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*Taxonomy and Floristics / Taxonomía y Florística*

# A New Species of *Guadua* (Poaceae: Bambusoideae: Bambuseae) Endemic to Nayarit, Mexico

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**Abstract**

**Background:** We found a flowering population of *Guadua* near the town of Heroico Batallón de San Blas, Nayarit. Unlike previously known populations of *Guadua* in the state, all of which appear to be *G. paniculata*, this population was morphologically similar to *G. amplexifolia*, a species known from southern Mexico, Central America, and northern South America but apparently absent from Nayarit.
**Question:** Does the Nayarit population of *Guadua* represent a new species?
**Studied species:** *Guadua, Guadua lacerata.*
**Study site and dates:** Nayarit, Mexico, September 2023, April 2024.
**Methods:** We did field observations and collected herbarium vouchers, measuring morphological vegetative and reproductive characters in the herbarium specimens and living plants. We used scanning electron microscopy to describe the foliage leaf, lemma, and palea micromorphology. Finally, we completed a conservation assessment.
**Results:** This population of *Guadua* from Nayarit differed from *G. amplexifolia* in that it had relatively short culm leaf blades compared to the sheath, with the sheaths shredding from the base with age, highly floriferous pseudospikelets, and relatively short, densely pubescent lemmas. We describe the *Guadua* comprising this population as a new species named *Guadua lacerata*. We hypothesize that this species would be listed as Critically Endangered.
**Conclusions:** Currently, *Guadua lacerata* is considered a new Critically Endangered species endemic to Nayarit, Mexico.
**Keywords:** genetic diversity, Guaduinae, micromorphology, Neotropical woody bamboos, tropical subdeciduous forest.

**Resumen**

**Antecedentes:** Encontramos una población de *Guadua* cerca del pueblo Heroico Batallón de San Blas, Nayarit. Es diferente a las poblaciones de *Guadua* previamente conocidas para el estado, todas ellas determinadas como *G. paniculata*. Esta población es morfológicamente más similar a *G. amplexifolia*, especie conocida solo del sur de México, Centroamérica y Sudamérica, pero aparentemente ausente para Nayarit.
**Pregunta:** ¿La población de *Guadua* de Nayarit representa una especie nueva?
**Especies de estudio:** *Guadua, Guadua lacerata.*
**Sitio y años de estudio:** Nayarit, México, septiembre 2023, abril 2024**.**
**Métodos:** Realizamos observaciones de campo y recolectamos muestras de herbario, medimos caracteres morfológicos vegetativos y reproductivos en los especímenes de herbario y plantas vivas. Usamos microscopía electrónica de barrido para describir la micromorfología de las láminas foliares, lemas y páleas. Finalmente, evaluamos el estado de conservación.
**Resultados:** La población de *Guadua* de Nayarit se diferenció de *G. amplexifolia* en tener láminas de las hojas del culmo relativamente cortas en comparación con la vaina, vainas que se desgarran desde la base con la edad, pseudoespiguillas con muchos flósculos y lemas relativamente cortas y densamente pubescentes. Describimos la *Guadua* que comprende esta población como una nueva especie nombrada *Guadua lacerata*. Planteamos la hipótesis de que esta especie estaría catalogada como En Peligro Crítico.
**Conclusiones:** Por el momento, se considera que *Guadua lacerata* es una especie nueva en peligro crítico de extinción endémica de Nayarit, México.
**Palabras clave:** Bambúes leñosos Neotropicales, bosque tropical subcaducifolio, diversidad genética, Guaduinae, micromorfología.

*Guadua* Kunth is the most speciose genus in the Guaduinae subtribe of Neotropical woody bamboos, with 36 described species (Ruiz-Sanchez *et al*. 2021, 2024, Afonso *et al.* 2023, Londoño & Ruiz-Sanchez 2024). The geographical distribution of *Guadua* species extends from central Mexico to Uruguay and Argentina in South America (Judziewicz *et al*. 1999, Ruiz-Sanchez *et al*. 2021). Mexico has eight of the 36 species, with four of the eight species endemic to the country (*G. guzmanii* Ruiz-Sanchez, Anaya & Londoño*, G. inermis* E.Fourn.*, G. tuxtlensis* Londoño & Ruiz-Sanchez*,* and *G. velutina* Londoño & L.G.Clark); additionally, *G. angustifolia* Kunth was introduced for cultivation in several regions of the country (Ruiz-Sanchez *et al*. 2015, 2024).

In addition to *Guadua*, five other genera are currently included in Guaduinae: *Apoclada* McClure, *Eremocaulon* Soderstr. & Londoño, *Olmeca* Soderstr., *Otatea* (McClure & E.W.Sm.) C.E.Calderón & Soderstr., and *Tibisia* C.D.Tyrrell, Londoño & L.G.Clark (Tyrrell *et al*. 2018, Ruiz-Sanchez *et al.* 2021). Phylogenetic analyses have found that *Guadua* is sister to *Eremocaulon*, and with *Apoclada*, these three genera form a clade. The clade including *Guadua, Eremocaulon,* and *Apoclada* is sister to the *Olmeca+Otatea* clade, and sister to the rest of Guaduinae genera is *Tibisia* (Tyrrell *et al.* 2018, Gallaher *et al.* 2022).

During September of 2023, a flowering population of *Guadua* belonging to an unknown species was located in Nayarit along the Mazatlán-Tepic highway, along a small, tree-lined stream between two farm fields about 4.25 km northwest from Pantano Grande and 0.5 km southwest of the town of Heroico Batallón de San Blas. Although the only previously known *Guadua* species from Nayarit is *G. paniculata* Munro (Ramírez-Ojeda *et al.* 2021, Perez-Garcia & Ruiz-Sanchez 2023), this population, at 8-10 m tall, with solid or nearly solid culms to about eight centimeters in diameter, prominent supra- and infranodal bands of white hair, and auriculate culm leaves with persistent blades, did not closely resemble members of the *G. paniculata* species complex or *G. guzmanii* of Jalisco, instead appearing most similar to *G. amplexifolia* J.Presj (Londoño & Ruiz-Sanchez 2014, Ruiz-Sanchez *et al.* 2015, 2024). Although *G. amplexifolia* has a few populations in the Pacific state of Oaxaca (*e.g.*, *Clark et al. 474, Clark et al. 1144*), these populations are over 1,000 km from the population of flowering *Guadua* in Nayarit. Furthermore, this population bore clear differences in its vegetative and floral morphology from *G. amplexifolia* or any other known *Guadua* species, most strikingly in the way that culm leaf sheaths shredded from the base when retained on the culm, the length and shape of many pseudospikelets, and the number of fertile florets per pseudospikelet, indicating that it represents a previously undescribed species.

In this study, we provide descriptions of the macromorphology and foliar and floral bract micromorphology of this new species of Pacific *Guadua*, a preliminary conservation assessment, a tabular morphological comparison of the Mexican *Guadua* species with persistent culm leaf blades and conspicuous supra- and infranodal bands of hair, and a map of the known range of this species. Additionally, we present photos of this new species *in situ*, scanning electron microscopy (SEM) images of its foliage leaves and floral bracts, and an updated dichotomous key to the *Guadua* of Mexico. We also estimated genetic diversity within the population with single sequence repeat (SSR) genotyping to calculate heterozygosity ($H_O$), expected heterozygosity ($H_E$), allele richness ($A_R$), average number of alleles per locus (Na), the effective number of alleles per locus ($A_e$), and Wright's fixation index (F).

## Materials and methods

*Field observations, collection, and macromorphological description.* Field observations and collection of herbarium vouchers took place on 8 September 2023 and 8 April 2024. Herbarium vouchers included living culm leaves, branches with foliage leaves, and branches with pseudospikelets, which were measured using a centimeter scale ruler in the herbarium after drying; culms and rhizomes were photographed and measured in the field using a ruler and flexible measuring tape with centimeter scale. Photographs taken in the field were deposited in an Iowa State University DataShare Repository and available at https://doi.org/10.25380/iastate.27287805. Descriptive terminology for macromorphological characters primarily followed that of Judziewicz *et al.* (1999). Pseudospikelets were described using the terminology of Londoño & Ruiz-Sanchez (2024), with structures labeled "glumes" by Judziewicz *et al*. (1999) termed "sterile lemmas". "Clusters" of pseudospikelets referred to the number of pseudospikelets in a branch-

ing group. Measurement, description, and location of additional *Guadua* species referenced specimens from IBUG, IEB, ISC, MEXU, and US (Thiers 2024), with additional reference to descriptions from Presl (1830), Fournier & Bescherelle (1886), Swallen (1938), Clark & Londoño (1991), Londoño & Ruiz-Sanchez (2014), and Ruiz-Sanchez *et al.* (2015, 2024). Descriptions of *G. amplexifolia* were limited to specimens collected in Mexico and Central America.

In April 2024 we collected fresh foliage leaves from the only eight individuals that comprised the population. Every individual was separated from each other for a few meters. The foliage leaf samples were kept in silica gel until processing in the laboratory.

*Scanning Electron Microscopy.* We used scanning electron microscopy to observe and describe the foliage leaf, lemma, and palea micromorphology of the new species. Foliage leaf and floral bract samples were obtained from *E.K. McMurchie & E. Ruiz-Sanchez 1681* and prepared and imaged following a slightly modified version of the procedure of McMurchie *et al.* (2022). The modifications to this procedure comprised the following: foliage leaf and floral bract samples were submerged in xylene three times to remove epicuticular wax, iridium was used to sputter coat samples, and floral bracts were flattened under weights following xylene treatment so that the abaxial surface was presented for imaging. Samples were imaged at the Iowa State University Roy J. Carver High Resolution Microscopy Facility using a Hitachi SU4800 FE_SEM field emission scanning microscope and deposited in an Iowa State University DataShare repository available at https://doi.org/10.25380/iastate.27287805. Foliage leaf and floral bract morphology were described using the terminology of Ellis (1979), although silica bodies that Ellis (1979) described as "dumb-bell shaped" and "elliptical" were described as "bilobate" and "rondel-shaped", respectively, in keeping with the International Code for Phytolith Nomenclature (ICPT 2019), and "nodular" silica bodies were described following Cunha-Santana (2017). Due to difficulty in observing the costal and intercostal zones of the lemma and palea, the differences between these zones were not described.

*Conservation assessment and map.* The conservation assessment, including calculation of area of occupancy (AOO), followed the guidelines of the International Union for Conservation of Nature (IUCN 2012, 2018, 2024). With only one known population of this species, there were too few collections to estimate the extent of occurrence (EOO). The geographic distribution map was elaborated using QGIS v. 2.16.3 (QGIS 2016) and base map was provided by INEGI (https://www.inegi.org.mx/app/geo2/elevacionesmex/).

*DNA extraction and SSR genotyping.* DNA was isolated using the CTAB method (Doyle & Doyle 1987), modified by Cota-Sánchez *et al*. (2006), from 100 mg of dry leaf tissue preserved in silica gel. Plant tissue was pulverized using a TissueLyser LT (QIAGEN, Hilden, Germany). The DNA was dissolved in 100 µL in Tris EDTA buffer solution (TE). DNA concentration and the purity were measured using a NanoDrop 2000TM Spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). We amplified six SSR loci: one developed for *Aulonemia aristulata* (Döll) McClure (Aar12) (Abreu *et al.* 2011), one developed for *Guadua angustifolia* (FJ476075) (MERPDC *et al.* 2009), and four developed for *G. chacoensis* (Rojas Acosta) Londoño & P.M. Peterson (Gcha01, Gcha04, Gcha07 and Gcha13) (Rossarolla *et al.* 2020).

The volume of each amplified sample was 5.5 µl containing 0.5 µl of each primer (10 µM). The forward primer was labeled with the fluorescent dyes FAM™ (Aar12, FJ476075, Gcha07, Gcha13), HEX™ (Gcha01, Gcha04), 2.5 µl of Multiplex PCR Kit Mix (QIAGEN Germantown, Maryland, USA), 1.5 µl of molecular grade water, and 1.0 µl of DNA. The polymerase chain reaction (PCR) was performed in an AERIS™ thermal cycler (Esco Healthcare, Singapore) under the following conditions: initial denaturation at 95 °C for 15 min, 30 denaturation cycles, initiation step at 94 °C for 30 sec, hybridization at 54-55 °C for 1.5 min, and extension at 72 °C for 1.5 min, followed by a final extension at 72 °C for 10 min. The PCR products were assessed on a 1 % agarose gel using GelRed, visualized with a UV Transilluminator (UVP), and then analyzed in an automatic sequencer with 0.5 µl of GeneScan 500 ROX Size standard or GeneScan 500 LIZ Size Standard (Applied Biosystems, Foster City, California, USA), 9.5 µl of Formamida (Applied Biosystems) and 1.0 µL of PCR reaction mix (diluted to 1:20). The amplified products were run on a SeqStudio-232000826 (Applied Biosystems®) to determine the allele sizes in the Laboratorio Nacional de Identificación y Caracterización Vegetal (LaniVeg, University of Guadalajara). The genotype configuration was determined using Microsatellite Analysis Software (MSA), which is a microsatellite genotyping module available on Thermo Fisher

Cloud and Peak Scanner CE Fragment Sizing (Thermo Fisher™). The Peak Scanner module offers peak identification and fragment sizing. We infer the number of alleles as a function of the peak area for each individual and each locus.

*Estimates of genetic diversity*. Deviations from Hardy-Weinberg equilibrium (HWE) were evaluated for each individual across all loci and per locus in GenAlEx 6.5 (Peakall & Smouse 2006). The observed heterozygosity ($H_O$), expected heterozygosity ($H_E$), allele richness ($A_R$), average number of alleles per locus (Na), effective number of alleles ($A_e$), and Wright's fixation index (F) were obtained with SPAGeDi v. 1.3a (Hardy & Vekemans 2002).

## Results

**Guadua lacerata** Ruiz-Sanchez & McMurchie, sp. nov. (Figures 1, 2, 3).

*Type*. Mexico. Nayarit, Santiago Ixcuintla Municipality, beside small stream between two pastures about 4.25 km northwest from Pantano Grande along Mazatlán-Tepic highway, 16 m asl, 21.8986°, -105.1659°, 8 September 2023(fl), *E.K. McMurchie & E. Ruiz-Sanchez 1681* (Holotype: IBUG; Isotypes: ISC, MEXU, US).

*Diagnosis. Guadua lacerata* differs from all other known species of *Guadua* by the following combination of characters: Supra- and infranodal bands of hair conspicuous and subequal; culm leaves 19.0-27.0 cm long, the sheath 2-3 times as long as the blade, abaxially glabrous when young developing light brown hairs 0.3-0.4 mm long that fall away as the sheath dies, shredding from the base in a twisted pattern where persistent on culm; foliage leaf blades 3.2-9.0 times as long as the width, the pseudospikelets 3.4-14.7 cm long, straight to strongly falcate, somewhat laterally compressed; 6-31 fertile florets per pseudospikelet; lemmas densely pubescent, 8.4-10.8(-13.0) mm long.

*Morphological description.* Rhizomes pachymorph, rhizome necks short, 9-10 cm long, 9-10 cm in diameter. Culms 8-10 m tall, 4-8 cm in diam., erect and arching above, some culms slightly sinuous and forming a zig-zag pattern. Internodes 14-34 cm long, terete with sulcus running from just above bud to distal nodal line, solid or hollow, if hollow with walls of 1.6-1.8 cm thick, lumen 0.8-1 cm in diam., when young mostly dark green, yellowish where covered by culm leaves and dark brown just beneath the infranodal band, becoming darker and duller in color as the culm matures, with soft, white pubescence that is sometimes slightly matted on young culms and wears away with age. Nodes solitary, the nodal line nearly horizontal, dipping very slightly below bud, with a supranodal band ca. 1 cm wide and an infranodal band 0.8-1 cm wide, both with dense, soft, velvety white hairs, the supranodal ridge inconspicuous; bud single, triangular, the prophylls 4-5 cm long, ca. 3 cm wide, white, glabrous at the center, the margins densely pubescent with purple and light brown hairs that form vertical stripes. Culm leaves 19.0-27.0 cm long, 13.0-19.0 cm wide at the base, coriaceous when young, retaining liquid under growing sheath, becoming chartaceous with age, retained on culm from base to ca. 2 m, deciduous above; where persistent, sheath shredding from base in twisted pattern, triangular, blade and sheath easily distinguished by color at juncture; sheaths 12.7-18.5 cm long, 2-3 times as long as blade, green to yellowish green faintly mottled with yellow when young, sometimes vertically striped with purple nearer to margins, becoming light brown with age as the leaf dies, abaxially glabrous when young, developing hairs with age, hairs 0.3-0.4 mm long, soft, light brown, these later falling away as the leaf dies, adaxially glabrous and shiny, the margins densely ciliate with hairs 1.0-1.8 mm long, white to brown; auricles always present on the overlapping side of the leaf, single or very rarely double, absent or rarely present on the underlapping side, always single, 3.7-10.0 mm long on the overlapping side, 2.7-5.2 mm long on the underlapping side when present, falcate to straight, brown, densely fimbriate; fimbriae (1.5-)2.0-5.3(-12) mm long, brown abaxially, white adaxially, curved to curly; oral setae absent; outer ligules absent; inner ligules 0.8-1.0 mm long, extending the full width of the sheath, slightly arched in the center, glabrous and shiny, the margin ciliate; blades 5.8-7.2(-9.5) cm long, 6.6-8.5 cm wide at base, broadly triangular, often rounded to slightly basally constricted, sometimes splitting vertically with age, erect, persistent, green to yellowish green faintly mottled with yellow, often purplish around juncture of sheath and blade and sometimes striped vertically with purple up blade when young, turning light brown as the blade dies, the blade typically browning before the sheath; adaxially sparsely hispid along the veins, densely hispid at the base and the apex, hairs 0.5 mm long, dark brown and shiny, abaxially glabrous when young, developing hairs as the leaf matures, which later fall away as the

blade dies; the margins ciliate, hairs similar to those of the sheath, 1.0-1.8 mm long, white to brown, the apex mucronate, mucro 0.5-1 mm long. Branching extravaginal, branching beginning at node 4-7(-12) aboveground, below which buds do not develop; typically consisting of a single branch per node, occasionally 2-3 branches per node in upper half of culm, primary branches in apical half frequently producing 1-3 slender, secondary branches along upper nodes; primary branches 3-5 m long, 0.8-2 cm wide; thorns absent from culm nodes; branches in basal 2 meters of culm often developing with many thorns and few leaves, apical branches with few or no thorns, the thorn complements consisting of a central thorn 1.5-2 cm long, slightly curved or recurved, and two lateral thorns 0.7-0.8 cm long, slightly curved. Foliage leaves 5-9 per complement; sheaths green, often mottled with very small yellow spots, carinate, glabrous, the margin entire; pseudopetioles 3-4 mm long, 1-1.5 mm wide, distinct, keeled, adaxially hispidulous, hairs 0.1-0.4 mm long, hyaline, abaxially glabrous or hispidulous; auricles present on one side of the sheath, 1.0-1.2 mm long, falcate to straight, green, densely fimbriate; fimbriae (1.0-)2.0-5.0(-7.0) mm long, shiny, white, straight to curly, the side without auricles developing fimbriae of the same size, color and form as those on auricles; oral setae absent; outer ligules 0.1-0.2 mm long, glabrous, truncate, the margin erose; inner ligules 0.05-0.1 mm long, glabrous, truncate, the margin minutely ciliate; blades (8.6-)13.0-16.7(-19) cm long, (1.8-)2.0-3.2(-5.2) cm wide, L : W = 3.2-9.0, 19-22 nerved, lanceolate, not tessellate, adaxially mostly glabrous, a few hyaline hairs 0.1-0.3 mm long trailing up blade from pseudopetiole, most dense at base of blade, abaxially glabrous, the base rounded, the midrib centric, visible for full length of blade, the margins cartilaginous, scabrous, the apex acute and mucronate, the mucro 0.8-2.0 mm long. Synflorescences terminating leafless or few-leaved branches on leafy culms, open, with clusters of two to three pseudospikelets with up to two orders of branching, the main axis puberulent; pseudospikelets 3.4-14.7 cm long, 4.6-4.8(-6.0) mm wide, typically falcate, sometimes straight, slightly laterally compressed, green when young, sometimes with some purple hairs, becoming brown with age, consisting of a subtending bract, a prophyll, 1 gemmiparous bract, 1 sterile lemma, 6-31 fertile florets, and a rudimentary terminal floret; subtending bracts 4-6 mm long, abaxially soft pubescent, apex with a short mucro; prophylls 3.0-3.3 mm long, abaxially soft pubescent, with ciliolate keels; gemmiparous bracts 6.0-7.0 mm long, pubescent with very short mucro; sterile lemmas 6.0-9.0 mm long, pubescent, mucronate, mucro 0.1-0.2 mm long; rachilla segments 3.5-5.0(-6.0) mm long, pubescent at the apex, the hairs white, appressed, minute and sparse at base, becoming dense and longer toward apex, 0.4-0.7 mm at rim, segments disarticulating at base of each lemma; fertile florets 6-31, with paleas typically completely enclosed within lemmas, rarely the winged keels of the palea laterally exceeding lemma by up to 0.3 mm on one side only; lemmas 8.4-10.8(-13.0) mm long, 5.9-8.0 mm wide, 15-21 nerved, ovate-lanceolate, green with faint yellow mottling and brown at apex and shoulders when young, becoming light brown with age, abaxially densely pubescent, hairs 0.1-0.2 mm long, appressed, pointing towards apex, longest on the shoulders and near apex, mostly translucent, hairs within 1 mm of lemma margin often purple, with a few purple hairs scattered throughout, these fading to brown with age; adaxially mostly glabrous, scurfy in upper 1/4, the apex with translucent hairs 0.1 mm long, the apex mucronate, the mucro (0.3-)0.4-0.5 mm long, slightly curved at the tip; paleas 6.8-8.8(-12.0) mm long, 2.5-3.4 mm wide, pale green when young, becoming stramineous to light brown with age, the apex acute, ciliate, with hairs 0.2-0.4 mm long, the sulcus 1.3-1.6 mm, 4-6 nerved, the lower 2/3 nearly glabrous with sparse hairs 0.1 mm long, the upper 1/3 with dense hairs 0.1-1.4 mm long, most dense towards apex, the enfolding margins 2-3 nerved, glabrous or mostly glabrous, sometimes with a few appressed hairs 0.1 mm long toward the apex, the keels winged, the wings 0.4-0.7 mm wide, 2-nerved, abaxially pubescent with translucent hairs 0.1-0.3 mm long, appressed, pointing toward apex, adaxially glabrous in lower 2/3, pubescent in upper 1/3 minute, appressed hairs pointing toward apex, the margins glabrous at the base the apex with cilia 0.2-0.4 mm long, one keel crossing over the other at the apex, not prolonged to prolonged 0.2 mm beyond the apex of the sulcus. Lodicules 3, lanceolate, the anterior pair 2.6–4.4 mm long, 0.5-0.7 mm wide, glabrous except for one or two hairs at the apex ca. 0.5 mm long, the posterior one 2.0-4.3 mm long, 0.4-0.5 mm wide, glabrous. Stamens 6, the anthers 3.0-5.5(-7.0) mm long, 0.8-1.5 mm wide, yellow to purple when fresh, drying yellow to light brown, basally sagittate, apically apiculate, the filaments free, 2.8-10 mm long. Ovaries 1.2-2.6 mm long, the basal part quadrangular, 0.5-1.5 mm long, 0.4-0.7 mm wide, light brown to stramineous, glabrous, the apical part blunt, 0.6-1.1 mm long, 0.6-1.0 mm wide, the style forming a hood over the apex of the ovary, typically much wider than the base but sometimes only slightly so, stramineous, densely pubescent with hairs 0.2-0.3 mm long; styles 0.6-1.0 mm long, stramineous, densely pubescent with hyaline hairs ca. 0.2-0.4 mm long, stigmas 3, plumose, white when fresh, 1.7-2.4 mm long. Caryopses when immature 11 mm long, amber; mature caryopses not seen.

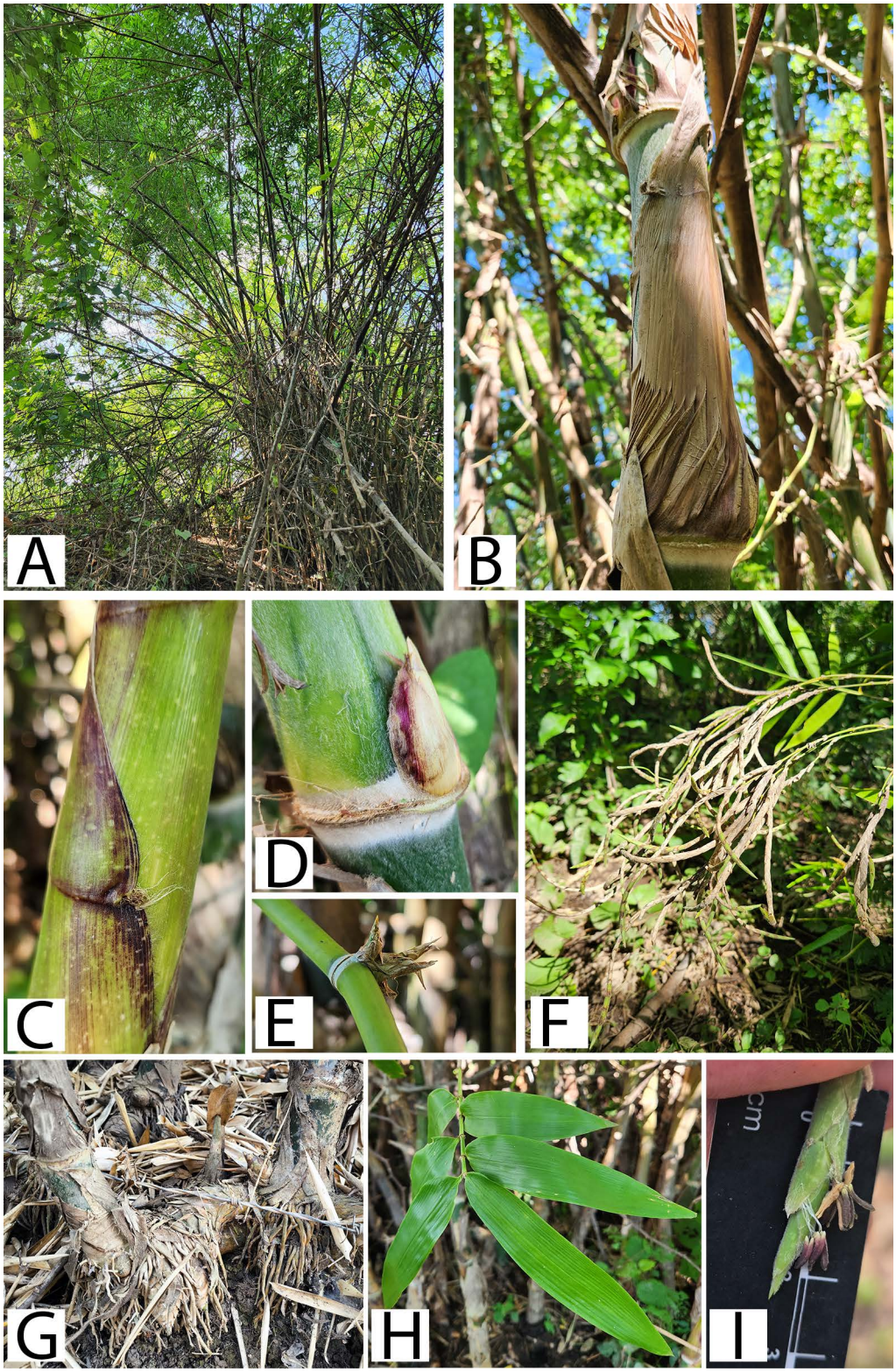


**Figure 1.** *Guadua lacerata* in the field. A. Habitat and habit. B. Mature culm leaf. C. Young culm leaf juncture of sheath and blade. D. Nodal region and bud. E. Branch thorn complement. F. Synflorescence. G. Rhizomes. H. Foliage leaves. I. Fertile florets. A-F and H by E.K. McMurchie, 8 September 2023; G and I by E. Ruiz-Sanchez, 24 April 2024.


**Figure 2.** Macromorphology of *Guadua lacerata*. A. Foliage leaf complement. B. Young culm leaf, adaxial view; B1. Closeup of culm leaf auricle; B2. Closeup of culm leaf inner ligule and adaxial blade pubescence. C. Foliage leaf ligular area. D. Pseudospikelet. E. Prophyll. F. Gemmiparous bract. G. Stamen. H. Gynoecium. I. Lemma. J. Palea. K. Posterior locidule. L-M. Anterior pair of lodicules. Illustration by Emma Hoover-Grinde based on *McMurchie & Ruiz-Sanchez 1681* (A-G; I-J) and *Ruiz-Sanchez & Perez-Garcia 816* (H; K-M).

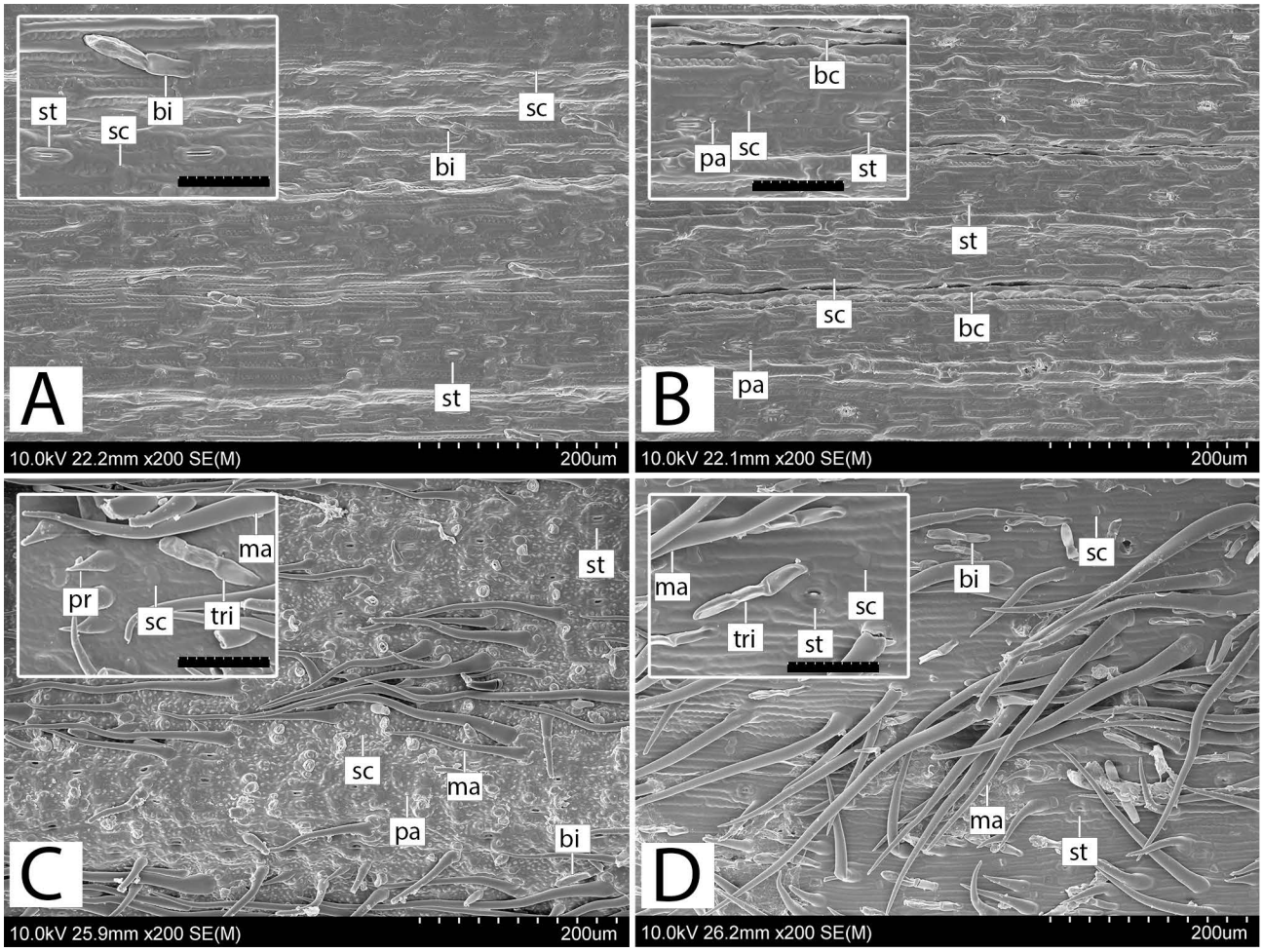


**Figure 3.** Micromorphology of foliage leaves and floral bracts of *Guadua lacerata* from *McMurchie & Ruiz-Sanchez 1681*. A. Foliage leaf abaxial surface. B. Foliage leaf adaxial surface. C. Lemma abaxial surface. D. Palea sulcus abaxial surface. Abbreviations: bc = bulliform cell; bi = bicellular microhair; ma = macrohair; pa = papilla; pr = prickle; sc = silica cell; st = stomatal apparatus; tri = tricellular microhair. Inset scale bars 50 µm.

*Foliage leaf and floral bract micromorphology*. Foliage leaf adaxial surface.- Long cells elongated horizontally. Bulliform cells elongated horizontally, individual cells wider than other cells in the intercostal zone. Short cells typically containing silica bodies, the silica cells alternating with long cells, occasionally occurring in files of two or three between the long cells in the costal zone. Silica bodies vertically elongated; bilobate to smooth saddle-shaped in the costal zone; bilobate, reniform, or nodular in the intercostal zone. Papillae sometimes absent; when present, surrounding stomatal apparatuses, simple, with up to eight surrounding the stomatal apparatus. Prickles absent. Microhairs in the intercostal zones, flanking bulliform cells, non-silicified, bicellular; distal cell about one and a half times as long as basal cell; basal cell parallel sided and not tapering at the base; distal cell broadly rounded at apex. Macrohairs absent. Stomatal apparatuses in one or less commonly two rows on both sides of a costal zone; subsidiary cells low dome-shaped to parallel sided.

Foliage leaf abaxial surface.- Long cells elongated horizontally. Short cells typically containing silica bodies and alternating with long cells. Silica bodies vertically elongated; bilobate to smooth saddle-shaped in the costal zone; bilobate, reniform, nodular, or rarely elongate with a smooth outline in the intercostal zone. Papillae absent. Prickles absent. Microhairs bicellular, non-silicified, scarce, located at the centers of the interstomatal region of intercostal

zone and costal zone; distal cell approximately the same length as basal cells to about one and a half times as long; basal cell typically not constricted at base and nearly parallel-sided, with a slight expansion at base, less commonly constricted at base, cupule-shaped; distal cell broadly rounded to slightly tapered at apex. Macrohairs absent. Stomatal apparatus in two or more commonly three rows on both sides of a costal zone; subsidiary cells low dome-shaped to parallel sided.

Lemma abaxial surface.- Long cells elongated horizontally. Short cells, excluding silicified trichomes, typically containing silica bodies and alternating with long cells. Silica bodies rondel-shaped, cross-shaped, or vertically or horizontally elongated and bilobate or reniform in the costal and intercostal zones. Papillae abundant on long and short cells of much of lemma excluding area near margin, simple. Prickles present in both intercostal and costal zones, interspersed with macrohairs, in three to five files, frequent to infrequent on most of lemma, frequent to scarce near margin; primarily pointing toward apex; the base of the prickle small; the barb long. Microhairs including two types, non-silicified, found only near margin, apparently in intercostal zone, scarce; one type tricellular, with a basal, central, and distal cell; basal cell about twice as long as distal cell; central cell about two thirds as long as basal cell and slightly narrower than basal and distal cells; basal cell only slightly tapering at base, parallel-sided with narrow point of attachment; central cell parallel-sided; distal cell broadly rounded at apex; the other type bicellular; distal cell approximately the same length as basal cell to one and a half times as long as basal cell; basal cell about twice as long as the width, very slightly constricted at base, cupule-shaped; distal cell broadly rounded at apex. Macrohairs abundant except for near margin, where they are abundant to scarce, located in intercostal and costal zones; primarily pointing toward apex of lemma; unicellular, hard, the base of the hair swollen. Stomatal apparatuses in one to five rows near center of lemma, in one irregular row nearer to lemma margin; subsidiary cells low dome-shaped to parallel sided.

Palea abaxial surface.- Long cells elongated horizontally and about four to 20 times as long as the width. Short cells, excluding silicified trichomes, typically containing silica bodies, though nearer to margin sometimes lacking silica bodies, alternating with long cells. Silica bodies most commonly rondel-shaped or cross-shaped, occasionally horizontally elongated and bilobate, short and smooth saddle-shaped, or reniform, rarely vertically elongated and smooth saddle-shaped or rounded. Papillae absent. Prickles irregular and frequent to sparse on the enfolding margin, inner surface of the winged keel, and sulcus; pointing toward apex; the base of the prickle medium in size; the barb long. Microhairs non-silicified, including two types; one type scarce to abundant on the palea enfolding margin, abundant on the sulcus and inner surface of winged keel, tricellular with a basal, central, and distal cell; basal cell similar in size to slightly longer than the distal cell, central cell slightly shorter to about half as long and narrower than the distal cells; basal cell very slightly tapering at base and inverted cone-shaped to cupule-shaped; central cell parallel sided; distal cell slightly tapered to a rounded apex or broadly rounded at apex; the other type scarce on the palea enfolding margin and sulcus, bicellular; the distal cell similar in size to about one and a half times as long as the basal cell; the basal cell tapering at the base and cupule-shaped; the distal cell broadly rounded at apex. Macrohairs on the enfolding margin, absent in some locations and abundant in others; abundant on sulcus and inner surface of winged keel; primarily pointing toward apex; unicellular, hard, lacking specialized epidermal cells associated with base of hair; the base of the hair swollen. Stomatal apparatuses infrequent on both the palea sulcus and enfolding margin; subsidiary cells low dome-shaped.

*Distribution and ecology*. Santiago Ixcuintla Municipality, Nayarit, Mexico; eight clumps of culms of this species seen growing along a small, slow-moving stream between two pastures on muddy soil near several clumps of *Bambusa*; 16 m asl; highly disturbed habitat with some remnant tropical subdeciduous forest.

*Phenology. Guadua lacerata* appears to flower sporadically. At the time of collection, six culms were observed bearing flowers, one of these older and having lost most of its flowers already. At the second visit to this population, seven

months after the initial visit, we saw that all the culms that flowered in September had died, with more new culms flowering. At least seven new seedlings were seen in April. It appears that only the flowering culms die off, while sterile culms remain alive.

*Etymology.* This species is named for the morphology of the culm leaf sheaths, which become lacerate *in situ* with age.

*Conservation status*. *Guadua lacerata* has been located and collected only in the state of Nayarit, Mexico, in an unprotected area between two farm fields. With the observed area covered by the plant estimated at less than about 100 $m^2$, area of occupancy (AOO) is estimated to be only 4 $km^2$ (IUCN 2018), with much of this space taken up by farmland. As this species is known from only a single population and is found in an area of highly degraded habitat potentially imperiled by further development, we hypothesize that this species would be listed as Critically Endangered (CR) under criteria B2ab(iii) were a formal conservation assessment to take place (IUCN 2012, 2024).

*Notes.* Vegetatively, this species most closely resembles *G. amplexifolia,* but differs from it in that in *G. lacerata*, the supranodal and infranodal bands are subequal in size, the culm leaf is only 19.0-27.0 cm long (as opposed to 22.8-45.4 cm long in *G. amplexifolia*), with the culm leaf sheath 2-3 times as long as the blade (as opposed to the sheath being about 1-2.5 times as the blade in *G. amplexifolia*), and the culm leaf sheath shreds from the base in a twisted pattern where retained on the culm as the leaf ages (Table 1). When fertile, *Guadua lacerata* is distinguished from all other Mexican *Guadua* with known inflorescences by the length and shape of its pseudospikelets, as well as the number of fertile florets per pseudospikelet. The pseudospikelets are typically falcate but sometimes straight in shape and 3.4-14.7 cm in length with 6-31 fertile florets, often exceeding the maximum pseudospikelet length and number of fertile florets of other *Guadua* species with similar vegetative morphology (Table 1). In contrast, the lemmas are typically shorter than those of most species of *Guadua* in Mexico excluding *G. inermis* and *G. paniculata*, at just 8.4-10.8(-13.0) mm long (Table 1). In addition to their shorter length, the lemmas of *G. lacerata* also differ from those of the morphologically similar *G. amplexifolia* in that they are densely pubescent (compared to the glabrous or sparsely pubescent lemmas of *G. amplexifolia*) (Table 1).

*Additional specimens examined.* Mexico. Nayarit, Santiago Ixcuintla Municipality, about 4.25 km northwest from Pantano Grande along Mazatlán-Tepic highway, 16 m asl, 21.8986°, -105.1659°, 8 April 2024 (fl), *E. Ruiz-Sanchez & M.L. Perez-Garcia 816* (IBUG, IEB, MEXU).

*Macromorphological key to the species of* Guadua *in Mexico.*

1. Culms 1-3.5(-5) cm in diameter at base; supra- and infranodal bands of hair absent or inconspicuous, grayish-white; culm leaf blades deciduous……..……..……..……..... 2
1. Culms 2-15 cm in diameter at base; supra- and infranodal bands of hair conspicuous, white; culm leaf blades persistent……..……..…….....4
2. Supra- and infranodal bands of hair present; culm leaf sheaths and inner ligules roughly symmetrical.... *G. paniculata*
2. Supra- and infranodal bands of hair absent; culm leaf sheaths and inner ligules slightly to strongly asymmetrical.....3
3. Culm internodes hollow, thin-walled; culm leaf sheaths and inner ligules strongly asymmetrical; culm leaf blades adaxially glabrous; foliage leaf pseudopetioles adaxially and abaxially hispid……..…..….*G. longifolia*
3. Culm internodes solid or hollow but thick-walled; culm leaf sheaths and inner ligules slightly asymmetrical; culm leaf blades adaxially pubescent; foliage leaf pseudopetioles adaxially and abaxially glabrous…..... *G. guzmanii*
4. Culm internodes hollow with lumen diameter at least half that of internode; culm leaves 39-69 cm long…..... 5
4. Culm internodes solid or hollow with lumen diameter less than half that of internode; culm leaves 19-46(-63) cm long…..……..……..……..…….....6

5. Culm leaf sheath to blade length ratio 5-10(-15); culm leaf auricles absent; foliage leaf pseudopetioles 4-7 mm long……..……..……..*G. aculeata*
5. Culm leaf sheath to blade length ratio 2.5-3.8; culm leaf auricles present; foliage leaf pseudopetioles 2-4 mm long……..…….……..*G. tuxtlensis*
6. Supra- and infranodal bands of hair subequal in size; culm leaves 19-27 cm long; culm leaf sheaths shredding at base with age; fertile florets 6-31 per pseudospikelet……..……..... *G. lacerata*
6. Supranodal band of hair narrower than infranodal band, typically about half as wide; culm leaves 23-46(-63) cm long; culm leaf sheaths not shredding at base with age; fertile florets 3-12 per pseudospikelet…….....……. 7
7. Culm leaf sheaths densely pubescent with both dark brown hairs and minute hyaline hairs; foliage leaf pseudopetioles 2-3 mm long, adaxially pilose……..…….....……..... *G. velutina*
7. Culm leaf sheaths pubescent with light brown hairs, minute hyaline hairs present or absent; foliage leaf pseudopetioles 2-6(-11) mm long, adaxially hispidulous or glabrous……...……..... 8
8. Thorns on lower branches abundant; culm leaf auricles absent or present; pseudospikelets (3.5-)4.5-6.5 cm long; fertile florets (3-)5-12; lemmas (11.7-)13.1-17.8 cm long, glabrous to sparsely pubescent……. *G. amplexifolia*
8. Thorns on lower branches absent or few; culm leaf auricles present; pseudospikelets 2.5-4.5 cm long, fertile florets 4-6; lemmas 5.4-10.4 cm long, pubescent…….……...……..... *G. inermis*

*Genetic diversity*. We amplified eight individuals for six microsatellites. We found 30 alleles ($A_R$), with an average of 3.83 alleles per locus (Na); the effective number of alleles ($A_e$) was 2.54. The average expected heterozygosity ($H_E$) for the six microsatellites was 0.516 and the observed heterozygosity ($H_O$) was 0.506. The F (Wright's fixation index) was 0.016.

**Table 1.** Morphological comparison of Mexican *Guadua* with persistent culm leaf blades and conspicuous nodal bands.

| **Species** | ***Guadua lacerata*** | ***Guadua aculeata*** | ***Guadua amplexifolia*** | ***Guadua inermis*** | ***Guadua tuxtlensis*** | ***Guadua velutina*** |
|---|---|---|---|---|---|---|
| Culm diameter (cm) | 4-8 | 5-10(-15) | 3-8(-15) | 2-8 | 8-14 | 2-10 |
| Culms solid or hollow | Solid or hollow with thick walls | Hollow | Solid or hollow with thick walls | Solid or hollow with thick walls | Hollow | Solid or hollow with thick walls |
| Supra- and infranodal band widths (cm) | 1; 0.8-1 | 0.4-1.5; 1.0-1.5 | (0.5-)0.8-1; (1-)1.7-2 | 0.5-1.0; 1.3-2.5 | 0.8; 1.0 | 0.5-1; (0.5-) 1.6-2.5 |
| Culm leaf length (cm) | 19.0-27.0 | 38.8-66.9 | 22.8-45.4 | 32-46(-63) | 47.4-56.0 | 24.5-46.0 |
| Culm leaf sheath to blade length ratio | 2-3 | 5-10(-15) | 1.2-2.6 | 1-2 | 2.5-3.8 | 1.3-2.5 |
| Culm leaf auricle presence | Present | Absent | Present or absent | Present | Present | Present |
| Number of fertile florets | 6-31 | 3-7 | (3-)5-12 | 4-6 | Unknown | 3-8(-11) |
| Lemma length (mm) | 8.4-10.8(-13.0) | 9-14.5 | (11.7-)13.1-17.8 | 5.4-10.4 | Unknown | 12-15.5 |
| Lemma abaxial pubescence | Densely pubescent | Glabrous | Glabrous to sparsely pubescent | Pubescent | Unknown | Densely pubescent |

## Discussion

Among all described *Guadua* species, *Guadua lacerata* represents one of the most extreme northwesternmost in its distribution, rivaled only by the wide-ranging *Guadua paniculata* (Perez-Garcia & Ruiz-Sanchez 2023). Two additional described species found along the Mexican Pacific coast, *G. guzmanii* and *G. amplexifolia*, are found at more southern latitudes, with *G. lacerata* representing the only known species of *Guadua* endemic to Nayarit (Perez-Garcia & Ruiz-Sanchez 2023, Ruiz-Sanchez *et al.* 2024). *Guadua lacerata* appears most morphologically similar to *G. amplexifolia*, with fairly high morphological similarity to *G. inermis* and *G. velutina* as well (Table 1). Despite their morphological similarity, these species do not live in close proximity to *G. lacerata*, with the closest populations hundreds of kilometers away and *G. inermis* and *G. velutina* limited to states surrounding the Gulf of Mexico (Figure 4).

Although the documentation of *G. lacerata* appears to be the first time a *Guadua* larger in size than *G. paniculata* has been located in Nayarit, ecological modeling has previously suggested that the lowland, coastal part of the state could contain suitable habitat for several *Guadua* species (Ruiz-Sanchez *et al.* 2018, Ramírez-Ojeda *et al.* 2021, Flores-Garnica *et al.* 2024). In particular, Flores-Garnica *et al.* (2024) found that using the environmental variables of elevation (reported as "altitude"), annual evapotranspiration, temperature annual mean, and annual precipitation, the coastal lowland of Nayarit contained areas of very good suitability for growth of *G. amplexifolia* and to a lesser extent *G. inermis*, with very small areas of half to good suitability for *G. velutina*. While *G. lacerata* bears clear morphological differences from *G. amplexifolia*, *G. inermis*, and *G. velutina*, the confirmation of a large, morphologically similar *Guadua* species in this area supports the use of these suitability estimates to locate additional *Guadua* populations.

The only currently known population of *G. lacerata* is located in an unprotected area between two farm fields, raising concerns for its continuing survival. This population is potentially threatened not only by development, but also by climate change, which is projected to shrink the potential suitable habitat of other Mexican bamboos, including *G. inermis* (Ruiz-Sanchez *et al.* 2018). Systematic surveys of nearby remaining patches of forest may reveal more populations of this species, especially if targeted to nearby waterways. In the riparian species *G. velutina*, Perez-Garcia *et al*. (2023) found that waterways appeared to be the primary facilitators of gene flow, likely through seed dispersal by hydrochory. As *G. lacerata* appears to be similarly associated with waterways, future surveys could focus on small waterways interconnected with the stream along which the known population was located.

In contrast with other species of *Guadua* in Mexico, *G. lacerata* displayed surprisingly high apparent genetic diversity, with average expected heterozygosity for all loci, $H_E$, of 0.516 and observed heterozygosity, $H_O$, of 0.506, compared to $H_E = 0.38$ and $H_O = 0.21$ for *G. amplexifolia*, $H_E = 0.30$ and $H_O = 0.20$ for *G. inermis*, $H_E = 0.33$ and $H_O = 0.38$ for *G. tuxtlensis*, and $H_E = 0.322$ and $H_O = 0.339$ for *G. velutina* (Pérez-Alquicira *et al.* 2021, Perez-Garcia *et al.* 2023). It is possible that unknown populations of *G. lacerata* could contribute to its relatively high genetic diversity. However, as *G. inermis* and *G. velutina* each have over a dozen known populations in Mexico, some within a few kilometers of each other, we hypothesize that the relatively high genetic diversity of *G. lacerata* is not due to the presence of many unknown populations but instead the unusual flowering pattern seen in this species. *Guadua lacerata* appears to exhibit sporadic flowering, although the timing of the flowering cycles of *G. lacerata* remains unknown. The term "sporadic flowering" is somewhat broad and encompasses all bamboo flowering events where only a few clumps or groups of bamboo within small area of a population of bamboo flower, regardless of whether only individual flowering clumps or entire flowering stems die, in contrast to massive synchronized monocarpy (Zheng *et al.* 2020). In *G. lacerata,* the mode of sporadic flowering differs somewhat from that of the morphologically similar *G. amplexifolia*, *G. inermis*, and *G. velutina* in that only the flowering culms and not the entire genetic individual dies on flowering (Perez-Garcia & Ruiz-Sanchez 2023). Cultivated *G. angustifolia* Kunth has shown a similar mode of sporadic flowering; although the flowering cycles of wild *G. angustifolia* remain largely unknown, they have shown slightly higher genetic diversity ($H_E = 0.71$ and $H_O = 0.56$) than that of *G. lacerata* (Posso Terranova 2011, Borah *et al*. 2021, Perez-Garcia & Ruiz-Sanchez 2023). *Guadua lacerata* was observed to have flowering culms in both Sep-

tember of 2023 and April of 2024. On the second occasion in which the population was observed, young seedlings were observed and only the few culms that were seen to flower in September of the previous year had died. Pseudospikelets observed in April of 2024 appeared relatively shorter and straighter than those seen in September of 2023, while those observed in September of 2023 typically contained numerous older, brown florets near the base, possibly indicating that the pseudospikelets of this species continue to produce additional fertile florets over the growing season even as older florets develop fruits.

Among the pseudospikelets we observed in *G. lacerata* in September of 2023 were some of the largest and most floriferous seen in any *Guadua* species. The pseudospikelets of *G. lacerata* include the longest recorded in Mexico, exceeding those of previous record holder, *G. longifolia* (E.Fourn.) R.W.Pohl, which has straight pseudospikelets of about 3-10 cm long (Swallen 1938). *Guadua macrospiculata* Londoño & L.G.Clark of the western Amazon Basin is the only known *Guadua* species to have pseudospikelets exceeding the length of those of *G. lacerata*, its pseudospikelets sometimes reaching 17 cm in length; however, *G. macrospiculata* has far fewer fertile florets, with a maximum number of 17 compared to the 31 seen in *G. lacerata* (Londoño & Clark 2002).

*Guadua amplexifolia* has relatively few flowering records in Mexico compared to other species of *Guadua*, complicating comparison of this species to *G. lacerata* (Perez-Garcia & Ruiz-Sanchez 2023). Relocation of the type population of *G. amplexifolia* or other potential extant populations nearby has been precluded by uncertainty surrounding its location. Tadeáš Haenke, the collector of the type material, is known to have visited both San Blas, Nayarit, and Acapulco, Guerrero, during his accompaniment of the Malaspina expedition in 1791; the type of *G. amplexifolia* is simply labeled "Mexico" (Hitchcock 1919). Due to the uncertainty surrounding the type locality of *G. amplexifolia* and the observation of Presl (1830) that the culm leaves were glabrous, unlike those of more recent collections, we considered the possibility that this type material may have been collected in San Blas and represent the species we here name *G. lacerata*. However, Presl (1830) described *G. amplexifolia* as displaying

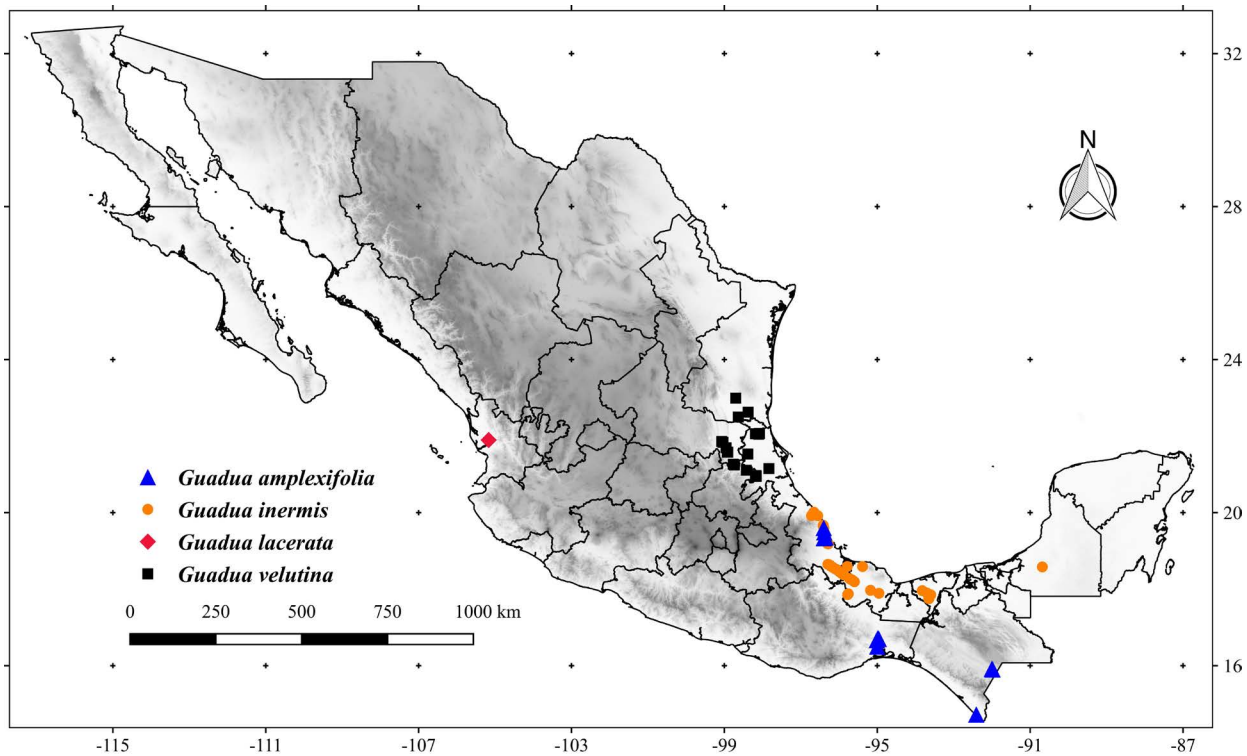


**Figure 4.** Geographical distribution of *Guadua lacerata* and morphologically similar *Guadua* species in Mexico.

glabrous, cylindrical pseudospikelets, in contrast to the densely pubescent, laterally compressed pseudospikelets that we observed in *G. lacerata*. Furthermore, Haenke spent only a few days in San Blas in October of 1791 due to rainy weather during the resupply visit by the Malaspina expedition; he had previously separated from the ship that visited San Blas in the spring, instead focusing on collecting inland from Acapulco (David *et al.* 2003). In light of these findings, we believe the *G. amplexifolia* type to truly represent *G. amplexifolia* as primarily identified in Mexico and not *G. lacerata*.

*Guadua amplexifolia* is one of the most wide-ranging species of *Guadua*, found from southern Mexico through northern South America (Young & Judd 1992). Populations of *Guadua* currently considered *G. amplexifolia* range from bamboos of modest size (*e.g*., *Clark et al. 1144*, with culms 3-6 cm in diameter and 6-7 m tall) to very large (*e.g., Stevens 8606*, with culms 15 cm in diameter and 15 m tall). A careful examination of morphology and population genetics of wild populations of *G. amplexifolia* is needed to clarify the identity of this species and whether certain populations may represent species currently undescribed. Additionally, micromorphology of foliage leaves and floral bracts may be useful for species delimitation in *Guadua* similar in appearance to *G. amplexifolia*. Foliage leaf micromorphology has been used in other Neotropical woody bamboo taxa to support taxonomic hypotheses (*e.g.*, Leandro *et al.* 2016, 2017), and there appear to be differences in foliar micromorphology of various *Guadua* species (Cunha-Santana 2017, Filgueira & Viana 2024). Although only two *Guadua* species, *G. variegata* Lizarazu and *G. leonardoana* Afonso, L.G. Clark & P.L. Viana, have previously been described with foliar micromorphology, these two species differ from *G. lacerata* in several ways, including that they lack papillae on the adaxial surface and bear prickles on both leaf surfaces (Lizarazu *et al.* 2013, Afonso *et al.* 2023). The micromorphology of floral bracts remains largely unstudied in *Guadua*, but floral and foliar micromorphology of *G. amplexifolia* were briefly described by Montiel *et al*. (2006). In our observation of the foliar and floral micromorphology of *G. lacerata*, we note several features not mentioned by Montiel *et al.* (2006), including papillae surrounding the adaxial stomatal complexes of foliage leaves and on the abaxial surface of the lemma. However, we considered the structures that Montiel *et al*. 2006) identified as operculated papillae to be silica bodies that were damaged or partially separated from the surrounding tissue, with papillae absent from the palea. As Montiel *et al.* (2006) limited their description of the micromorphology of *G. amplexifolia* to a single population from Guanacaste, Costa Rica, the micromorphology that they described may not be representative of that of *G. amplexifolia* of Mexico. A systematic evaluation of micromorphology of different *G. amplexifolia* populations in relation to morphologically similar species including *G. inermis, G. velutina,* and *G. lacerata* could supplement traditional taxonomy and molecular systematics in aiding our understanding of these species.

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