Zontehuitz near summit, [16.49659°N, 92.45225°W], 2130 m alt., Jan 1965, D.E. Breedlove and P.H. Raven 8119 (US). **Municipio Unión Juárez**, Volcán Tacaná, 500 m al E de Talquián, [15.09306218°N, 92.08369755°W], 1700 m alt., 26 Apr 1987, E. Martínez and A. Reyes 20291 (MEXU [*]). **Chihuahua: Municipio Casas Grandes**, near Colonia Garcia in the Sierra Madres, [29.97622543°N, 108.3352935°W], 2286 m alt.,

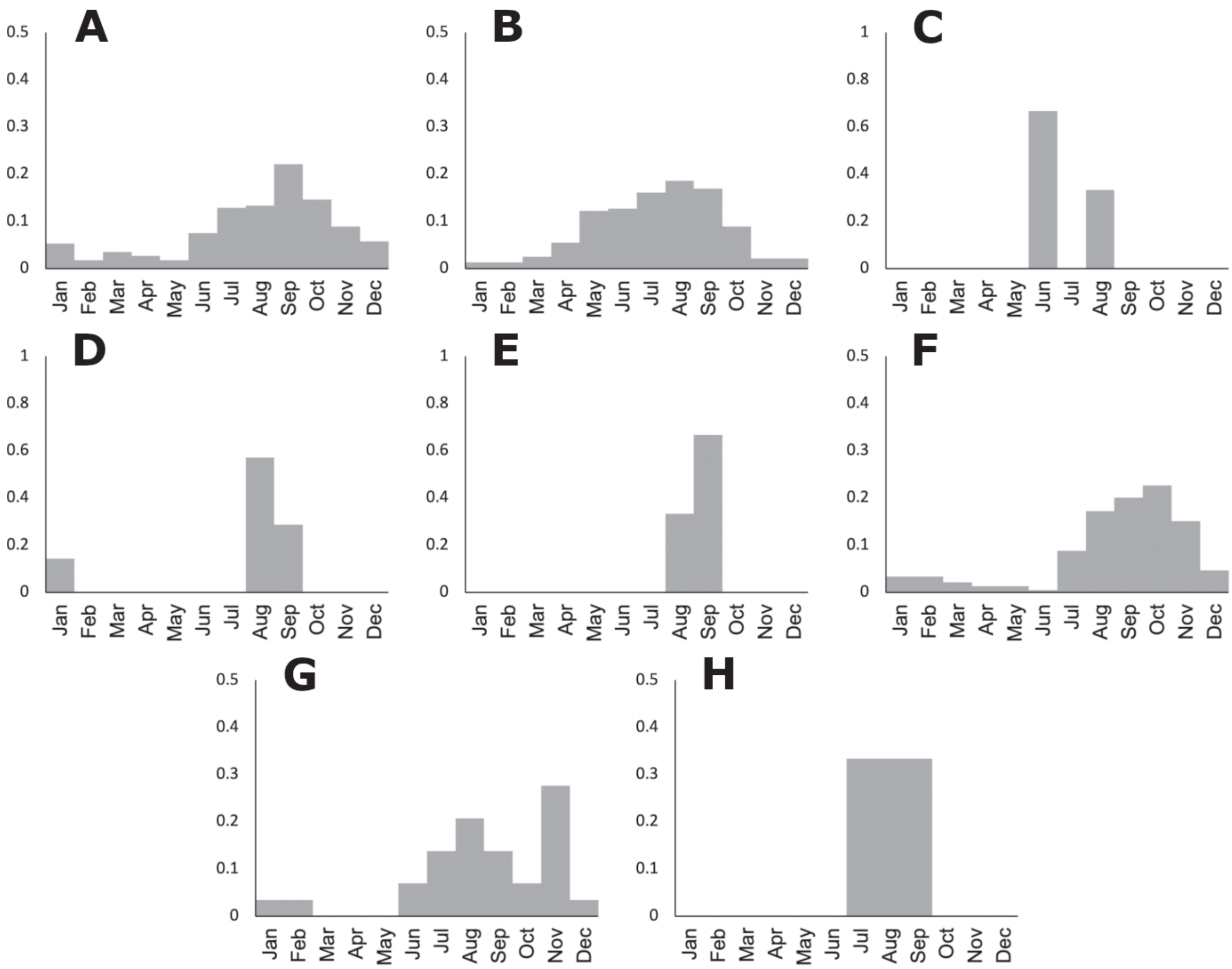

Figure 28. Phenology histograms of *Agrostis* species **A** *A. perennans* **B** *A. scabra* **C** *A. stolonifera* **D** *A. subpatens* **E** *A. subrepens* **F** *A. tolucensis* **G** *A. turrialbae* **H** *A. variabilis*.

22 Aug 1899, C.H.T. Townsend and C.M. Barber 276 (US). **Durango: Municipio Durango**, 5 mi W of Llano Grande along Durango–Mazatlán highway, [23.86°N, 105.25°W], 2500 m alt., 9 Sep 1967, J.R. Reeder and C.G. Reeder 4908 (MEXU, US). **Guanajuato: Municipio San Felipe**, club campestre El Vergel de la Sierra, [21.38504722°N, 101.6354389°W], 2627 m alt., 14 Jul 1997, J. Macías 898a (MEXU). **Guerrero: Municipio General Heliodoro Castillo**, cerro Teotepec, [17.46666667°N, 100.2166667°W], 3350 m alt., 5 Dec 1963, J. Rzedowski 18168 (ENCB). **Hidalgo: Municipio Omitlán de Juárez**, Santa Elena, km 15 de la carretera federal 105 Pachuca–Huejutla, [20.15722222°N, 98.65833333°W], 2640 m alt., 14 Jul 1994, J.P. Pérez 141 (MEXU [*]). **Municipio Tepeapulco**, cerro Santa Ana, [19.764°N, 98.5293°W], 2850 m alt., 8 Sep 1976, A. Ventura 2082 (FCME [**], MEXU, UAMIZ, XAL). **Jalisco: Municipio San Gabriel**, NW slopes of Nevado de Colima, above Jazmín, barranca near upper end of water-line 2–3 km above settlement of El Isote, [19.65°N, 103.7°W], 2600–2800 m alt., 26 Mar 1949, R. McVaugh 10048 (MEXU, US). **México: Municipio Amecameca**, km 18 de la carretera Amecameca–Tlamacas, [19.0917039°N, 98.67702965°W], 3400 m alt., 14 Jan 1982, R. Sánchez 81 (CIIDIR, IEB, MEXU). **Municipio Ocuilan**, carretera Santa Martha–Zempoala, km 2–14, [19.05°N, 99.33333333°W], 2900 m alt., 1 Aug 1987, J. Castañeda 280 (MEXU [*]). **Mexico City:**

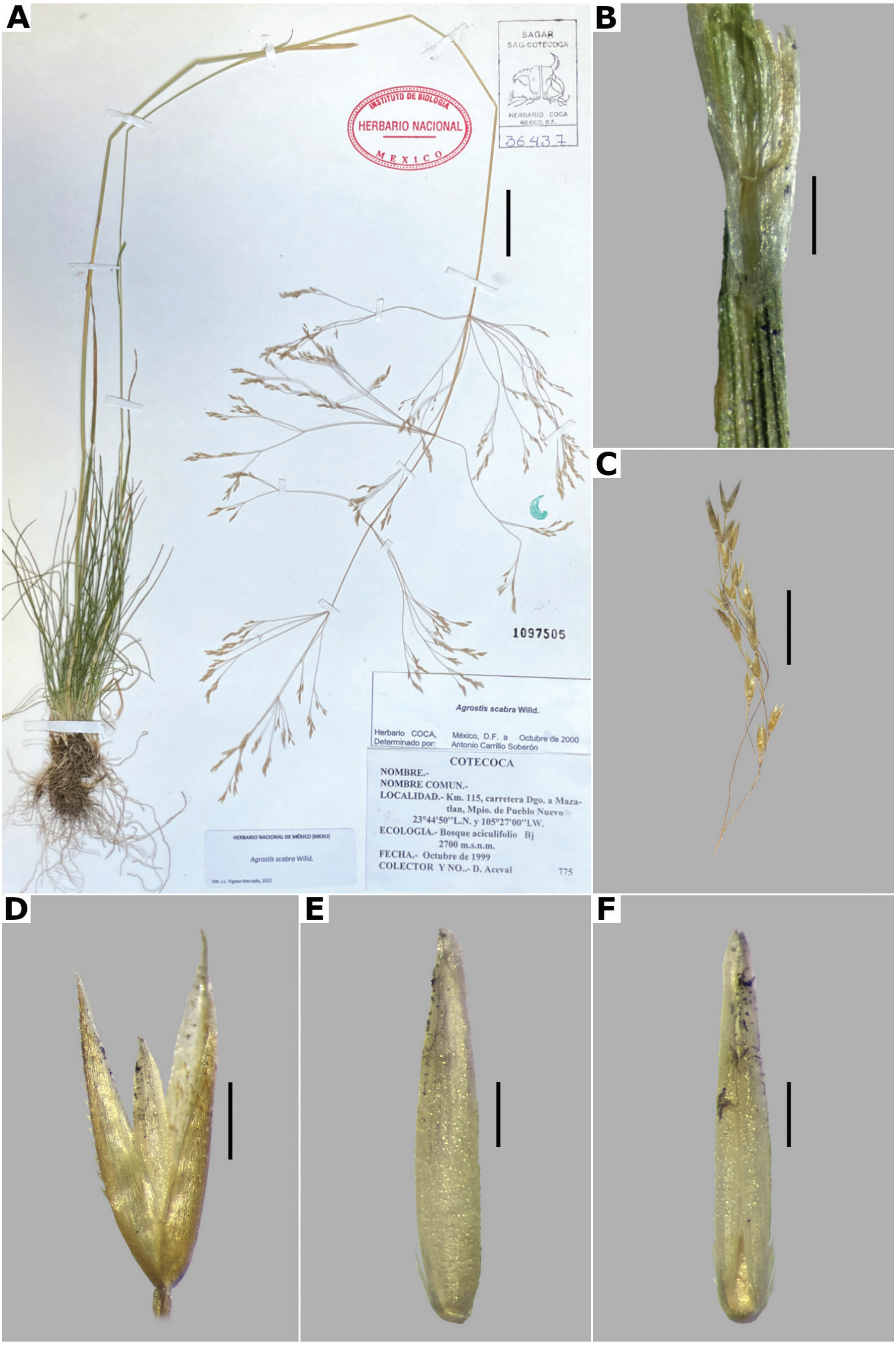

Figure 29. *Agrostis scabra* **A** whole plant **B** ligular area **C** detail of a terminal branche of the panicle **D** spikelet, **E** floret, abaxial view, **F** floret, adaxial view. Based on Aceval 775 (MEXU). Scale bars: 3 cm (**A**); 5 mm (**B, C**); 0.5 mm (**D**); 0.3 mm (**E, F**).

Alcaldía Magdalena Contreras, Eslava, [19.291667°N, 99.246389°W, 2530 m alt.], 19 Sep 1938, E. Lyonnet 2532 (CHAPA, MEXU, US). Los Dinamos, 2800 m alt., 27 Aug 1979, A. Ventura 3506 (FCME [*], MEXU, UAMIZ, XAL). **Alcaldía Tlalpan**, top of cerro Ajusco, [19.2069°N, 99.2597°W], 3937 m alt., 12 Jul 1959, J.H. Beaman 2794 (US). **Michoacán: Municipio Erongarícuaro**, 1 km al SE de Zínciro, sobre el camino a Eronguarícaro, [19.66463889°N, 101.7333194°W], 2400 m alt., 2 Nov 1989, J. Rzedowski 49202 (CHAPA, CIIDIR, MEXU). **Municipio Salvador Escalante:** alrededores de San Gregorio, [19.39238889°N, 101.5304389°W], 2650 m alt., 14 Sep 1988, E. Pérez-Calix 205 (CHAPA, CIIDIR, IBUG, IEB, MEXU [*,**], TEX). **Morelos: Municipio Tlalnepantla**, 2 km al S de CICITEC, Tlalnepantla, [19.06036734°N, 98.96226062°W], 2750 m alt., 26 Mar 1981, G. Ayala 19 (MEXU [*]); carretera Milpa Alta–Oaxtepec, camino viejo al CICITEC, [19.064835°N, 98.927786°W], 2770 m alt., 21 Oct 1993, A. Miranda et al. 881 (MEXU); **Oaxaca: Municipio San Juan Yaeé**, Santa María Lachichina, [17.43962564°N, 96.285451°W], 2700 m alt., 15 Apr. 2003, A. Flores s.n. (CHAPA, MEXU [*]). **Municipio San Miguel Suchixtepec**, campamento Río de Molino, 4 km al SO de San Miguel Suchixtepec, [16.07677493°N, 96.47030551°W], 2250 m alt., 21 Sep 1965, J. Rzedowski 21046 (CHAPA, IBUG, MEXU). **Puebla: Municipio Hueytamalco**, El Popual, [20.027434°N, 97.274122°W], 1450 m alt., 3 Jun 1970, F. Ventura 1211 (IBUG, MEXU). **Municipio Tlatlauquitepec**, Xucayucan, [19.89833333°N, 97.47833333°W], 1600 m alt., 5 Oct 1998, J.L. Contreras 5886 (MEXU [*,**]). **Querétaro: Municipio Colón**, parte más alta del cerro Zamorano, [20.93305556°N, 100.1797222°W], 3200–3270 m alt., 13 Nov 1971, J. Rzedowski and R. McVaugh 459 (US). **Tlaxcala: Municipio Huamantla**, ladera N del cerro de La Malinche, [19.23705301°N, 98.01935192°W], 3800 m alt., 12 Oct 1986, L. Aragón et al. 46 (MEXU). **Veracruz: Municipio Jilotepec**, El Rincón, 19.60694444°N, 96.94444444°W, 1100 m alt., 19 Jun 1993, M.J. Lizama 26 (CHAPA, CIB, MEXU [*], XAL); comunidad Jilotepec, camino La Cuesta–Zacatal, 19.61527778°N, 96.95138889°W, 1500 m alt., 12 Oct 1993, M.J. Lizama 81 (CHAPA, CIB, MEXU [*,**], XAL); comunidad El Pueblito, camino a La Concepción, 19.59722222°N, 96.925°W, 622 m alt., 17 Jan 1996, M.J. Lizama 622 (CIB). **Zacatecas**, **Municipio Monte Escobedo**, límite entre los estados de Zacatecas y Jalisco, por la terracería a Mezquitic, [22.31821648°N, 103.5748305°W], 2190 m alt., 21 Sep 1989, J. Balleza 2266b (CHAPA). See Suppl. materials 2, 3 for additional examined specimens.

14. *Agrostis scabra* Willd., Sp. Pl. 1(1): 370. 1797.
Figs 4M, 29, 30A

= *Trichodium laxiflorum* Michx., Fl. Bor. Amer. 1: 42. 1803, nom. illeg. superfl. *Agrostis laxa* Schreb. ex Pursh, Fl. Amer. Sept. 1: 61. 1814 [1813], pro syn. *Agrostis laxiflora* (Michx.) Richardson, Narr. Journey Polar Sea: 731. 1823, nom. illeg. hom., non Poir., 1810. *Agrostis michauxii* Zuccagni var. *laxiflora* A. Gray, N. Amer. Gram. 1: 17. 1834. *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb. var. *laxiflora* (Michx.) Beetle, Phytologia 52: 11. 1982. Type. USA. Hab. In humidis et praetensibus a sinu Hudsonis ad Floridam, A. Michaux s.n. (holotype: P).

Trichodium scabrum (Willd.) Muhl., Cat. Pl. Amer. Sept. 10. 1813.

= *Agrostis geminata* Trin., Gram. Unifl. Sesquifl. 207. 1824. *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb. var. *geminata* (Trin.) Hitchc., U.S.D.A. Bur. Pl. Industr. Bull. 68: 44. 1905. *Agrostis scabra* Willd. var. *geminata* (Trin.) Swallen, Proc. Biol. Soc. Washington 54: 45. 1941. *Agrostis scabra* Willd. var. *geminata* (Trin.) Hultén, Fl. Alaska Yukon 2: 156. 1942, nom. illeg. hom. Type: USA. Alaska: Unalaschka, J.F. Eschscholtz s.n. (holotype: LE-TRIN (LE01026091 [image!]); isotypes: LE-TRIN (LE00009321 [image!]), US [fragm. ex LE-TRIN] (US00156432 [image!])).

Agrostis laxiflora (Michx.) Richardson var. *scabra* (Willd.) Torr., Fl. New York 2: 442. 1843.

Agrostis hyemalis (Walter) Britton, Sterns & Poggenb. var. *scabra* (Willd.) H.L. Blomq., Grass. North Carolina 82. 1948.*

Type. America borealis, Anonymous s.n. (lectotype, designated by Vigosa-Mercado (2022a: 3): B-W (BW01732020 [image!]); isolectotype: B-W (BW01732010 [image!])).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 15–90 cm long, erect, nodes usually 1–2(–3), sometimes more, glabrous, internodes glabrous. ***Leaves*** mostly basal, sometimes cauline leaves well developed; sheaths 1.5–13 cm long, the lower ones usually longer than the internodes, the upper ones shorter, glabrous or scaberulous; ligules 0.5–5 mm long, usually longer than wide, dorsally scaberulous, apices rounded to truncate, sometimes acute, erose to lacerate; blades 3–14 cm long, (0.3–)0.5–2(–3) mm wide, the lower ones usually filiform and involute, the upper ones linear and flat, scaberulous on both surfaces. ***Panicles*** (4–)8–30 cm long, (2.2–)4–20(–26) cm wide, open, lax, ovate, lax, usually long-exserted from the upper sheaths; branches spreading, sometimes ascending, rebranching in the upper third, scaberulous, without spikelets near their base, spikelets usually clustered at the tips, inferior branches 1.5–13 cm long; pedicels (0.5–)1–7(–10) mm long, appressed, scaberulous. ***Spikelets*** 2–3(–3.4) mm long, greenish to purplish; glumes subequal to unequal, lanceolate, apices shortly acuminate, 1-veined, scaberulous on the keel, lower glume 1.8–2.8(–3.2) mm long, upper glume 2–3(–3.2) mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1.3–2 mm long, elliptic, apices entire, obtuse, sometimes toothed, 5-nerved, veins prominent distally, unawned, rarely awned from above mid-length, awn up to 2 mm long, inserted 0.8–1.5 mm above the base, straight; paleas absent or up to 0.2 mm long, veinless, glabrous; anthers 3, 0.5–1.4 mm long. ***Caryopsis*** 0.8–1.5 mm long, elliptic; endosperm liquid to soft. 2n= 42 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows medium-sized, wide; adaxial ribs rounded; keel absent; first order bundles circular to slightly elliptical in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 31A–C). Lemmas with transversal thickenings oblong, wider than the unthickened portions of the wall; prickle hairs abundant (Fig. 32A).

* See Suppl. material 1 for other heterotypic synonyms.

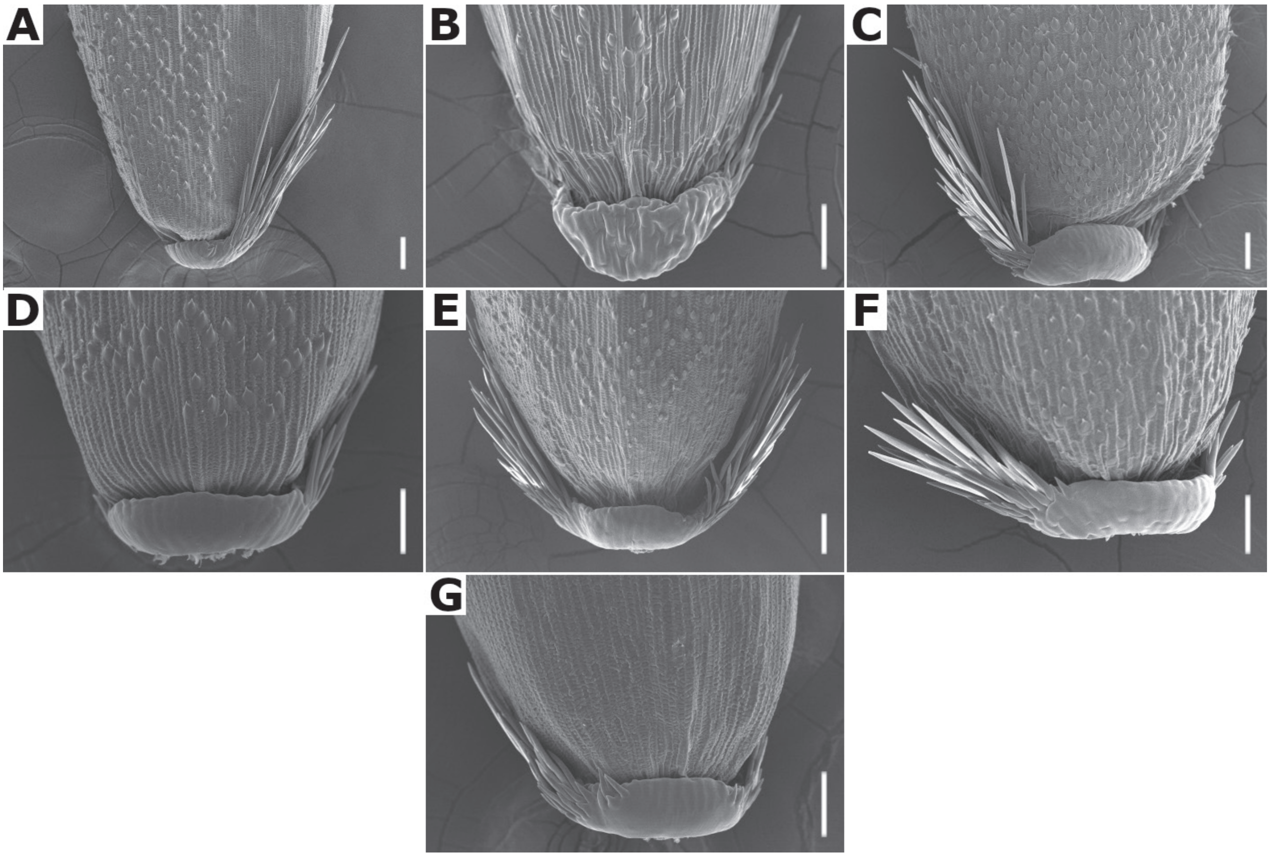

Figure 30. Calluses of *Agrostis* species observed with SEM **A** *A. scabra* **B** *A. stolonifera* **C** *A. subpatens* **D** *A. subrepens* **E** *A. tolucensis* **F** *A. turrialbae* **G** *A. variabilis*. Scale bars: 50 µm.

Distribution and habitat. *Agrostis scabra* is native from Alaska to Guatemala. It has been introduced in Argentina and Chile (Rúgolo and Molina 1997), Venezuela, the West Indies and Europe (Dorr 2014). In the study zone, this species has been collected in the USA states of Arizona, California, New Mexico and Texas; in the Mexican states of Baja California, Baja California Sur, Chiapas, Chihuahua, Coahuila, Durango, Guanajuato, Jalisco, México, Michoacán, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Veracruz and Zacatecas; in the Guatemalan state of Huehuetenango (Fig. 26B). It has also been reported from Mexico City, and the Mexican states of Aguascalientes, Hidalgo, and Tlaxcala (Dávila et al. 2018; Sánchez-Ken 2019), but no specimens from these states were found. *Agrostis scabra* grows in open areas of temperate forests, with conifers and *Quercus*, also in cloud forests, alpine grasslands, stream edges and shrublands, between 630–3500 m a.s.l. (Fig. 27B).

Phenology. Specimens with spikelets have been collected year round, but most of them between the months of April and October (Fig. 28B).

Commentaries. The plants of this species are variable and at least two forms were observed in the study zone: 1) plants with very conspicuous basal leaves, with filiform and involute blades, distributed in Mexico and Guatemala; 2) plants with well-developed cauline leaves, with broader leaf blades, common in southern USA. *Agrostis scabra* is often confused with *A. perennans*, which share several leaf anatomy and lemma micromorphology characters (see the note under the description of that species). *Agrostis scabra* has been considered a synonym or a variety of *A. hyemalis* and is often confused with it (see the note under the description of that species).

Conservation status. *Agrostis scabra* is a common and widespread species in the study zone. It is represented by 240 collections, with several populations occurring in 25 protected areas. The EOO is 2,076,712 km^2 and the AOO is 712 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Guatemala. Huehuetenango: Municipio Chiantla, Chancol, 15.4999°N, 91.34986°W, 3300 m alt., 28 Aug 2000, M. Véliz et al. 10046 (MEXU [*]). La Capellanía, 15.42111111°N, 91.44027778°W, 3150 m alt., 20 Jul 2004, M. Véliz 15309 (MEXU [*]). **Mexico. Baja California: Municipio Ensenada**, Sierra San Pedro Mártir, moist stream banks, La Víbora, arroyo La Grulla, 4 km SW of La Grulla, [30.86667°N, 115.50833°W], 1900 m alt., 9 Aug 1977, R. Moran 24402 (MEXU [*], SD). **Baja California Sur: Municipio La Paz**, arroyo Encinos Blancos, Sierra la Laguna, [23.38333333°N, 109.9833333°W], 1870 m alt., 13 Aug 1987, J.L. León de la Luz 2722 (MEXU). **Chiapas: Municipio Jitotol**, 5 km SE of Jitotol, along road to Bochil, [17.03092769°N, 92.8499077°W], 1600 m alt., 24 Feb 1982, D.E. Breedlove 58514 (MEXU, TEX). **Municipio Venustiano Carranza**, ejido Laja Tendida, km 17 carretera Venustiano Carranza–Tuxtla Gutiérrez, 2 km a Flores Magón, [16.342325°N, 92.669313°W], 630 m alt., 5 Sep 1997, A. Miranda 1275 (MEXU [*]). **Chihuahua: Municipio Ocampo**, Parque Nacional de la Cascada de Basaseachic, [28.16666667°N, 108.2083333°W], 1600 m alt., 25 Apr 1987, R. Spellenberg et al. 8428 (MEXU [*,**]); **Municipio Temosachic**, Nabogame, [28.49543744°N, 108.4808032°W], 1800 m alt., 25 Mar 1988, J.E. Laferrière 1419 (MEXU, TEX). **Coahuila: Municipio Arteaga**, El Morro, Sierra de Arteaga, límites con Nuevo León, [25.21307327°N, 100.2847136°W], 2900 m alt., 25 Sep 1991, J.A. Villareal and M.A. Carranza 6300 (CIIDIR, MEXU, XAL). **Durango**: **Municipio Pueblo Nuevo**, ejido El Brillante, lago de Puentecillas, 23.6725°N, 105.4563889°W, 2744 m alt., 28 Oct 2011, S. Heynes et al. 264 (CIIDIR, MEXU [*,**], UAMIZ). **Municipio Santiago Papasquiaro**, Bajío de Vacas (Hacienditas), [25.040833°N, 105.407778°W], 2659 m alt., 5 Oct 1990, A. Benítez 2633 (CHAPA, CIIDIR, MEXU [*], UAMIZ). **Guanajuato: Municipio Guanajuato**, Bufas de Guanajuato, [21.02596283°N, 101.2580131°W], 2140 m alt., 12 May 1981, R. Santillán and A. Mora, 28-R (MEXU). **Jalisco: Municipio Ojuelos**, Cañón de Bacieros, 14 km SO de Ojuelos, [21.81239946°N, 101.6801703°W], 2350 m alt., 4 Jun 1983, M. Alcocer s.n. (CHAPA, MEXU [*]). **México: Municipio Temascaltepec**, 11 km sobre la desviación a Tequesquipan, carretera Toluca–Temascaltepec, [19.06454704°N, 99.94451928°W], 2350 m alt., 15 Feb 1983, E. Manrique 161 (MEXU). **Michoacán: Municipio Pátzcuaro**, La Laguna, cerca de San Gregorio, [19.41886944°N, 101.4982472°W], 2700 m alt., 26 Oct 1985, J.S. Martínez 1013 (IEB). **Morelos: Municipio Huitzilac**, shore of Laguna Zempoala, 20 km NW of Cuernavaca, [19.04991306°N, 99.31567672°W], 2800 m alt., 8 Dec 1950, N.C. Fassett 28453 (F, US). **Nuevo León: Municipio Galeana**, cima del cerro Potosí, [24.87220276°N, 100.232885°W], 3500 m alt., 16 Aug 1989, A. García and S. González 196 (CIIDIR, IBUG, IEB, MEXU, UAMIZ). **Oaxaca: Municipio San Miguel El Grande**, 36 km de Tlaxiaco rumbo a Chalcatongo, [17.08138782°N, 97.61677573°W], 2559 m alt., 25 Jun 1980, A.A. Beetle M-4760 (CHAPA, IBUG, MEXU). **Puebla: Municipio Huachinango**, near Huachinango, [20.11°N, 98.03°W], 1890 m alt., 12 Apr 1962, A.A. Beetle M-567 (UTC). **Querétaro: Municipio Pinal de Amoles:**

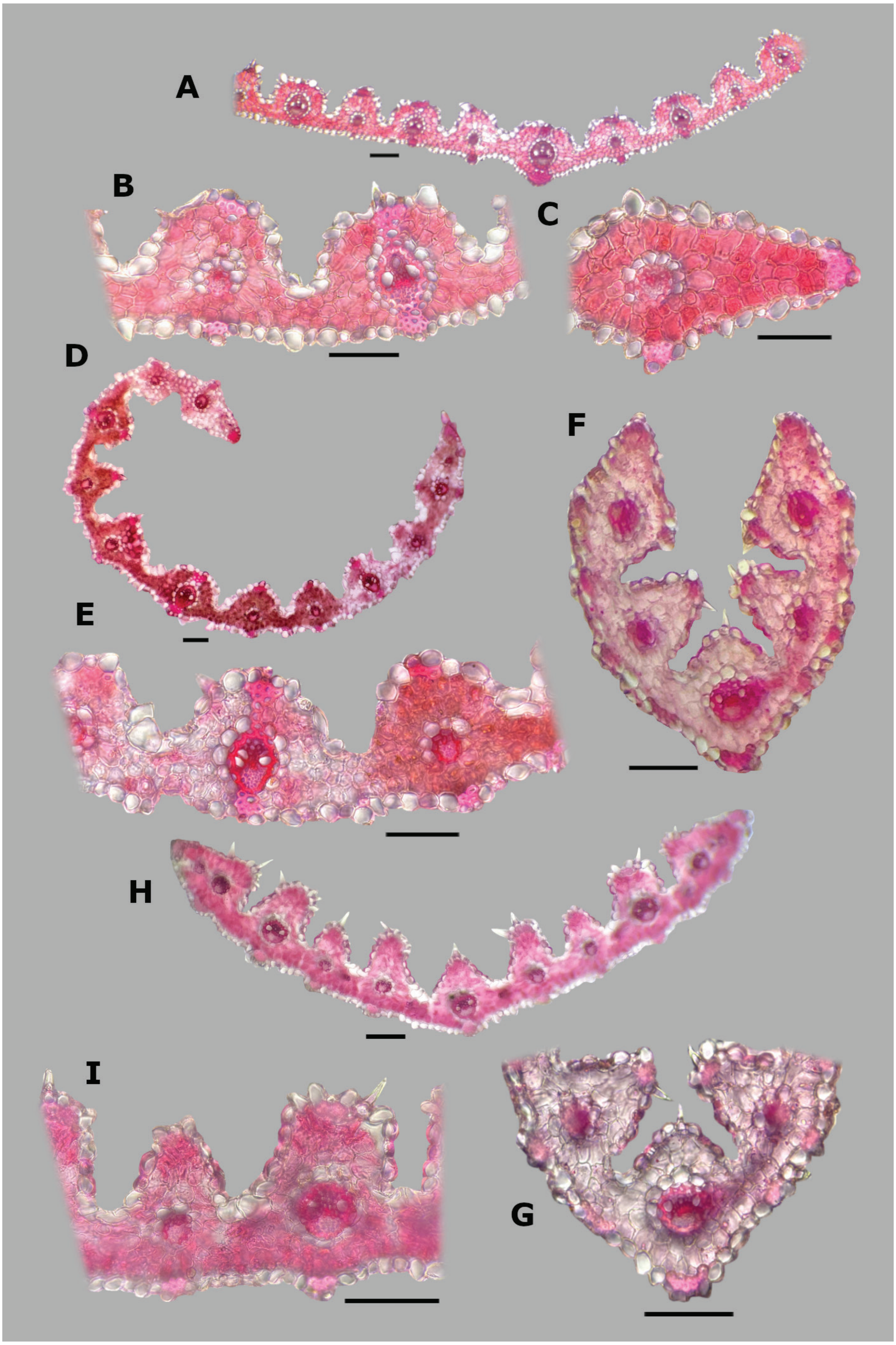

Figure 31. Leaf blade anatomy in transversal section of *Agrostis* species, in general view, and details of lateral bundles. **A**–**C** *A. scabra* **D**–**E** *A. stolonifera* **F**–**G** *A. subpatens* **H**–**I** *A. subrepens*. Scale bars: 0.1 mm.

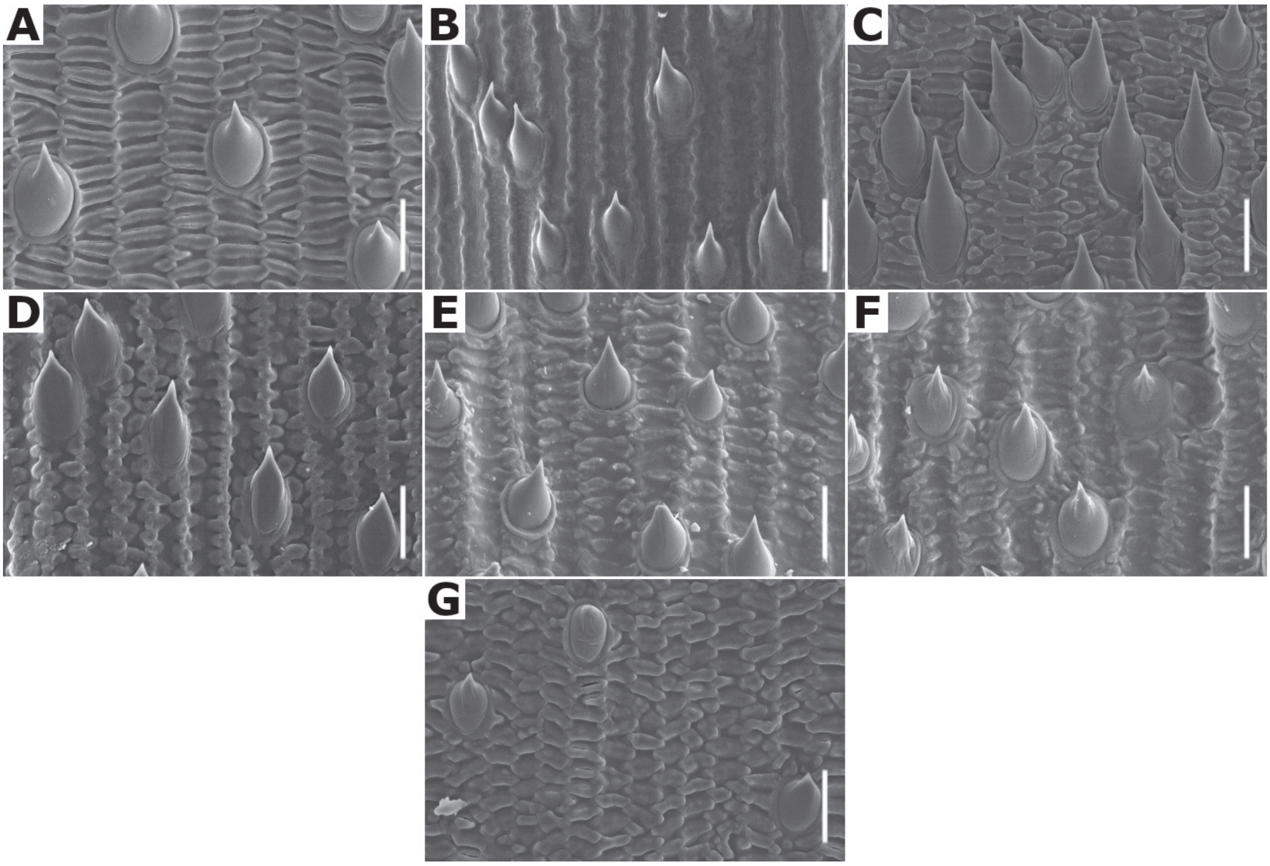

Figure 32. Lemma surface of *Agrostis* observed with SEM **A** *A. scabra* **B** *A. stolonifera* **C** *A. subpatens* **D** *A. subrepens* **E** *A. tolucensis* **F** *A. turrialbae* **G** *A. variabilis*. Scale bars:15 µm.

Puerto de los Velázquez, [21.12092778°N, 99.67360833°W], 2650 m alt., 17 Sep 1993, V. Jaramillo et al. 813 (IEB, MEXU). **San Luis Potosí: Municipio Villa de Arriaga**, near the village of San Francisco in the Sierra de San Miguelito ca 25 km SW of San Luis Potosi**.,** [22N, 101.14W], 2200–2400 m alt., 5 Sep 1954, E.R. Sohns 1070 (US). **Sinaloa: Municipio Concordia,** El Palmito, en el parteaguas, 8 km al O del poblado, [23.55579174°N, 105.8468406°W], 2350 m alt., 18 Nov 1984, R. Vega 1385 (MEXU). **Sonora: Municipio Yécora**, arroyo El Otro Lado, 3.9 Km E of Yecora on Mex 16, 28.375°N, 108.898333°W, 1560 m alt., 25 May 1998, T.R. Van Devender et al. 98-640 (ASU, MEXU, NY, TEX). **Veracruz: Municipio Las Vigas de Ramírez**, Toxtlacoaya, 19.63333333°N, 97.06111111°W, 2320 m alt., 15 Sep 91, H. Sandoval 97 (CHAPA, CIB, MEXU [*]). **Zacatecas: Municipio Jerez**, Sierra Los Cardos, 10.5 mi NW of Jerez, W of El Cargadero, on road towards Monte de los Garcia, 22.7099°N, 103.131°W, 2570 m alt., 19 Oct 2007, P.M. Peterson et al. 21406 (CAN, US). **USA. Arizona: Cochise County**, Coronado National Forest, ca. 6.6 miles E on Pinery Canyon road from fork to Chiricahua National Monument, [32.00439°N, 109.243154°W], 1676 m alt., 12 Jun 1987, L.R. Landrum and S.S. Landrum 5500 (ASC, ASU). **Pima County**, Rose Canyon Lake, E end, ca. 3 km S of Mount Bigelow, [32.3833°N, 110.708°W], 2113, 17 Sep 1992, M.A. Baker 10209 (ASU [*]). **California: San Diego County**, SW of Combs Peak, canyon off of Chihuahua-Lost Valley Road just NW of Sky Oaks Field Station, on Bureau of Land Management lands, 33.38207°N, 116.62718°W, 1405 m alt., 15 Aug 2010, J.P. Rebman 20319 (SD [*]). **New Mexico: Hidalgo County,** Peloncillo Mountains, Cloverdale Creek, just inside National Forest boundary, 31.40937429°N, 108.9147098°W, 1585 m alt., 1 May 1991, K.W. Allred 5232 (IBUG). **Texas: Jeff Davis County**, Madera Canyon, roadside park in canyon along highway 118, 30.7°N, 104.1°W, 1768 m alt., 29 Jun 1979, R.D. Worthington 4691 (COLO, UTEP). See Suppl. materials 2, 3 for additional examined specimens.

15. *Agrostis stolonifera* L., Sp. Pl. 1: 62. 1753.
Figs 4N, 30B, 33

= *Agrostis palustris* Huds., Fl. Angl. (Hudson) 27. 1762. *Agrostis stolonifera* L. var. *palustris* (Huds.) Farw., Rep. (Annual) Michigan Acad. Sci. 21: 351. 1920. *Agrostis polymorpha* Huds. var. *palustris* (Huds.) Huds., Fl. Angl. (ed. 2) 1: 32. 1778. *Agrostis alba* L. var. *palustris* (Huds.) Pers., Syn. Pl. 1: 76. 1805. *Apera palustris* (Huds.) Gray, Nat. Arr. Brit. Pl. 2: 148. 1821. *Agrostis stolonifera* L. subsp. *palustris* (Huds.) Tzvelev, Novosti Sist. Vyssh. Rast. 8: 58. 1971. Type: England. 119. Gramen Miliac. maj. panic. viridi. In Herb. Petiver (lectotype, designated by Widén (1971: 77): BM).

Agrostis polymorpha Huds. var. *stolonifera* (L.) Huds., Fl. Angl. (ed. 2) 1: 31. 1778.
Decandolia stolonifera (L.) Bastard, Essai Fl. Maine et Loire 29. 1809.
Vilfa stolonifera (L.) P. Beauv., Ess. Agrostogr. 16. 1812.
Milium stoloniferum (L.) Lag., Elench. Pl. Nov. 10. 1816.
Agrostis alba L. var. *stolonifera* (L.) Sm., Engl. Fl. 1: 93. 1824.
Agrostis vulgaris With. var. *stolonifera* (L.) G. Mey., Chloris Han.: 657. 1836.
Agrostis vulgaris With. var. *stolonifera* (L.) W.D.J. Koch, Syn. Fl. Germ. Helv. 782. 1837.
Agrostis tenuis Sibth. var. *stolonifera* (L.) Podp., Kvetena Moravy (Prace Marav. Prir. Spolc.) 6: 354. 1926.
Agrostis palustris Huds. var. *stolonifera* (L.) Druce, Fl. Oxfordshire (ed. 2) 473. 1927.
Agrostis capillaris L. var. *stolonifera* (L.) Druce, List Brit. Pl. 126. 1928.*

Type. Herb. A. van Royen s.n. (lectotype, designated by Widén (1971: 77): L (L0059234 [image!])).

Description. ***Plants*** perennial, stoloniferous. ***Tillers*** extravaginal, with cataphylls. **Stolons** up to 1(–2) m long. ***Culms*** (8–)15–60 cm long, erect, decumbent at the base, nodes (2–)3–7, glabrous, lower nodes rooting, internodes glabrous. ***Leaves*** mostly cauline; sheaths 2.5–8 cm long, usually shorter than the internodes, glabrous or scaberulous; ligules 1–7 mm long, longer than wide, dorsally scaberulous, apices rounded to truncate, erose to lacerate; blades (1–)2–10 cm long, (1–)2–6 mm wide, linear, flat, becoming convolute when dry scaberulous on both surfaces. ***Panicles*** (3–)4–20 cm long, 0.5–3 cm wide, open at anthesis, becoming contracted, dense, lanceolate, sometimes spiciform; branches appressed to ascending, branching from below mid-length, scaberulous, inferior branches 2–6 cm long, lateral branches often with spikelets near their base; pedicels 0.5–3.3 mm long, appressed to ascending, scaberulous. ***Spikelets*** 1.6–2 (–3) mm long, greenish, often tinged with purple; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the

* See Suppl. material 1 for other heterotypic synonyms.

keel, lower glume 1.6–2 (–3) mm long, upper glume 1.4–2(1.6–2 (–3) mm long; callus puberulous, with 2 bunches of short trichomes, sometimes inconspicuous; lemmas 1.4–2 mm long, elliptic to oblong, apices entire, acute to obtuse, sometimes toothed, 3(5)-veined, veins inconspicuous or prominent distally, unawned, rarely awned from above mid-length, awn up to 1.5 mm long, inserted 0.8–1.5 mm above the base, straight or weakly geniculate; paleas present, 0.7–1.4 mm long, 2-veined, glabrous; anthers 3, 0.9–1.5 mm long. ***Caryopsis*** 0.9–1.3, elliptic; endosperm solid. 2n= 28, 35, 42 (Harvey 2007).

Anatomy and micromorphology. Leaf blades flat to convolute in transversal section; adaxial furrows medium-sized to deep, wide; adaxial ribs rounded; keel absent; first order bundles circular to slightly elliptical in outline, sheath interrupted adaxially and abaxially, abaxial and adaxial sclerenchyma in girders, narrowing towards the bundle; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 31D, E). Lemmas without transversal thickenings, prickle hairs abundant to scarce (Fig. 32B).

Distribution and habitat. Introduced. *Agrostis stolonifera* is native to Eurasia and northern North America (Harvey 2007). In the study zone, this taxon has been collected from the Mexican states of Baja California and Veracruz (Fig. 26C). *Agrostis* has also been reported from the southern United States and Mexico City, also from the states of Chiapas, Chihuahua, Coahuila, Hidalgo, Jalisco, México, Michoacán, Nuevo León, Puebla, and Tlaxcala (Dávila et al. 2018; Sánchez-Ken 2019), but no specimens from these states have been seen. This taxon has been collected on stream edges and open areas of pine forests, between 1800–2100 m a.s.l. (Fig. 27C). There are more records of this species in the study zone, on databases (GBIF 2023d), but not all of them have images, and thus we were unable to confirm their identity.

Phenology. Specimens with spikelets have been collected from June to August (Fig. 28C).

Commentaries. *Agrostis stolonifera* is often confused with *A. gigantea* (see the note under the description of that species). This is a variable species and several infraspecific taxa have been recognized (e.g., Pohl and Davidse 1994; Rúgolo and Molina 1997). The plants from the study zone fit well in *A. stolonifera* var. *palustris*, which is distinguished from the typical variety in the more contracted panicles, up to 3 cm wide, and smaller spikelets of 1.6–2 mm long (vs. more open panicles, up to 6 cm wide, spikelets 2–2.5 mm long in the typical variety). The width of the panicles could be related to the age of the panicles, since they become contracted after anthesis, and thus varieties are not recognized here.

This taxon is also confused with *Polypogon viridis* (Gouan) Breistr., from which it is distinguished in the spikelets disarticulating above the glumes (vs. disarticulation below the glumes, with a pedicel fragment in *P. viridis*).

Conservation status. Since *Agrostis stolonifera* is an introduced taxon in the study zone, its conservation status is considered as Least Concern (LC).

Specimens examined. Mexico. Baja California: Municipio Ensenada, Sierra San Pedro Mártir, La Grulla, [30.88916°N, 115.46223°W], 2100 m alt., 21 Aug 1967, R. Moran and R.F. Thorne 14466 (SD). **Veracruz: Municipio Tatatila**, camino Las Vigas–Tatatila, 1 km antes de La Mancuerna, 19.675°N, 97.125°W, 1800 m alt., 7 Jun 1996, H.R. Sandoval and B.V. Hernández 370 (CIB), 380 (CIB, MEXU [*, **], XAL).

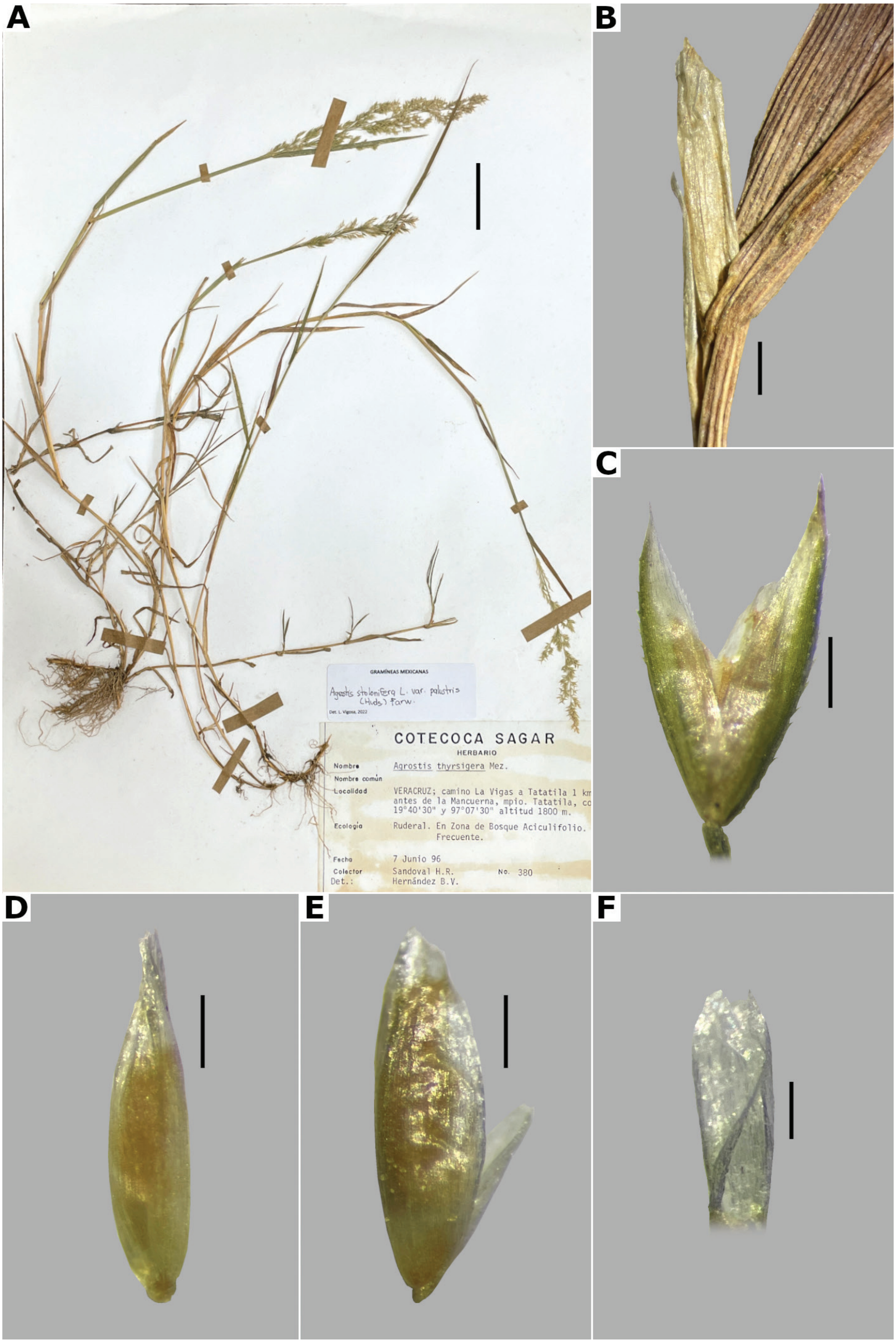

Figure 33. *Agrostis stolonifera* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view, **E** floret, lateral view showing the lemma and the palea **F** palea. Based on Sandoval and Hernández 380 (CIB). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**); 0.2 mm (**F**).

16. *Agrostis subpatens* Hitchc., in Britton, N. Amer. Fl. 17(7): 527. 1937.
Figs 4O, 30C, 34

= *Agrostis vinosa* Swallen, Contr. U.S. Natl. Herb. 29(9): 402. 1950. Type. Guatemala. Huehuetenango: alpine meadow, vicinity of Chémal, summit of Sierra de los Cuchumatanes, 3700–3750 m alt., 8 Aug 1942, J. Steyermak 50290 (holotype: US (US00131130); isotypes: F (F0046567F [image!]), MO (MO-501391 [image!]), US (US00624107 [image!])).

Type. Costa Rica. Cerro de la Muerte, 3100 m alt., Jan 1897, H. Pittier 10470 (holotype: US (US00131113); isotype: G (G00192032 [image!])).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** up to 30 cm long, erect, decumbent at the base, nodes 1–2, glabrous, internodes glabrous. ***Leaves*** mostly basal; sheaths 1–6 cm long, longer or shorter than the internodes, glabrous or scaberulous; ligules 2–3(5) mm long, longer than wide, dorsally scaberulous, apices acute, often lacerate; blades 2.2–10(15) cm long, 0.4–0.8 mm wide, filiform, conduplicate to convolute, sometimes flat at the base, scaberulous on both surfaces. ***Panicles*** 5–11.5 cm long, 0.5–4 cm wide, contracted to open, somewhat lax, linear to lanceolate, exserted from the upper sheaths; branches appressed to ascending, rebranching about mid-length or below, scaberulous, without spikelets near their base, inferior branches up to 2.8 cm long cm long; pedicels 2–7 mm long, usually longer than the spikelets, appressed to ascending, scaberulous. ***Spikelets*** 2.1–3 mm long, purplish; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume 2.1–3 mm long, upper glume 1.9–2.8 mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1.3–2.2 mm long, elliptic, apices toothed, 5-veined, veins prominent distally, awned near the base, awn 3–3.5 mm long, weakly geniculate, reaching the lemma apices; paleas absent; anthers 3, 0.9–1.5 mm long. ***Caryopsis*** 0.8–1.5 mm long, elliptic; endosperm solid. 2n= 28 (Pohl and Davidse 1971).

Anatomy and micromorphology. Leaf blades convolute to v-shaped in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded to triangular; keel absent; first order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma in strands; second order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 31F, G). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portion of the wall; prickle hairs abundant (Fig. 32C).

Distribution and habitat. *Agrostis subpatens* is distributed from Chiapas, Mexico to Costa Rica (Pohl and Davidse 1994). It has also been reported from Venezuela (Luteyn 1999). In the study zone, it has been collected in the Mexican state of Chiapas and in the Guatemalan departments of Chimaltenango and Huehuetenango (Fig. 26D). This species has also been reported from Mexico City and the Mexican states of Hidalgo, Jalisco, México, Michoacán, Oaxaca, Puebla, Querétaro, Tlaxcala and Veracruz (Villaseñor 2016; Dávila et al. 2018; Sánchez-Ken 2019; Vigosa-Mercado and Ruiz-Sánchez, 2020), but these records correspond to misidentified specimens of *A. tolucensis* and *A. turrialbae*.

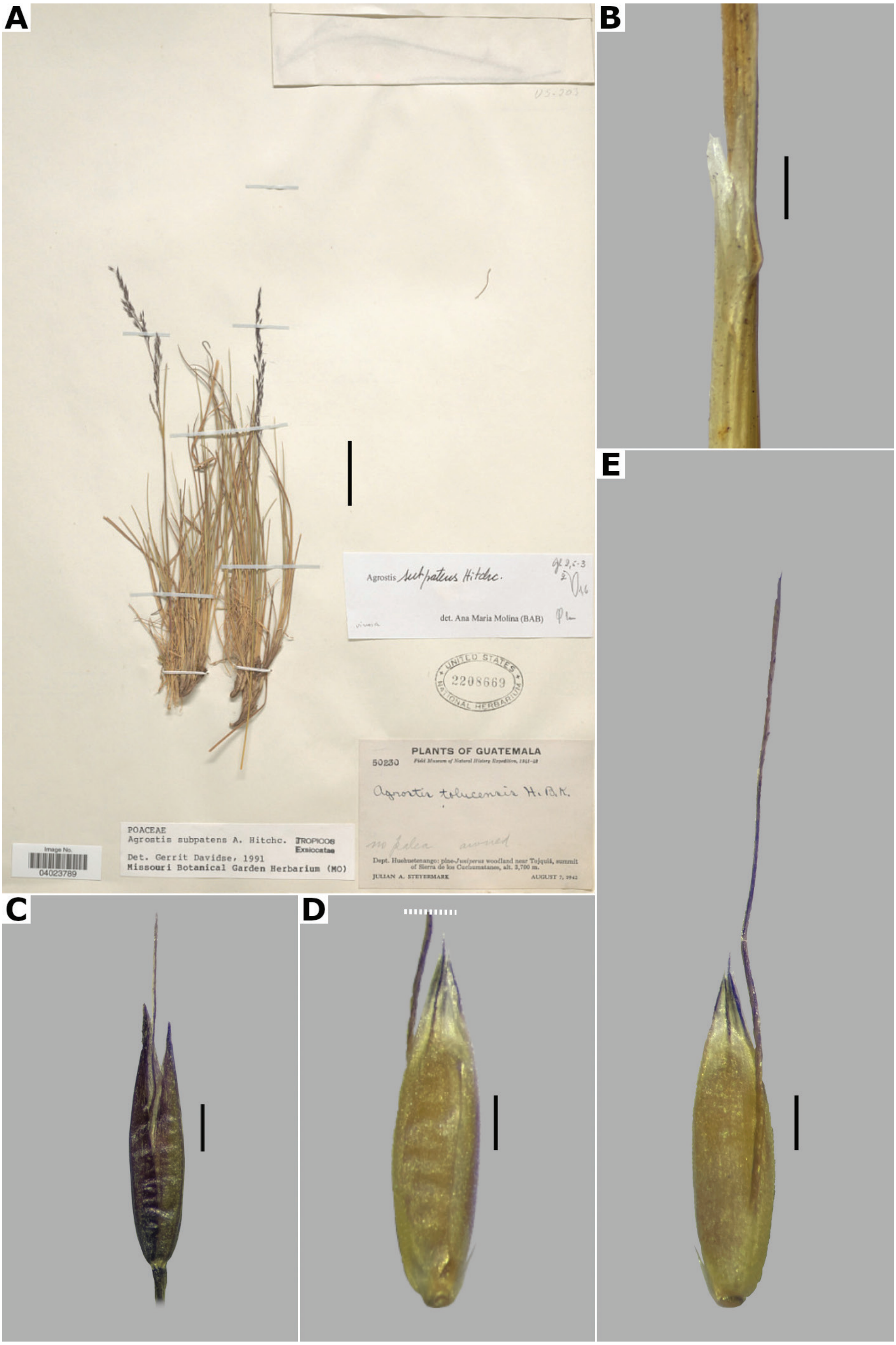

Figure 34. *Agrostis subpatens* **A** whole plant **B** ligular area **C** spikelet **D** floret, lateral view, **E** floret, abaxial view. A based on Steyermark 50230 (US), B–E based on Breedlove 40355 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D, E**).

Agrostis subpatens grows in open areas of temperate forests with *Pinus* and *Juniperus*, and in alpine grasslands, between 2900–3790 m a.s.l. (Fig. 27D).

Phenology. Specimens with spikelets have been collected in January, August and September (Fig. 28D).

Commentaries. This species is similar to *A. tolucensis* and *A. turrialbae*, with which it shares the basal filiform leaves, as well as several leaf blade anatomy and lemma micromorphology characters. *Agrostis subpatens* differs from *A. tolucensis* in the less dense and often more open panicles, with pedicels usually longer than the spikelets (vs. usually dense and spiciform panicles, pedicels usually shorter than the spikelets in *A. tolucensis*). It differs from *A. turrialbae* in the awned lemmas and absent palea (vs. unawned lemmas, palea up to 0.2 mm long in *A. turrialbae*).

Conservation status. *Agrostis subpatens* is known in the study zone from a few localities in southern Mexico and Guatemala. It is represented by seven collections, with several populations occurring in two protected areas. The EOO is 5,589 km^2 and the AOO is 20 km^2. Following the IUCN criteria, the preliminary assessment category is Endangered (EN).

Specimens examined. Guatemala. Chimaltenango: Municipio Acatenango, slopes of Volcán de Acatenango, above Las Calderas, [14.52463248°N, 90.87729338°W], 2900 m alt., 3 Jun 1939, P.C. Standley 61878 (F). **Huehuetenango: Municipio Chiantla**, Llano de Tsajualá, 3170 m alt., 26 Aug 1976, D.N. Smith 383 (F); cerca del cementerio, aldea San Nicolás, [15.43172006°N, 91.43878244°W], 3090 m alt., 3 Sep 1976, D.N. Smith 430 (F). **Municipio Todos Santos Cuchumatán**, Cerro Alto entre Llano de San Miguel y Todos Santos Cuchumatán, [15.54382199°N, 91.57855143°W], 3790 m alt., 29 Aug 1976, D.N. Smith 411 (F); near Tojquiá, summit of Sierra de los Cuchumatanes, [15.54360741°N, 91.56627528°W], 3700 m alt., 7 Aug 1942, J.A. Steyermark 50230 (F, US). **Mexico. Chiapas: Municipio Siltepec**, on the N and W slope of cerro Mozotal below the microwave tower along the road from Huixtla to El Porvenir and Siltepec, [15.4275°N, 92.341944°W], 3000 m alt., 19 Sep 1976, D.E. Breedlove 40355 (DS, MEXU [*, **]).

17. *Agrostis subrepens* (Hitchc.) Hitchc., in Britton, N. Amer. Fl. 17(7): 525. 1937.

Figs 4P, 30D, 35

Agrostis hyemalis (Walter) Britton, Sterns & Poggenb. var. *subrepens* Hitchc., U.S.D.A. Bur. Pl. Industr. Bull. 68: 44. 1905. Type: Mexico. Chihuahua: in wet places, pine plains, base of Sierra Madre Mountains, 28 Sep 1887, C.G. Pringle 1420 (holotype: US (US00131756 [image!]); isotypes: F (F-104784 [image!], F-2108718 [image!]), K (K000308371 [image!]), NY (NY-327645 [image!], NY-327646 [image!], US (US00131757 [image!])).

Type. Based on *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb. var. *subrepens* Hitchc.

Description. ***Plants*** perennial, rhizomatous or developing pseudostolons. ***Tillers*** extravaginal, with cataphylls. ***Rhizomes and pseudostolons*** up to 5 cm long. ***Culms*** 0.6–1 m long, erect, decumbent at the base, nodes 2–4, glabrous, internodes glabrous. ***Leaves*** mostly cauline; sheaths 3.5–7 cm long, usually shorter than the internodes, glabrous; ligules 1–2 mm long, longer than wide, dorsally scaberulous, apices truncate, erose; blades 3–5 cm long, 1–1.5 mm wide, linear, flat or involute, scaberulous on both surfaces. ***Panicles*** 9–22 cm long, 5–10 cm wide, open, lax, pyramidal, long-exserted from the upper sheaths; branches spreading, rebranching about mid-length, scaberulous, without spikelets near their base, inferior branches 2–8 cm long; pedicels 1–3 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.8–2.8 mm long, purplish; glumes subequal, lanceolate, apices acute, 1-veined, scaberulous on the keel, lower glume 1.8–2.8 mm long, upper glume 1.7–2.7 mm long; callus glabrous or with a few trichomes, Inconspicuous; lemmas 1.3–2 mm long, elliptic, apices entire, acute, 5-veined, veins prominent, unawned; paleas absent; anthers 3, 1–1.3 mm long. ***Caryopsis*** ca. 1.2 mm long, elliptic; endosperm solid. 2n= unknown.

Anatomy and micromorphology. Leaf blades flat in transversal section; adaxial furrows deep, narrow; adaxial ribs square to triangular; keel absent; first order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma in strands; second order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 31H, I). Lemmas with transversal thickenings irregular, wider than the unthickened portion of the wall; prickle hairs abundant (Fig. 32D).

Distribution and habitat. *Agrostis subrepens* was described from the Sierra Madre Occidental, in Chihuahua, Mexico (Fig. 26E). It has also been reported from South America, in Bolivia, Ecuador, Colombia, Paraguay, Perú and Venezuela (Soreng and Peterson 2003; Idárraga-Piedrahita et al. 2011), but the specimens from these countries were not seen, and could represent misidentifications of other species. In the study zone, *A. subrepens* grows in wet areas, in forests with *Pinus* and *Quercus*, between 2000–2168 m in elevation (Fig. 27E).

Phenology. Specimens with spikelets have been collected from August to September (Fig. 28E).

Commentaries. The status of *A. subrepens* as a distinct species and its distribution has been put in doubt recently (Sylvester et al. 2020a). This species is very similar to *A. perennans* sensu lato and other awnless species of the study zone, but differs from them in the presence of pseudostolons, leaf blades with square to triangular adaxial ribs, and lemmas with irregular thickenings (vs. caespitose plants, leaf blades with rounded adaxial ribs, lemmas with usually polygonal thickenings). Some individuals of *A. perennans* sensu lato sometimes develop pseudostolons, but despite the leaf anatomy, there are few differences between the two taxa. We recognise *A. subrepens* as a distinct species, until more evidence is available.

It could also be confused with *A. pallens* from California and Baja California, but it is distinguished in the more open panicles, and unawned lemmas (vs. panicles often contracted, often awned lemmas), as well as the leaf anatomy.

Conservation status. *Agrostis subrepens* is known in the study zone from a few localities in Chihuahua, Mexico. It is represented by five collections, with no populations occurring in protected areas. The EOO is 74 km^2 and the AOO is 12 km^2. Following the IUCN criteria, the preliminary assessment category is Endangered (EN).

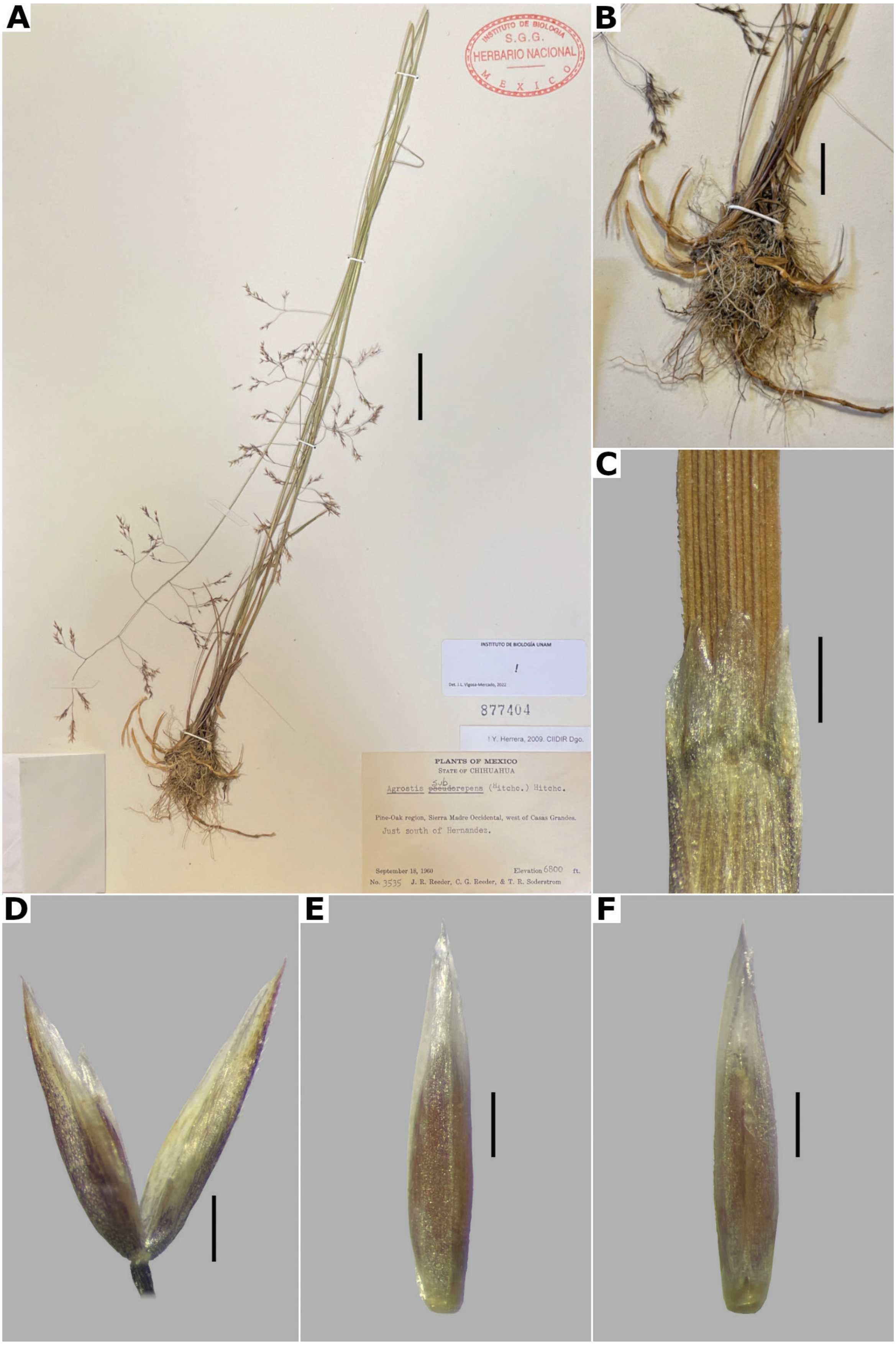

Figure 35. *Agrostis subrepens* **A** whole plant **B** detail of the pseudostolons **C** ligular area **D** spikelet **E** floret, abaxial view **F** floret, adaxial view. Based on Reeder et al. 3535 (MEXU). Scale bars: 3 cm (**A**); 1 cm (**B**); 1 mm (**C**); 0.5 mm (**D**); 0.3 mm (**E, F**).

Specimens examined. Mexico. Chihuahua: Municipio Casas Grandes, Sierra Madre Occidental, W of Casas Grandes, just S of Hernández [30.04186415°N, 108.2901759°W], 2000 m alt., 18 Sep 1960, J. Reeder et al. 3535 (MEXU [*, **], US). **Municipio Madera**, Chuhuichupa, [29.60543842°N, 108.3736947°W, 2168 m alt.], Aug–Sep 1936, H. LeSueur 87 (US), 198 (US), near Colonia Garcia, in the Sierra Madre, [29.9833°N, 108.333°W, 2149 m alt.], 1 Aug 1899, E.W. Nelson 6195 (US).

18. *Agrostis tolucensis* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 1: 135. 1816.

Figs 4Q, 30E, 36

= *Agrostis virescens* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 1: 135–136. 1816. *Agrostis tolucensis* Willd. ex Steud., Syn. Pl. Glumac. 1: 164. 1854, nom. inval., pro syn. Type: Mexico. State of México: in planitie Tolucana, A. Humboldt and A. Bonpland s.n. (holotype: P (P00669395 [image!]); isotypes: LE-TRIN, P (P00136912 [image!], P00740428 [image!], P00740429 [image!], P00740430 [image!])).*

Type. Mexico. State of México: crescit in apricis, aridis regni Mexicani, prope urbem Toluca et Islahuaca [Ixtlahuaca], 1380 hexap. alt., A. Humboldt and A. Bonpland s.n. (holotype: P (P00669394 [image!]); isotypes: P (P00136913 [image!]), P00136914 [image!], P00136915 [image!], P00740426! [image!]), US [fragm. ex P] (US00156505 [image!]).

Description. ***Plants*** perennial, caespitose, or shortly rhizomatous. ***Tillers*** extravaginal and intravaginal, with cataphylls. ***Rhizomes*** if present, up to 1 cm, ascendent. ***Culms*** 5–30(–60) cm long, erect, nodes 1–3, glabrous, internodes glabrous. ***Leaves*** mostly basal or basal and cauline; sheaths 1–10 cm long, the lower ones longer than the internodes, the upper ones shorter, glabrous or scaberulous; ligules 2–5(–6) mm long, longer than wide, dorsally scaberulous, apices acute to truncate, erose or lacerate; blades 3–10(–19) cm long, 0.5–3(–4) mm wide, filiform to linear, conduplicate to involute, sometimes flat, scaberulous on both surfaces. ***Panicles*** (3–)5–12 cm long, (0.3–)0.5–1 cm wide, contracted, dense, spiciform, linear to lanceolate, often interrupted at the base, often partially included in the upper foliage sheats; branches appressed, rebranching below mid-length, scaberulous, with spikelets near their base, inferior branches up to 3 cm long; pedicels 0.5–3 mm long, appressed, scaberulous. ***Spikelets*** 2–3(–3.6) mm long, greenish to purplish; glumes subequal to unequal, lanceolate, apices acute to shortly acuminate, 1-veined, scaberulous on the keel, lower glume 2–3(–3.6) mm long, upper glume 1.8–2.8(–3.4) mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1.2–2 mm long, elliptic, apices toothed, 5-veined, veins prominent, awned near the base, sometimes above mid-length, rarely awnless, awn 1.5–3.5 mm long, geniculate, reaching the lemma apices; paleas absent or up to 0.2 mm long; anthers 3, 0.5–1 mm long. ***Caryopsis*** 0.7–1.5 mm long, elliptic; endosperm soft to solid . 2n= 28 (Pohl and Davidse 1971).

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* See Suppl. material 1 for other heterotypic synonyms.

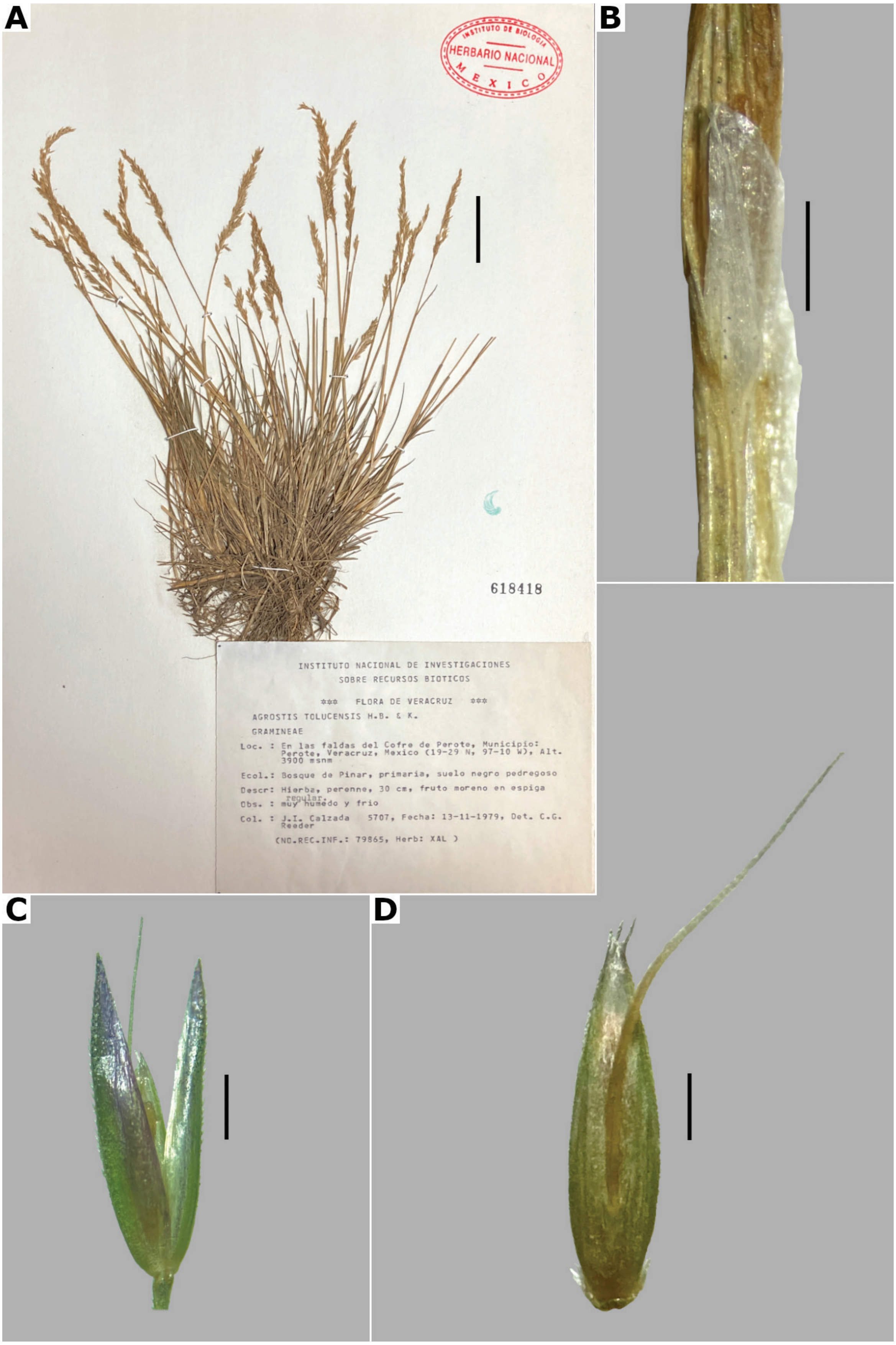

Figure 36. *Agrostis tolucensis* **A** whole plant **B** ligular area **C** spikelet **D** floret, abaxial view. Based on Calzada 5707 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C**); 0.3 mm (**D**).

Leaf anatomy. Leaf blades involute to v-shaped in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded to triangular; keel absent; first order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma in strands; second order bundles circular in outline, sheath not interrupted, abaxial and adaxial sclerenchyma; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 37A, B). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portion of the wall; prickle hairs abundant (32E).

Distribution and habitat. *Agrostis tolucensis* is distributed from northern Mexico to Chile. In the study zone, it has been collected in Mexico City, and the Mexican states of Chiapas, Durango, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Tlaxcala, and Veracruz; in the Guatemalan departments of Sacatepéquez and San Marcos (Fig. 26F). It has also been reported from the Mexican states of Colima, Guanajuato, and San Luis Potosí (Villaseñor 2016; Sánchez-Ken 2019), but no specimens from these states were found. *Agrostis tolucensis* grows in open areas of temperate forests with *Abies*, *Pinus*, and *Quercus*, and alpine grasslands, between 1330–4520 m a.s.l. (Fig. 27F).

Phenology. Specimens with spikelets have been collected year round, but most of them between the months of July and November (Fig. 28F).

Commentaries. It has been reported that South American populations of this species develop long rhizomes (e.g. Renvoize 1998). This species is often confused with *A. exarata* and *A. subpatens* (see the notes under the description of these species). *Agrostis tolucensis* is a variable species, and several infraspecific taxa have been described, none of which are recognized in this work. In the study zone, at least three forms have been observed, but there is a continuous interval of variation in the populations of this species: 1) small plants with narrow leaf blades and panicles shortly exceeding the foliage, 2) larger plants with narrow leaf blades and panicles long-exserted from the foliage, 3) larger plants with broader leaf blades, more open panicles, and lemmas with awn inserted above mid-length of the lemma. The plants of the latter form have been called *A. virescens*, but they fit well in the continuous interval of variation of the populations. This species is also confused with *A. meyenii* Trin. (see the note under excluded species).

Conservation status. *Agrostis tolucensis* is a common and widespread species in the study zone. It is represented by 244 collections, with several populations occurring in 17 protected areas. The EOO is 439,417 km^2 and the AOO is 432 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Guatemala. San Marcos: Municipio Sibinal, Volcán Tacaná, 500 m al E de Talquián, 15.13055556°N, 92.10694444°W, 4028 m alt., 24 May 2000, N. Gallardo et al. 8851 (MEXU). **México. Chiapas: Municipio Unión Juárez**, SE side of the summit of Volcán Tacaná, [15.09306218°N, 92.08369755°W], 3600 m alt., 10 Nov 1972, D.E. Breedlove 29340 (MEXU [*], MO); cráter del Volcán Tacaná, [15.09306218°N, 92.08369755°W], 4000 m alt., 9 Oct 1987, E. Martínez 20869 (MEXU [*]). **Durango: Municipio San Dimas**, 3 mi S of Guachichiles, upper slopes of cerro Huehento, 24.0786°N, 105.743°W, 3078–3249 m alt., 30 Sep 2008, P.M. Peterson and

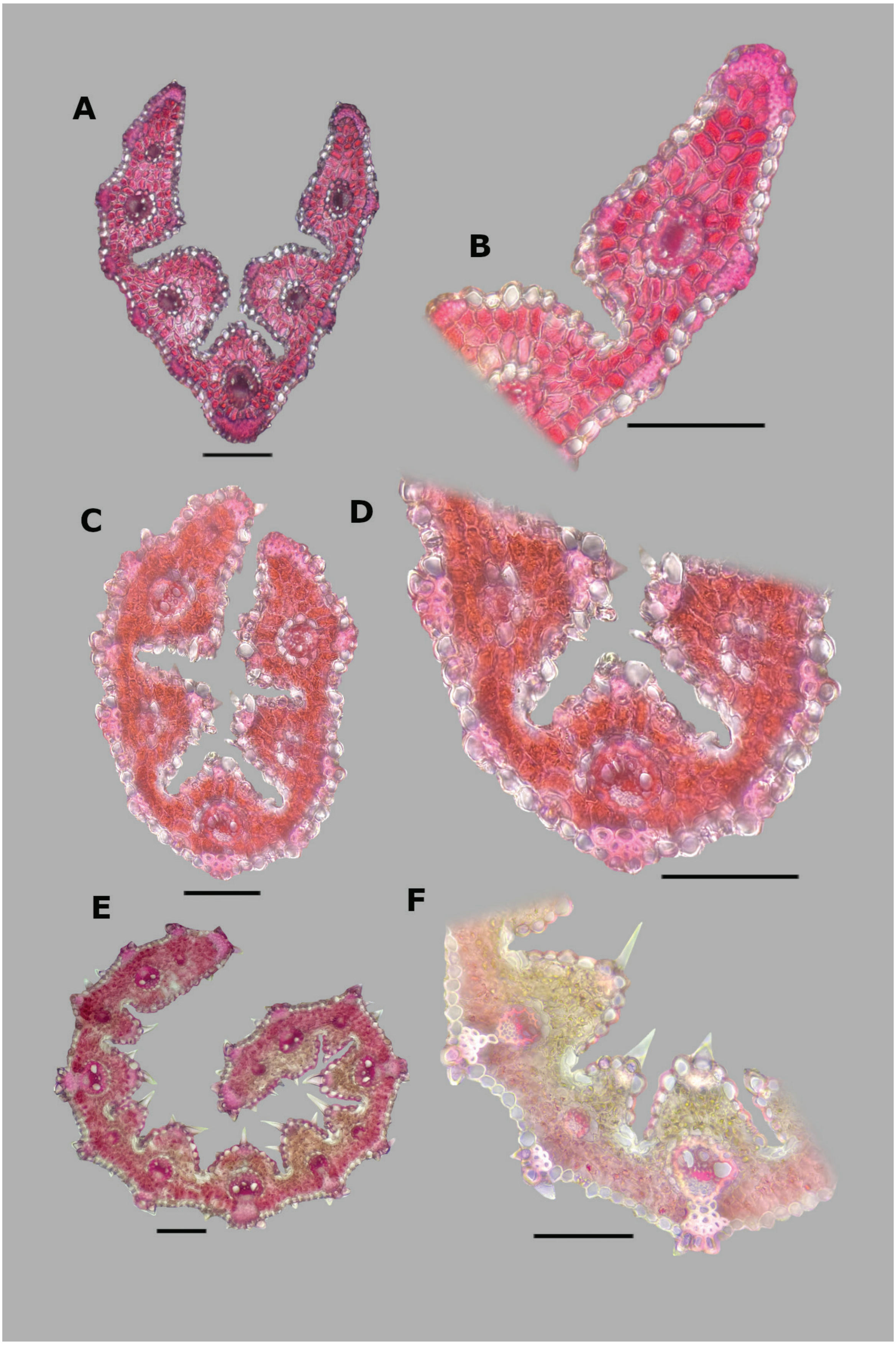

Figure 37. Leaf blade anatomy in transversal section of *Agrostis* species, in general view, and details of lateral bundles. **A**, **B** *A. tolucensis* **C**, **D** *A. turrialbae* **E**, **F** *A. variabilis*. Scale bars: 0.1 mm.

J.M. Saarela 22445 (CAN, US). **Guerrero: Municipio General Heliodoro Castillo**, cerro Teotepec, [17.46666667°N, 100.2166667°W], 3200 m alt., 17 Oct 1999, E. Domínguez 1200 (FCME [*]), 5 Dec 1993, M. González and C. Catalán 564 (CHAPA, MEXU). **Hidalgo: without municipality**, pasando desviación a Pachuca, autopista a México, 19 Jul 1976, J.J. Soto s.n. (IBUG). **Jalisco: Municipio Ciudad Guzmán**, 2 km antes de llegar a La Casita, camino El Refugio–Nevado de Colima, 2860 m alt., 3 Feb 1994, J. Reynoso 1735 (CIIDIR, IBUG). **Municipio San Gabriel**, N slopes of Nevado de Colima, [19.60110761°N, 103.5808018°W, 3000 m alt.], 19 Sep 1980, A.A. Beetle and R. Guzmán M-5380 (IBUG, MEXU [*]). **Mexico: Municipio Amecameca**, La Joya de Alcalican, pies de Iztaccíhuatl, [19.141667°N, 98.675°W], 3950 m alt., 23 Nov 1975, L. Alonso 66 (CHAPA, IBUG, MEXU); SW del Volcán Iztaccíhuatl, 1.5 km al SE de La Joyita, 19.13291667°N, 98.64144444°W, 3997 m alt., 15 Nov 2012, R. Hernández-Cárdenas and L. Arredondo-Amezcua 867 (MEXU [*]); km 20 carretera Amecameca–Tlamacas, [19.0917039°N, 98.67702965°W, 3402 m alt.], 2 Oct 1992, A. Miranda and G. Villegas 650 (MEXU [*]); La Joya de Alcalican, extremo SW del Iztaccíhuatl, [19.152778°N, 98.673333°W], 3900 m alt, 26 Nov 1978, H.J. Soriano 116 (ASU, CIIDIR, MEXU [*], XAL). **Municipio Zinacantepec,** camino al Nevado, [19.1225°N, 99.77888889°W], 3200 m alt., 1 Oct 1992, A. Miranda et al. 598 (MEXU [*, **]). **Mexico City**, **Alcaldía Tlalpan**, volcán Pelado, [19.151°N, 99.2171°W], 3100 m alt., 1 Jul 1985, A. Miranda et al. 25 (MEXU). **Michoacán: Municipio Angangeueo**, alrededores del Llano de las Papas, [19.65618889N, 100.2717278], 3200 m alt., 9 Oct 1988, J. Rzedowski 47403 (CHAPA, CIIDIR, IBUG, IEB, MEXU [**], XAL). **Morelos: Municipio Huitzilac**, Zempoala, [19.05034984°N, 99.31696647°W, 2812 m alt.], 1938, E. Lyonnet 2497 (MEXU, US). **Municipio Oaxtepec**, Oaxtepec, [18.90219847°N, 98.96287658°W], 1333 m alt., Aug 1952, F. Gallegos 438 (MEXU). **Oaxaca: Municipio San Miguel Amatlán**, 8.3 mi N of San Cualimojoyas on road towards Santa Maria Yavesia, 17.1819°N, 96.4445°W, 2794 m alt., 20 Sep 2008, P.M. Peterson and J.M. Saarela 22308 (US). **Puebla: Municipio Atzitzintla**, Sierra Negra, SW of Pico de Orizaba, summit of mountain, [18.98528°N, 97.310745°W], 4520 m alt., 10 Sep 1958, J.H. Beaman 2506 (MEXU, US). **Municipio San Nicolás de los Ranchos**, 6 km al SE de Paso de Cortés, brecha a Xalitzintla, [20.18°N, 98.44°W], 3400 m alt., 14 Sep 1988, P. Tenorio 15092 (MEXU, TEX); Buenavista, 5 km al E de Xalitzintla, [19.1°N, 98.55°W], 3300 m alt., 15 Feb 1988, P. Tenorio 15099 (MEXU [**]). **Tlaxcala: Municipio Huamantla**, volcán La Malinche, 4200 m alt., 4 Nov 1988, R. Acosta 2556 (CIB, MEXU [*]); parte alta de La Malinche, [19.25666667°N, 98.02833333°W], 3500 m alt., 7 Oct 1993, R. Hernández 96 (CIIDIR, MEXU). **Veracruz: Municipio Perote**, Cofre de Perote, 500 m al NO de la estación de televisión, [19.496389°N, 97.151389°W], 4030 m alt., 10 Sep 1992, B.V. Hernández 66 (MEXU [*], CHAPA, CIB, XAL). See Suppl. material 2 for the full list of examined specimens.

19. *Agrostis turrialbae* Mez, Repert. Spec. Nov. Regni Veg. 18(1–3): 4. 1922.
Figs 4R, 30F, 38

= *Agrostis arcta* Swallen, Contr. U.S. Natl. Herb. 29(9): 405. 1950. Type. Guatemala. Chimaltenango: moist roadside at Santa Elena, 17 Jul 1933, A.F. Skutch 422 (holotype: US (US00131720)).

= *Agrostis vesca* Swallen, Contr. U.S. Natl. Herb. 29(9): 405. 1950. Type. Guatemala. Chimaltenango: moist roadside at Santa Elena, 17 Jul 1933, A.F. Skutch 420 (holotype: US (US00131129)).

Type. Costa Rica. Cartago: plateau au field W du Turrialba, 2600 m alt., 27 Jan 1884, H. Pittier 855 (holotype: B; isotypes: US (US00131127, US04023770 [image!])).

Description. ***Plants*** perennial, caespitose. ***Tillers*** extravaginal, with cataphylls. ***Culms*** 13–32 cm long, erect, nodes 1–2, glabrous, internodes glabrous. ***Leaves*** mostly basal; sheaths 0.8–6.5(–10) cm long, usually longer than the internodes, glabrous or scaberulous; ligules 0.5–1.6 mm long, longer than wide, dorsally scaberulous, apices acute to rounded, erose or lacerate; blades 1–9 cm long, 0.2–0.5 mm wide, filiform, conduplicate to involute, rarely flat in the upper leaves, scaberulous on both surfaces. ***Panicles*** 3.8–10 cm long, 1.7–5(–8) cm wide, open, lax, ovate, exserted from the upper sheaths; branches ascending to spreading, rebranching about or slightly above mid-length, scaberulous, without spikelets near their base, inferior branches 0.7–2.5 cm long; pedicels 0.7–4 mm long, ascending to spreading, scaberulous. ***Spikelets*** 1.5–2.4 mm long, purplish; glumes subequal to unequal, lanceolate, apices acute, 1-veined, scaberulous on the keel, lower glume 1.5–2.4 mm long, upper glume 1.4–2.3 mm long; callus pubescent, with 2 bunches of trichomes; lemmas 1.3–1.8 mm long, elliptic, apices entire, acute, sometimes irregularly toothed, 5-veined, veins prominent, unawned, rarely awned near the apices, awn ca. 0.2 mm long, straight; paleas absent or up to 0.2 mm long, veinless, glabrous; anthers 3, ca. 0.7 mm long. ***Caryopsis*** 1.5–2.2 mm elliptic; endosperm solid. 2n= unknown.

Anatomy and micromorphology. Leaf blades v-shaped to involute in transversal section; adaxial furrows deep, narrow; adaxial ribs rounded to triangular; keel absent; first order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma present, abaxial; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 37C, D). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portion of the wall; prickle hairs present, abundant (Fig. 32F).

Distribution and habitat. *Agrostis turrialbae* is distributed from central Mexico to Costa Rica. It has also been reported from Colombia and Venezuela (Luteyn 1999; Soreng and Peterson 2003). In the study zone, this species has been collected in the Mexican states of Chiapas, México, Querétaro, Tlaxcala, and Veracruz, and the Guatemalan departments of Huehuetenango and San Marcos (Fig. 39A). It has also been reported from Hidalgo (Sánchez-Ken 2019), but no specimens from this state were seen. *Agrostis turrialbae* grows in open areas of temperate forests, with *Pinus* and *Quercus*, and alpine grasslands, between 1600–4240 m a.s.l. (Fig. 27G).

Phenology. Specimens with spikelets have been collected from June to February (Fig. 28G).

Commentaries. Populations of this species from central Mexico have been confused with *A. subpatens* by some authors (e.g., Acosta 2001; Vigosa-Mercado and Ruiz-Sánchez 2020) (see the note under the description of that species).

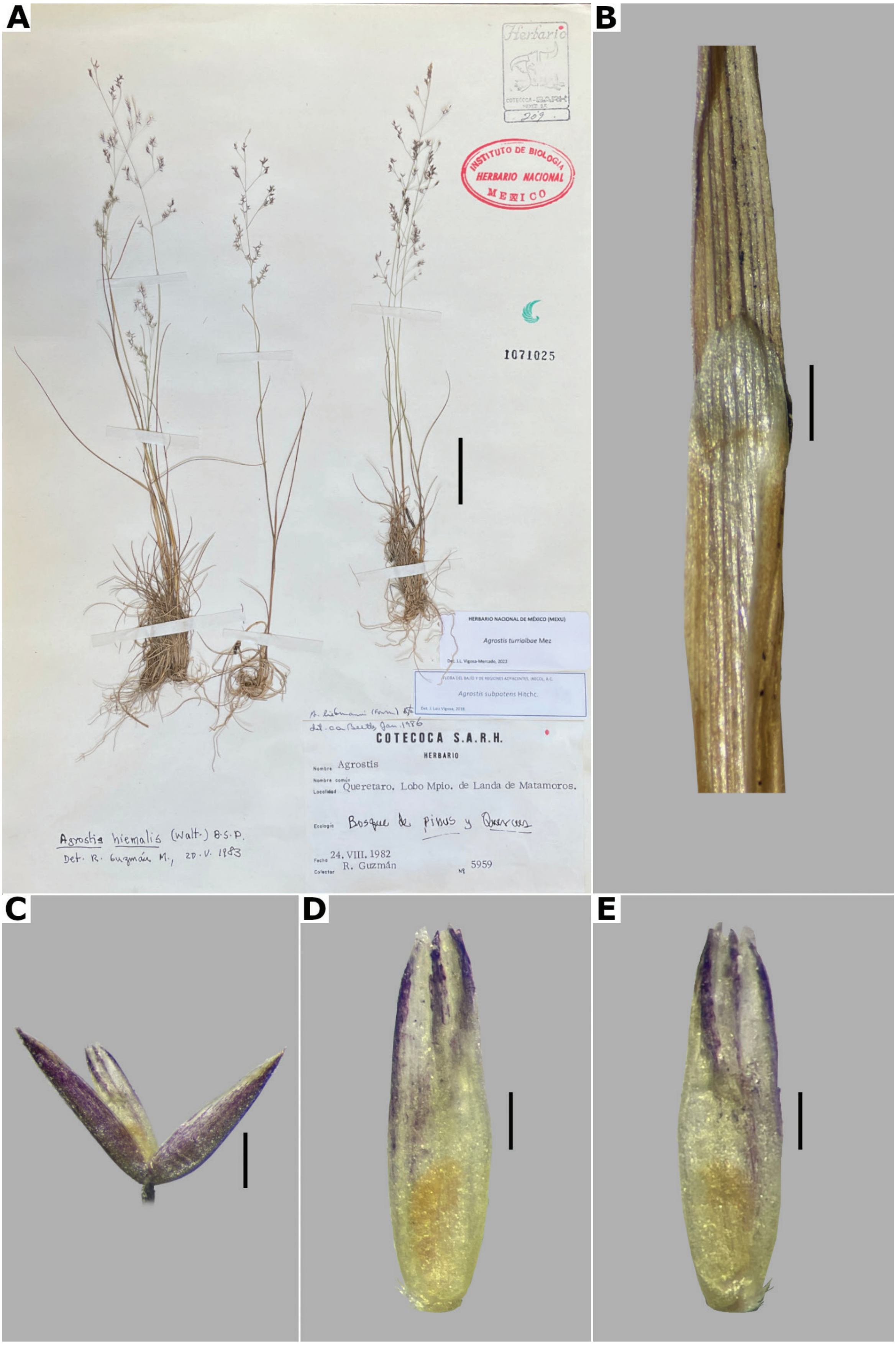

Figure 38. *Agrostis turrialbae* **A** whole plant **B** ligular area **C** spikelet **E** floret, abaxial view **F** floret, adaxial view. Based on Guzmán 5959 (MEXU). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.5 mm (**C**); 0.2 mm (**D, E**).

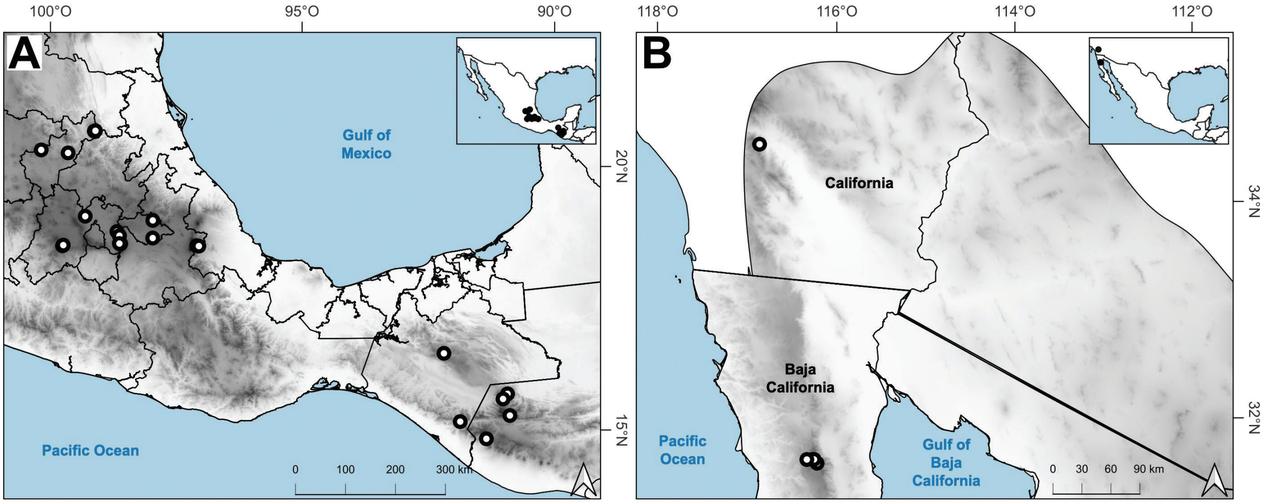

Figure 39. Map of known geographic distribution of *Agrostis* species, based on herbarium specimen data **A** *A. turrialbae* **B** *A. variabilis*.

Agrostis turrialbae is similar to *A. perennans* sensu lato, and its identity has been put in doubt recently by Sylvester et al. (2020a). Both species share open panicles and unawned lemmas, as well as several lemma micromorphology characters. In the study zone, it has been found that the plants identified as *A. turrialbae* are consistently different from *A. perennans*, and are characterized by the small size of the plants, mostly basal leaves, leaf blades narrow and conduplicated to involute, with adaxial ribs rounded to triangular, with abaxial intercostal sclerenchyma, and purplish spikelets (vs. usually larger plants, usually basal and cauline leaves, but the basal ones often drying at anthesis, leaf blades wider and flat, with rounded adaxial ribs, without intercostal sclerenchyma, greenish to purplish spikelets in *A. perennans*). This species is scarcely different from *A. idahoensis*, from the southern USA (see the note under the description of that species).

Conservation status. *Agrostis turrialbae* is a widespread species in the study zone. It is represented by 30 collections, with several populations occurring in six protected areas. The EOO is 183,426 km^2 and the AOO is 84 km^2. Following the IUCN criteria, the preliminary assessment category is Least Concern (LC).

Representative specimens examined. Guatemala. Huehuetenango: Municipio Santa Eulalia, top of cerro Chemalito, Sierra de los Cuchumatanes, 3.5 mi W of Santa Eulalia, [15.7822223°N, 91.5111111°W], 3100–3150 m alt., 2 Aug 1942, J.A. Steyermark 49905 (F, US). **San Marcos: Municipio San Marcos**, between San Sebastián and summit of Volcán Tajumulco, [15.04824546°N, 91.86726456°W, 3353 m alt.], 13 Feb 1940, J.A. Steyermark 35477 (F). **Mexico. Chiapas: Municipio Motozintla**, near summit of cerro Mozotal., [15.419722°N, 92.336667°W], 2750 m alt., 24 Nov 1981, D.E. Breedlove and B.M. Bartholomew 55845 (MO). **México: Municipio Amecameca:** ladera SW del volcán Iztaccíhuatl, rumbo al primer Portillo, 19.13697222°N, 98.64898611°W, 4050 m alt., 8 Nov 2014, R. Hernández and S. Villalobos 2057 (IEB, MEXU [**]). **Querétaro: Municipio Colón**, antena El Zamorano, [20.93305556°N, 100.1797222°W], 3355 m alt., 24 Nov 1981, A. Mora and J. Ramírez 401-AMB (MEXU [*,**]). **Municipio Landa**, Lobo, [21.29275°N, 99.11930833°W], 1600 m alt., 24 Aug 1982, R. Guzmán 5959 (MEXU [*, **]). **Tlaxcala: Municipio Huamantla**, ladera N del Volcán La Malinche, 19.23486111°N, 98.03338889°W, 4190 m alt., 29 Jun 2013, R. Hernández-Cárdenas and L. Arredondo-Amezcua 1123 (IEB), 1929 (IEB). **Veracruz: Municipio Calcahualco**, La Cuchilla, camino al Pico de Orizaba, por Coscomatepec, [19.06728503°N, 97.19152382°W], 3160 m alt., 22 Jul 1982, R. Guzmán 5847 (MEXU). See Suppl. material 2 for the full list of examined specimens.

20. *Agrostis variabilis* Rydb., Mem. New York Bot. Gard. 1: 32. 1900.

Fig. 4S, 30G, 40

Agrostis varians Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 314. 1841, nom. illeg. hom., non Thuillier 1799. Type: America borealis [Rocky Mountains?], J.D. Hooker T-217 (holotype: LE-TRIN; isotypes: MO (MO-992441 [image!], NY (NY327643 [image!], US (US00156511 [image!])).

Type. Based on *Agrostis varians* Trin.

Description. ***Plants*** perennial, slender, usually caespitose, rarely rhizomatous. ***Tillers*** extravaginal, with cataphylls. ***Rhizomes*** if present, up to 2 cm long. ***Culms*** 10–45 cm long, erect, nodes 1–2, glabrous, internodes glabrous. ***Leaves*** mostly basal; sheaths 0.8–6(–10) cm long, the lower ones longer than the internodes, the upper ones shorter, scaberulous; ligules 1–2.2 mm long, longer than wide, dorsally scaberulous, apices acute, erose to lacerate; blades 1–7 cm long, 0.5–1 mm wide, filiform, conduplicate to convolute, scaberulous on both surfaces. ***Panicles*** 1.5–13 cm long, 0.2–0.7 cm wide, contracted, dense, spiciform, linear, sometimes interrupted at the base, sometimes partially included in the upper sheaths; branches appressed, rebranching from below mid-length, scaberulous, with spikelets near their base, inferior branches up to 1 cm long; pedicels 0.3–2.2 mm long, appressed, scaberulous. ***Spikelets*** 1.4–2 mm long, greenish to stramineous, often tinged with purpure; glumes subequal, lanceolate, apices acute, 1-veined, scaberulous on the keel, lower glume 1.4–2 mm long, upper glume 1.3–1.9 mm long; callus glabrous; lemmas 1–1.4 mm long, elliptic, apices entire, acute, 5-veined, veins prominent distally, usually unawned, rarely awned above mid-length, awn up to 1 mm long, straight, not reaching the lemma apices; paleas absent; anthers 3, 0.3–0.6 mm long. ***Caryopsis*** 0.9–1.2 mm long, elliptic; endosperm solid. 2n= 28 (Harvey 2007).

Anatomy. Leaf blades convolute to v-shaped in transversal section; adaxial furrows medium-sized to deep, narrow; adaxial ribs rounded to triangular: keel absent; first order bundles circular in outline, sheath interrupted abaxially, abaxial sclerenchyma in strands or girders, narrowing towards the bundle, adaxial sclerenchyma in strands; second order bundles circular in outline, sheath interrupted abaxially, abaxial and adaxial sclerenchyma in strands; intercostal sclerenchyma absent; leaf margins with well-developed sclerenchyma caps, rounded; colorless cells absent (Fig. 37E, F). Lemmas with transversal thickenings irregular to oblong, wider than the unthickened portion of the wall; prickle hairs present, scarce (32G).

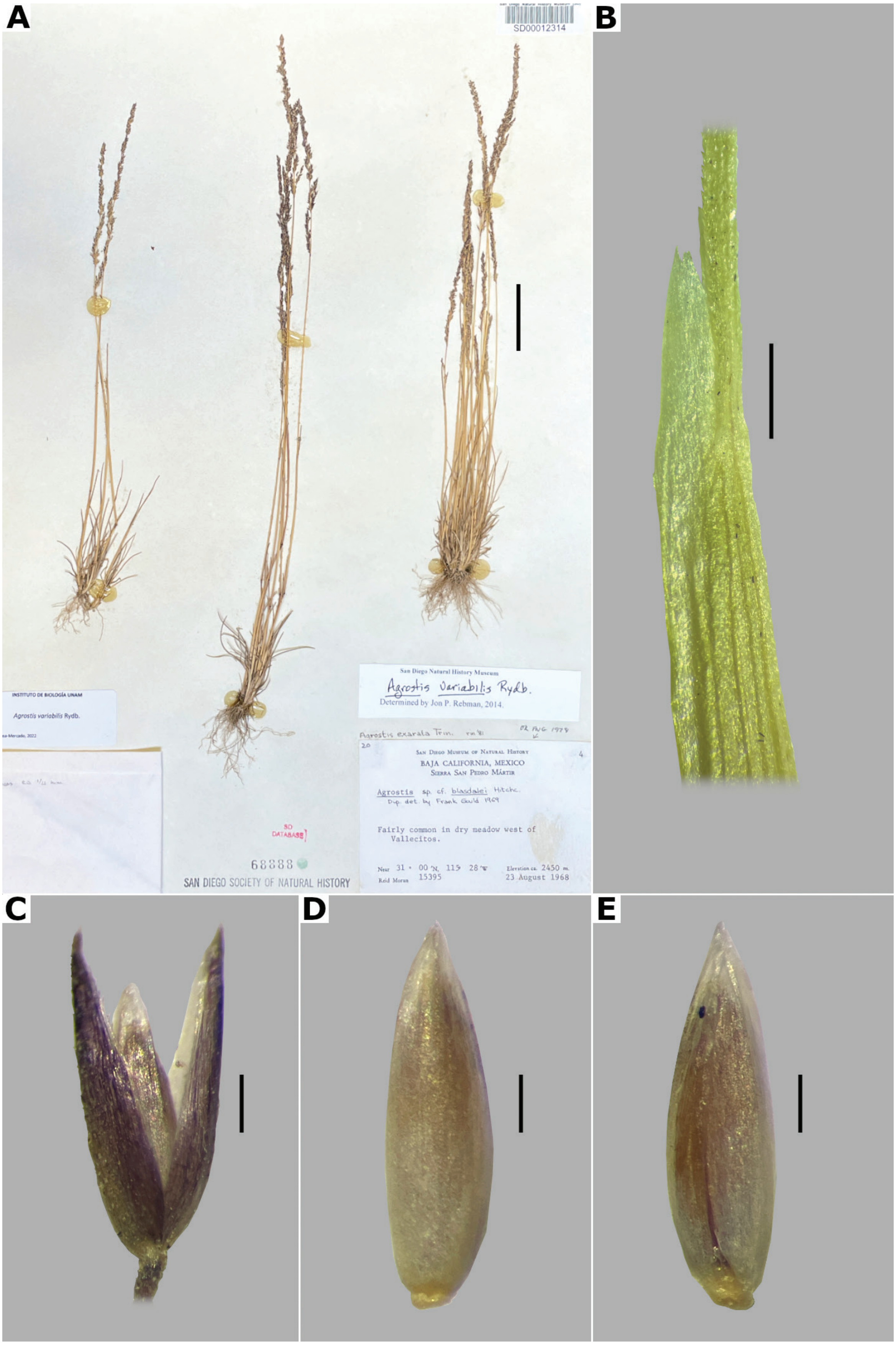

Figure 40. *Agrostis variabilis* **A** whole plant **B** ligular area **C** spikelet **E** floret, abaxial view **F** floret, adaxial view. Based on Moran 15395 (SD). Scale bars: 3 cm (**A**); 1 mm (**B**); 0.3 mm (**C**); 0.2 mm (**D, E**).

Distribution and habitat. *Agrostis variabilis* is distributed from Alaska to the northern peninsula of Baja California, Mexico. In the study zone, it has been collected in the USA state of California, and the Mexican state of Baja California (Fig. 39B). This species has also been reported from Chihuahua (Sánchez-Ken 2019), but no specimens from this state were seen. *Agrostis variabilis* grows in open areas of temperate forests with *Pinus*, between 2400–2639 m a.s.l. (Fig. 27H).

Phenology. Specimens with spikelets have been collected from July to September (Fig. 28H).

Commentaries. It has been reported for other regions that the spikelets can reach 2.5 mm long (Harvey 2007). This species is often confused with the smaller forms of *A. exarata*, but differs from them in the mostly basal leaves, with filiform and convolute to involute leaf blades, 0.5–1 mm wide (vs. basal and cauline leaves, leaf blades linear, flat, 1.5–4(–8) mm wide in *A. exarata*).

Conservation status. *Agrostis variabilis* is apparently a rare species in the study zone. It is represented by six collections, with its populations occurring in two protected areas. The EOO is 1,621 km^2 and the AOO is 16 km^2. Following the IUCN criteria, the preliminary assessment category is Endangered (EN).

Specimens examined. Mexico. Baja California: Municipio Ensenada, Sierra San Pedro Mártir, fairly common in dry meadow W of Vallecitos, 31.01089°N, 115.49504°W, 2450 m alt., 23 Aug 1968, R. Moran 15395 (SD [*,**], UC); common on gravelly arroyo bank, Tasajera, ca. 3 km NW of Los Llanitos, 30.98333°N, 115.44167°W, 2500 m alt., 3 Sep 1979, R. Moran 28010 (SD); Sierra San Pedro Mártir, fairly common in arroyo, Jeffrey Pine forest, Yerba Buena, 31.01292°N, 115.48002°W, 2475 m alt., 16 Aug 1967, R. Moran and R.F. Thorne 14157 (SD). Sierra San Pedro Mártir, 25 Sep 1982, A. Preciado 299 (MEXU [*,**]); Sierra San Pedro Mártir, campground and main gate area, 31N, 115.557W, 2461 m alt., 14 Jul 2013, S. Ratay et al. 235 (SD). **USA. California: Riverside County**, Mt. San Jacinto State Park, N side of Hidden Lake, 33.80022°N, 116.64119°W, 2639 m alt., 12 Jul 1999, L. Hendrickson 10430 (BSCA).

Excluded names

***Agrostis alba* L., Sp. Pl. 1: 63. 1753.**

The rhizomatous plants with paleate spikelets were formerly treated under this name, but the original material corresponds to *Poa nemoralis* L., so currently *A. alba* is a synonym of the latter.

***Agrostis avenacea* J.F. Gmel., Syst. Nat., ed. 13 2(1): 171. 1791.**

This name is a synonym of *Lachnagrostis filiformis* (G. Forst.) Trin., which differs from *Agrostis* species in the hairy lemmas, well developed paleas and the rachilla prolongated as a hairy bristle.

***Agrostis blasdalei* Hitchc., Proc. Biol. Soc. Washington 41: 160–161. 1928.**

This species is distributed from Mendocino to Santa Cruz Counties, in California USA, where it grows in shrublands, and coastal cliffs and dunes (Harvey 2007). *Agrostis blasdalei* has been reported in Baja California, Mexico (Sánchez-Ken

2019), but the records of this species in the study zone appear to be erroneous identifications of specimens of *A. exarata*, from which differs in the panicles included in the upper sheaths at maturity, callus of the floret glabrous, and lemma shortly dentate (vs. panicles usually exserted, callus with at least a few trichomes, lemmas usually entire in *A. exarata*).

Agrostis borealis **Hartm., Handb. Skand. Fl. (ed. 3) 17. 1838.**

This name is a synonym of *A. mertensii* Trin. (see below). It has been reported in the state of Mexico (Beetle et al. 1983).

Agrostis castellana **Boiss. & Reut. Diagn. Pl. Nov. Hisp. 26. 1842.**

This species is native to Europe. It has been reported from Durango, México (Sánchez-Ken 2019), but specimens from this state have not been seen. *Agrostis castellana* is often confused with *A. capillaris*, which shares the rhizomatous habit, and paleate spikelets. *Agrostis castellana* is distinguished in the ligules longer than wide, panicle branches densely scaberulous, lemmas often awned, and lemma of the terminal spikelet of each branchlet with callus and dorsal surface pubescent (vs. ligules usually shorter than wide, panicle branches scarcely scaberulous and lemmas usually unawned, with a glabrous callus or with a few and inconspicuous trichomes in *A. capillaris*)

Agrostis densiflora **Vasey, Contr. U.S. Natl. Herb. 3(1): 72. 1892.**

This species is distributed from coastal Oregon to California (Harvey 2007). The records of *A. densiflora* in the study zone appear to be erroneous identifications of specimens of *A. exarata*. It is distinguished in the dentate lemmas and anthers of 0.5–1.2 mm long (vs. lemmas usually entire, anthers of 0.3–0.7 mm long in *A. exarata*).

Agrostis exserta **Swallen, Contr. U.S. Natl. Herb. 29(9): 404. 1950.**

This species has recently been transferred to the genus *Podagrostis*, under the name *P. exserta* (Swallen) Sylvester & Soreng (Sylvester et al. 2020b). It is distributed from Oaxaca, Mexico, to Guatemala (Vigosa-Mercado, 2022b). *Podagrostis* species are distinguished from *Agrostis* in the glumes as long as the floret, paleas well developed and rachilla prolonged as a glabrous bristle (vs. glumes longer than the floret, paleas often absent or minute, rachilla not prolonged).

Agrostis humilis **Vasey, Bull. Torrey Bot. Club 10(2): 21. 1883.**

This species has been recognized as part of the genus *Agrostis* or *Podagrostis*. The molecular and morphological evidence confirms *Podagrostis* as a distinct genus (Peterson et al. 2020; Sylvester et al. 2020b). *Podagrostis humilis* (Vasey) Björkman is distributed in Canada and USA (Molina et al. 2021). See the note under *A. exserta* for the differences between *Agrostis* and *Podagrostis* species.

Agrostis liebmannii **(E. Fourn.) Hitchc., in Britton, N. Amer. Fl. 17(7): 519. 1937.**

This species has recently been transferred to the genus *Podagrostis*, under the name *P. liebmannii* (Swallen) Sylvester & Soreng (Sylvester et al. 2020b). It is endemic to Mexico, known in the states of Hidalgo, Puebla and Veracruz (Vigosa-Mercado, 2022b). See the note under *A. exserta* for the differences between *Agrostis* and *Podagrostis* species.

Agrostis mertensii **Trin., Linnaea 10(3): 302. 1836.**

This species has a disjunct distribution in Scandinavia, Europe, Canada, Alaska to North Carolina, USA, and South America (Harvey 2007; Sylvester et al. 2020a). *Agrostis mertensii* has been reported from central Mexico (Harvey 2007; Villaseñor 2016; Dávila et al. 2018). Some authors consider that *A. ghiesbreghtii* could be a synonym of this species (Steven P. Sylvester pers. communication). We have checked descriptions and type material of *A. mertensii* and its synonyms. At first glance, *A. ghiesbreghtii* fits well in the interval of variation of *A. mertensii*, and Mexican populations could represent large and robust forms of the latter. However, we have not seen a great number of specimens of *A. mertensii*, nor studied the anatomy and micropmorphology. At this moment, we prefer to recognize *A. ghiesbreghtii* as a distinct species, until more evidence is available.

Agrostis meyenii **Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(3–4): 312. 1841.**

This species is distributed from Bolivia to Tierra del Fuego, Chile (Rúgolo and Molina 1997). *Agrostis meyenii* has been reported in the study zone from misidentified specimens of *A. tolucensis*, but is distinguished from it in the lemmas unawned or awned from the upper third, awn up to 1.2 mm long, straight, and paleas of 0.2–0.7 mm long (lemmas awned from mid-length or near the base, awn 1.5–3.5 mm long, geniculate, paleas absent or up to 0.2 mm long in *A. tolucensis*).

Agrostis novogaliciana **McVaugh, Fl. Novo-Galiciana 14: 41–42, f. 10. 1983.**

This species has recently been transferred to the genus *Podagrostis*, under the name *P. novogaliciana* (McVaugh) A.M. Soriano & Rúgolo (Molina et al. 2021). It is endemic to Jalisco, Mexico. See the note under *A. exserta* for the differences between *Agrostis* and *Podagrostis* species.

Agrostis pittieri **Hack., Oesterr. Bot. Z. 52(2): 60. 1902.**

This species is endemic to Costa Rica (Pohl and Davidse 1994). *Agrostis pittieri* has been reported in the study zone from misidentified specimens of *A. subpatens*, but differs from it in the paleas of 0.5–1 mm long (vs. paleas absent or up to 0.2 mm long in *A. subpatens*).

***Agrostis rosei* Scribn. & Merr., Bull. Div. Agrostol., U.S.D.A. 24: 21, f. 5. 1901.**

This species has recently been transferred to the genus *Podagrostis*, under the name *P. rosei* (Swallen) Sylvester & Soreng (Sylvester et al. 2020b). It is endemic to Mexico, known from the states of Durango and Zacatecas (Vigosa-Mercado, 2022b). See the note under *A. exserta* for the differences between *Agrostis* and *Podagrostis* species.

***Agrostis semiverticillata* (Forssk.) C. Chr., Dansk Bot. Ark. 4(3): 12. 1922.**

This name is a synonym of *Polypogon viridis* (Gouan) Breistr., which differs from *Agrostis* species in the spikelets disarticulating below the glumes, with a fragment of the pedicel (vs. disarticulation above the glumes).

***Agrostis tandilensis* (Kuntze) Parodi., Darwiniana 6: 158. 1943.**

This species is native to South America, introduced to USA, where it is known to occur in vernal pools in coastal zones of Monterrey, San Diego, and Solano Counties (Rúgolo 2007), outside the study zone. It has also has been reported from Baja California, Mexico (Beetle et al. 1983), but no herbarium specimens associated with this record have been found. Some authors have treated this and other South American species as part of the genus *Bromidium*. *Agrostis tandilensis* differs from other *Agrostis* species in the hairy lemmas, with lateral veins excurrent as two long teeth (vs. lemmas glabrous or with hairs only on the callus, veins not or shortly excurrent).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Acosta S (2001) *Agrostis*. In: Calderón de Rzedowski G, Rzedowski J (Eds) Flora fanerogámica del Valle de México (2nd edn.) Instituto de Ecología, A.C., Comisión Nacional para el Conocimiento y uso de la Biodiversidad, Pátzcuaro, Michoacán, 1014–1017. https://www.biodiversidad.gob.mx/publicaciones/librosDig/pdf/Indice_Flora_del_Valle_de_Mx.pdf

Beetle AA, Guzmán R, Jaramillo V, Guerrero MP, Manrique E, Chimal A, Shariff C, Núñez I (1983) Las Gramíneas de México (Vol. I) Comisión Técnico Consultiva para la Determinación de Coeficientes de Agostadero, Ciudad de México, 1–260.

Björkman SO (1960) Studies in *Agrostis* and related genera. Symbolae Botanicae Upsalienses 17: 1–112.

Carlbom CG (1967) A biosystematic study of some North American species of *Agrostis* L. and *Podagrostis* (Griesb.) Scribn. & Merr. PhD thesis, Oregon State University, Corvallis, Oregon, USA. http://hdl.handle.net/1957/47745

CCH2 Portal (2022) Consortium of California Herbaria. https://cch2.org/portal/index.php [Accessed 1.12.2022]

Clayton WD, Renvoize SA (1986) Genera graminum. Grasses of the world. Her Majesty's Stationery Office, London, 1–389.

Dauby G (2020) ConR: Computation of Parameters Used in Preliminary Assessment of Conservation Status. R package version 1.3.0. https://CRAN.R-project.org/package=ConR

Dávila P, Mejía-Saulés MT, Gómez-Sánchez M, Valdés-Reyna J, Ortiz JJ, Morín C, Castrejón J, Ocampo A (2006) Catálogo de las gramíneas de México. Universidad Nacional Autónoma de México, Comisión para el Conocimiento y Uso de la Biodiversidad, Mexico City, 1–671.

Dávila P, Mejía-Saulés MT, Soriano-Martínez AM, Herrera-Arrieta Y (2018) Conocimiento taxonómico de la familia Poaceae en México. Botanical Sciences 96(3): 462–514. https://doi.org/10.17129/botsci.1894

Dorr LJ (2014) Flora of Guaramacal (Venezuela): Monocotyledons. Smithsonian Contributions to Botany (Vol. 100) Smithsonian Institution, Washington, D.C., 1–289. https://doi.org/10.5479/si.19382812.100

Ellis RP (1976) A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. Bothalia 12(1): 65–109. https://doi.org/10.4102/abc.v12i1.1382

Ellis RP (1979) A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12(4): 641–671. https://doi.org/10.4102/abc.v12i4.1441

Espejo-Serna A, López-Ferrari AR, Valdés-Reyna J (2000) Poaceae. Las monocotiledóneas mexicanas, una sinopsis florística. Lista de referencia Partes IX a XI. Pandanaceae a Zosteraceae. Consejo Nacional de la Flora de México, A.C., Universidad Autónoma Metropolitana, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, 7–236.

Ferrusquía-Villafranca I (1993) Geology of Mexico: A Synopsis. In: Ramamoorthy TP, Bye R, Lot A, Fa J (Eds) Biological diversity of Mexico: Origins and distribution. Oxford University Press, New York, 3–107.

Fournier E (1886) Mexicanas Plantas, pars secunda, Gramineae. Ex Typographeo Reipublicae, Paris, 1–160. https://doi.org/10.5962/bhl.title.475

García E (2004) Modificaciones al sistema de clasificación climática de Köppen. Universidad Nacional Autónoma de México, Instituto de Geografía: Ciudad de México, 1–90. http://www.publicaciones.igg.unam.mx/index.php/ig/catalog/book/83

GBIF (2023a) *Agrostis elliottiana* Schult. https://doi.org/10.15468/dl.z6ex48 [Accesed 27.7.2023]

GBIF (2023b) *Agrostis idahoensis* Nash. https://doi.org/10.15468/dl.shx37k [Accesed 27.7.2023]

GBIF (2023c) *Agrostis microphylla* Steud. https://www.gbif.org/occurrence/1894824218 [Accesed 27.7.2023]

GBIF (2023d) *Agrostis stolonifera* L. https://doi.org/10.15468/dl.qez3gb [Accesed 29.7.2023]

Gollotte A, Van Tuinen D, Atkinson D (2004) Diversity of arbuscular mycorrhizal fungi colonising roots of the grass species *Agrostis capillaris* and *Lolium perenne* in a field experiment. Mycorrhiza 14(2): 111–117. https://doi.org/10.1007/s00572-003-0244-7

Harvey MJ (2007) *Agrostis*. In: Barkworth ME, Capels KM, Long S, Anderton LK, Piep MB (Eds) Flora of North America North of Mexico (Vol. 24) Oxford University Press, New York, 633–662. http://floranorthamerica.org/Agrostis

Herrera-Arrieta Y (2001) Las gramíneas de Durango. Instituto Politécnico Nacional, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, 1–478.

Herrera-Arrieta Y, Peterson PM (2018) Grasses of Chihuahua, Mexico. Smithsonian Contributions to Botany (Vol. 107) Smithsonian Institution, Washington, D.C., 1–380. https://doi.org/10.5479/si.1938-2812.107

Herrera-Arrieta Y, Peterson PM, Cortés A (2010) Gramíneas de Zacatecas. Sida Botanical Miscellany (Vol 32) Botanical Research Institute of Texas, Fort Worth, Texas, 1–239. https://repository.si.edu/handle/10088/9724

Hitchcock AS (1905) North American species of *Agrostis*. United States Department of Agriculture Bureau of Plant Industry Bulletin 68: 1–68.

Hitchcock AS (1913) Mexican grasses in the United States National Herbarium. Contributions from the United States National Herbarium 17: 181–389. https://www.jstor.org/stable/23492202

Hitchcock AS (1920) The genera of grasses of the United States, with special reference to the economic species. Bulletin of the United States Department of Agriculture 772: 1–307. https://doi.org/10.5962/bhl.title.64674

Hitchcock AS (1937) *Agrostis*. In: Britton NL (Ed.) North American Flora (Vol. 17(7)). New York Botanical Garden, New York, 515–534.

Idárraga-Piedrahita A, Ortiz RC, Callejas-Posada R, Merello M [Eds] (2011) Listado de las plantas vasculares del departamento de Antioquia. In: Flora de Antioquia: Catálogo de las Plantas Vasculares (Vol. 2) Universidad de Antioquia, Medellín, 127–923. https://www.tropicos.org/projectimages/Antioquia/Flora%20Antioquia%20Vol%20II.pdf

INEGI (2022) Mapa Digital de México V.6. Instituto Nacional de Geografía y Estadística http://gaia.inegi.org.mx/mdm6/

IUCN (2012) IUCN Red list categories and criteria: Version 3.1. Second edition. International Union for Conservation of Nature, Gland, Switzerland, 1–32. https://portals.iucn.org/library/node/10315

Jarvis CE (1992) Seventy-two proposals for the conservation of types of selected Linnaean generic names, the report of subcommittee 3C on the lectotypification of Linnaean generic names. Taxon 41(3): 552–583. https://doi.org/10.2307/1222833

Jarvis CE (2007) Order out of chaos. Linnaean plant names and their types. The Linnaean Society of London and Natural History Museum, London, 1–1016.

Linnaeus C (1737) Genera Plantarum. Conradum Wishoff, Leiden, 1–384. https://doi.org/10.5962/bhl.title.70902

Linnaeus C (1753) Species Plantarum. Impensis Laurentii Salvii, Stockholm, 1–560. https://doi.org/10.5962/bhl.title.669

Llorente J, Ocegueda S (2008) Estado del conocimiento de la biota. In: Sarukhán J (Ed.) Capital natural de México I: conocimiento actual de la biodiversidad. Comisión para el Conocimiento y Uso de la Biodiversidad, Mexico City, 283–322. https://bioteca.biodiversidad.gob.mx/janium/Documentos/6456.pdf

Luteyn JL (1999) Páramos, a checklist of plant diversity, geographical distribution, and botanical literature. Memoirs of the New York Botanical Garden (Vol. 84). New Work Botanical Garden, New York, 1–278.

McNeill J, Odell EA, Consaul LL, Katz DS (1987) American code and later lectotypifications of Linnaean generic names dating from 1753: A case study of discrepancies. Taxon 36(2): 350–401. https://doi.org/10.2307/1221430

McVaugh R (1983) Gramineae. In: Anderson WR (Ed.) Flora Novo-Galiciana (Vol. 14) Michigan University Press, Ann Arbor, Michigan, 1–436.

Mejía-Saulés MT, Dávila P (1992) Gramíneas útiles de México. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, 1–298.

Microsoft Corporation (2022) Microsoft Excel. https://office.microsoft.com/excel

Molina AM, Rúgolo ZE, Ferrero MA, Palacio PC, Guerreiro C, Vega AS (2021) Taxonomic revision of the genus *Podagrostis* (Poaceae, Pooideae, Poeae). Annals of the Missouri Botanical Garden 106: 245–270. https://doi.org/10.3417/2021642

Orton LM, Barberá P, Nissenbaum MP, Peterson PM, Quintanar A, Soreng RJ, Duvall MR (2021) A 313 plastome phylogenomic analysis of Pooideae: Exploring relationships among the largest subfamily of grasses. Molecular Phylogenetics and Evolution 159: 107110. https://doi.org/10.1016/j.ympev.2021.107110

Pacheco D, Dávila P, Mejía-Saulés MT (2012) Poaceae. In: García-Mendoza A, Meave J (Eds) Diversidad Florística de Oaxaca. Universidad Nacional Autonoma de Mexico, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, 339–349.

Peterson PM, Sylvester SP, Romaschenko K, Soreng RJ, Barberá P, Quintanar A, Aedo C (2020) A phylogeny of species near *Agrostis* suporting the recognition of two new genera, *Agrostula* and *Alpagrostis* (Poaceae, Pooideae, Agrostidinae) from Europe. PhytoKeys 167: 57–82. https://doi.org/10.3897/phytokeys.167.55171

Philipson WR (1937) A revision of the British species of the genus *Agrostis* Linn. Journal of the Linnean Society. Botany 51: 73–15. https://doi.org/10.1111/j.1095-8339.1937.tb01905.x

Pohl RW, Davidse G (1971) Chromosome numbers of Costa Rican grasses. Brittonia 23(3): 293–324. https://doi.org/10.2307/2805632

Pohl RW, Davidse G (1994) *Agrostis*. In: Davidse G, Sousa Sánchez M, Chatter AO (Eds) Flora Mesoamericana (Vol. 6) Instituto de Biología, Universidad Nacional Autonoma de Mexico, Mexico City, 237–240. http://legacy.tropicos.org/NamePage.aspx?nameId=40034657&projectId=3

Portal de Biodiversidad de Guatemala (2022) Bienvenidos al Portal de Biodiversidad de Guatemala. https://biodiversidad.gt/portal/index.php [Accessed 1.12.2022]

QGIS.org (2022) QGIS Geographic Information System. Version 3.22. QGIS Association. http://www.qgis.org [Accessed 1.12.2022]

Renvoize SA (1998) Gramíneas de Bolivia. Royal Botanical Gardens, Kew, 1– 644.

Romero-García AT, Blanca-López G, Morales-Torres C (1988) Revisión del género *Agrostis* L. (Poaceae) en la península Ibérica. Ruizia (Vol. 7) Real Jardín Botánico, Madrid, 5–160. https://bibdigital.rjb.csic.es/idurl/1/1525839

Royen A (1740) Florae Leydensis Prodromus. Samuelen Luchtmans academiae typographum, Leiden, 1–538. https://doi.org/10.5962/bhl.title.693

Rúgolo ZE (1982) Revalidación del género *Bromidium* Nees et Meyen emend. Pilger (Gramineae). Darwiniana 24: 187–216. https://www.jstor.org/stable/23216517

Rúgolo ZE (2007) *Bromidium*. In: Barkworth ME, Capels KM, Long S, Anderton LK, Piep MB (Eds) Flora of North America North of Mexico (Vol. 24) Oxford University Press, New York, 633–662. http://floranorthamerica.org/Bromidium

Rúgolo ZE, Molina AM (1997) Las especies del género *Agrostis* L. (Gramineae: Agrostideae) de Chile. Gayana. Botánica 54: 91–156. http://www.biodiversitylibrary.org/item/91363

Rzedowski J (1991) Diversidad y orígenes de la flora fanerogámica de México. Acta Botánica Mexicana 14(14): 3–21. https://doi.org/10.21829/abm14.1991.611

Saarela JM, Liu Q, Peterson PM, Soreng RJ, Paszko B (2010) Phylogenetic of the grass Aveneae-type plastid DNA clade (Poaceae: Pooideae, Poeae) based on plastid and ribosomal DNA sequence data. In: Seberg O, Petersen G, Barfod AS, Davis JI (Eds) Diversity, phylogeny, and evolution in the monocotyledons. Aarhus University Press, Aarhus, Denmark, 557–587.

Saarela JM, Bull RD, Paradis MJ, Ebata SN, Peterson PM, Soreng RJ, Paszko B (2017) Molecular phylogenetics of cool-season grasses in the subtribes Agrostidinae, Anthoxanthinae, Aveninae, Brizinae, Calothecinae, Koeleriinae and Phalaridinae (Poaceae, Pooideae, Poeae, Poeae chloroplast group 1). PhytoKeys 87: 1–139. https://doi.org/10.3897/phytokeys.87.12774

Sánchez-Ken JG (2019) Riqueza de especies, clasificación y listado de las gramíneas (Poaceae) de México. Acta Botánica Mexicana 126: e1379. https://doi.org/10.21829/abm126.2019.1379

Sánchez-Ken JG, Cerros-Tlatilpa R (2016) Listado florístico de la familia Poaceae en el estado de Morelos, México. Acta Botánica Mexicana 116(116): 65–105. https://doi.org/10.21829/abm116.2016.1119

SEINet (2022) Arizona-New Mexico Chapter. https://swbiodiversity.org/seinet/index.php [Accessed 1.12.2022]

Soreng RJ, Peterson PM (2003) *Agrostis*. In: Soreng RJ, Peterson PM, Davidse G, Judziewicz EJ, Zuloaga FO, Filgueiras TS, Morrone O (Eds) Catalogue of New World Grasses (Poaceae): IV. Subfamily Pooideae. Contributions from the United States National Herbarium 48: 42–89. https://archive.org/details/mobot39088011697067

Soreng RJ, Peterson PM, Zuloaga FO, Romaschenko K, Clark LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA, Li DZ, Davidse G (2022) A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. Journal of Systematics and Evolution 60(3): 476–521. https://doi.org/10.1111/jse.12847

Sylvester SP, Cuta-Alarcón LE, Bravo-Pedraza WJ, Soreng RJ (2020a) *Agrostis* and *Podagrostis* from páramos of Boyacá, Colombia: Synoptic taxonomy including a key to Colombian species. PhytoKeys 151: 107–160. https://doi.org/10.3897/phytokeys.151.50538

Sylvester SP, Peterson PM, Romaschenko K, Bravo-Pedraza WJ, Cuta-Alarcon LE, Soreng RJ (2020b) New combinations and updated descriptions in *Podagrostis* (Agrostidinae, Poaceae) from the Neotropics and Mexico. PhytoKeys 148: 21–50. https://doi.org/10.3897/phytokeys.148.50042

Templeton AR (1989) The meaning of species and speciation: A genetic perspective. In: Otte D, Endler JA (Eds) Speciation and its Consequences. Sinauer Associates, Sunderland, Massachusetts, 3–27.

Thiers B (2022) Index herbariorum. New York Botanical Garden. http://sweetgum.nybg.org/science/ih/ [Accessed 1.12.2022]

Tkach N, Schneider J, Döring E, Wölk A, Hochbach A, Nissen J, Winterfeld G, Meyer S, Gabriel J, Hoffmann MH, Röser M (2020) Phylogenetic lineages and the role of hybridization as driving force of evolution in grass supertribe Poodae. Taxon 69(2): 234–277. https://doi.org/10.1002/tax.12204

TORCH (2022) Texas Oklahoma Regional Consortium of Herbaria. https://portal.torcherbaria.org/portal/index.php [Accessed 1.12.2022]

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW JMcNeill J, Monro AM, Prado J, Price MJ, Smith GF [Eds] (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress, Shenzhen, China, July 2017. Regnum Vegetabile (Vol. 159) Koeltz Botanical Books, Glashütten, 1–254. https://doi.org/10.12705/Code.2018

Valdés-Reyna J (2015) Gramíneas de Coahuila. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, 1–556.

Vigosa-Mercado JL (2017) Poaceae, subfamilia Pooideae. In: Medina-Lemos R (Ed.) Flora del Valle de Tehuacán-Cuicatlán (Vol. 138) Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, 1–121.

Vigosa-Mercado JL (2022a) Typification of names in Mexican species of Pooideae (Poaceae). Phytoneuron 2022–44: 1–4. https://www.phytoneuron.net/wp-content/uploads/2022/10/44PhytoN-PooideaeLectotypes.pdf

Vigosa-Mercado JL (2022b) Un nuevo registro de *Podagrostis* (Poaceae, Pooideae, Poeae) para México. Acta Botánica Mexicana 129: 1993. https://doi.org/10.21829/abm129.2022.1993

Vigosa-Mercado JL, Ruiz-Sánchez E (2020) Familia Gramineae, Subfamilia Pooideae. In: Rzedowski J, Hernández-Ledesma P (Eds) Flora del Bajío y de Regiones Adyacentes (Vol. 219) Instituto de Ecología, A.C., Pátzcuaro, Mexico, 1–214. https://doi.org/10.21829/fb.311.2020.219

Villaseñor JL (2016) Checklist of the native vascular plants of México. Revista Mexicana de Biodiversidad 87(3): 559–902. https://doi.org/10.1016/j.rmb.2016.06.017

Ward DB (2007) Thomas Walter typification project, IV: Neotypes and epitypes for 43 Walter names, of genera A through C. Journal of the Botanical Research Institute of Texas 1(2): 1091–1100. https://www.jstor.org/stable/41971537

Widén KG (1971) The genus *Agrostis* L. in eastern Fennoscandia. Taxonomy and distribution. Flora Fennica 5: 1–209. http://hdl.handle.net/10138/36219

Supplementary material 1

Other heterotypic synonyms

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Research Article

A new species of *Schlegelia* (Schlegeliaceae) from wet montane forest of Colombia and a key for the species of the genus

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Abstract

In this paper we describe and illustrate *Schlegelia longirachis* a new species from montane forest remnants (1200–1900 m) in the Western slope of the Eastern Cordillera of Colombia ("Serranía de Las Quinchas" and Virolín county) in the Departments of Boyacá and Santander. A root-climbing liana, the new species is contrasted to *S. fuscata*, *S. monachinoi* and *S. parviflora*, the three most morphologically similar species of *Schlegelia*. This new species is differentiated from its putative close relatives by vegetative (texture, colour, pubescence and shape in leaves, bracts, bracteoles pedicel, calyx and corolla), inflorescences as well as floral characters (staminode absent). We provide an updated key to 24 known species of *Schlegelia*. For the identification key, *S. fuscata* and *S. roseiflora* are regarded here as different from *S. parviflora*. *S. urbaniana* is considered a synonym of *S. axillaris*, whereas *S. fastigiata* is separated from *S. sulphurea* as a recognizable species. *Schlegelia* has its center of distribution in Colombia, where 17 of the species are known to occur.

Resumen

En este artículo se describe e ilustra *Schlegelia longirachis* una nueva especie de los remanentes de bosques montanos húmedos (1200–1900 m) localizados en la vertiente occidental de la Cordillera Oriental de Colombia, en la Serranía de Las Quinchas y corregimiento de Virolín, en los departamentos de Boyacá y Santander (respectivamente). Esta nueva especie es una liana trepadora por raíces, la cual comparte varias similaridades con *S. fuscata*, *S. monachinoi* y *S. parviflora*. Sin embargo, difiere de estas especies en la textura, colores, pubescencia, forma de las hojas, brácteas, bractéolas, pedicelo, cáliz y corola, en el tipo de inflorescencia y por la ausencia del estaminodio. Se presenta una clave actualizada para diferenciar las especies del género *Schlegelia*. Para la clave, en un contexto geográfico y taxonómico, *S. fuscata* y *S. roseiflora* son tratadas como especies diferentes de *S. parviflora*. Por otra parte, *S. urbaniana* es considerada un sinónimo de *S. axillaris* y *S. fastigiata* es separada de *S. sulphurea*, y es reconocida como una especie válida. La presente contribución incrementa a 24 las especies de *Schlegelia*, 17 de éstas se conocen en Colombia, el país con la mayor diversidad del género.

Key words: Climbing plants, Flora of Colombia, Lamiales, lianas, montane wet forests, Serranía de Las Quinchas, Virolín

Palabras clave: plantas trepadoras, Flora de Colombia, Lamiales, lianas, bosques húmedos montanos, Serranía de Las Quinchas, Virolín

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Introduction

Schlegelia comprises 24 species (including the new species described herein), as presently circumscribed in the key provided here. The genus occurs from the states of Chiapas, Oaxaca and Veracruz in Mexico (i.e., *S. nicaraguensis* Standl.; *sensu* Villaseñor Ríos 2016), the Antilles (i.e., *S. parasitica* (Sw.) Miers ex Griseb.), Central America, the Chocó Region, and Northern South America from the Guayana Shield to the Amazonia of Brazil, Colombia, Peru and Venezuela; at elevations from sea level to 2100 m (Gentry 1973, 1977, 1982a, 1982b, 1997, 2001, 2009). The genus is recognized by its conspicuous climbing habit, which consists of lianas climbing by adventitious roots, without tendrils (Gentry 1973, 1980). Its leaves are simple, with axillary pseudostipules (prophylls). The inflorescences are axillary racemes or terminal thyrses. Calyces are cupular or irregularly lobed. Corollas are tubular, tubular-campanulate infundibuliform-campanulate or hypocrateriform-campanulate. Petals are white, pink, red, yellow, or purple. Ovaries have an incompletely bilocular placenta. The fruit is a globose berry, up to 5 cm diam., with a persistent calyx (Gentry 1980, 2009).

Schlegelia was described from a collection made by Hendrick C. Focke, a Dutch Guianan lawyer, botanist, and ethnologist, who made numerous plant collections in Suriname between 1835–1850 (Pulle 1906). He sent his collections to Freidrich A. W. Miquel, who described the genus along with *S. lilacina* Miquel [= S. violacea (Aubl.) Griseb.; Miquel, 1844]. From its inception the relationships of *Schlegelia* were not clear; Miquel described the genus under the tribe Crescentiaeae as conceived by Endlicher (1839). Crescentieae was considered part of Gesneriaceae by Endlicher and consequently Miquel. However, Don, De Candolle, Martius and Fenzl considered Crescentieae part of Bignoniaceae (Miquel 1844).

Schlegelia, currently belongs into its own family, the Schlegeliaceae Reveal (1995: 74–75), a Neotropical family that includes four genera, two of them monotypic: *Exarata* Gentry (*E. chocoensis* A. H. Gentry), from the Chocó Region, and *Synapsis* Griseb. (*S. ilicifolia* Griseb.) from Cuba; and two relatively larger genera *Gibsoniothamnus* L.O.Williams (ca. 10 species) distributed in Mesoamerica and the Antilles, and *Schlegelia* Miq. (1844: 785). Before Schlegeliaceae was considered as a formal family by Reveal (1995), A. H. Gentry had proposed a new tribe Schlegelieae Gentry of the Bignoniaceae (Gentry 1980). The tribe was suggested as it was difficult to place these genera within Bignoniaceae or Scrophulariaceae (Gentry 1980; Armstrong 1985). Phylogenetic analyses confirmed Schlegeliaceae as monophyletic and distinct from Bignoniaceae and Scrophulariaceae (Spangler and Olmstead 1999; Olmstead et al. 2009). The most recent phylogenetic reconstruction based on chloroplast and nuclear genes place Schlegeliaceae (a) sister to Martyniaceae and Thomandersiaceae (BS<90, Liu et al. 2020); (b) sister to a clade including Pedaliaceae, Lentibulariaceae, Acanthaceae, Bignoniaceae and Verbenaceae (BS=98, 80 cp genes, Fonseca 2021); or (c) sister to Bignoniaceae and Verbenaceae (BS=65, 410 nuclear genes, Fonseca 2021). The relationship of Schlegeliaceae to other families of Lamiales is still not well understood; a better sampling of the family within molecular phylogenetic analyses should shed some light on the placement of Schlegeliaceae within this diverse order.

No comprehensive monograph of *Schlegelia* has been completed to date, although the genus has been treated largely as part of Bignoniaceae for Flora of Panama (Gentry 1973), Flora of Ecuador (Gentry 1977), Flora de Venezuela (Gentry 1982a), Flora de Veracruz (Gentry 1982b), Flora of the Venezuelan Guayana (Gentry 1997), Flora of Costa Rica (Burger and Barringer 2000), Flora de Nicaragua (Gentry 2001), Flora de Colombia (Gentry 2009) and Manual de Plantas de Costa Rica (Morales 2015). In addition, the genus has been treated in: Checklist of the plants of the Guiana Shield (Funk et al. 2007), Catálogo de las plantas vasculares nativas de México (Villaseñor Ríos 2016), Catalogue of seed plants of the West Indies (Acevedo-Rodriguez and Strong 2023), and Catálogo de plantas y líquenes de Colombia (Gradstein 2016).

The present work describes and illustrates a new species of *Schlegelia*, found in an isolated population located in highly fragmented montane forest. This new species was detected during the academic fieldwork conducted by "Herbario de la Universidad Militar Nueva Granada" (UMNG-H). Currently, the distribution of this new species is known only from "Serranía de Las Quinchas" and "Virolín" region, in Municipalities of Otanche and Charalá, Boyacá and Santander departments. Further botanical explorations of the area and the nearby municipalities are expected to uncover additional populations of this species as they share similar habitats. The present contribution increases to 24 the number of *Schlegelia* species, 17 of them known from Colombia, the country with the highest diversity of the genus.

Materials and methods

We examined 120 herbarium specimens of *Schlegelia* from South America deposited at "Herbario de la Universidad Nacional de Colombia" (COL). In addition, all type specimens, as well as general collections, hosted by virtual herbaria, were consulted, including those maintained by the Field Museum (F; http://emuweb.fieldmuseum.org/botany/taxonomic.php), Instituto Nacional de Pesquisas da Amazônia (INPA; http://inct.florabrasil.net/en/), JSTOR Global Plants (http://plants.jstor.org), Museum of Natural History, Paris (P; http://www.mnhn.fr), Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/), speciesLink (https://specieslink.net/), Smithsonian Institution (US; https://collections.si.edu/search/), Universidad de Antioquia, Colombia (HUA; http://www2.udea.edu.co/herbario/paginas/consultas/consultarEjemplares.iface), Universidad Nacional Autónoma de México (MEXU; https://datosabiertos.unam.mx/biodiversidad/), and the National Herbarium of The Netherlands (U; https://www.nationaalherbarium.nl/). The herbarium codes after Thiers (2019).

This publication is based on morphological assessments of herbaria collections. The description of the new species is based on field observations (flower and fruit material was preserved in ethanol) as well as on herbaria specimens. The flowers from herbaria specimens were rehydrated for three days before measuring using a 1:1 combination of glycerin and 0.9 NaCl solution.

Plants of the World (POWO, https://powo.science.kew.org) and taxonomic literature on *Schlegelia* were consulted to assemble the species key; in particular, Bignoniaceae for Flora of Panama (Gentry 1973), Flora of Ecuador (Gentry 1977), Flora of Venezuela (Gentry 1982a), Flora of Venezuelan Guayana (Gentry 1997) and Flora of Colombia (Gentry 2009). The Catálogo de plantas y líquenes de Colombia (Gradstein 2016) was also reviewed. Additionally, the International Plant Names Index (https://www.ipni.org/), the online botany collections of the Smithsonian National Museum of Natural History (https://naturalhistory.si.edu/research/botany), and Tropicos (http://legacy.tropicos.org/Home.aspx) were consulted to update the current nomenclature and geographical information. Terminology for vegetative characters, inflorescences, flowers, and fruit morphology follow Gentry (1977, 2009) and Font-Quer (2001).

To determine the conservation status (according to IUCN categories and criteria; IUCN Standards and Petitions Committee 2022), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Bachman et al. 2011), which is continually updated (https://geocat.kew.org/). The EOO is defined by the IUCN Standards and Petitions Committee (2022) as the minimum convex polygon encompassing all known occurrences of a species. In addition, AOO is the area within the EOO, which is comprised of 2 × 2 km grid cells containing known occurrences records.

Taxonomic treatment

Schlegelia longirachis **Aymard & M.A.Jaram., sp. nov.**
urn:lsid:ipni.org:names:77325154-1

Type. Colombia. Boyacá. Municipio Otanche. Serranía de Las Quinchas, sector la Y, Finca Lote Terreno, 5°41'42.6"N, 74°19'37.5"W, 1200 m, 26 Oct 2022 (fl, fr). *M. Alejandra Jaramillo*, *Andrés F. Majin-Ladino*, *Lucindo Galvis & estudiantes de Taxonomía vegetal 2022-1*. (Holotype: COL!; Isotypes: UMNG-H!, HUA!). Figs 1, 2.

Schlegelia longirachis resembles *S. monachinoi*, but can be differentiated from this species by the longer internodes, 4–8cm long in *S.longirachis*, vs. 1.5–4.5cm in *S. monachinoi*. The leaf blades densely black punctuated on the adaxial surface, vs. sparsely punctuated towards the base of the blade on both surfaces in *S. monachinoi*. The inflorescences are longer 4–18 cm long in *S. longirachis*, vs. 3–11 cm in *S. monachinoi*. Bracts are oblong vs. lanceolate-triangular in *S. monachinoi*.

Description. ***Root-climbing liana*** internodes 4–8 cm long, ca. 3cm in diameter, pale brown when dry, branches sparsely lenticelate. ***Leaves*** simple, opposite; petioles 12–20 mm long, glabrous; leaf blade lanceolate, lanceolate-elliptic, rarely oblanceolate, 4–22 × (3.2) 4.5–9 cm; coriaceous, densely black punctuated on the adaxial surface (Fig. 1C), glabrescent or with simple trichomes located near base and in the midrib on the abaxial surface (Fig. 1B), base obtuse-rounded or cuneate, apex rounded or acute, margins entire, black-brown upon drying; venation brochidodromous, midrib prominent on the abaxial surface, 6–7 pairs of secondary veins, the tertiary veins conspicuously reticulate on the abaxial surface. ***Inflorescence*** axillary, narrowly thyrsic with dichasial partial inflorescences; rachis puberulous to sparsely adpressed pubescent (5–12 cm long in flower, 12–18 cm long in fruit); flowers 14–20, produced in long-peduncled, 2–3-flowered dichasia along the rachis, each flower subtended by a bract and 2 bracteoles (Fig.

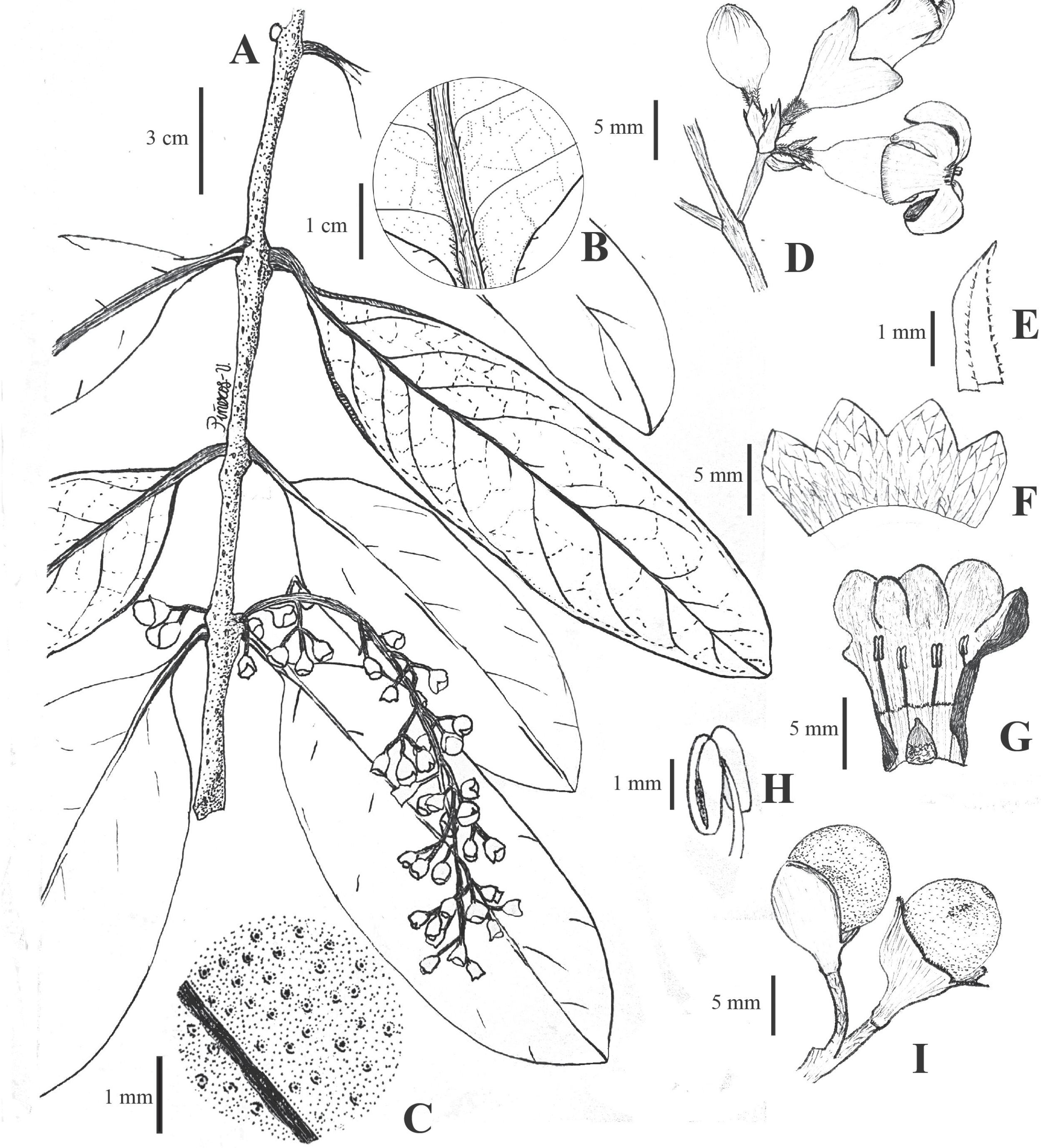

Figure 1. *Schlegelia longirachis* **A** a flowering branch **B** detail of the leaf abaxial surface **C** detail of the leaf adaxial surface showing the black punctations **D** inflorescence showing the bract and bracteoles **E** bract **F** calyx extended **G** corolla and adnate stamens extended **H** detail of a stamen **I** fruits. Illustration by Paola Piñeros.

1D), bracts 2–3 mm long, oblong, glabrous, ciliate at the margins; bracteoles ca. 1 mm long, triangular, ciliate at the margins; pedicels 3.5–4.5 mm in flower, 7.5–8.5 in fruit, adpressed pilose. ***Calyx*** cupular ca. 6 × 5 mm, bilabiate fused, 4-lobed, lobes oblong, 2–2.5 (3.2) mm long, apex rounded-acute, white, sparsely puberulent and with white disk-shape glands on the outer surface (visible in dry collections), glabrous and reticulate veined inside. ***Corolla*** campanulate-hypocrateriform with 5 reflexed lobes, white, deep pink at

Figure 2. *Schlegelia longirachis* **A** a flowering branch **B** detail of the inflorescence. Photos by Andrés Majín.

the throat (Fig. 2B); tube 7–8 mm long, ca. 4 mm wide in the mouth; lobes 3–4 × 3 mm, glabrous inside, minutely puberulous outside. ***Stamens*** didynamous (Fig. 1H), subexserted, filament 3–4 mm long, pilose at the base, inserted at ca. 4 mm from base of corolla; anthers ca. 1.5 mm long, oblong, glabrous; staminode absent. ***Pistil*** with conical ovary, ca. 1.5 × 1.5 mm, glabrous; nectariferous disk fused and not clearly differentiated from the ovary base. ***Fruit*** a berry, 6.6–8 mm in diam., spherical, drying black, glabrous with conspicuous papillae, covered to the middle by a persistent calyx (Fig. 1I, 2B). **Seeds** not seen.

Phenology. Collected in flower in March, and in flower and fruit in October.

Etymology. The specific epithet refers to the long rachis of the inflorescences that is present in this new species. The long rachis of *S. longirachis* displays the flowers away from the foliage, a characteristic that may have some bearing on the pollination strategy of the species.

Distribution and habitat. The species is known to occur in montane forest remnants between 1200 and 1900 m. In the type locality, *S. longirachis* grows in forest consisting of medium to tall trees.

Conservation status. This species is known only from the type and two additional localities; however, it is reported here as a very rare species. It should be regarded as Endangered (EN) due to the low number of known localities, its estimated Area of Occupancy (AOO) of 12,000 km^2, and its estimated Extent of Occurrence (EOO) of 755,768 km^2 (IUCN Standards and Petitions Committee 2022). Additionally, the conservation of these forests is at risk due the continuous deforestation and degradation of the "Serranía de Las Quinchas" and their surrounding areas on middle Magdalena river, and the Virolín Region (Galindo-T. et al. 2003) especially in the years during the pre- and post-conflict period (peace agreement was signed in 2017). The expansion of deforestation, degradation and water pollution continues (Salgado et al. 2022), with significantly greater agricultural use, pasture, selective logging, illicit crops and mining (Restrepo et al. 2021). Although conservation status assessments can be made for species with such small numbers of collections (Rivers et al. 2011), it may be difficult to assess whether the appearance of rarity in a species is due to the lack of, or outdated, data, or to its actual rarity (Verspagen and Erkens 2022). Fortunately, the area where *S. longirachis* occurs is protected as part of the Regional Natural Park Serranía de las Quinchas (Stiles and Bohórquez 2000; Bohorquez-Osorio et al. 2020) and Fauna and Flora Santuary Guanentá-Alto Rio Fonce (Galindo-T. et al. 2003).

Additional specimens. Colombia. Santander. Municipio de Charalá. Corregimiento de Virolín. Vereda El Reloj, Camino a Olival, aprox. 6°08'N, 73°20'W, 1680–1700 m, 03 Mar 1981, *S. Díaz Piedrahita 2273* (COL); Municipio de Charalá, Virolín, Vereda Palmar, 6°03'44.8"N, 73°12'50.4"W, 1894 m, 06 Oct 2009, *M. Blanco et al. 53* (COL).

Notes. The species described here is morphologically similar to three taxa *S. fuscata* A. H. Gentry *S. monachinoi* Moldenke and *S. parviflora* as characterized in Table 1. However, it is most similar to *S. monachinoi* from the Andean wet forests in Colombia, Ecuador and Venezuela (Gentry 1977, 1982a, 2009). Both species have elongate, narrow axillary thyrses, the corolla and lobes lilac inside and fruit 0.5–2.5 cm in diam. *S. longirachis* differs from *S. monachinoi* in the characters presented in diagnosis. The new species can be distinguished with the key to the species presented below.

Table 1. Comparison of diagnostic morphological characters of *Schlegelia longirachis*, with morphologically similar species. [1]In the *S. monachinoi* description, H. Moldenke mentioned that the bract is lanceolate, 2–5 mm long (Moldenke 1949). However, Gentry (2009) quoted that the bract is triangular, 1–2 mm long. Our examination of the type material deposited in COL confirmed the Gentry´s observation.

Character	*S. longirachis*	*S. fuscata*	*S. monachinoi*	*S. parviflora*
Leaves	3–9 cm wide, lanceolate, lanceolate-elliptic, rarely oblanceolate, coriaceous, with simples trichomes on the abaxial surface, black-brown when dry, base obtuse-rounded or cuneate	5–12 cm wide, widely-elliptic to elliptic, oblanceolate, rigid-coriaceous, with lepidote trichomes and disk-shape glands located near base of midrib on the abaxial surface, brown when dry, base truncate or widely-cuneate	5–11 cm wide, elliptic, oblanceolate, rarely narrowly ovate, rigid-coriaceous, with lepidote trichomes and disk-shape glands located near base of midrib on the abaxial surface, yellowish when dry, base acute	4.5–15 cm wide, obovate or elliptic-obovate, coriaceous, glabrescent or with lepidote trichomes and disk-shape glands located near base of midrib on the abaxial surface, olive green or brown when dry, base cuneate
Inflorescences	4–18 cm long, elongate, racemose to narrowly paniculate, puberulent or glabrous	1–(4)–5 cm long, shorter, racemose or narrowly subpaniculate, inconspicuous puberulent	4–15 cm long, elongate, racemose to narrowly paniculate, densely hirsute-puberulent (with lax trichomes)	2–5 cm long, shorter, contracted panicle, almost often fasciculate, glabrous to inconspicuous puberulent
Bract	2–3 mm long, oblong, sparsely puberulent outside, ciliate at the margins	2–5 mm long, lanceolate, glabrous on both sides, ciliate at the margins	1–2 mm long, triangular[1], densely puberulous on both sides, short-puberulous along the margins	1–2 mm long, subulate, short-puberulous at least along the margins
Calyx	ca. 6 × ca. 5 mm, basally fused, 3–4-lobes, sparsely puberulent outside, brown when dried	6–7 × 5–6 mm, 3–5-lobed, inconspicuous lepidote, puberulent at the apex outside, black when dried	4–6 × 3--5 mm, 2–3-lobed, inconspicuous lepidote or subpuberulous at least in the base, yellowish-brown when dried	4–6 × 3–5 mm, 2–3-lobed, glabrescent or inconspicuous lepidote or subpuberulous at least in the base, brown when dried
Corolla	7–8 mm long, 4 mm wide in the mouth, campanulate-hypocrateriform, lilac inside, lobes 3–4 mm long, minutely (not-glandular) puberulous outside	10–11 mm long, 4 mm wide in the mount, tubular, lilac inside, lobes 3–4 mm long, glandular-lepidote to glandular puberulous inside	10–12 mm long, 5 cm wide in the mount, tubular, lilac inside, lobes ca. 5 mm long, glandular-lepidote to glandular puberulous inside	10–12 mm long, 5 cm wide in the mount, tubular, yellow inside, lobes 4–6 mm long, glandular-lepidote to glandular puberulous inside
Staminode	Absent	Present	Present	Present

[1]In the *S. monachinoi* description, H. Moldenke mentioned that the bract is lanceolate, 2–5 mm long (Moldenke 1949). However, Gentry (2009) quoted that the bract is triangular, 1–2 mm long. Our examination of the type material deposited in COL confirmed the Gentry´s observation.

Key to the species of *Schlegelia*

Modified from Gentry (2009) species indicated with an asterisk (*) are endemic to Colombia.

Careful analysis of the literature and herbarium specimens led us to deem *Schlegelia fuscata* A. H. Gentry and *S. roseiflora* Ducke to be different from *S. parviflora* (Oerst.) Monach (see Table 1). *Schlegelia urbaniana* K. Schum. ex Duss is considered a synonym of *S. axillaris* Griseb., whereas *S. fastigiata* Schery in separated from *S. sulphurea* Diels as a recognizable species.

1 Inflorescences cauliflorous, ramiflorous..**2**
– Inflorescences terminal or axillary **10**
2 Corolla tubular-campanulate, > 3.5 cm long, ca. 1.1 cm wide at the mouth of the tube, purple or magenta, rarely white; lobes > 5 mm long; fruit ca. 4 cm diam...**3**
– Corolla tubular or narrowly tubular, 0.8–2.5 cm long, 0.2–0–4 cm wide at the mouth of the tube, white with apex pink, yellow, red or orange; lobes 1–4 mm long; fruit 1–1.5 cm diam. **4**
3 Leaves strongly coriaceous, bullate, usually > 30 cm long; inflorescences a multifloral thyrse, densely contracted, subtended by a conspicuous fascicle of basal bracts .... ***S. dresslerii* A.H.Gentry (Panamá, Colombia, Ecuador)**
– Leaves subcoriaceous or coriaceous, not bullate, usually < 11 cm long; inflorescences a pauciflorous thyrse; not subtended by basal bracts............. ....***S. nicaraguensis* (México, Mesoamérica, Colombia)**
4 Pseudostipules present; corolla tube white (the lobes apex and calyx pink), pink or yellow; inflorescences a crowded (densely branched) or slightly contracted thyrse...**5**
– Pseudostipules inconspicuous or absent; corolla (tube and lobes) red, red-orange or red-purple, calyx red or brown; inflorescence a paucifloral thyrse...**8**
5 Inflorescence a crowded, densely branched thyrse; corolla tube 1.8–2.5 cm long; ovary lepidote **6**
– Inflorescence a slightly or laxer contracted thyrse; corolla 0.8–1.2 cm long; ovary glabrous **7**
6 Pseudostipules subulate; corolla tube yellow .... ***S. sulphurea* (Panamá, Colombia; Ecuador)**
– Pseudostipules lanceolate; corolla tube white (the lobes apex and calyx pink) .... ***S. fastigiata* (Guatemala, Costa Rica, Panamá, Colombia, Ecuador)**
7 Pseudostipules subulate; leaves 10–25 × 7–20 cm, elliptic or obovate; corolla tube white (the lobes apex and calyx pink) or pink; 1–1.2 cm long....... .... ***S. macrophylla* Ducke (Brazil, Colombia, Perú)**
– Pseudostipules lanceolate; leaves 7–11 × 2.5–5 cm, elliptic-oblong or obovate-oblong; corolla tube pink, ca. 0.8 cm long .... ***S. roseiflora* (Brazil, French Guiana, Perú)**
8 Leaves densely hirsute along primary and secondary veins on abaxial surface; primary and secondary veins impressed on the adaxial surface.......... .... ***S. hirsuta* A.H.Gentry (Colombia)**
– Leaves glabrous or lepidote on the abaxial surface, primary and secondary veins flat on the adaxial surface..**9**

9 Leaves chartaceous to subcoriaceous, elliptic to wide-elliptic, two times as long as wide, 15–26 cm long, the base auriculate with rolled up lobes; inflorescence thyrse with reduced partial inflorescences; calyx 5–7 mm long; corolla tube 2–2.5 cm long, red-purple .... ***S. spruceana*** **K. Schum. (Brazil, Colombia, Guyana, Venezuela)**

– Leaves coriaceous, narrowly elliptic, more than two times longer than wide, 9–16 cm long, the base rounded or cuneate; inflorescences glomerulate, of several condensed thyrses; calyx 3–5(–6) mm long; corolla tube 1.8–2 cm long, red............................***S. cauliflora*** **A.H.Gentry (Brazil, Colombia, Perú)**

10 Inflorescences terminal, 14–40 cm long **11**

– Inflorescences axillary, 0.5–21 cm long **13**

11 Inflorescences with foliaceous bracts, 1–2.5 × 1–2 cm; a species endemic to the Choco Region .... ***S. darienensis*** **Sandwith (Colombia, Ecuador, very probably Panamá)**

– Inflorescences with obsolete bracts, 1–2× ca. 1 mm; Amazonian and Guiana Shield species...**12**

12 Calyx subtruncate, 4–5 mm long; corolla tube ca. 2 mm wide; fruit 1–1.6 cm diam., 1/3 to 1/4 covered by a persistent, subtruncate calyx........................ ....***S. scandens*** **Sandwith (Brazil, Colombia, Perú, Suriname, Venezuela)**

– Calyx irregularly 2–3-labiate, 5–9 mm long; corolla tube ca. 3 mm wide; fruit ca. 1 cm diam., with lower 2/3 covered by a persistent, distinctly toothed calyx ....***S. violacea*** **(Brazil, Guianas, Venezuela)**

13 Fruits 3.5–5 cm in diam. **14**

– Fruit 0.5–2.5 cm in diam. **15**

14 Leaves broadly obovate or rarely elliptic, coriaceous, apex rounded, base acute and decurrent on petiole, not lepidote; inflorescences 2.5–3.5 cm long, hispidulous; fruits 4.5–5 cm diam.......................***S. macrocarpa*** **Lundell (Guatemala)**

– Leaves elliptic-obovate, chartaceous, or subcoriaceous, apex apiculate, base broadly cuneate; sparsely lepidote on both surfaces; inflorescences 1–1.2 cm long, puberulent; fruits 3.5–4 cm diam.. ....***S. nicaraguensis*** **(México, Mesoamérica, Colombia)**

15 Leaves panduriform (fiddle shape), the base strongly auriculate ....***S. pandurata*** **(Moldenke) A.H.Gentry (Colombia, Ecuador)**

– Leaves elliptic, obovate, elliptic-obovate, wide-ovate, lanceolate, oblanceolate, oblong-ovate or oblong-elliptic, the base cuneate, rounded or abrupt subcordate, slightly or not auriculate..**16**

16 Corolla golden yellow, lobes 1–2 mm long; calyx toothed, lobes 2–2.5 mm ....***S. aurea*** **Ducke (Brazil)**

– Corolla white with pink tip, lilac, creamy or purple, lobes 3–6 mm long; calyx truncate, subtruncate or slightly toothed, lobes 0.5–1 mm long **17**

17 Inflorescences a crowded, contracted thyrse, densely branched, the branchlets short and conspicuously jointed ....***S. sulphurea*** **(Panamá, Colombia, Ecuador)**

– Inflorescences lax thyrses or axillary thyrsic fascicles, 1–several flowered **18**

18 Inflorescences fasciculate or very branched thyrses; corolla campanulate or infundibuliform-campanulate, 5– 6 mm wide toward the end of the tube **19**

– Inflorescences contracted or elongate thyrses, more or less fasciculate (*S. parviflora*) or a lax thyrse; corolla campanulate-hypocrateriform or tubular, 0.4–0.5 cm wide toward the end of the tube...**23**

19 Inflorescences a very short thyrse; corolla tube 0.6–0.8 cm long **20**
– Inflorescences fasciculate thyrses; corolla tube 1–3.5 cm long................**21**
20 Leaves 2.5–5 cm wide, elliptic-oblong or obovate-oblong; corolla tube pink, ca. 0.8 cm long ....***S. roseiflora*** **(Brazil, French Guiana, Perú)**
– Leaves 7–9 cm wide, widely obovate or widely elliptic; corolla tube white, 5–6 cm long..***S. axillaris*** **(Antilles)**
21 Leaves 4–7 cm long,, obovate; corolla 1.3–1.9 cm long .... ***S. brachyantha*** **Griseb. (Antilles, Colombia, Costa Rica, Panamá, Venezuela)**
– Leaves 10–20 cm long, elliptic, oblong or elliptic-oblong; corolla 2.5–3.5 cm long..**22**
22 Leaves coriaceous; calyx tubular-campanulate, ca. 1 cm long, green; corolla ca. 3.5 cm long ....***S. paraensis*** **Ducke (Brazil, Guianas, Venezuela)**
– Leaves chartaceous; calyx campanulate, 0.4–0.5 cm long, violet; corolla 2.5–3 cm long...***S. parasitica*** **(Antilles)**
23 Young branches with conspicuous and dense, raised lenticels; base of leaves abruptly truncate or subcordate; petioles stout, 0.5–1.3 cm long; corolla 1.2–1.3 cm long, white with yellow throat.. ...... ***S. chocoensis*** **A.H.Gentry (Colombia, Ecuador, very probable in Panamá)**
– Young branches with inconspicuous or sparse lenticels; base of leaves rounded, cuneate or nearly so; petioles slender, 1–2.5 cm long; corolla ≤ 1.2 cm long, white or lilac or lavender, the throat lilac or lavender...................**24**
24 Leaves 13–30 cm long; inflorescences a contracted thyrse, the main axis 1–(4)–5 cm long..**25**
– Leaves 4–22 cm long; inflorescences thyrse or a lax thyrse, the main axis (4)–18 cm long **26**
25 Inflorescences a slightly contracted thyrse; peduncle and pedicel stout and woody ....***S. macrophylla*** **Ducke (Brazil, Colombia, Perú)**
– Inflorescences a contracted thyrse, almost often fasciculate; peduncle and pedicel slender and herbaceous...................................***S. parviflora*** **(Mexico, Mesoamerica, Brazil, Colombia, Ecuador, French Guiana, Peru, Venezuela)**
26 Leaves widely-elliptic to elliptic or oblanceolate, brown when dry; inflorescences 1–(4)–5 cm long, narrowly thyrsic, calyx black when dried...***S. fuscata*** **A.H.Gentry (Nicaragua, Costa Rica, Panamá, Colombia, Ecuador, French Guiana, Venezuela)**
– Leaves lanceolate, lanceolate-elliptic, elliptic, rarely narrowly ovate, or oblanceolate, black- brown or yellowish when dry; inflorescences 4–18 cm long, narrowly thyrsic; calyx brown to yellowish when dry **27**
27 Leaves lanceolate, lanceolate-elliptic, coriaceous, glabrescent or with simple trichomes, densely punctuated on the adaxial surface, black-brown when dry; inflorescences rachis puberulent to sparsely pilose; bracts 2–5 mm long, oblong, ciliate along the margins; calyx sparsely puberulent on outer surface, brown when dry; staminode absent ....***S. longirachis**** **(Colombia)**
– Leaves elliptic, oblanceolate, rarely narrowly ovate, rigid-coriaceous, with lepidote trichomes and sparsely punctuated near base of midrib on both surfaces, yellowish when dry; inflorescences rachis densely hirsute-puberulent, bracts 1–2 mm long, triangular, short- puberulous along the margins; calyx lepidote or subpuberulous at least at the base, yellowish when dry; staminode present ....***S. monachinoi*** **(Colombia, Ecuador, Venezuela)**

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Acevedo-Rodríguez P, Strong MT (2023) Catalogue of Seed Plants of the West Indies. Online version.

Armstrong JE (1985) The delimitation of Bignoniaceae and Scrophulariaceae based on floral anatomy, and the placement of problem genera. American Journal of Botany 72(5): 755–766. https://doi.org/10.1002/j.1537-2197.1985.tb08336.x

Bachman S, Moat J, Hill AW, de laTorre J, Scott B (2011) Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Bohorquez-Osorio AF, Ulian T, Diazgranados M (2020) Guía de plantas útiles de la Serranía de las Quinchas. Ecología, Economía y Ética, Rutas Turísticas por los Bosques y la Paz. Royal Botanic Gardens, Kew, E3, UK.

Burger WC, Barringer KA (2000). Schlegeliaceae. Fieldiana 41: 69–77.

Endlicher S (1839) Crescentieae. Genera plantarum secundum ordines naturales disposita. Vindobonae, 273 pp.

Fonseca LHM (2021) Combining molecular and geographical data to infer the phylogeny of Lamiales and its dispersal patterns in and out of the tropics. Molecular Phylogenetics and Evolution 164: 107287. https://doi.org/10.1016/j.ympev.2021.107287

Font-Quer P (2001) Diccionario de Botánica. Ediciones Península, Barcelona.

Funk VA, Hollowell TH, Berry PE, Kelloff CL, Alexander S (2007) Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Contributions from the United States National Herbarium 55: 1–584.

Galindo-T R, Betancur J, Cadena-M JJ (2003) Estructura y composición florística de cuatro bosques andinos del santuario de flora y fauna Guanentá-alto río Fonce, Cordillera Oriental colombiana. Caldalsia 25: 313–335.

Gentry AH (1973) *Schlegelia* (Bignoniaceae). Flora of Panama. Ann. Missouri Botanical Garden 60: 922–930.

Gentry AH (1977) Bignoniaceae. In: Harling GW, Sparre BB (Eds) Flora of Ecuador. University of Göteborg & Swedish Museum of Natural History, Göteborg & Stockholm, 1–172.

Gentry AH (1980) Bignoniaceae: Part I, (Crescentieae and Tourretieae). Flora Neotropica 25. New York Botanical Garden Press, New York, NY, 1–131.

Gentry AH (1982a) Bignoniaceae. In: Febres ZL de, Steyermark J (Eds) Flora de Venezuela. Instituto Nacional de Parques. Dirección de Investigaciones Biológicas, Caracas, Venezuela, 1–464.

Gentry AH (1982b) Bignoniaceae. Flora of Veracruz 24: 1–222.

Gentry AH (1997) Bignoniaceae. In: Steyermark JA, Berry PE, Yatskievych K, Holst BK (Eds) Flora of the Venezuelan Guyana, Vol. 3, (Araliaceae-Cactaceae). Missouri Botanical Garden Press, Saint Louis, MO, 403–491.

Gentry AH (2001) *Schlegelia* (Bignoniaceae). In: Stevens DW, Ulloa Ulloa C, Pool A, Montiel OM (Eds) Flora de Nicaragua. Monographs in Systematic Botany from the Missouri Botanical Garden 85: 424–425.

Gentry AH (2009) Bignoniaceae. Flora de Colombia No 25. Universidad Nacional de Colombia. Facultad de Ciencias. Instituto de Ciencias Naturales, Bogotá, 462 pp.

Gradstein SR (2016) Schlegeliaceae. Catálogo de plantas y líquenes de Colombia Vol. I., 2393–2394.

IUCN Standards and Petitions Committee (2022) 1 Guidelines for Using the IUCN Red List Categories and Criteria.

Liu B, Tan YH, Liu S, Olmstead RG, Min DZ, Chen ZD, Joshee N, Vaidya BN, Chung RCK, Li B (2020) Phylogenetic relationships of *Cyrtandromoea* and *Wightia* revisited: A new tribe in Phrymaceae and a new family in Lamiales. Journal of Systematics and Evolution 58(1): 1–17. https://doi.org/10.1111/jse.12513

Miquel FAG (1844) Bemerkunger über *Schlegelia* und über die Verwandtschaftwn der Crecentieen Endl. Botanische Zeitung (Berlin) 2: 785–789.

Moldenke HN (1949) New and Noteworthy Plants VIII. Phytologia 3: 106–121. https://doi.org/10.5962/bhl.part.10091

Morales JF (2015) Schlegeliaceae. Monographs in Systematic Botany from the Missouri Botanical Garden 131: 143–148.

Olmstead RG, Zjhra ML, Lohmann LG, Grose SO, Eckert AJ (2009) A molecular phylogeny and classification of Bignoniaceae. American Journal of Botany 96(9): 1731–1743. https://doi.org/10.3732/ajb.0900004

Pulle A (1906) An enumeration of the vascular plants known from Suriname, together with their distribution and synonymy: 5. The Netherlands, 614 pp. https://doi.org/10.5962/bhl.title.57150

Restrepo IC, Aldana AM, Stevenson PR (2021) Forest dynamics in different scenarios: Selective logging in the middle Magdalena (Colombia). Sustainable Forestry 4(2): 72. https://doi.org/10.24294/sf.v4i2.1613

Reveal JL (1995) Newly required suprageneric names in vascular plants. Phytologia 79: 68–76. http://biostor.org/reference/62999

Rivers MC, Taylor L, Brummitt NA, Meagher TR, Roberts DL, Lughadha EMN (2011) How many herbarium specimens are needed to detect threatened species? Biological Conservation 144(10): 2541–2547. https://doi.org/10.1016/j.biocon.2011.07.014

Salgado J, Shurin JB, Vélez MI, Link A, Lopera-Congote L, González-Arango C, Jaramillo F, Åhlén I, de Luna G (2022) Causes and consequences of recent degradation of the Magdalena River basin, Colombia. Limnology and Oceanography Letters 7(6): 451–465. https://doi.org/10.1002/lol2.10272

Spangler RE, Olmstead RG (1999) Phylogenetic analysis of Bignoniaceae based on the cpDNA gene sequences rbcL and ndhF. Annals of the Missouri Botanical Garden 86(1): 33–46. https://doi.org/10.2307/2666216

Stiles F, Bohórquez CI (2000) Evaluando el estado de la biodiversidad: El caso de la avifauna de La Serranía De Las Quinchas, Boyacá, Colombia. Caldasia 22: 61–92.

Thiers B (2019) Index Herbariorum A global directory of public herbaria and associated staff. http://sweetgum.nybg.org/ih/

Verspagen N, Erkens RHJ (2022) A method for making Red List assessments with herbarium data and distribution models for species-rich plant taxa: Lessons from the Neotropical genus *Guatteria* (Annonaceae). Plant, People and Planet: 1–11. https://doi.org/10.1002/ppp3.10309

Villaseñor Ríos JL (2016) Checklist of the native vascular plants of Mexico. Catálogo de las plantas vasculares nativas de México. Revista Mexicana de Biodiversidad 87(3): 559–902. https://doi.org/10.1016/j.rmb.2016.06.017

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Research Article

Hedyotis longiramulis (Rubiaceae), a new species from south China

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Abstract

Hedyotis longiramulis **sp. nov.** (Rubiaceae) is described from Guangdong Province, China. It is similar to *H. caudatifolia* but differs in having puberulent, more or less tetragonal and decussately sulcate juvenile stems, waxy leaf surface, short inflorescence peduncles, high length ratio of corolla lobe to tube, and subglobose capsules. The phylogenetic analysis reveals that *H. longiramulis* is sister to *H. pubirachis*. Dimorphism concerning pollen size was observed in the heterostylous flowers. The complete chloroplast genome of the new species comprises a typical quadripartite structure of 153,616 bp in length, with two inverted repeats of 25,457 bp, a large single-copy of 85,050 bp and a small single-copy of 17,652 bp. It contains 112 unique genes, including 79 protein-coding genes, 29 tRNA genes, and four rRNA genes, the GC content of the chloroplast genome is 32.4%. The new species is provisionally evaluated as "Least Concern" because it is common and well-protected in two Provincial Nature Reserves.

Key words: Chloroplast genome, *Hedyotis-Oldenlandia* complex, phylogeny, taxonomy

Introduction

The genera *Hedyotis* L. and *Oldenlandia* L. are two taxonomically disputed genera and usually considered as a taxonomic complex in the tribe Spermacoceae of Rubiaceae. These two genera include more than 500 species distributed in tropical and subtropical regions worldwide (Dutta and Deb 2004). Taxonomical treatment of several genera within the tribe, especially regarding to generic delimitation, has much been debated (e.g., Lamarck 1792; Willdenow 1797; Bremekamp 1952; Dutta and Deb 2004). Recent phylogenetic analyses proved that the *Hedyotis-Oldenlandia* complex was polyphyletic and a narrow generic delimitation was then proposed accordingly (Guo et al. 2013; Gibbons 2020). Currently, *Hedyotis* s. str. is characterized by having an erect and robust herbaceous or shrubby habit, homo- or heterostylous flowers, triangular or ovate stipules with serrate marginal glands and tipped colleters, mostly diplophragmous capsules (loculicidal dehiscence first and then septicidal dehiscence along the septum) and fruticosa-type seeds (dorsiventrally flattened, lenticular with irregularly narrow wing-like margin). The distribution center of *Hedyotis* s. str. is the Asian-Pacific region (Terrell and Robinson 2003).

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With the rapid development of high-throughput sequencing technologies, whole chloroplast genome dataset is increasingly used for simulating phylogenetic relationships (Liu et al. 2018; Song et al. 2019; Charr et al. 2020; Rono et al. 2020; Zhang et al. 2021). However, all of the present molecular phylogenetic analyses on the *Hedyotis-Oldenlandia* complex are based on a handful of nuclear or chloroplast DNA markers. Therefore, a more reliable phylogenetic relationship with robust support based on the whole chloroplast genome dataset is strongly anticipated. But unfortunately, for *Hedyotis* s. str., only the whole chloroplast genome dataset of *H. ovata* Thunb. ex Maxim. is available (MK203877) up to now (Zhang et al. 2019).

During a field collection in Guangdong Ehuagnzhang Provincial Nature Reserve, we found a sub-shrubby species of *Hedyotis* s. str. with purplish and puberulent young stems and long axillary branches. It is similar to *H. caudatifolia* Merr. & F.P.Metcalf with respect to its erect subshrubby habit, ovate to lanceolate leaf shape, and long lateral branches bearing several terminal and axillary inflorescences, but conspicuously differs by its puberulent, more or less tetragonal and decussately sulcate juvenile stems. After detailed morphological comparison and phylogenetic analysis, we confirm that this species is a hitherto undescribed one.

Materials and methods

Morphological examination

Morphological data of the new species was observed on living individuals and herbarium specimens deposited at IBSC and CANT (herbarium code follows https://sweetgum.nybg.org/science/ih/).

For micromorphology, scanning electron microscopy (SEM, JSM-6360LV) was applied under 15.00 kV accelerating voltage. Pollen grains were put in 70% alcohol, washed by an ultrasonic cleaner (WIGGENS UA10MFD, 100W, 59KHZ) for 5 min, and then centrifuged at 8000 rpm for 5 min. After this, we removed the supernatant and added 70% alcohol to the sediment. These steps were repeated three times. Finally, the pollen suspension was dropped on the sample stubs with conductive double sided adhesive carbon tapes. The pollen samples were gilded by sputter coater (LEICA EM ACE600, 10 μm, 20 mA) once dried in room conditions. Seed samples were cleaned using the same method as for pollen grains and then transferred to sample stubs for gilding after drying. Leaf material was cleaned by brushing lightly and rinsing gently in warm water and then transferred to sample stubs after drying.

Pollen terminology for description followed Hesse et al. (2009), seed terminology followed Neupane et al. (2015), and foliar epidermal terminology followed David (1974).

Conservation assessment

The conservation assessment was undertaken according to the guidelines for assessing the conservation status of species (IUCN 2022). Estimation of the extent of occurrence (EOO) and area of occupancy (AOO) were performed in GeoCAT (Bachman et al. 2011) with 2 × 2 km grid cells.

Genomic DNA extraction and sequencing

Leaf material for DNA extraction was dried in silica gel. Total DNA was extracted using the modified cetyltrimethylammonium bromide (CTAB) protocol (Doyle 1991). Primers for polymerase chain reaction (PCR) are listed in Table 1, and the methods for PCR followed Guo et al. (2011). PCR products were purified and sequenced by Sangon Biotech Limited Company (Shanghai, China). For whole genome sequencing, the DNA samples were sent to Beijing Genomics Institute (Shenzhen, China) for genomic library construction and *de novo* sequencing (paired-end, PE=150 bp) using the BGISEQ-500. Raw reads were filtered and trimmed using SOAPnuke v.1.5.6 with software parameters "-n 0.01 -l 20 -q 0.3 -A 0.25 --cutAdaptor -Q 2 -G --polyX 50 --minLen 150".

Chloroplast genome assembly and annotation

A total of 2 Gb clean reads were obtained and assembled using GetOrganelle v.1.7.3.5 (Jin et al. 2020). With reference to *H. ovata* (GenBank: MK203877), the genome was first annotated using GeSeq (https://chlorobox.mpimp-golm.mpg.de/geseq.html) (Tillich et al. 2017) and PGA (Qu et al. 2019), and then manually adjusted using Geneious v.11.0.3. A circular map of the chloroplast genome was drawn using OGDRAW v.1.3.1 (https://chlorobox.mpimp-golm.mpg.de/OGDraw.html) (Greiner et al. 2019).

Molecular phylogenetic analyses

Twenty-three morphologically similar and sympatric *Hedyotis* taxa, as well as two accessions of the new species (see Table 2), were selected as ingroup operational taxonomic units (OTUs) for molecular phylogenetic analyses. Two Spermacoceae species, *Dentella repens* (L.) J.R.Forst. & G.Forst. from Australia and *Pentodon pentandrus* Vatke from Zambia were chosen as outgroup OUTs (see Table 2).

Five DNA markers (ITS, *petD*, *rps16*, *trnH-psbA* and *trnL-F*) were employed to reconstruct the phylogenetic trees. Sequences were aligned using MAFFT v.7.017 (Katoh et al. 2002) and then concatenated together in Geneious. Maximum Likelihood (ML) analyses were accomplished with IQ-TREE v.2.0 (Nguyen

Table 1. Primers used for PCR in the present study.

DNA region	Primer name	Sequence	References
ITS	P17	5'-CTACCGATTGAATGGTCCGGTGAA-3'	Popp and Oxelman 2001
	26S-82R	5'-TCCCGGTTCGCTCGCCGTTACTA-3'	
petB-petD	PIpetB1365F	5'-TTGACYCGTTTTTATAGTTTAC-3'	Löhne and Borsch 2005
	PIpetD738R	5'-AATTTAGCYCTTAATACAGG-3'	
rps16	rps16F	5'-GTGGTAGAAAGCAACGTGCGACTT-3'	Oxelman et al. 1997
	rps16R3	5'-CGATAGACGGCTCATTGGGATA-3'	
trnH-psbA	trnH-05	5'-CGCGCATGGTGGATTCACAATCC-3'	Tate and Simpson 2003
	psbA3	5'-GTTATGCATGAACGTAATGCTC-3'	Sang et al. 1997
trnL-F	TabC	5'-CGAAATCGGTAGACGCTACG-3'	Taberlet et al. 1991
	TabF	5'-ATTTGAACTGGTGACACGAG-3'	

Table 2. Taxa, vouchers, localities, and GenBank accession numbers of ITS, *petD*, *rps16*, *trnH-psbA* and *trnL-F* sequences for phylogenetic analysis.

Taxon	Voucher (herbarium)	ITS	*petD*	*rps16*	*trnH-psbA*	*trnL-F*
Dentella repens J.R.Forst. & G.Forst	Australia: Andersson 2262 (GB)	AM939440	EU557693	AF333370	/	EU543091
Hedyotis acutangula Champ. ex Benth.	China: unknown BW21 (CUHK)	HQ148749	/	HM752907	HM640307	HM752822
Hedyotis acutangula Champ. ex Benth.	China: Ruijiang Wang HA-02 (IBSC)	JX111197	JX111085	JX111241	JX111160	JX111316
Hedyotis cantoniensis F.C.How ex W.C.Ko	China: Ruijiang Wang et al. 1250 (IBSC)	JF699912	JF700061	JX111247	JF699773	JX111322
Hedyotis caudatifolia Merr. & F.P.Metcalf	China: Ruijiang Wang et al. 1229 (IBSC)	JF699915	JF700064	JX111255	JF699776	JX111328
Hedyotis caudatifolia Merr. & F.P.Metcalf	China: Ruijiang Wang et al. 1269 (IBSC)	JF699916	JF700065	JX111256	JF699777	JX111329
Hedyotis communis W.C.Ko	China: Bo Li LB0172 (IBSC)	JX111208	JX111094	JX111257	JX111167	JX111330
Hedyotis consanguinea Hance	China: Ruijiang Wang 1254 (IBSC)	JF699923	JF700071	JX111258	JF699783	JX111331
Hedyotis effusa Hance	China: Ruijiang Wang et al. 1268_1 (IBSC)	JF699933	JF700083	JX111262	JF699790	JX111335
Hedyotis exserta Merr.	China: Guobin Jiang and Xinxin Zhou 1124 (IBSC)	MT345066	MT347606	MT792387	MT792403	MZ514116
Hedyotis interrupta G.B.Jiang & R.J.Wang	China: Guobin Jiang and Xinxin Zhou 1136_2 (IBSC)	MT345072	MT347612	MT792393	MT792409	MZ514117
Hedyotis loganioides Benth.	China: Ruijiang Wang 1253-1 (IBSC)	JF699910	JF700059	JX111246	JF699771	JX111320
Hedyotis longiexserta Merr. & F.P.Metcalf	China: Mingdeng Yuan et al. YS60 (IBSC)	MW396581	MW405435	MW405424	/	MZ514123
Hedyotis longipetala Merr.	China: Ruijiang Wang 1334 (IBSC)	JX111216	JX111102	JX111268	JX111175	JX111342
Hedyotis longiramulis Y.D.Xu & R.J.Wang	China: Yida Xu and Fan Su AP0138 (IBSC)	MZ326005*	MZ425928**	MZ425928**	MZ425928**	MZ425928**
Hedyotis longiramulis Y.D.Xu & R.J.Wang	China: Dan Liang et al. WP1366 (IBSC)	MZ411390*	MZ403800*	MZ417507*	MZ403809*	MZ417501*
Hedyotis matthewii Dunn	China: Ruijiang Wang et al. 1251 (IBSC)	JF699900	JF700049	JX111243	JF699761	JX111318
Hedyotis nankunshanensis R.J.Wang & S.J.Deng	China: Ruijiang Wang et al. 1688 (IBSC)	JN975969	JN975964	OQ723460*	OQ723461*	OQ723462*
Hedyotis nanlingensis R.J.Wang	China: Mingdeng Yuan et al. YS228 (IBSC)	MW396579	MW405437	MW405426	MZ514110	MZ514124
Hedyotis ovata Thunb. ex Maxim.	China: Guobin Jiang et al. 1508 (IBSC)	MZ326003	MZ403799	MZ343053	MZ403807	MZ403793
Hedyotis puberulifolia Y.D.Xu & R.J.Wang	China: Ruijiang Wang and Yida Xu 6216 (IBSC)	MW169047	MW196744	OQ723463*	OQ723464*	OQ723465*
Hedyotis pubirachis Y.D.Xu & R.J.Wang	China: Yida Xu and Fan Su AP0147 (IBSC)	MW264177	MW266052	MZ447121	MZ447124	MZ447126
Hedyotis pulcherrima Dunn	China: Ruijiang Wang 1233-1 (IBSC)	JF699946	JF700096	JX111274	JF699801	JX111348
Hedyotis taishanensis G.T.Wang & R.J.Wang	China: Yida Xu et al. WP1330 (IBSC)	MZ479676	MZ514102	MZ514103	MZ514108	MZ514121
Hedyotis tenuipes Hemsl.	China: Ruijiang Wang 1234_1 (IBSC)	JF699960	JF700110	JX111280	JF699812	JX111354
Hedyotis xanthochroa Hance	China: Ruijiang Wang 1361 (IBSC)	JX111227	JX111110	JX111286	JX111183	JX111361
Hedyotis xinyiensis X.Guo & R.J.Wang	China: Ruijiang Wang 1182 (IBSC)	JF699970	JF700120	JX111288	JF699820	JX111362
Hedyotis yangchunensis W.C.Ko & Zhang	China: Ruijiang Wang 1270-1 (IBSC)	JF699972	JF700122	JX111290	JF699821	JX111364
Pentodon pentandrus Vatke	Zambia: Dessein et al. 598 (BR)	AM939528	EU557759	EU543066	/	EU543154

*indicates that the sequences are newly obtained by PCR sequencing.
**indicates that the sequences are newly obtained by whole genome sequencing.

et al. 2015). The best-fit nucleotide substitution model of GTR+F+R2 was selected by using ModelFinder (Kalyaanamoorthy et al. 2017). Bayesian inference (BI) analyses were accomplished with MrBayes v.3.1.2 (Ronquist et al. 2012).

GTR+G+I was selected to be the best-fit nucleotide substitution model by MrModeltest v.2.3 (Nylander 2004). The sampled species along with their voucher information and GenBank accession numbers are listed in Table 2.

Results

A new species based on morphological and molecular evidence

Morphology

During our examination of herbarium material, we found that *Hedyotis longiramulis* was often misidentified as either *H. caudatifolia* or *H. communis* W.C.Ko because of the subshrubby habit, the ovate to lanceolate leaves and the triangular stipules. A detailed morphological comparison is therefore provided to elucidate the differences among them (Table 3).

Molecular analysis

BI and ML analyses based on the combined nuclear ITS and four plastid markers (*petD*, *rps16*, *trn*H-*psbA* and *trnL-F*) result in the same tree topology. The two accessions of the new species form a monophyletic clade that is sister to *H. pubirachis* Y.D.Xu & R.J.Wang with robust support (PP = 1, BS = 98) (Fig. 1). The two species share common characters, such as subshrubby habit and ovate to lanceolate leaf shape, but differ in other characters. A comparison of the morphological characters is given in Table 3.

Table 3. Diagnostic characters of *Hedyotis longiramulis*, *H. pubirachis* (sister species in molecular analysis), *H. caudatifolia* and *H. communis* (two morphologically similar species).

Characters	*H. longiramulis*	*H. caudatifolia*	*H. communis*	*H. pubirachis*
Stem	more or less tetragonal and decussately sulcate at juvenile internodes, puberulent	terete or slightly flattened, glabrous	terete or slightly flattened, glabrous	terete with inconspicuous ridges, glabrous
Leave surface	waxy on both side	glabrous on both side	glabrous on both side	glabrous on both side
Petiole length (mm)	5–15 on main stem and 2–5 on lateral branches	3–15	subsessile	3–10
Stipules	triangular, densely puberulent abaxially	triangular, glabrous abaxially	narrowly triangular, glabrous abaxially	triangular to broadly ovate, glabrous abaxially
Inflorescences	growing on lateral branches, terminal and axillary in the upper nodes	growing on lateral branches, terminal and axillary in the upper nodes	growing on main stem and on lateral branches, strictly axillary	growing on main stem and on lateral branches, terminal and axillary in the upper nodes
Peduncle length (cm)	0.5–2.0	2.0–10.0	0.5–2.5	2.5–7.0
Calyx lobes length (mm)	ca. 0.9	0.8–1.0	2–3	ca. 0.5
Calyx lobes shape	ovate-triangular with blunt or rounded apex	triangular with acute apex	narrowly triangular with acute apex	broadly triangular
Ratio of calyx lobe length to its basal width	ca. 1:1	1–1.5:1	2.5–3:1	ca. 0.8:1
Corolla tube length (mm)	3.5–3.8	3.0–4.0	4.0–5.0	2.8–3.3
Corolla lobe length (mm)	3.5–3.8	2.0–2.7	2.5–4.0	2.0–2.2
Length ratio of corolla lobe to tube	0.9–1.0	ca. 0.8	0.6–0.8	ca. 0.7
Capsule shape	subglobose	ellipsoid-oblong or ellipsoid	obovoid or subglobose	ellipsoid to subglobose

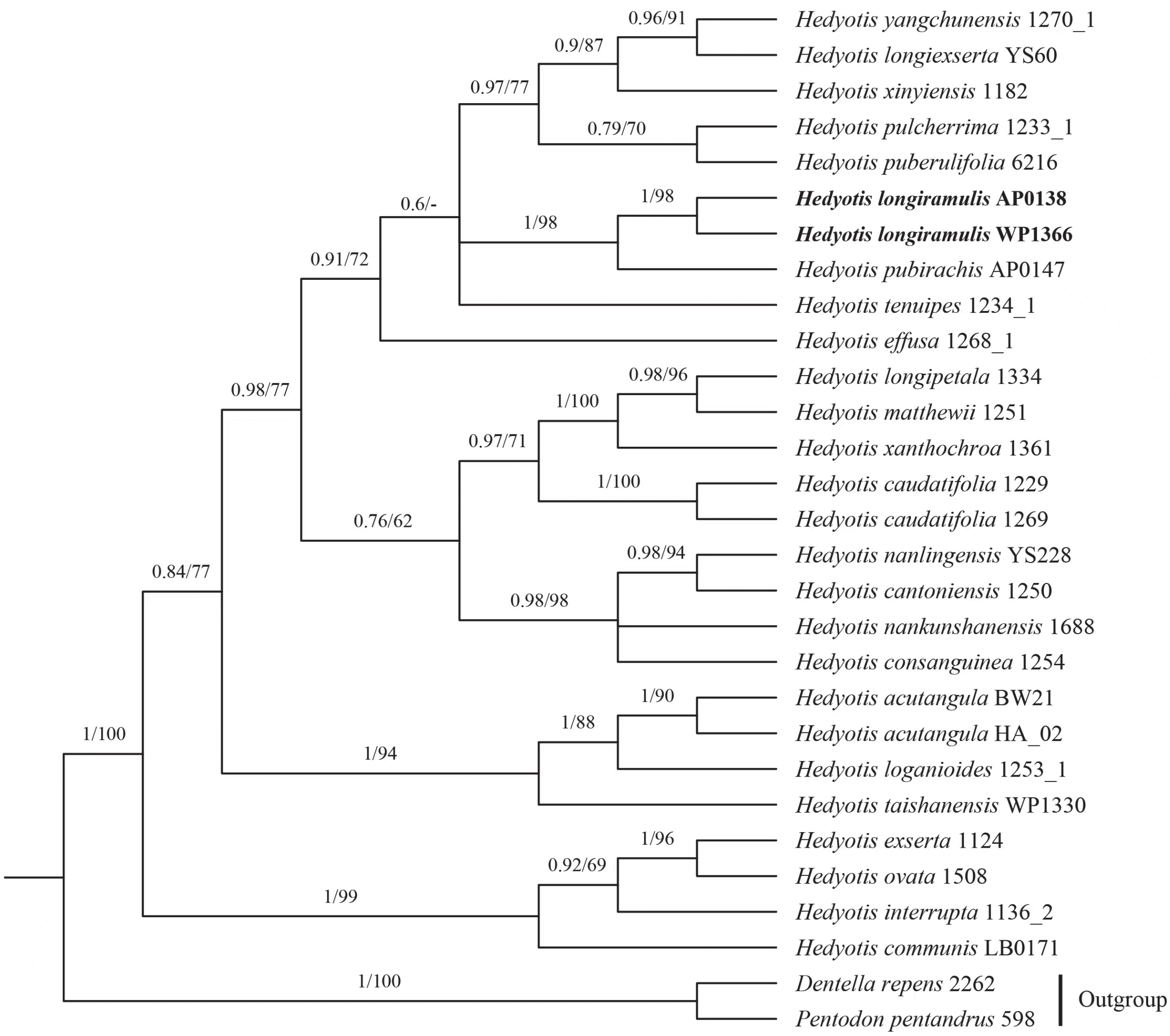

Figure 1. Phylogenetic relationships of *Hedyotis* based on combined nuclear ITS and four plastid markers (*petD*, *rps16*, *trnH-psbA* and *trnL-F*). Bootstrap values (BS≥50%, right) and Bayesian Posterior Probabilities (PP≥0.5, left) are labeled above the branches. Field collection numbers are labeled after species names.

Taxonomic treatment

Hedyotis longiramulis **Y.D.Xu & R.J.Wang, sp. nov.**
urn:lsid:ipni.org:names:77325483-1
Figs 2, 3
鹅凰嶂耳草 (é Huáng Zhàng ěr Cǎo)

Type. China. Guangdong Province: Yangchun City, Bajia Town, Guangdong Ehuangzhang Provincial Nature Reserve, roadsides, 21°52'N, 111°25'E, elev. 643 m. April 9, 2021, *Y.D. Xu & R.J. Wang 6540* (holotype: IBSC [IBSC0865777!]; isotype: IBSC [IBSC0865778!]).

Diagnosis. The species is similar to *H. caudatifolia* in having a subshrubby habit, ovate to lanceolate leaves, and long lateral branches with several terminal and axillary inflorescences, but differs from it by having puberulent, more or less tetragonal and decussately sulcate juvenile stems (versus glabrous and terete in *H. caudatifolia*), waxy leaf surface (versus non-waxy in *H. caudatifolia*), shorter peduncles (0.5–2.0 cm versus 2.0–10.0 cm in *H. caudatifolia*), a higher length ratio of corolla lobe to tube (0.9–1.0 versus approximately 0.8 in *H. caudatifolia*), and subglobose capsules (versus ellipsoid-oblong or ellipsoid in *H. caudatifolia*).

Description. Perennial woody subshrubs, 40–120 cm tall. ***Stem*** more or less tetragonal and decussately sulcate at juvenile internodes, becoming terete with age, purplish, puberulent, branched at upper part. ***Leaves*** opposite, 5–16 × 1.5–4 cm on main stem and 1.0–6.5 × 0.3–1.5 cm on lateral branches, ovate to lanceolate, coriaceous, dark green adaxially, greyish-green or sometimes purplish abaxially, both surfaces waxy, apex acute or subacute, base cuneate or shortly decurrent; petiole 5–15 mm long on main stem and 2–5 mm long on lateral branches, waxy or puberulent; midrib depressed adaxially and prominent abaxially, secondary veins usually 5–6 on each side, sometimes indistinct adaxially; ***stipules*** 4–10 × 3–6 mm, triangular, apex acute to acuminate, margin sparsely glandular serrate, puberulent abaxially. ***Inflorescences*** growing on long lateral branches, terminal and axillary in the upper nodes, 1.5–3.5 cm long, cymose or paniculate-cymose; inflorescence axes tetragonal, sulcate; peduncles 0.5–2.0 cm long; bracts ca. 1 mm long, subulate. ***Flowers*** heterostylous, pedicels 0.9–2.0 mm long. ***Hypanthium*** ca. 1 mm long, obconic to subglobose; lobes 4, ca. 0.9 × 0.9 mm, ovate-triangular, blunt or rounded at apex. ***Corolla*** white or purplish, tube 3.5–3.8 mm long, glabrous abaxially and densely or sparsely pubescent adaxially; lobes 4, 3.5–3.8 × 1.8–2.2 mm, ovate-triangular; stamens 4, anthers ca. 0.9 mm long; stigma bilobed, ca. 0.5 mm long, subglobose, papillate. ***Long-styled flowers*****:** stamens included, filaments ca. 0.6 mm long, adnate to the middle part of corolla tube; style ca. 7.6 mm long, exserted, glabrous. ***Short-styled flowers*****:** stamens exserted, filaments ca. 2.8 mm long, adnate to the throat of corolla tube; style ca. 2.7 mm long, included, glabrous. ***Fruits*** capsular, ca. 2.0 mm in diameter, subglobose, glabrous, dehiscent diplophragmously; seeds several, ca. 1 mm long, cymbiform, with reticulate surface. (Fig. 3A–C.)

Distribution and habitat. *Hedyotis longiramulis* is only known from Yangchun City of Guangdong Province, China. It grows mainly in damp places under broad-leaved forests, sometimes on roadsides at the elevation of 500–700 m. The associated species are mainly (Hance ex Benth.) Krass. (Melastomataceae), *Melastoma sanguineum* Sims (Melastomataceae), *Dunnia sinensis* Tutcher (Rubiaceae), *Dicranopteris ampla* Ching & P.S.Chiu (Gleicheniaceae) and *Selaginella doederleinii* Hieron. (Selaginellaceae).

Phenology. Flowering from late March to July, fruiting from August to October.

Etymology. The specific epithet “longiramulis” of the new species refers to its long lateral branches bearing many inflorescences.

Palynology. The pollen grains of *Hedyotis longiramulis* are monads, isopolar, spheroidal, 3-colporate; the tectum is a double microreticulum, with a psilate suprareticulum and a microechinate infrareticulum. The pollen size is 22.5 (20.2–25.1) × 21.5 (19.0–22.8) μm with P/E value 1.04 in long-styled flowers (Fig. 3D–F) and 27.1 (25.2–29.3) × 27.1 (25.1–28.7) μm with P/E value 1.00 in short-styled flowers (Fig. 3G–I).

Foliar epidermal anatomy. The epidermal cells on the upper (Fig. 3J) and lower (Fig. 3K) surface of leaves of *H. longiramulis* are irregularly polygonal, randomly arranged and have striated and papillate surface ornamentation, with the striations thickened at the middle of the periclinal walls, and the papillae

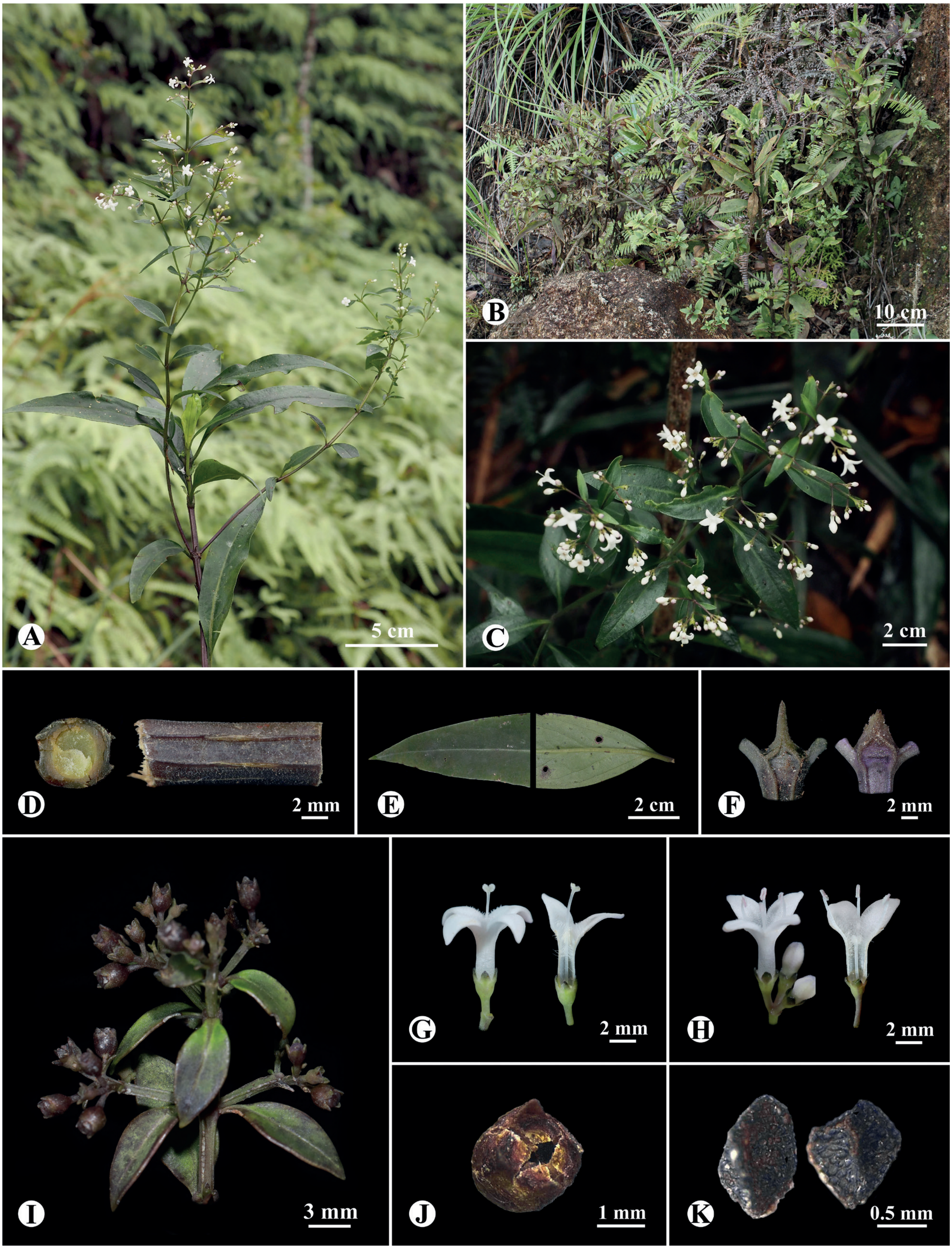

Figure 2. *Hedyotis longiramulis* Y.D. Xu & R.J. Wang **A** habit **B** habitat **C** inflorescences **D** part of stem (right) and its transverse section **E** adaxial (left) and abaxial (right) surgaces of leaf **F** Stipules **G** long-styled flower (left) and its longitudinal section (right) **H** short-styled flower (left) and its longitudinal section (right) **I** infructescence **J** diplophragmous capsule **K** dorsal (left) and ventral (right) view of seeds.

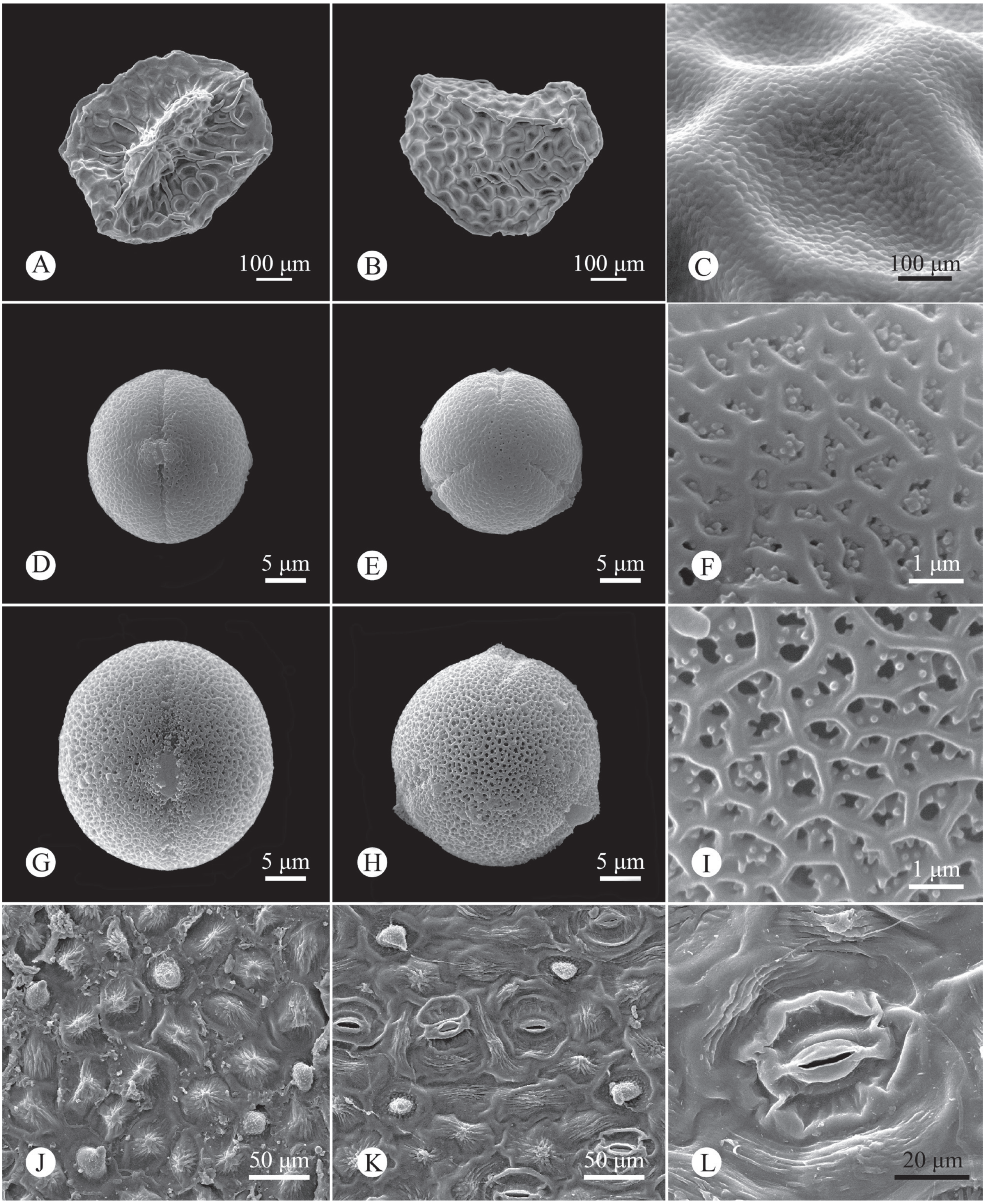

Figure 3. Micromorphology of seed, pollen and leaf epidermis of *Hedyotis longiramulis* using SEM **A–C** ventral view, dorsal view, and surface ornamentation of seeds, respectively **D, G, E, H, F, I** equatorial view, polar view, and reticulate ornamentation of pollen grains, respectively **J–L** leaf epidermis, adaxial and abaxial surfaces, and stomatal apparatus, respectively **A–C, J–L** *Yi-Da Xu & Fan Su AP0138* **D–F** *Rui-Jiang Wang & Yi-Da Xu 6540*, long-styled flower **G–I** *Rui-Jiang Wang & Yi-Da Xu 6541*, short-styled flower.

conical, with granular ornamentation on the surface. The anticlinal walls are straight in epidermis cells of the upper leaf surface and undulate in those of the lower leaf surface.

The leaves of *H. longiramulis* are hypostomatic, with the stomata randomly orientated over most of the lower surface. The stomata are paracytic, ca. 56.5 (51.4–63.4) × 42.8 (37.1–52.1) μm in size (Fig. 3L).

Additional specimens examined (paratypes). China. Guangdong Province: Yangchun City, Guigang Town, Baichong Provincial Nature Reserve, roadside, 13 Sept. 1990, Nian Liu et al. 424 (IBSC); ibid., 18 May 1991, Nian Liu et al. 1735 (IBSC). Yangchun City, Bajia Town, Guangdong Ehuangzhang Provincial Nature Reserve, mountain land and valley, 24 Oct. 1957, Kui Liang 69692 (CANT); ibid., 23 Oct. 1957, Bao-Han Liang 89654 (CANT); ibid., 11 Oct. 1990, Nian Liu et al. 866 and 899 (IBSC); ibid., 11 May 2001, Hua-Gu Ye et al. 5629 (IBSC); ibid., 7 Apr. 2019, Xin-Xin Zhou et al. ZXX0026 (IBSC); ibid., 12 Aug. 2020, Dan Liang et al. WP1366 (IBSC); ibid., 10 Sept. 2020, Yi-Da Xu & Fan Su AP0138 (IBSC); ibid., 9 Apr. 2021, Rui-Jiang Wang & Yi-Da Xu 6541 (IBSC).

Conservation status assessment. So far 10 subpopulations of *Hedyotis longiramulis* were found in Yangchun City (AOO 40 km^2, EOO 758 km^2), Guangdong Province, and their habitats are well protected. About 60 mature individuals were found in each of these subpopulations (within 2 × 2 km grid cells). We therefore estimated that there are at least 600 mature individuals in this area. According to the criteria D1 of IUCN Red List Categories and Criteria (IUCN 2022), the species can be assessed as “Vulnerable”. However, many other subpopulations of this species may be found in similar habitat nearby the vouchers’ localities in the nature reserves. Considering that this species has no economic uses and that there are no plausible threats since it occurs in two protected reserves, we recommend to evaluate it as “Least Concern”.

Characteristics of the chloroplast genome

The size of the complete chloroplast genome of *H. longiramulis* is 153,616 bp (GenBank: MZ425928, Fig. 4) with a typical quadripartite structure, including a small single-copy region (SSC, 17652 bp), a large single-copy region (LSC, 85050 bp), and a pair of inverted repeat regions (IRs, 25457 bp). It contains 112 unique genes, and the GC content is 32.4% (Table 4). The *rps19*, *ycf1*, *ndhF*, *rpl2* and *trnH* genes were found nearby the IR/Single-Copy (SC) region boundaries. Compared with *H. ovata*, the IR of *H. longiramulis* contracted to include only 4 bp of the 5’ end of *rps19* (vs. entirely included and occurring twice in IRs of *H. ovata*), and excludes the entire *ndhF* and 100 bp of the intergenic region (vs. including 32 bp of the 3’ end of *ndhF* in *H. ovata*) (Fig. 5). Detailed characteristics and statistics of the chloroplast genomes are listed in Tables 4, 5.

Discussion

Similar to other *Hedyotis* species described previously (Wang et al. 2018; Jiang and Wang 2019; Xu and Wang 2021; Jiang and Wang 2021), the pollen grains of *H. longiramulis* are dimorphic between long-styled and short-styled flowers, i.e., the pollen of the short-styled flowers is larger than that of the long-styled flow-

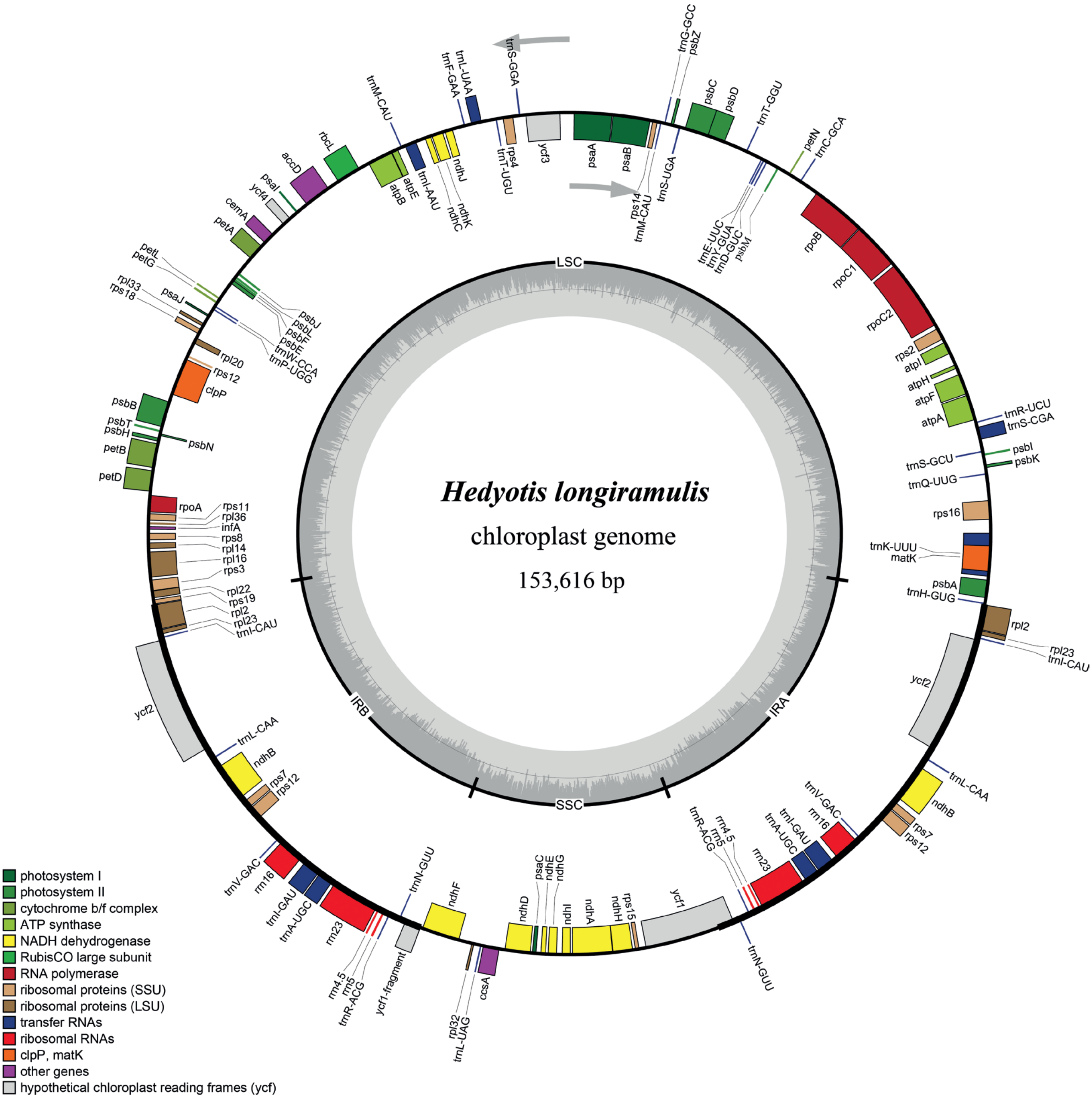

Figure 4. Chloroplast genome map of *Hedyotis longiramulis*. The thick lines on the outer complete circle identify the inverted repeat regions (IRa and IRb). The arrows indicate the transcription directions of the genes inside and outside of the circle. Genes belonging to different functional groups are color-coded. The dark gray in the innermost track corresponds to the GC content, the light gray to the AT content.

ers. This pattern was also found in other Rubiaceae with dimorphic flowers, e.g., *Damnacanthus* C.F.Gaertn. (Naiki and Nagamasu 2003) and *Arcytophyllum* Schult. & Schult.f. (Wolff and Liede-Schumann 2007).

The phylogenetic analysis shows that *H. longiramulis* is sister to *H. pubirachis* (Fig. 1), but it can be distinguished from this species by the puberulent stems and stipules (versus glabrous in *H. pubirachis*), the waxy leaf surface (versus non-waxy in *H. pubirachis*) and the inflorescences growing on long lateral branches (versus inflorescences on the main stem and lateral branches in *H. pubirachis*) (Table 3).

Table 4. Characteristics of the chloroplast genomes of *Hedyotis longiramulis* and *H. ovata*.

	Characteristics	*H. longiramulis* GenBank: MZ425928	*H. ovata* GenBank: MK203877
Size (bp)	Total	153,616	154,560
	LSC	85,050	84,579
	SSC	17,652	17,865
	IR	25,457	26,058
Number of unique genes	Total	112	112
	Protein-coding genes	79	79
	rRNA genes	4	4
	tRNA genes	29	29
GC%	Total	32.4	32.6
	LSC	35.9	36.0
	SSC	32.4	32.6
	IR	43.5	43.4
	protein-coding sequences (CDS)	38.4	38.9

Table 5. Genes encoded in the chloroplast genome of *Hedyotis longiramulis*.

Category	Group of genes	Names of unique genes
Self-replication	tRNA genes	*trnA-UGC*, *trnC-GCA*, *trnD-GUC*, *trnE-UUC*, *trnF-GAA*, *trnfM-CAU*, *trnG-GCC*, *trnH-GUG*, *trnI-CAU*, *trnI-GAU*, *trnK-UUU*, *trnL-CAA*, *trnL-UAA*, *trnL-UAG*, *trnM-CAU*, *trnN-GUU*, *trnP-UGG*, *trnQ-UUG*, *trnR-ACG*, *trnR-UCU*, *trnS-GCU*, *trnS-GGA*, *trnS-UGA*, *trnT-GGU*, *trnT-UGU*, *trnV-GAC*, *trnV-UAC*, *trnW-CCA*, *trnY-GUA*
	rRNA genes	*rrn4.5*, *rrn5*, *rrn16*, *rrn23*
	Ribosomal small subunit	*rps2*, *rps3*, *rps4*, *rps7*, *rps8*, *rps11*, *rps12*, *rps14*, *rps15*, *rps16*, *rps18*, *rps19*
	Ribosomal large subunit	*rpl2*, *rpl14*, *rps16*, *rpl20*, *rpl22*, *rpl23*, *rpl32*, *rpl33*, *rpl36*
	DNA-dependent RNA polymerase	*rpoA*, *rpoB*, *rpoC1*, *rpoC2*
Photosynthesis	Photosystem I	*psaA*, *psaB*, *psaC*, *psaI*, *psaJ*, *ycf3*, *ycf4*
	Large subunit of rubisco	*rbcL*
	Photosystem II	*psbA*, *psbB*, *psbC*, *psbD*, *psbE*, *psbF*, *psbH*, *psbI*, *psbJ*, *psbK*, *psbL*, *psbM*, *psbN*, *psbT*, *psbZ*
	NADH dehydrogenase	*ndhA*, *ndhB*, *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*, *ndhK*
	Cytochrome b/f complex	*petA*, *petB*, *petD*, *petG*, *petL*, *petN*
	ATP synthase	*atpA*, *atpB*, *atpE*, *atpF*, *atpH*, *atpI*
Other genes	Maturase	*matK*
	Subunit of acetyl-CoA carboxylase	*accD*
	Envelope membrane protein	*cemA*
	Protease	*clpP*
	C-type cytochrome synthesis	*ccsA*
	Conserved open reading frames	*ycf1*, *ycf2*
Peseudogene	Translation-related gene	*infA*

Comparing to chloroplast genome of the new species to that of *H. ovata*, we found that there was a 300 bp contraction that occurred in the IR regions of *H. longiramulis* excluding almost entirely the *rps19* gene from the IR/LSC boundaries (Fig. 5). However, we currently can't predict the fluctuation tendency in this genus due to insufficient chloroplast genomic data. We suggest that the complete chloroplast genome would be informative and would help resolve infrageneric relationships within the genus.

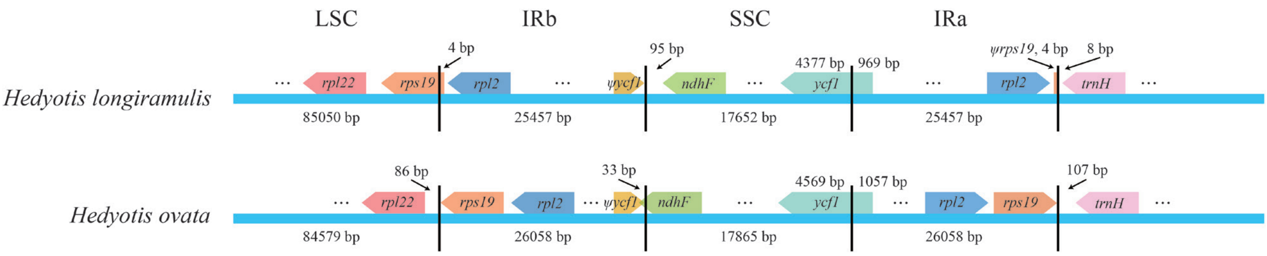

Figure 5. Sequence comparison of the IR/SC boundaries between *Hedyotis longiramulis* and *H. ovata*.

Key to the 24 *Hedyotis* species sampled in this study

1 Stem terete or slightly flattened **2**
– Stem tetragonal or sulcate, or at least so when juvenile **13**
2 Leaves ovate to ovate-triangular; inflorescences 1-flowered or 2–4-flowered and fasciculate .... ***H. pulcherrima***
– Leaves lanceolate, ovate-lanceolate, or lanceolate-elliptic; inflorescences cymose or paniculate cymose **3**
3 Stipules more or less puberulent abaxially **4**
– Stipules glabrous abaxially **6**
4 Leaves densely puberulent on both sides .... ***H. puberulifolia***
– Leaves glabrous on both sides or only puberulent on midrib adaxially **5**
5 Position of inflorescences strictly axillary .... ***H. loganioides***
– Position of inflorescences terminal and axillary in upper nodes.... ***H. tenuipes***
6 Position of inflorescences strictly axillary .... ***H. communis***
– Position of inflorescences terminal and axillary in upper nodes **7**
7 Inflorescences showing dichasial branching at sub-axes **8**
– Inflorescences showing monochasial branching at sub-axes **10**
8 Inflorescence axes terete .... ***H. cantoniensis***
– Inflorescence axes more or less 4-angled or sulcate **9**
9 Peduncles hollow, slightly sulcate; corolla tubes ca. 2.5 mm long .... ***H. nankunshanensis***
– Peduncles solid, 4-angled and sulcate; corolla tubes 3.0–4.0 mm long .... ***H. caudatifolia***
10 Inflorescence axes 4-angled and sulcate .... ***H. pubirachis***
– Inflorescence axes terete **11**
11 Leaves narrowly elliptic to lanceolate; stipules triangular.... ***H. nanlingensis***
– Leaves ovate, broadly elliptic or lanceolate; stipules broadly triangular.... **12**
12 Leaves ovate to lanceolate; capsules oblong-ellipsoid ...... ***H. longiexserta***
– Leaves ovate to broadly elliptic; capsules subglobose .... ***H. effusa***
13 Stems more or less puberulent or scabrous **14**
– Stems glabrous **17**
14 Leaves base broadly rounded or amplexicaul; leaves densely pilose on both sides .... ***H. xanthochroa***
– Leaves base cuneate, narrowly cuneate or shortly decurrent; leaves glabrous, waxy or puberulent on both sides **15**
15 Leaf surface waxy on both sides; inflorescences growing at lateral branches .... ***H. longiramulis***
– Leaves glabrous to puberulent on both sides; inflorescences growing at terminal and upper axillary of main stem **16**

16 Flowers not enclosed by two ovate leaflike bracts; corolla white or purplish abaxially; corolla tubes shorter than 3 mm .... ***H. matthewii***
– Flowers enclosed by two ovate leaflike bracts; corolla purple abaxially; corolla tubes longer than 15 mm .... ***H. yangchunensis***
17 Inflorescences axillary **18**
– Inflorescences terminal and axillary in upper nodes of stem **19**
18 Stipules broadly triangular, margins not reflexed, apex apiculate to aristate .... ***H. interrupta***
– Stipules ovate or triangular, margins becoming reflexed, apex acute to acuminate .... ***H. acutangula***
19 Corolla purple abaxially; corolla tubes longer than 5 mm **20**
– Corolla white or purplish abaxially; corolla tubes shorter than 3 mm **21**
20 Leaves lanceolate, narrowly lanceolate or narrowly elliptic, scabrous .... ***H. exserta***
– Leaves ovate, glabrous .... ***H. ovata***
21 Flowers homostylous; corolla tubes pilosulous adaxially **22**
– Flowers heterostylous; corolla tubes pubescent adaxially....................... **23**
22 Leaves narrowly lanceolate or lanceolate; corolla lobes longer than tube.... .... ***H. longipetala***
– Leaves narrowly elliptic, elliptic or lanceolate; corolla lobes nearly equal to tube in length .... ***H. matthewii***
23 Stipules broadly triangular, glabrous abaxially .... ***H. consanguinea***
– Stipules triangular, pubescent abaxially **24**
24 Inflorescences at terminal and upper axillary of main stem; peduncles shorter than 5 cm .... ***H. xinyiensis***
– Inflorescences at terminal of main stem; peduncles longer than 5 cm .... ***H. taishanensis***

Conclusion

The new species of *Hedyotis longiramulis* is described based on the combination of morphological and molecular evidence. In addition, the micromorphological characters of seed, pollen and leaf epidermal features were illustrated.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Bachman S, Moat J, Hill AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: Geospatial conservation assessment tool. ZooKeys 150: 117–126. https://doi.org/10.3897/zookeys.150.2109

Bremekamp CEB (1952) The African species of *Oldenlandia* L. sensu Hiern & K. Schumann. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde 48(2): 1–297.

Charr JC, Garavito A, Guyeux C, Crouzillat D, Descombes P, Fournier C, Ly SN, Raharimalala EN, Rakotomalala JJ, Stoffelen P, Janssens S, Hamon P, Guyot R (2020) Complex evolutionary history of coffees revealed by full plastid genomes and 28,800 nuclear SNP analyses, with particular emphasis on *Coffea canephora* (Robusta coffee). Molecular Phylogenetics and Evolution 151: e106906. https://doi.org/10.1016/j.ympev.2020.106906

David LD (1974) Approaches to the identification of angiosperm leaf remains. Botanical Review 40(1): 1–157. https://doi.org/10.1007/BF02860067

Doyle J (1991) DNA protocols for plants. In: Hewitt GM, Johnston AWB, Young JPW (Eds) Molecular Techniques in Taxonomy. Springer Berlin Heidelberg, Berlin, 283–293. https://doi.org/10.1007/978-3-642-83962-7_18

Dutta R, Deb DB (2004) Taxonomic Revision of *Hedyotis* L. (Rubiaceae) in Indian Sub-continent. Botanical Survey of India, 211 pp.

Gibbons KL (2020) *Hedyotis*, *Oldenlandia* and related genera (Rubiaceae: Spermacoceae) in Australia: New genera and new combinations in an Asian-Australian-Pacific lineage. Taxon 69(3): 515–542. https://doi.org/10.1002/tax.12236

Greiner S, Lehwark P, Bock R (2019) OrganellarGenomeDRAW (OGDRAW) version 1.3.1: Expanded toolkit for the graphical visualization of organellar genomes. Nucleic Acids Research 328(5979): 710–722. https://doi.org/10.1093/nar/gkz238

Guo X, Simmons MP, But PPH, Shaw PC, Wang RJ (2011) Application of DNA barcodes in *Hedyotis* L. (Spermacoceae, Rubiaceae). Journal of Systematics and Evolution 49(3): 203–212. https://doi.org/10.1111/j.1759-6831.2011.00130.x

Guo X, Wang RJ, Simmons MP, But PPH, Yu J (2013) Phylogeny of the Asian *Hedyotis-Oldenlandia* complex (Spermacoceae, Rubiaceae): Evidence for high levels of polyphyly and the parallel evolution of diplophragmous capsules. Molecular Phylogenetics and Evolution 67(1): 110–122. https://doi.org/10.1016/j.ympev.2013.01.006

Hesse H, Halbritter H, Zetter R, Weber M, Buchner R, Frosch-Radivo A, Ulrich S (2009) Pollen Terminology: An Illustrated Handbook. Springer Wien, New York, 261 pp.

IUCN Standards and Petitions Committee (2022) Guidelines for using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf

Jiang GB, Wang RJ (2019) *Hedyotis tonggulingensis* (Rubiaceae): A new species from Hainan, China. Phytotaxa 406(3): 191–198. https://doi.org/10.11646/phytotaxa.406.3.5

Jiang GB, Wang RJ (2021) Two new species of *Hedyotis* L. (Rubiaceae) from Hainan, China. Nordic Journal of Botany 39(6): e02934. https://doi.org/10.1111/njb.02934

Jin JJ, Yu WB, Yang JB, Song Y, dePamphilis CW, Yi TS, Li DZ (2020) GetOrganelle: A fast and versatile toolkit for accurate *de novo* assembly of organelle genomes. Genome Biology 21(1): 241–271. https://doi.org/10.1186/s13059-020-02154-5

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Misawa K, Kuma K-I, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30(14): 3059–3066. https://doi.org/10.1093/nar/gkf436

Lamarck JBPAM (1792) *Hedyotis*. In: Lamarck JBAPM, Poiret JLM (Eds) Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature. Botanique (Vol. 1(2)). Chez Panckoucke, Paris, 269–272. https://doi.org/10.5962/bhl.title.218

Liu WZ, Kong HH, Zhou J, Fritsch PW, Hao G, Gong W (2018) Complete chloroplast genome of *Cercis chuniana* (Fabaceae) with structural and genetic comparison to six species in Caesalpinioideae. International Journal of Molecular Sciences 19(5): e1286. https://doi.org/10.3390/ijms19051286

Löhne C, Borsch T (2005) Molecular evolution and phylogenetic utility of the *petD* group II intron: A case study in basal angiosperms. Molecular Biology and Evolution 22(2): 317–332. https://doi.org/10.1093/molbev/msi019

Naiki A, Nagamasu H (2003) Distyly and pollen dimorphism in *Damnacanthus* (Rubiaceae). Journal of Plant Research 25(1): 105–113. https://doi.org/10.1007/s10265-002-0075-1

Neupane S, Dessein S, Wikstrom N, Lewis P, Long CL, Bremer B, Motley T (2015) The *Hedyotis-Oldenlandia* complex (Rubiaceae: Spermacoceae) in Asia and the Pacific: Phylogeny revisited with new generic delimitations. Taxon 64(4): 299–322. https://doi.org/10.12705/642.8

Nguyen LT, Schmidt HA, Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Nylander JAA (2004) MrModeltest v2: Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Oxelman B, Liden M, Berglund D (1997) Chloroplast *rps*16 intron phylogeny of the tribe Sileneae (Caryophyllaceae). Plant Systematics and Evolution 206: 393–410. https://doi.org/10.1007/BF00987959

Popp M, Oxelman B (2001) Inferring the history of the polyploid *Silene aegaea* (Caryophyllaceae) using plastid and homoeologous nuclear DNA sequences. Molecular Phylogenetics and Evolution 20(3): 474–481. https://doi.org/10.1006/mpev.2001.0977

Qu XJ, Moore MJ, Li DZ, Yi TS (2019) PGA: A software package for rapid, accurate, and flexible batch annotation of plastomes. Plant Methods 15(1): 50–61. https://doi.org/10.1186/s13007-019-0435-7

Rono PC, Dong X, Yang JX, Mutie FM, Oulo MA, Malombe I, Kirika PM, Hu GW, Wang QF (2020) Initial complete chloroplast genomes of *Alchemilla* (Rosaceae): Comparative analysis and phylogenetic relationships. Frontiers in Genetics 11: e560368. https://doi.org/10.3389/fgene.2020.560368

Ronquist F, Teslenko M, Mark PVD, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sang T, Crawford DJ, Stuessy TF (1997) Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). American Journal of Botany 84(9): 1120–1136. https://doi.org/10.2307/2446155

Song Y, Chen Y, Lv JZ, Xu J, Zhu SF, Li MF (2019) Comparative chloroplast genomes of *Sorghum* species: Sequence divergence and phylogenetic relationships. BioMed Research International 5046958: 1–11. https://doi.org/10.1155/2019/5046958

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three noncoding regions of chloroplast DNA. Plant Molecular Biology 17(5): 1105–1109. https://doi.org/10.1007/BF00037152

Tate JA, Simpson BB (2003) Paraphyly of *Tarasa* (Malvaceae) and diverse origins of the polyploid species. Systematic Botany 28(4): 723–737.

Terrell EE, Robinson H (2003) Survey of Asian and Pacific species of *Hedyotis* and *Exallage* (Rubiaceae) with nomenclatural notes on *Hedyotis* types. Taxon 52(4): 775–782. https://doi.org/10.2307/3647351

Tillich M, Lehwark P, Pellizzer T, Ulbricht-Jones ES, Fischer A, Bock R, Greiner S (2017) GeSeq – versatile and accurate annotation of organelle genomes. Nucleic Acids Research 45(W1): W6–W11. https://doi.org/10.1093/nar/gkx391

Wang GT, Zhang Y, Liang D, Chen YQ, Wang RJ (2018) *Hedyotis taishanensis* (Rubiaceae): A new species from Guangdong, China. Phytotaxa 367(1): 38–44. https://doi.org/10.11646/phytotaxa.367.1.4

Willdenow KL (1797) Caroli a Linné Species Plantarum Exhibentes Plantas Rite Cognitas ad Genera Relatas, cum Differentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas (Tomus 1). Impensis G. C. Nauk, 1568 pp. https://doi.org/10.5962/bhl.title.60064

Wolff D, Liede-Schumann S (2007) Evolution of flower morphology, pollen dimorphism, and nectar composition in *Arcytophyllum*, a distylous genus of Rubiaceae. Organisms, Diversity & Evolution 7(2): 106–123. https://doi.org/10.1016/j.ode.2006.02.005

Xu YD, Wang RJ (2021) *Hedyotis puberulifolia* (Rubiaceae), a new species from Guangdong, China. Phytotaxa 502(2): 160–168. https://doi.org/10.11646/phytotaxa.502.2.4

Zhang XF, Wang JH, Zhao KK, Fan WW, Wang HX, Zhu ZX, Wang HF (2019) Complete plastome sequence of *Hedyotis ovata* Thunb. ex Maxim (Rubiaceae): An endemic shrub in Hainan, China. Mitochondrial DNA. Part B, Resources 4(1): 675–676. https://doi.org/10.1080/23802359.2019.1572467

Zhang Y, Wang ZF, Guo YN, Chen S, Xu XY, Wang RJ (2021) Complete chloroplast genomes of *Leptodermis scabrida* complex: Comparative genomic analyses and phylogenetic relationships. Gene 791: e145715. https://doi.org/10.1016/j.gene.2021.145715

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Research Article

A new lithophilous species of Gesneriaceae, *Petrocodon rubrostriatus*, from the karst area of South Yunnan, China

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Abstract

A new lithophytic species of Gesneriaceae, *Petrocodon rubrostriatus* K.Tan, X.Q.Song & M.X.Ren, **sp. nov.** from Lvchun County, South Yunnan, China, is described and illustrated here. It closest resembles *P. mollifolius* (W.T.Wang) A.Weber & Mich.Möller, but the new species is differentiated from it by red to brownish-red stripes in the yellow corolla throat and 4.5 mm long bract lobes, a ca. 10 mm long style, and staminodes inserted at 2.5–3 mm from the corolla base. The species is preliminarily assessed as 'Critically Endangered' (CR) according to IUCN criteria, since currently only one single locality is known with a few subpopulations on a fragmented limestone cliff, with fewer than 300 individuals.

Key words: Didymocarpoideae, flora of Yunnan, limestone, new taxon

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Introduction

Petrocodon Hance is a genus of lithophytic perennial herbs in the Gesneriaceae with currently 49 species and one variety (*P. dealbatus* var. *denticulatus*), mainly distributed in the limestone regions of southwestern China, and four species distributed on the northern Indo-China Peninsular (Huang et al. 2022; Yang et al. 2022; GRC 2023; POWO 2023; Zhang et al. 2023). Most species of *Petrocodon* are endemic to karst landscapes (Fan et al. 2020; Li et al. 2020 a, b), except for three species, *Petrocodon asterocalyx* F.Wen, Y.G.Wei & R.L.Zhang (Zhang et al. 2018), *P. chishuiensis* Z.B.Xin, F.Wen & S.B.Zhou (Xin et al. 2020), and *P. wui* F.Wen & R.B.Zhang (Zhang et al. 2023), which are distributed in Danxia landforms. After the revision based on molecular phylogenetic studies, several Chinese monotypic and small genera have been included in *Petrocodon*, such as *Calcareoboea* C.Y.Wu ex H.W.Li and *Lagarosolen* W.T.Wang (Weber et al. 2011), one species of *Wentsaiboea* D.Fang & D.H.Qin (Weber et al. 2011) and one species of *Primulina* Hance (Xu et al. 2014). *Petrocodon* is a genus with one of the highest diversity of floral traits in Chinese Gesneriaceae, which may have resulted from coevolution with their pollinators (Weber et al. 2011).

* The authors contributed equally to this paper.

In early August 2020, the authors carried out a field plant survey in the Lixianjiang river basin of Yunnan province, China. A flowering plant of Gesneriaceae was found growing on the tufa surface of a limestone cliff. Due to its typically lithophytic habit and gross vegetative characteristics, such as infundibuliform corolla, straight filaments, capsules dehiscing 4-valved, and capitate stigma, the authors provisionally determined that it belonged to the genus *Petrocodon* as originally defined. Some flowering individuals were collected as voucher specimens. Careful examination of those specimens in the lab and of living plants was made to compare vegetative and reproductive organs with other species of *Petrocodon*. The new taxon of *Petrocodon* is morphologically most close to *P. mollifolius* (W.T.Wang) A.Weber & Mich.Möller, but different from the latter mainly by the red stripes inside the pale to bright yellow corolla. Supported by molecular analyses, we confirmed it as a new species of *Petrocodon* sister to *P. mollifolius*.

Materials and methods

Morphological study

All available specimens of *Petrocodon* s.l. stored in the herbaria (IBK, KUN, and PE) in China, digital specimens on JSTOR Global Plants (http://plants.jstor.org) and the Chinese Virtual Herbarium (http://www.cvh.ac.cn), and relevant literature (e.g., Weber et al. 2011, 2020; Yang et al. 2022; Zhang et al. 2023) were examined and studied. We carried out morphological observation, measurements, and prepared a description based on living plants, dried specimens, and preserved materials of the new species. We described this new species using the terminology of Wang et al. (1990, 1998), Weber et al. (2011) and Zhang et al. (2023).

Phylogenetic analysis

Leaf material of the undescribed species was collected from the type locality in Lvchun County (Yunnan, China) and immediately dried in silica gel for DNA extraction (Chase and Hills 1991). Sequences of the nuclear ribosomal Internal Transcribed Spacer region (ITS) and plastid *trn*L-F intron-spacer region (*trn*L-F) of 38 samples representing 24 species and one variety of *Petrocodon* were downloaded from GenBank (Table 1). Four samples of the new species were newly sequenced for both markers following the DNA extraction, PCR amplification and sequencing protocol of Yang et al. (2022), using the primers for ITS and *trn*L-F of Taberlet et al. (1991) and Möller and Cronk (1997), respectively. Sequence alignment and phylogenetic analyses of the 44 samples followed Yang et al. (2022), with *Primulina dryas* (Dunn) Mich.Möller & A.Weber and *P. pinnata* (W.T.Wang) Yin Z.Wang as outgroups, based on previous phylogenetic analyses (Möller et al. 2009; Weber et al. 2011; Zhang et al. 2018, 2023). A partition homogeneity test (Farris et al. 1995) was conducted in PAUP 4.0a169 (Swofford 2003) with 1000 replicates to determine whether the *trn*L-F and ITS datasets contained phylogenetic conflict. We performed phylogenetic analyses, based on the combined dataset of *trn*L-F and ITS sequences using Maximum Likelihood (ML). We employed IQ-TREE v.2.0.6 (Nguyen et al. 2015) with 1000

Table 1. Voucher and GenBank accession numbers for the samples used in this study.

Species	Voucher number	*trn*L-F	ITS
Petrocodon ainsliifolius W.H. Chen & Y.M. Shui	Y.M.Shui et al. 44071	HQ632941	HQ633038
	CWH88	KF202298	KF202291
Petrocodon asterocalyx F.Wen, Y.G.Wei & R.L.Zhang	FW-2013	KC904957	KC904954
Petrocodon chishuiensis Z.B. Xin, F. Wen & S.B. Zhou	FW-2014	KF680503	KF680504
Petrocodon coccineus (C.Y.Wu ex H.W.Li) Y.Z.Wang	G80E	FJ501516	FJ501341
	CWH14B	KF202299	KF202292
Petrocodon coriaceifolius (Y.G.Wei) Y.G.Wei & Mich.Möller	M.Moeller & Y.G.Wei MMO 06-913	HQ632943	HQ633040
Petrocodon dealbatus Hance	LJM-2003-104	GU350668	GU350636
	G12B	FJ501537	JF697578
	LJM1209291	KR476565	KR337020
Petrocodon dealbatus var. *denticulatus* (W.T. Wang) W.T. Wang	Y.G. Wei 2010-03	JF697590	JF697578
Petrocodon ferrugineus Y.G. Wei	M.Moeller & Y.G.Wei MMO 06-784	HQ632946	HQ633043
Petrocodon hancei (Hemsl.) A.Weber & Mich.Möller	M.Moeller & Y.G.Wei MMO 08-1342	HQ632944	HQ633041
	–	KC904958	KC904955
	–	KC904959	KC904956
	GDLC05	KF498253	KF498051
Petrocodon hechiensis (Y.G.Wei, Yan Liu & F.Wen) Y.G.Wei & Mich. Möller	M.Moeller & Y.G.Wei MMO 07-1077	HQ632942	HQ633039
	–	KR476563	KR337018
Petrocodon hispidus (W.T. Wang) A.Weber & Mich.Möller	CWH87	KF202300	KF202293
	CWH101	KF202301	KF202294
Petrocodon hunanensis X.L. Yu & Ming Li	WF190107-02	MK941180	MK941179
Petrocodon integrifolius (D. Fang & L.Zeng) A.Weber & Mich.Möller	M.Moeller & Y.G.Wei MMO 06-865	HQ632940	HQ633037
Petrocodon lithophilus Y.M. Shui, W.H. Chen & Mich. Möller	CWH89	KF202302	KF202295
	CWH103	KF202303	KF202296
Petrocodon lui (Yan Liu & W.B.Xu) A.Weber & Mich.Möller	Y.G.Wei 8012	HQ632938	HQ633035
Petrocodon mollifolius (W.T. Wang) A.Weber & Mich.Möller	HEAC:LJM1108211	KR476547	KR337000
Petrocodon multiflorus F. Wen & Y.S. Jiang	HJ01-2	KM232660	KJ475411
Petrocodon nivelolanosus (D. Fang & W.T. Wang) A.Weber & Mich. Möller	–	JF697588	JF697576
Petrocodon pulchriflorus Y.B. Lu & Q. Zhang	Q.Zhang 01	KX579059	KX579058
Petrocodon retroflexus Q. Zhang & J. Guo	–	KX579061	KX579060
Petrocodon rubrostriatus sp. nov.	20TK0811008	OQ955752	OQ968808
	20TK0811008	OQ955753	OQ968809
	20TK0811008	OQ955754	OQ968810
	20TK0811008	OQ955755	OQ968811
Petrocodon scopulorus (Chun) Y.Z.Wang	–	GU350669	GU350637
	W.Fang 2010-02	HQ632947	HQ633044
	LJM06753	KR476567	KR337023
Petrocodon tiandengensis (Yan Liu & B.Pan) A.Weber & Mich.Möller	9413	JX506850	JX506960
Petrocodon tongziensis R.B.Zhang & F.Wen	Ren-Bo Zhang SBQ09383	MF872618	MF872617
Petrocodon viridescens W.H. Chen, Mich. Möller & Y.M. Shui	Y.M.Shui et al. 82661	HQ632939	HQ633036
	CWH41	KF202304	KF202297
Petrocodon wui F.Wen & R.B.Zhang	WF065	OQ716553	OQ694978
Primulina dryas (Dunn) Mich.Möller & A.Weber	C7a	FJ501524	FJ501348
Primulina pinnata (W.T.Wang) Yin Z.Wang	G26	FJ501526	FJ501349

Note. "–" indicates authors did not provide voucher number.

bootstrap replicates (Hoang et al. 2018). K3Pu+F+G4 was selected as the best model for *trn*L-F and GTR+F+G4 for ITS using ModelFinder (Kalyaanamoorthy et al. 2017). Tree visualization was carried out in FigTree v.1.4.4 (Rambaut 2018). The tree and sequence matrices are available in the TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S30602).

Results

As the partition homogeneity test for the *trn*L-F and ITS datasets showed no statistically significant incongruence (*P* = 0.09), the datasets were analysed combined. The aligned matrix of the plastid gene (*trn*L-F: 846 bp) and nuclear region (ITS: 693 bp) comprised 1539 bp, of which 1151 sites were identical, 237 (15.4%) were parsimony informative, and 151 parsimony-uninformative variable characters.

The phylogenetic tree revealed that all sampled *Petrocodon* taxa clustered together were monophyletic (BP = 100%) (Fig. 1). The four specimens of the new species, *P. rubrostriatus*, resolved in one clade with maximum support (BS = 100%). The new species together with its most similar species (*P. mollifolius*) belonged to a moderately-supported subclade (BP = 77%), which was on the first diverging lineage of *Petrocodon*.

In comparing the morphology between the new species (*P. rubrostriatus*) and the other species in *Petrocodon*, we found that the morphologically most similar species was *P. mollifolius*, but can be easily distinguished by its red to brownish-red stripes in the yellow corolla throat and corolla lobes. Other characters, such as bract size and insertion of staminodes inside corolla, pistil indumentum, disc margin and other characteristics also distinguished the two species (Table 2, Fig. 2). In conclusion, both the molecular phylogenetic analysis and morphological comparisons indicated that the new species and *P. mollifolius* are most closely allied, but could be distinguished.

Taxonomic treatment

Petrocodon rubrostriatus **K.Tan, X.Q.Song & M.X.Ren, sp. nov.**
urn:lsid:ipni.org:names:77325486-1
Fig. 2

Diagnosis. The new species resembles *Petrocodon mollifolius* (W.T.Wang) A.Weber & Mich.Möller in leaf blade shape and size, flower base colour and size (Figs 2, 3), but can be easily distinguished from the latter by corolla lobes with red to brownish longitudinal stripes (*vs*. corolla purely yellow), shorter lanceolate bracts, ca. 4.5 mm long (*vs*. linear, 12–20 mm long); longer style length ca. 10 mm (*vs*. 6–8 mm), and staminode insertion at 2.5–3 mm from corolla base (*vs*. inserted at the corolla base).

Type. China. Yunnan Province: Lvchun county, Banpo township, Emaluoba community, 22°36'N, 102°16'E, altitude ca. 390 m, August 13, 2020, *Ke Tan 20TK0811008* (Holotype: IBK! IBK00449896; Isotypes: HUTB, IBK! IBK00449897)

Description. Perennial herb. ***Rhizomatous stem*** 1–2 cm long, 5–8 mm in diam., sometimes inconspicuous. ***Roots*** fibrous, numerous, pale brown to brown. ***Leaves*** in a densely crowded basal rosette, (6–)9–12; petioles 1.5–4 cm long, densely whitish villous; lamina adaxial surface dark green,

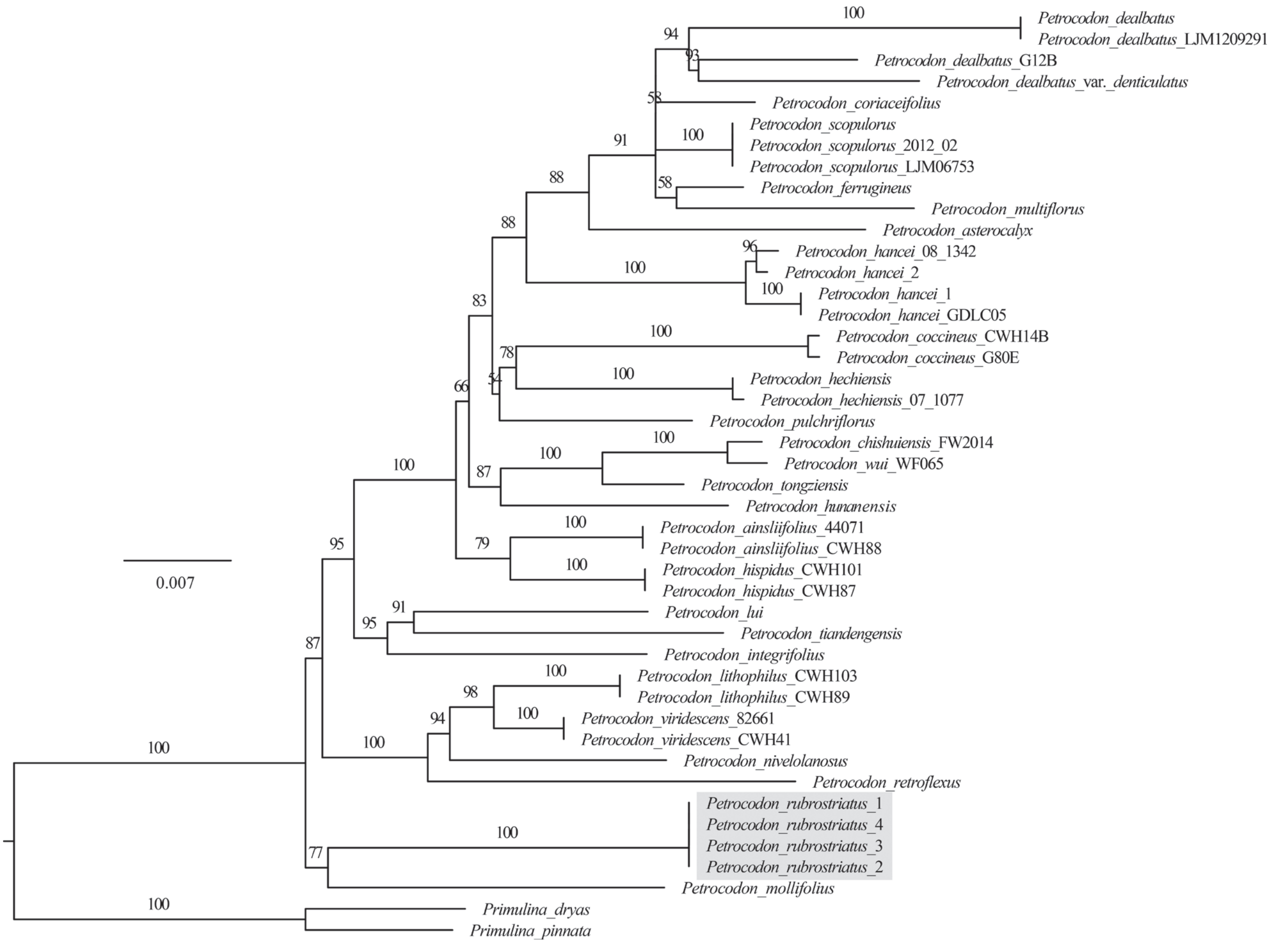

Figure 1. Phylogenetic tree of *Petrocodon* generated by Maximum Likelihood (ML) of combined *trn*L-F and ITS datasets. Numbers above the branches indicate ML bootstrap values (≥ 50%).

abaxial surface green, both surfaces whitish pubescent, herbaceous, elliptic, broadly elliptic to ovate, or rhombic ovate, 5.5–11.5 × 2.3–3.5 cm, margin serrate; 4–5 pairs of lateral veins on each side, ascending, tertiary venation also distinctive; apex acute, occasionally obtuse, base cuneate, occasionally asymmetric. ***Inflorescences*** 1–4 per plant, axillary, cymose, 3–5-flowered; peduncles green to pale brownish green, puberulent, interspersed with a few longer hairs, 6.5–8.5 cm long; bracts 2, opposite, green to pale green, lanceolate, ca. 4.5 mm long, ca. 1 mm across at base, abaxially pubescent, adaxially nearly glabrous, margin entire; bracteoles 2, opposite, narrowly triangular, colour and hairs same as bracts; pedicels 8–12 mm long, ca. 1 mm in diam., hairs same as peduncle. Calyx 5-sect to base, lobes green to pale green, lanceolate, ca. 2.5 × 0.5 mm, abaxially pubescent, adaxially nearly glabrous, margin entire. ***Corolla*** pale yellow to bright yellow, 1.9–2.2 cm long, base near-spherical, outside pubescent interspersed with few glandular hairs, inside glabrous; tube infundibuliform, tubular at the base and widening around the middle, ca. 15 mm long, ca. 4 mm in diam. at the base, ca. 7.5 mm in diam. at orifice, abaxial lip much longer than adaxial lip, adaxial lip 2-lobed to near base, slightly obliquely semicircular, lobes ca. 8 mm long, ca. 6 mm wide at base, margin entire, apex rounded, each lobe with two to three red to brownish-red longitudinal stripes, abaxial lip 3-lobed to more than middle, elliptical, lateral ones slightly oblique and smaller than the central one, lobes ca. 13 mm long, ca. 5 mm wide at base, margin entire, apex

Table 2. Morphological comparison between *Petrocodon rubrostriatus* and *P.mollifolius*.

Characters		*P. rubrostriatus*	*P. mollifolius*
Leaf blade	Shape	elliptic, broadly elliptic to ovate, or rhombic ovate	ovate to narrowly ovate, or ovate-oblong
Bracts	Shape	lanceolate	linear
	Length	ca. 4.5 mm long	12–20 mm long
	indumentum	abaxially pubescent, adaxially nearly glabrous	both sides densely puberulent
Calyx	Shape	broad lanceolate	lanceolate-linear
	indumentum	sparsely puberulent	densely villous
Corolla	Shape	infundibuliform corolla tube	nearly tubular
	colour	pale yellow with two or three red to brownish longitudinal stripes	pale yellow without stripes
Filament	Length	ca. 8 mm long	ca. 6.5 mm long
	indumentum	sparsely eglandular and glandular-puberulent from the middle to the top, and glands from the middle to the bottom	glandular puberulent
Pistil	Length	ca. 21 mm long, ovary 10 mm long and style ca. 10 mm long	ca. 17 mm long, ovary 10 mm long and style 6 mm long
	indumentum	densely puberulent	densely glandular- pubescent
Staminodes		3, inserted at 2.5–3 mm from corolla base	3, inserted at corolla base
Disc		sinuate	annular

rounded, each lobe with one red to brownish-red longitudinal stripe. ***Stamens*** 2, inserted in tube ca. 6 mm from corolla base; filaments pale green, ca. 8 mm long, straight, sparsely eglandular and glandular puberulent from the middle to the top and with glands from the middle to the bottom; anthers pale brownish yellow, elliptic, ca. 1.5 × 2.2 mm, glabrous, cohering face to face; staminodes 3, inserted 2.5–3 mm from corolla base, ca. 2 mm long, glabrous. ***Disc*** brownish green, ca. 0.9 mm high, glabrous, margin sinuate. ***Pistil*** ca. 21 mm long; ovary pale green, densely puberulent, ca. 10 mm long, ca. 1 mm wide; style whitish green, ca. 10 mm long, sparsely eglandular pubescent; stigma pale green, ca. 1 mm long, ca. 0.7 mm wide, disc-like. ***Capsule*** cylindrical, green when young, 1.7–2.1 cm long, ca. 1.5 mm wide, pubescent, becoming grey-brown and dehiscing into four valves when mature. ***Seeds*** unappendaged, long ellipsoid, ca. 0.4 mm long, ca. 0.2 mm wide.

Phenology. Flowering in August, fruiting from October to November based on field observations.

Etymology. The name *rubrostriatus* refers to the bright red to brownish stripes in the yellow corolla. This is noticeably different from the corolla colours of previously published *Petrocodon* species.

Vernacular name. Hóng Wén Shí Shān Jù Tái (红纹石山苣苔). The first two words, “Hóng Wén”, mean red stripes of the corolla, and the following four words, “Shí Shān Jù Tái”, mean *Petrocodon* in Chinese.

Distribution and habitat. *Petrocodon rubrostriatus* is only known from the type locality, near Lixianjiang river, Emaluoba community, Banpo township, Lvchun county, Yunnan. The species grows on moist, shady tufa surfaces of a limestone cliff in a monsoon rainforest at ca. 400 m. Thus, it is exposed to a warm environment with high air humidity in a moderately shaded monsoon rainforest.

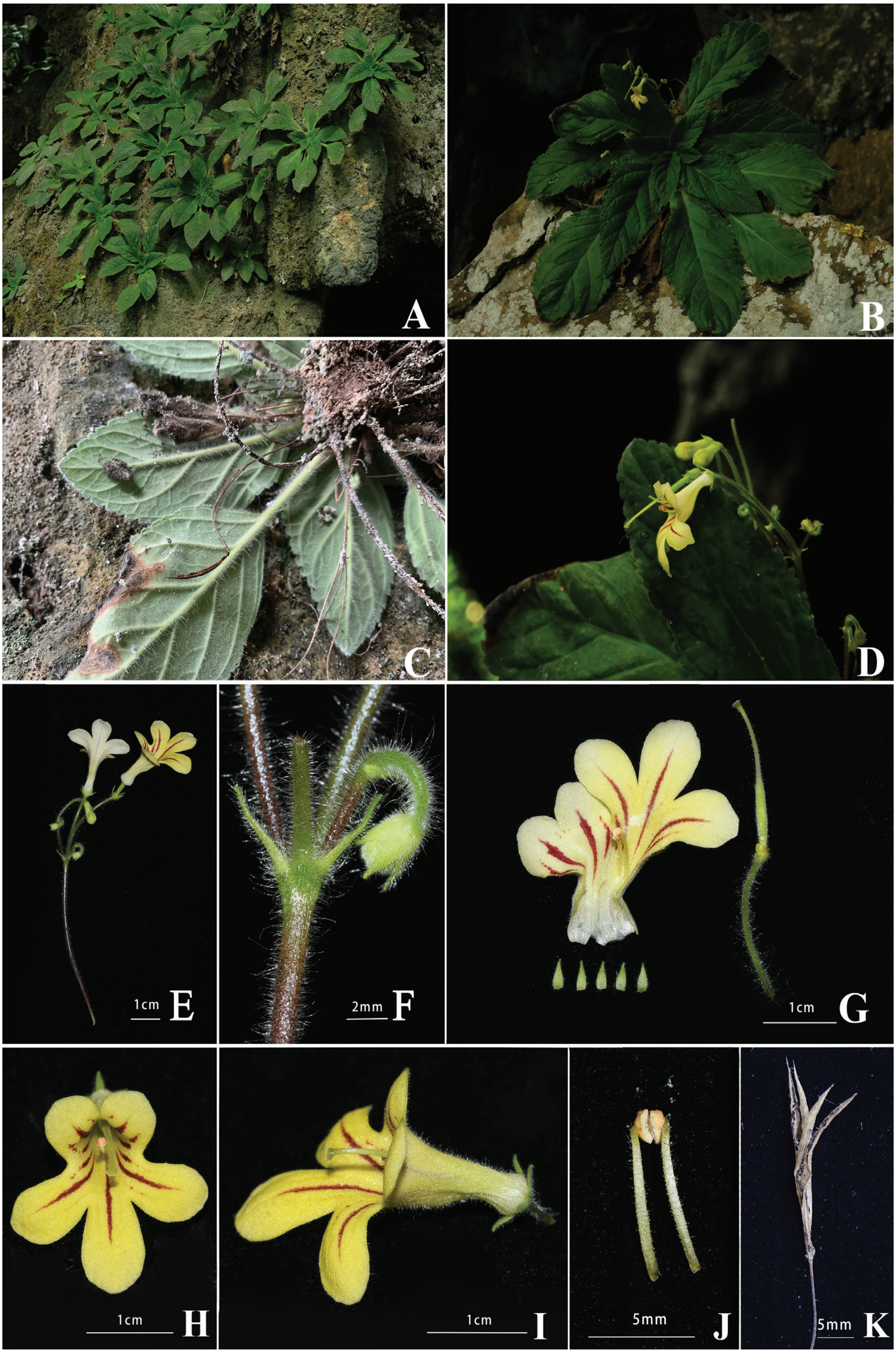

Figure 2. *Petrocodon rubrostriatus* K.Tan, X.Q. Song & M.X.Ren, sp. nov. **A** habitat **B** habit **C** underside of plant **D** oblique side view of flower and buds **E** cyme **F** bracts and flower bud **G** dissected calyx lobes, pistil with opened corolla **H** front view of flower **I** side view of flower **J** stamens with coherent anthers **K** dehisced capsule (Photographs by D.C. Meng).

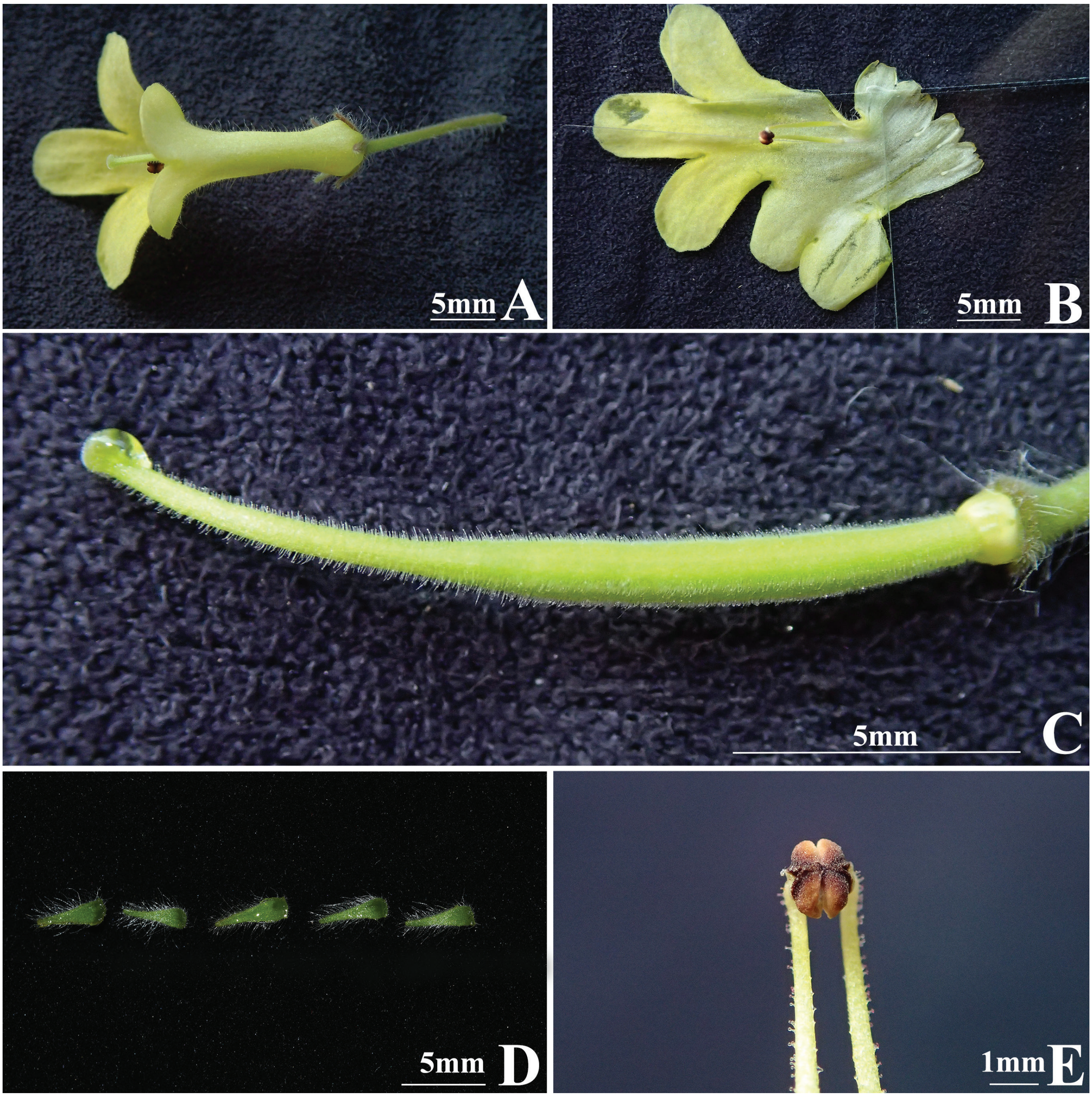

Figure 3. *Petrocodon mollifolius* (W.T.Wang) A.Weber & Mich.Möller **A** adaxial view of flower **B** opened corolla with two fertile stamens and three staminodes **C** pistil with disc **D** dissected calyx lobes **E** stamens with coherent anthers (Photographs by D.C. Meng).

Preliminary conservation assessment. *Petrocodon rubrostriatus* is currently only known from the type locality in the Lixianjiang river basin, where only one small population was observed. In total in 2020, there were fewer than 300 mature individuals in five separate subpopulations, clustered together in a fairly small site of ca. 100 m^2, on a moist cliff on the rock surface of an unnamed limestone hill close to the Lixianjiang river. The area of occupancy (AOO), is significantly smaller than the smallest AOO unit of IUCN (10 km^2 for Critically Endangered under B2). In 2022, we revisited the type locality and observed a decline in habitat quality caused by a prolonged drought in Southwest China, and a reduction in mature plants to only about 100. This suggests that the new species is extremely vulnerable and easily disturbed by the persistent drought and also the activities of local people. According to the IUCN red list criteria (IUCN 2022), the category of 'Critically Endangered' [CR, B2a,b (iii,iv,v)] is proposed here.

Taxonomic notes. The new species is morphologically similar to *Petrocodon mollifolius*, but most easily distinguished by the longitudinal stripes of red to brownish-red on the petal lobes. With the new species here, there are now 50 species and one variety in *Petrocodon*, and 47 species are distributed in China. South and Southwest China are the distribution and diversity centres of *Petrocodon*. The distribution pattern of a few species extends to the northern Indo-China Peninsula, namely *P. coccineus* (C.Y.Wu ex H.W.Li) Yin Z.Wang and *P. hispidus* (W.T.Wang) A.Weber & Mich.Möller which are both distributed in South China and Northern Vietnam (Wei 2018; Wei et al. 2022), *P. vietnamensis* Z.B.Xin, T.V.Do & F.Wen is endemic of Vietnam (Xin et al. 2021; Wei et al. 2022), *P. bonii* (Pellegr.) A.Weber & Mich.Möller is distributed from Thailand to Vietnam (GRC 2023, POWO 2023), and *P. flavus* D.J.Middleton & Sangvir. is an endemic of North Thailand (Middleton et al. 2015). The new species is found in the karst region near the Lixianjiang river, the boundary of China with Vietnam and Laos, and thus, the new species may also extend to these countries. Currently, the new species is tentatively considered an endemic to China until detailed field investigations are carried out in its neigbouring countries.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: DYC. Writing - original draft: KT. Writing - review and editing: MXR, XQS.

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Data availability

All of the data that support the findings of this study are available in the main text.

References

Chase MW, Hills H (1991) Silica gel: An ideal material for field preservation of leaf samples for DNA studies. Taxon 40(2): 215–220. https://doi.org/10.2307/1222975

Fan ZW, Cai L, Yang JW, Tang S-H, Wen F (2020) *Petrocodon luteoflorus* (Gesneriaceae), a new species from karst region in Guizhou, China. PhytoKeys 157: 167–173. https://doi.org/10.3897/phytokeys.157.32316

Farris JS, Källersjö M, Kluge AG, Bult C (1995) Testing significance of incongruence. Cladistics 10(3): 315–319. https://doi.org/10.1111/j.1096-0031.1994.tb00181.x

GRC (2023 [continuously updated]) Gesneriaceae Resource Centre. Royal Botanic Garden Edinburgh. https://padme.rbge.org.uk/GRC [Accessed 7 Jul 2023]

Hoang DT, Vinh LS, Flouri T, Stamatakis A, von Haeseler A, Minh BQ (2018) Mpboot: Fast phylogenetic maximum parsimony tree inference and bootstrap approximation. BMC Evolutionary Biology 18(1): 1–11. https://doi.org/10.1186/s12862-018-1131-3

Huang H, Wen F, Li MJ, Zhang JQ, Zhou YL, Li QY, Bai XX (2022) Characteristics of potential suitable areas of *Petrocodon* Hance and its environmental driving factors. Guihaia 43(7): 1–180. https://doi.org/10.11931/guihaia.gxzw202202034

IUCN (2022) Guidelines for using the IUCN Red List Categories and Criteria. Version 15. Prepared by the Standards and Petitions Committee. https://www.iucnredlist.org/documents/RedListGuidelines.pdf

Kalyaanamoorthy S, Minh BQ, Wong TK, Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Li S, Pan B, Xin ZB, Fu LF, Wen F (2020a) *Petrocodon ionophyllus*, a new species of Gesneriaceae from the limestone areas of south China. Rheedea 30(1): 150–158. https://doi.org/10.22244/rheedea.2020.30.01.09

Li ZL, Qin WH, Wen F, He DM, Hong X (2020b) *Petrocodon wenshanensis*, a new species of Gesneriaceae from southwestern China. PhytoKeys 157: 183–189. https://doi.org/10.3897/phytokeys.157.39624

Middleton DJ, Sangvirotjanapat S, La-Ongsri W (2015) A new species of *Petrocodon* (Gesneriaceae) from Thailand. Thai Forest Bulletin 43: 15–17. [Botany]

Möller M, Cronk QCB (1997) Origin and relationships of *Saintpaulia* (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. American Journal of Botany 84(7): 956–965. https://doi.org/10.2307/2446286

Möller M, Pfosser M, Jang CG, Mayer V, Clark A, Hollingsworth ML, Barfuss MHJ, Wang YZ, Kiehn M, Weber A (2009) A preliminary phylogeny of the ‘Didymocarpoid Gesneriaceae’ based on three molecular data sets: Incongruence with available tribal classifications. American Journal of Botany 96(5): 989–1010. https://doi.org/10.3732/ajb.0800291

Nguyen LT, Schmidt HA, Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Interne. http://www.plantsoftheworldonline.org/ [Accessed 07 July 2023]

Rambaut A (2018) FigTree, V1.4.4. Institute of Evolutionary Biology, University of Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/

Swofford DL (2003) PAUP*: Phylogenetic Analysis Using Parsimony (* and other Methods). Version 4. Sinauer Associates, Sunderland.

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17(5): 1105–1109. https://doi.org/10.1007/BF00037152

Wang WT, Pan KY, Zhang ZY, Li ZY (1990) Gesneriaceae. In: Wang WT (Ed.) Flora Reipublicae Popularis Sinicae (Vol. 69). Science Press, Beijing, 125–581.

Wang WT, Pan KY, Li ZY, Weitzman AL, Skog LE (1998) Gesneriaceae. In: Wu ZY, Raven PH (Eds) Flora of China. 18. Scrophulariaceae through Gesneriaceae. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis, 244–401.

Weber A, Wei YG, Puglisi C, Wen F, Mayer V, Möller M (2011) A new definition of the genus *Petrocodon* (Gesneriaceae). Phytotaxa 23(1): 49–67. https://doi.org/10.11646/phytotaxa.23.1.3

Weber A, Middleton DJ, Clark JL, Möller M (2020) Keys to the infrafamilial taxa and genera of Gesneriaceae. Rheedea 30(1): 5–47. https://doi.org/10.22244/rheedea.2020.30.01.02

Wei YG (2018) The distribution and conservation status of native plants in Guangxi, China. China Forestry Publishing House, Beijing, 876 pp.

Wei YG, Do VT, Wen F (2022) A Checklist to the Plants of Northern Vietnam. China Forestry Publishing House, Beijing, 606 pp.

Xin ZB, Fu LF, Huang ZJ, Li S, Maciejewski S, Wen F, Zhou SB (2020) *Petrocodon chishuiensis* (Gesneriaceae), a new species endemic to Guizhou, China. Taiwania 65(2): 181–186. https://doi.org/10.6165/tai.2020.65.181

Xin ZB, Do TV, Fu LF, Huang ZJ, Maciejewski S, Wen F (2021) *Petrocodon vietnamensis* sp. nov. (Gesneriaceae) from karst caves in northern Vietnam. Nordic Journal of Botany 39(4): njb.02996. https://doi.org/10.1111/njb.02996

Xu WB, Meng T, Zhang Q, Wu WH, Liu Y, Chung KF (2014) *Petrocodon* (Gesneriaceae) in the limestone karsts of Guangxi, China: Three new species and a new combination based on morphological and molecular evidence. Systematic Botany 39(3): 965–974. https://doi.org/10.1600/036364414X681437

Yang ZM, Chou WC, Zhao FC, Wen F, Wei YG (2022) *Petrocodon asterostriatus* (Gesneriaceae), a species from Guangxi, China. Annales Botanici Fennici 59(1): 285–294. https://doi.org/10.5735/085.059.0141

Zhang RL, Fu LF, Li S, Wei YG, Maciejewski S, LoFurno M, Wen F (2018) *Petrocodon asterocalyx*, a new species of Gesneriaceae from Guangxi, China. Phytotaxa 343(3): 259–268. https://doi.org/10.11646/phytotaxa.343.3.6

Zhang RB, Deng T, Li N, Wen F (2023) *Petrocodon wui* (Gesneriaceae), a new species from Guizhou, China. PhytoKeys 225: 41–51. https://doi.org/10.3897/phytokeys.225.99660

PhytoKeys 230: 301–307 (2023)
DOI: 10.3897/phytokeys.230.102754

Research Article

An unexpected new tree species from Gansu, China: *Illicium gansuense* (Schisandraceae)

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Abstract

We describe the newly-discovered species *Illicium gansuense* (Schisandraceae), discovered in the Yuhe area of Giant Panda National Park, Gansu, China. Morphologically, *I. gansuense* resembles *I. ternstroemioides* and *I. arborescens*. However, the new species can be distinguished by its smaller leaf size, the larger number of tepals, tepal margin ciliate, and distinct flowering and fruiting seasons.

Key words: Austrobaileyales, basal angiosperms, Gansu, Giant Panda National Park, Illiciaceae, Yuhe area

Introduction

The genus *Illicium* L., which belongs to the family Schisandraceae (APG IV 2016), consists of 35 species distributed across the southeastern United States, Mexico, the West Indies (five species), and eastern Asia (approximately 30 species) (Keng 1993). Linnaeus (1759) published the 10th edition of Systema Naturae, which included the first named species of *Illicium* (*I. anisatum* L.) based on Kaempfer's monograph. In 1947, Smith published the first comprehensive study of the genus *Illicium*, "The Families Illiciaceae and Schisandraceae", which divided the genus into two subgenera based on perianth morphology: 1) *I.* subgen. *Illicium* with thin, membranaceous and narrowly oblong or ligulate inner perianth segments; and 2) *I.* subgen. *Cymbostemon* with carnose to papyraceous and usually ovate to suborbicular inner perianth segments (Spach 1839; Smith 1947; Lin 1997). Both Hao's and Morris' results suggested that the previous division based on perianth morphology wasn't monophyletic (Hao et al. 2000). Morris et al. (2007) utilized a distinguishable seed character to reflect their evolution history: *I.* sect. *Cymostemon* contains seven species with a hilar rim around seed hilum; and *I.* sect. *Illicium* consists of all the other species which do not have a hilar rim.

China, especially the southwest and southeast parts of the country, is home to many species of *Illicium* species. In particular, the species *I. henryi* Diels. is known to occur only in southern Gansu Province.

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Illicium has considerable economic value, with *I. verum* Hook.f. being particularly valuable domestically in China and exported worldwide. The fruits of *I. verum* are used as a spice, and the leaves and fruits are steam distilled to create an aromatic oil (star anise oil) for use as a flavoring, as well as a therapeutic agent in traditional Chinese medicine (TCM). Other species of *Illicium* are used ornamentally or as a source of fine wood for furniture.

While surveying plants in the Yuhe area of the Giant Panda National Park, Gansu, in October 2020, we discovered an unknown species of *Illicium*. Based on field surveys, morphological and phenological studies, and taxonomic literature reviews, we concluded that this species should be included in *I.* sect. *Cymbostemon* (Spach) A.C.Smith (Smith 1947). However, because the specimen differed from other members in the section, we named and established the specimen as a new species (*I. gansuense*), as described herein.

Material and method

All morphological data were obtained from field observations carried out in the Yuhe Area of the Giant Panda National Park, Longnan City, Gansu Province, eastern China. Plants were photographed with a Nikon D750 digital camera. Digital specimens were deposited at the IBSC, KUN, PE, IBK, and WUK herbaria through the Chinese Virtual Herbarium (https://www.cvh.ac.cn/). Physical specimens were deposited at the NWTC Herbarium. All terminology used in the present study is in accordance with the Flora of China (Lu and Rabeler 2001), as well as the Plant Photo Bank of China (PPBC) and the Chinese Field Herbarium (CFH). The conservation status of the new species was assessed according to the standards of the IUCN (2012).

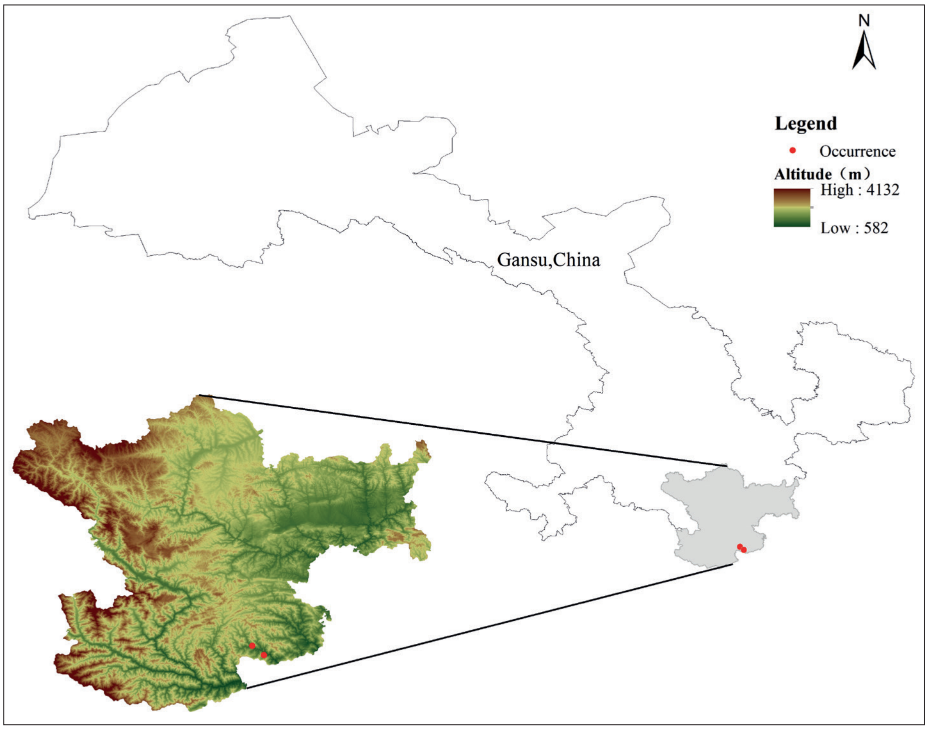

Figure 1. Distribution of *Illicium gansuense*.

Taxonomic treatment

Illicium gansuense **Z.F.Bai & Xue L.Chen, sp. nov.**
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Figs 2–4

Type. China. Gansu: Longnan City, Yuhe Area of Giant Panda National Park, altitude ca. 1200 m, 4 April 2020, *Zengfu Bai & Xuelin Chen 2020001* (***holotype*:** NWTC!; ***isotype*:** NNBG!).

Diagnosis. *Illicium gansuense* is similar to *I. ternstroemioides* and *I. arborescens* in overall form, leaf characters, red flowers, location, and population density. *Illicium gansuense* can be distinguished from *I. ternstroemioides* and *I. arborescens* based on leaf-blades size (7–12 × 1.8–3.5 cm in *I. gansuense* vs. 7–13 × 2–5 cm in *I. ternstroemioides* vs. 6–12 × 2–4.5 cm in *I. arborescens*), tepal number and pubescence (10–17 tepals with ciliate margins vs. 10–14 tepals with glabrous margins vs. 14–21 tepals with glabrous margins), number of carpels (10–13 vs. 12–14 vs. 12–16), number and size of the stamens (23–27, 2–3 mm long vs. 22–30, 1.8–3.4 mm long vs. 39–41, 2–3 mm long), and ovary length (1–1.5 mm long vs. 1.3–2.5 mm long vs. 1–1.8 mm long). (Table 1).

Description. Trees 4–12 m tall, whole plant with an aniseed aroma. Trunk 22.5 cm diam. at chest height, outer bark grayish-brown, with irregular longitudinal cracks; canopy tower or conical and branches are dense and spread horizontally; twigs pubescent, perules ca. 3 × 2 mm, ovoid, yellowish-brown, caducous, margins finely ciliate. Leaves clearly spirally-alternate to pseudoverticillate (clustered in sets of 2–5 at the apex of twigs); petioles 8–12 mm long, 1–2 mm diam.; blades 7–12 × 1.8–3.5 cm, oblanceolate, coriaceous, translucent oil spots visible against the light, adaxially dark to medium green, glossy, abaxially light green, base cuneate, margin glabrous, apex acuminate; midvein adaxially slightly impressed, abaxially prominently round, lateral veins pairs 6–9, inconspicuous. Inflorescences 1-flowered, but flowers sometimes clustered in groups of 2–6 at the apex of branches, axillary, pedunculate; peduncle 8–14 mm long, 2 mm diam., brown, bracteoles 2–4 × 2–3 mm, ovate. Flowers 12–18 mm diam., bisexual, androgynous scented, anthesis diurnal; floral buds 5–10 × 3–6 mm, ovoid, brown; pedicels 5–12 mm long, 2 mm diam., brown; tepals 10–17, in 2–3 whorls, outer whorl with 5–7 tepals, 6–8 × 5–7 mm, ovate, sepaloid, yellowish-green, base round, margin red, ciliate, apex acuminate or

Table 1. Morphological, geographic, and phenological comparison of *Illicium gansuense*, *I. ternstroemioides*, and *I. arborescens*.

Trait	*I. gansuense*	*I. ternstroemioides*	*I. arborescens*
Leaf blades	7–12 × 1.8–3.5 cm	7–13 × 2–5 cm	6–12 × 2–4.5 cm
Tepals	10–17, margin ciliate	10–14, margin glabrous	14–21, margin glabrous
Carpels	10–13	12–14	12–16
Stamens	23–27, 2–3 mm long	22–30, 1.8–3.4 mm long	39–41, 2–3 mm long
Ovaries	1–1.5 mm long	1.3–2.5 mm long	1–1.8 mm long
Distribution	Gansu (eastern China)	Fujian, Hainan (southeastern China)	Taiwan
Flowering time	March–April	January–August	January–April

Figure 2. *Illicium gansuense* Z.F.Bai & Xue L.Chen **A** flowering branch **B** adaxial and abaxial leaf surface **C** flower **D** tepals **E** removal of tepals showing gynoecium and stamens **F, G** stamens, dorsal and ventral views **H** carpel **I** fruiting branch **J, K** fruits **L** seed. (Drawn by Jianlu Bai based on type specimen).

Figure 3. *Illicium gansuense* Z.F.Bai & Xue L.Chen **A** habitat **B, C** flowering branch **D** bark.

obtuse, inner whorls with 8–10 tepals, 8–12 × 4–8 mm, widely ovate to widely obovate to widely elliptic, petaloid, fleshy, red, base broadly cuneate, margin ciliate, apex acuminate; stamens 23–27, in 2–3 whorls, 1.3–3.5 mm long, filament 0.3–1.5 mm long, stout, widely obovoid to widely ellipsoid, pink, connective truncate to emarginate, pink, anther 1–2 × 0.6–1 mm, introrsely rimose, pollen grains trisyncolpate, blackish-brown *in vivo*; carpels 10–14, 3–5.5 × 1.6–2 mm, ovaries 1–1.5 mm long, stigmatic crest 1.3–1.8 mm long, slightly longer than the ovary, subulate. Follicetum 12–16 × 4–7 mm; peduncle 1–1.5 cm long; follicles 10–13, 15–25 × 5–8 mm, 2–4 mm thick, woody, dark brown, apex aristate due to the persistent and hardened stigmatic crest, 3–6 mm long, slightly curved at apex. Seeds 4.5–6 × 4–5 mm, 1.5–2.5 mm thick, ovoid, testa smooth, brown.

Distribution and habitat. Currently, only one population of *I. gansuense* has been identified in Yuhe Town, Longnan City, southern Gansu Province. This area is characterized by a northern subtropical subhumid climate and a mountainous terrain containing high peaks and steep slopes. Specimens of *I. gansuense* were found growing in a deciduous broadleaf forest at an elevation of 1200 m. The dominant species of this forest community include *Trachycarpus fortunei* (Hook.) H.Wendl. (Arecaceae), *Cinnamomum septentrionale* Hand.-Mazz. (Lauraceae), *Lindera aggregata* (Sims) Kosterm. (Lauraceae), and *Deyeuxia effusiflora* Rendle (Poaceae). (Fig. 1)

Phenology. Flowering from March to April, fruiting from May to November.

Conservation status. There is only one known location, and fewer than three individuals of *I. gansuense* were found during our fieldwork in the Yuhe area of Giant Panda National Park in 2020 and 2022. However, investigations of the natural distribution of this species are insufficient. According to the IUCN Red List criteria (2019), this new species is better assessed as Data Deficient (DD; criteria B1ab(i–v) + 2ab(i–v)).

Etymology. The specific epithet '*gansuense*' refers to a province in eastern China. 甘肃八角 (gān sù bā jiǎo) is suggested as a suitable Chinese name for it.

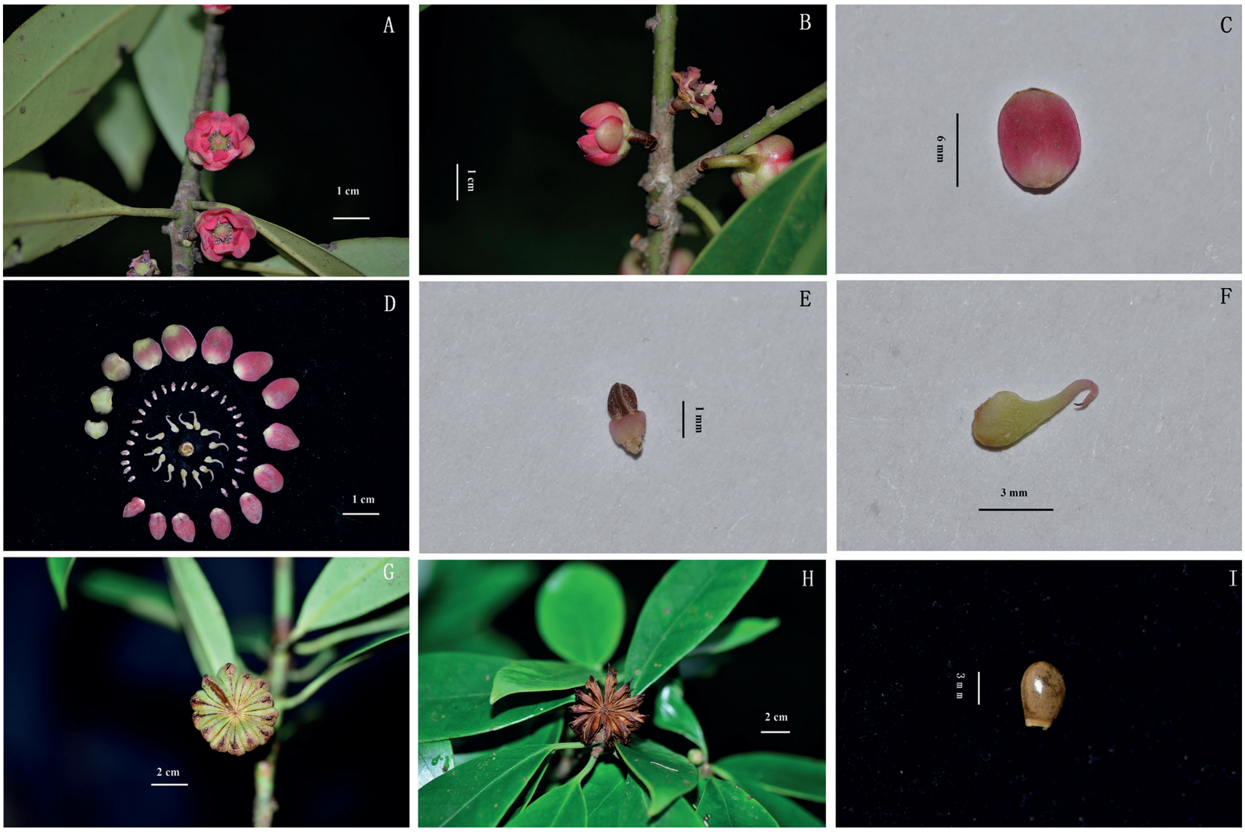

Figure 4. *Illicium gansuense* Z.F.Bai & Xue L. Chen **A** flower at front view **B** flower at side view **C** the largest tepals **D** all parts of flower **E** stamen **F** follicle **G** fruit at front view **H** fruit at side view **I** seed. Photographed by Zengfu Bai.

Notes. *Illicium gansuense* is similar to *I. ternstroemioides* and *I. arborescens* in overall form, that are all trees, leaf characteristics, flower color, location, and population density. However, as noted above, the three species can be distinguished according to both morphological features and distribution. Specifically, in relation to *I. ternstroemioides* and *I. arborescens*, *I. gansuense* is characterized by smaller leaf blades, tepals with ciliate margins (rather than glabrous), fewer carpels, and smaller ovaries. Additionally, *I. gansuense* blooms from March to April and *I. arborescens* blooms from January to April. (Table 1).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Methodology: ZZ. Writing – review and editing: ZB, XC, JZ.

Data availability

All of the data that support the findings of this study are available in the main text.

References

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181(1): 1–20. https://doi.org/10.1111/boj.12385

Hao G, Saunders RMK, Chye M-L (2000) A phylogenetic analysis of the Illiciaceae based onsequences of internal transcribed spacers (ITS) of nuclear ribosomal DNA. Plant Systematics and Evolution 223(1–2): 81–90. https://doi.org/10.1007/BF00985328

IUCN (2012) IUCN Red List Categories and Criteria, Version 3.1. (2nd edn.). IUCN, Gland.

Keng H (1993) Illiciaceae. In: Kubitzki K, Rohwer JG, Bittrich V (Eds) The Families and Genera of Vascular Plants. II Flowering Plants–Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families. Springer, Berlin, 344–347. https://doi.org/10.1007/978-3-662-02899-5_42

Lin Q (1997) Systematics and evolution of the family Illiciaceae. PhD Thesis. Forestry College, South China Agricultural University, Guang Zhou, China. [In Chinese]

Linnaeus C von (1759) Systema Naturae. Editio Decima 2: 1042. [1050, 1370.]

Lu DQ, Rabeler RK (2001) Pseudostellaria. In: Wu ZY, PH Raven, Hong DY (Eds) Flora of China. Science Press, Missouri Botanical Garden Press, St. Louis, Beijing, 7–10.

Morris AB, Bell CD, Clayton JW, Judd WS, Soltis DE, Soltis PS (2007) Phylogeny and divergence time estimation in *Illicium* with implications for New World biogeography. Systematic Botany 32(2): 236–249. https://doi.org/10.1600/036364407781179734

Smith AC (1947) The families Illiciaceae and Schisandraceae. Sargentia 7: 1–224. https://doi.org/10.5962/p.265318

Spach E (1839) Histoire Naturelle des Végétaux: Phanérogames, Tome 7. Librairie encyclopédique de Roret, Paris, 444 pp.