

2012

Kalinia, a New North American Genus for a Species Long Misplaced in Eragrostis (Poaceae, Chloridoideae)

Hester L. Bell

Rancho Santa Ana Botanic Garden, Claremont, California

J. Travis Columbus

Rancho Santa Ana Botanic Garden, Claremont, California

Amanda L. Ingram

Wabash College, Crawfordsville, Indiana

Follow this and additional works at: <http://scholarship.claremont.edu/aliso>

 Part of the [Botany Commons](#), and the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Bell, Hester L.; Columbus, J. Travis; and Ingram, Amanda L. (2012) "Kalinia, a New North American Genus for a Species Long Misplaced in Eragrostis (Poaceae, Chloridoideae)," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 30: Iss. 2, Article 3. Available at: <http://scholarship.claremont.edu/aliso/vol30/iss2/3>

KALINIA, A NEW NORTH AMERICAN GENUS FOR A SPECIES LONG MISPLACED IN ERAGROSTIS
(POACEAE, CHLORIDOIDEAE)

HESTER L. BELL,^{1,3} J. TRAVIS COLUMBUS,¹ AND AMANDA L. INGRAM²

¹Rancho Santa Ana Botanic Garden and Claremont Graduate University,
1500 North College Avenue, Claremont, California 91711, USA;

²Department of Biology, Wabash College, PO Box 352, Crawfordsville, Indiana 47933, USA

³Corresponding author (hester.bell@cgu.edu)

ABSTRACT

Eragrostis obtusiflora (Poaceae, Chloridoideae), a species distributed from the southwestern United States to central Mexico, has long been recognized for exhibiting morphological and anatomical features atypical of *Eragrostis*. Phylogenetic analyses of nuclear internal transcribed spacer sequences and plastid sequences demonstrate that *E. obtusiflora* should be excluded from *Eragrostis* (Eragrostideae) and instead be placed in Cynodonteae, although its position within this tribe was unresolved. Additional data, including anatomical and micromorphological characters, suggest a close relationship with *Distichlis*. However, differences in spikelet and rhizome characters prevent its inclusion in *Distichlis*. Therefore, the species is transferred to a newly described genus, *Kalinia*, as *K. obtusiflora*.

RESUMEN

Eragrostis obtusiflora (Poaceae, Chloridoideae), una especie distribuida de los E.E.U.U. al sudoeste a México central, se reconoce por exhibir características morfológicas y anatómicas atípicas en *Eragrostis*. Los análisis filogenéticos de las secuencias nucleares del espaciador internos transcritos ribosomal y las secuencias de cloroplasto demuestran que *E. obtusiflora* debe ser excluida de *Eragrostis* (Eragrostideae) y ser colocada dentro de Cynodonteae, aunque su posición dentro de la tribu esté sin resolver. Datos adicionales, incluyendo caracteres anatómicos y micromorfológicos, sugieren una posible relación cercana con *Distichlis*. Sin embargo, diferencias en caracteres de la espiguilla y del rizoma previenen su inclusión en *Distichlis*. Por lo tanto, la especie se transfiere a un género nuevo descrito, *Kalinia*, como *K. obtusiflora*.

Key words: alkaline soils, bicellular microhair, Cynodonteae, halophytic grass, *Kalinia*, lemma micromorphology.

INTRODUCTION

In the fall of 2001, as part of a systematic study of *Distichlis* Raf. and relatives (Poaceae, Chloridoideae; Bell and Columbus 2008), the first two authors collected *D. spicata* (L.) Greene from numerous populations in the southwestern USA and Mexico. At Willcox Playa (Cochise County, Arizona, USA) and Salinas de Hidalgo (San Luis Potosí, Mexico) few plants of *D. spicata* were found to be in flower. We noted many non-flowering plants that were similar to *D. spicata* in overall appearance and habit but differed by having markedly pungent-tipped leaves, in contrast to the pointed but not pungent leaf blades of *D. spicata*. Subsequent analyses of DNA sequences of the nuclear internal transcribed spacer (ITS; nrDNA) and *trnL-F* (cpDNA) regions revealed that sequences of pungent-leaved plants from the distant localities were nearly identical, yet differed from other sequences of *D. spicata*, and, indeed, all other species of *Distichlis*.

In fall 2003 we revisited Willcox Playa and found the pungent-leaved plants in flower. The flowers were hermaphroditic in contrast to the unisexual flowers of dioecious *Distichlis*. In addition, the 3-nerved lemmas, versus 5–13 in *Distichlis*, helped us identify the plants as *Eragrostis obtusiflora* (E.Fourn.) Scribn. (Eragrostideae), a species distributed from the southwestern USA (Arizona, New Mexico) to central Mexico in saline/alkaline soils of inland playas (Pleistocene

lake beds; Rosen 1994; Briere 2000). *Distichlis spicata* is often sympatric with *E. obtusiflora*, and, as pointed out by McVaugh (1983), non-flowering plants are easily confused. Both species are rhizomatous and have rigid, often conspicuously orthostichous leaf blades.

In morphological and anatomical studies of *Eragrostis* Wolf, a large, worldwide genus of ca. 400 species (Clayton et al. 2006 onwards), Van den Borre and Watson (1994) and Gómez Sánchez and Koch (1998) reported that *E. obtusiflora* is anomalous within *Eragrostis*. In particular, *E. obtusiflora* differs from other species of *Eragrostis* in having pungent-tipped leaves, a 3-nerved upper glume, bundle sheaths that are not interrupted, bulliforms consisting of two large cells and associated with girders of colorless cells to the abaxial epidermis, and papillae present on intercostal long cells. In contrast, similarities between *E. obtusiflora* and members of Monanthochloinae (Clayton and Renvoize 1986), including *Distichlis*, have been noted by a number of authors, specifically in overall growth habit, presence of well developed rhizomes, and occurrence in saline and/or alkaline habitats (Ogden 1897; Scribner 1897; Gómez Sánchez and Koch 1998; Bell and Columbus 2008). In addition, *E. obtusiflora* shares two characteristics with species of *Distichlis*: bicellular microhairs where the basal cell is sunken into the mesophyll (also present in other halophytic grasses) and, in the intercostal zones of abaxial leaf blade surfaces, microhairs are surrounded and

sometimes overarched by groups of four papillae (Bell and Columbus 2008).

The Grass Phylogeny Working Group II [GPWG II] (2012) conducted a family-wide analysis based upon three plastid loci and using a broad sample of Chloridoideae that included *E. obtusiflora*. *Eragrostis obtusiflora* resolved in the Cynodonteae clade, distant from the Eragrostideae clade where all other sampled *Eragrostis* species resolved. Although sister to *Distichlis* in the tree, the relationship had low statistical support.

Based on Ogden (1897), Van den Borre and Watson (1994), Gómez Sánchez and Koch (1998), and GPWG II (2012), there is growing evidence that *E. obtusiflora* is misplaced in *Eragrostis*. We test this hypothesis by analyzing DNA sequences of additional loci from samples of *E. obtusiflora* and many representatives of Chloridoideae, including *Distichlis* and a large number of *Eragrostis* species. In addition, the abaxial surfaces of leaf blades and lemmas and blade transectional anatomy of *E. obtusiflora* are further examined and compared to other chloridoid grasses.

MATERIALS AND METHODS

Sampling

All specimens used in this study are listed in Appendix 1. Specimens of *E. obtusiflora* from Arizona, USA, (Bell 295) and, in Mexico, San Luis Potosí (Bell 251) and Jalisco (Bell 318) were dried in silica gel for DNA extraction and sequencing. ITS and *trnL-F* sequences were added to the data sets from Columbus et al. (2007) which include a broad sample of Chloridoideae. The *rps16* (cpDNA) region of Bell 251 was sequenced and added to the data set from Ingram and Doyle (2007). This data set contains a large sample of *Eragrostis* species representing both subgenera (Van den Borre and Watson 1994) and most of the major morphological groups in the genus based upon spikelet disarticulation type.

Specimens from across the geographical range of *E. obtusiflora* were examined for leaf blade transectional anatomy (Bell 295, 305, 318) and for micromorphology of the abaxial surfaces of leaf blades (Bell 295, 310, 318) and lemmas (Bell 239, 295, 305). As described in Bell and Columbus (2008), segments of living leaf blades were liquid-preserved in the field for anatomical study.

DNA Sequencing and Analysis

Sequences of ITS, *trnL-F*, and *rps16* from *E. obtusiflora* were obtained following the methods in Columbus et al. (2007) and Ingram and Doyle (2004). The sequences were manually aligned with the data sets of Columbus et al. (2007) and Ingram and Doyle (2004) and analyses of these data were carried out as described in those studies. GenBank accession numbers for newly generated sequences are provided in Appendix 1. We also performed a Kishino-Hasegawa test (Kishino and Hasegawa 1989) and a Templeton test (Templeton 1983) using the combined ITS and *trnL-F* data set in PAUP vers. 4.0b (Swofford 2002) to compare the length of the most parsimonious trees with the length obtained when *E. obtusiflora* was constrained as a member of Eragrostideae (sensu Columbus et al. 2007).

Micromorphology

The abaxial surfaces of fully expanded leaf blades and mature lemmas were examined using scanning electron microscopy following the methods of Bell and Columbus (2008).

Leaf Blade Transectional Anatomy

Preparation of blade transections followed the methods described in Columbus (1996) and Bell and Columbus (2008). Permanent microscope slides are deposited at RSA. Descriptive terminology for leaf anatomy and micromorphology follows Ellis (1976, 1979).

RESULTS

Analyses of DNA Sequences

In maximum parsimony analyses of the separate (trees not shown) and combined (Fig. 1) data sets of ITS and *trnL-F*, *E. obtusiflora* resolved within Cynodonteae, apart from the other species of *Eragrostis*. However, due to limited resolution and clade support, the phylogenetic position of *E. obtusiflora* within Cynodonteae is uncertain. In maximum parsimony analysis of *rps16*, *E. obtusiflora* likewise was not placed with other *Eragrostis* species and instead resolved in a clade among members of Cynodonteae (Fig. 2). Descriptive statistics for the analyses are given in Table 1. Results of a Kishino-Hasegawa test indicated that tree length was significantly longer when *E. obtusiflora* was constrained as part of Eragrostideae (length difference = 42, $p = 0.001$; see Fig. 1). A Templeton test provided almost identical results.

Micromorphology

As seen in Fig. 3, costal and intercostal zones of the abaxial leaf blade surface are distinct in *E. obtusiflora*. Macrohairs and prickle hairs were not observed. Microhairs, papillae, and stomata are only present in the intercostal zone. The shape of intercostal long cells is obscured by the numerous large rounded papillae. There are two rows of stomata each restricted to one edge of the intercostal zone; subsidiary cells are low-dome shaped. Intercostal short cells generally occur singly; they are vertically oblong or reniform. Microhairs are distributed along the middle of the intercostal zone and are each surrounded and slightly overarched by groups of papillae. From anatomical studies we know that the microhairs are bicellular (Fig. 7); however, in the surface view only the distal cell is visible and frequently is collapsed, indicating the cell wall is thin.

The costal zone is raised and made up of seven to nine files of cells. The center file contains short cells that alternate in shape between round and more-or-less square with smooth walls. On both sides of the center file there are files of narrow long cells with undulating margins intermixed with short cells of both kinds.

Overall, the abaxial surfaces of blades and lemmas (Fig. 4) of *E. obtusiflora* are quite different from each other. The blade surface has a regular pattern of alternating costal and intercostal zones determined by the numerous veins. Lemmas have three nerves and the costal and broad intercostal zones are not as distinct. Long cells have deeply undulating walls. Short cells are oval to reniform in shape and occur singly between long cells. Lemmas of *E. obtusiflora* have few papillae,

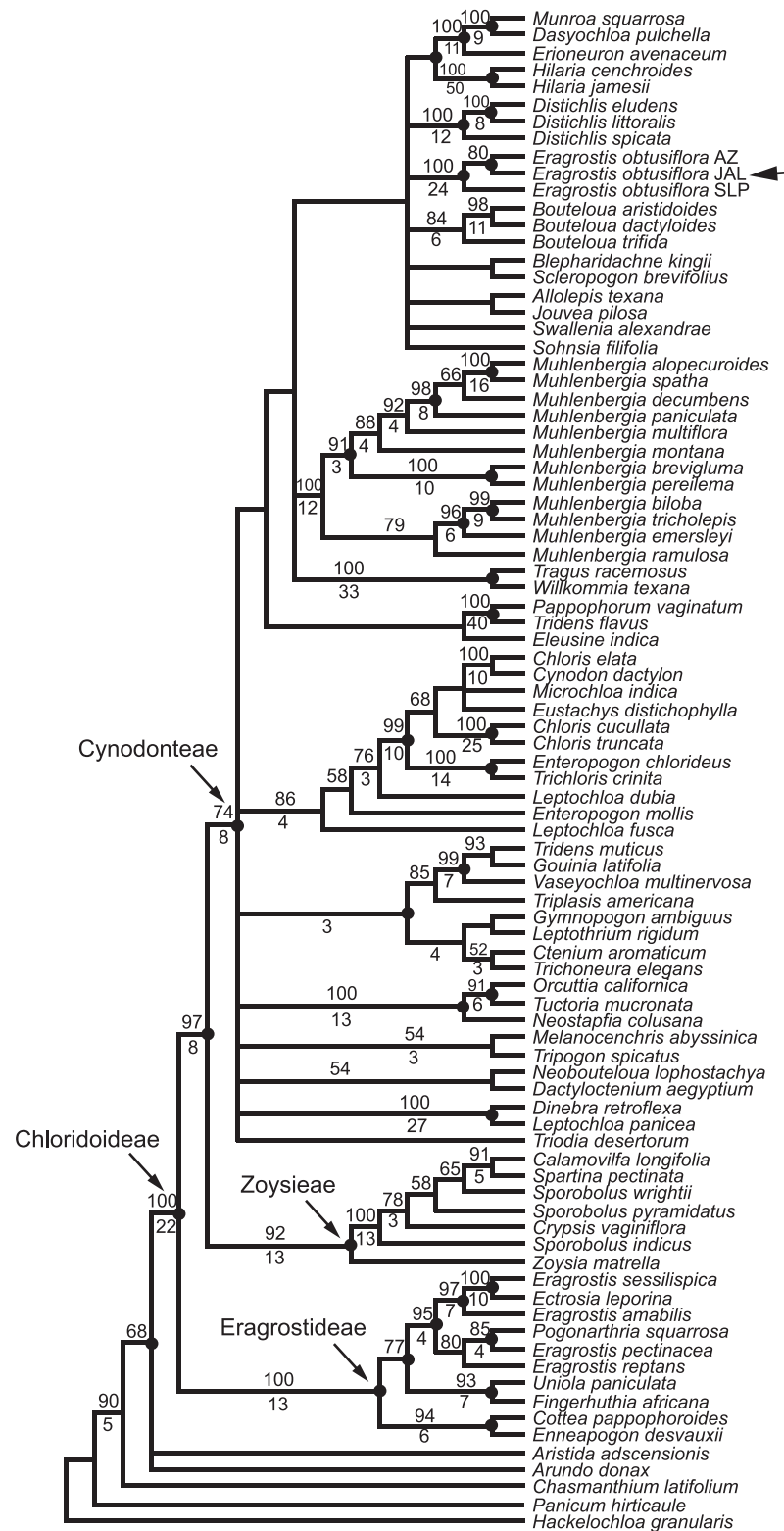


Fig. 1. Strict consensus of 126 most parsimonious trees from analysis of combined ITS and *trnL-F* sequences (length = 4826; CI = 0.38; RI = 0.54). Bootstrap values ≥ 50 are given above the branches and Bremer decay values ≥ 3 are below the branches. Bulleted nodes are found in the strict consensus of separate parsimony analyses of ITS (13 trees) and *trnL-F* (360,726 trees). Phylogenetic analysis methods are described in Columbus et al. (2007). Tribal classification follows Columbus et al. 2007 and Peterson et al. 2007. (AZ = Arizona, JAL = Jalisco, SLP = San Luis Potosi).

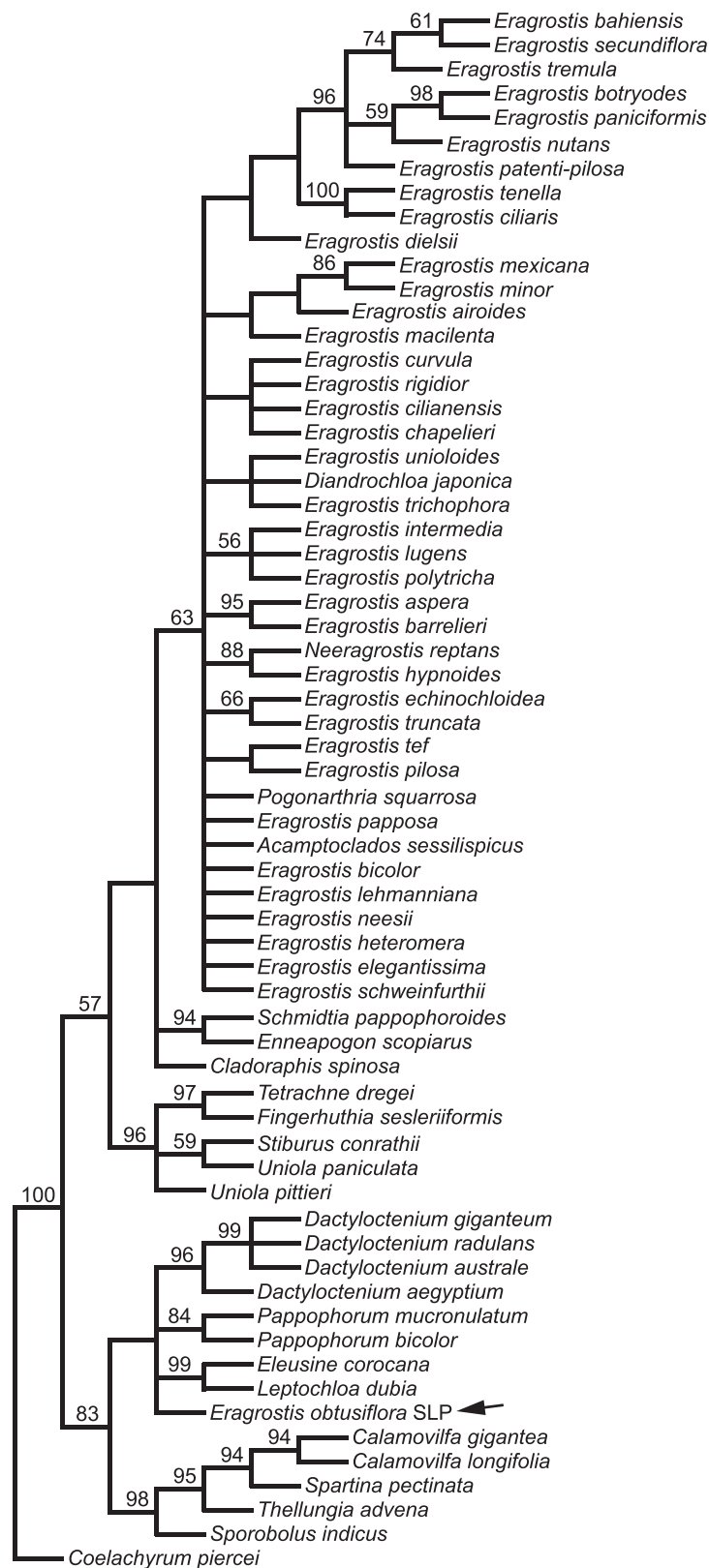


Fig. 2. Strict consensus of 840 most parsimonious trees from analysis of *rps16* sequences (length = 235; CI = 0.68; RI = 0.88). Bootstrap values ≥ 50 are given above the branches. Phylogenetic analysis methods are described in Ingram and Doyle (2004, 2007).

Table 1. Summary information for the data sets and results of the analyses. PIC = parsimony informative characters, CI = consistency index, RI = retention index.

	Aligned length	PIC	Indels scored	Tree length	Number of trees	CI	RI
ITS	812	382	0	3705	13	0.28	0.51
<i>trnL-F</i>	1715	244	39	1091	360, 726	0.69	0.69
ITS + <i>trnL-F</i>	2527	626	39	4826	126	0.38	0.54
<i>rps16</i>	951	118	11	235	840	0.68	0.88

prickle hairs, stomata, and microhairs (Fig. 4). Stomata on lemmas have a similar shape to those on the leaf blades with low-dome-shaped subsidiary cells. Papillae are found adjacent to and sometimes overarching both stomata and microhairs. Apically pointing prickle hairs are distributed in the costal and intercostal zones. Microhairs on lemmas are the chloridoid bicellular type.

The observations reported in this study are generally in agreement with those of Gómez Sánchez and Koch (1998) with the exception that their illustration of the abaxial blade surface shows five files of cells in the costal zone (versus 7–9 in the present study) and they do not show any round short cells in these files. Gómez Sánchez and Koch (1998) did note rows of stomata with overarching papillae in the intercostal zones. Liu et al. (2010) did not find stomata on lemmas of the five *Eragrostis* species that were included in their study.

Leaf Blade Anatomy

Transectional leaf anatomy of *E. obtusiflora* is distinctive with large ridges of colorless cells on the adaxial side of all vascular bundles except those at the margins (Fig. 5, 6). The outline of the blade forms a broad, continuously curved U. There are deep, narrow furrows between all vascular bundles on the adaxial side and shallow furrows on the abaxial side. The median vascular bundle is not distinct as a midrib and there is no keel. The blade has 19–25 vascular bundles with five 1st order bundles regularly arranged with two or three 2nd order bundles between the 1st order and a single 3rd order bundle at each margin.

The shape of all vascular bundles is elliptical or slightly pointed adaxially. The vascular bundles have a double bundle sheath, the outer of which is even in outline and contains chloroplasts that are centripetally arranged within the cells, features that are predictive of the NAD-ME type of C₄ photosynthesis (Prendergast and Hattersley 1987). In the 1st order vascular bundles, parenchyma cells adjoin the inner sheath. Metaxylem is slightly narrower than the outer sheath cells and has thickened walls. Bundle sheaths are complete; on the abaxial side some outer sheath cells lack chloroplasts. Adaxial bundle sheath extensions consist of large, thin-walled, colorless cells that are separated from the epidermis by a narrow sclerenchyma strand. Abaxial sclerenchyma forms small girders. At each margin there is a small, slightly pointed sclerenchyma cap. The mesophyll is radiate, composed of tabular cells, and separated from adjacent vascular bundles by bi- or multiseriate columns of colorless cells of irregular size and shape. At the base of the furrows there are bulliform cells associated with the colorless cells.

There are numerous papillae and/or prickle hairs on the adaxial surface and, consistent with the micromorphological study, fewer papillae on the abaxial surface between vascular bundles. Dumbbell or flask-shaped bicellular microhairs are

present on both surfaces; the basal cell is partially sunken below the epidermis into colorless or mesophyll cells (Fig. 7).

The results of the present study are in general agreement with previous work, with the exception that Gómez Sánchez and Koch (1998) did not distinguish 2nd order and 3rd order vascular bundles in blades of *E. obtusiflora*. However, distinct metaxylem is evident in the 1st order vascular bundles (Ellis 1976) as noted by Ogden (1897) and Bell and Columbus (2008).

DISCUSSION

Eragrostis obtusiflora has long been positioned in *Eragrostis* because of its multiple florets per spikelet and 3-nerved, awnless, and glabrous lemmas. However, based on other characteristics, including leaf anatomy, taxonomists have found it to be a puzzling species with enigmatic affinities (Ogden 1897; Scribner 1897; Hitchcock 1951; McVaugh 1983; Van den Borre and Watson 1994; Gómez Sánchez and Koch 1998; Calderón de Rzedowski and Rzedowski 2001). Most of these researchers have noted similarities in vegetative appearance and in habitat requirements between *E. obtusiflora* and members of Monanthochloinae, especially *D. spicata*. *Distichlis spicata* and *E. obtusiflora* frequently co-occur in saline/alkaline habitats, and both species are strongly rhizomatous. However, rhizomes of *E. obtusiflora* are thicker (>5 mm) and generally golden yellow with distinctive scale scars while rhizomes of *D. spicata* are more slender (<4 mm) and brownish with persistent scale leaves. In addition, lemma nerve number (3 in *E. obtusiflora* vs. 7–13 in *D. spicata*) and floral sexuality (hermaphroditic in *E. obtusiflora* vs. unisexual in *D. spicata*) clearly distinguish these species.

Analyses of molecular data from the nuclear and chloroplast genomes confirm that *E. obtusiflora* has been misplaced taxonomically (GPWG II 2012; Fig. 1, 2). It does not form a clade with other species of *Eragrostis* in tribe Eragrostideae. When *E. obtusiflora* is constrained as part of Eragrostideae (in the analysis of combined ITS and *trnL-F*, Fig. 1), tree length is significantly longer (Templeton 1983; Kishino and Hasegawa 1989). Rather, it resolves in Cynodonteae. In both GPWG II (2012) and the present study, it resolves with the same group of genera but with a lack of statistical support making its exact relationship to these genera uncertain based upon these data and analyses.

Another source of evidence disputing the current placement of *E. obtusiflora* comes from micromorphological and anatomical data. Amarasinghe and Watson (1988, 1990) studied bicellular microhair morphology in 74 *Eragrostis* species and reported three types of microhairs: chloridoid (short, broad, and distal cell thick walled), panicoid (long, narrow, and distal cell thin walled), and intermediate (long, distal cell inflated). While *Eragrostis* microhairs are variable, the dumbbell or flask-shaped microhairs observed in *E. obtusiflora* (Fig. 7) have

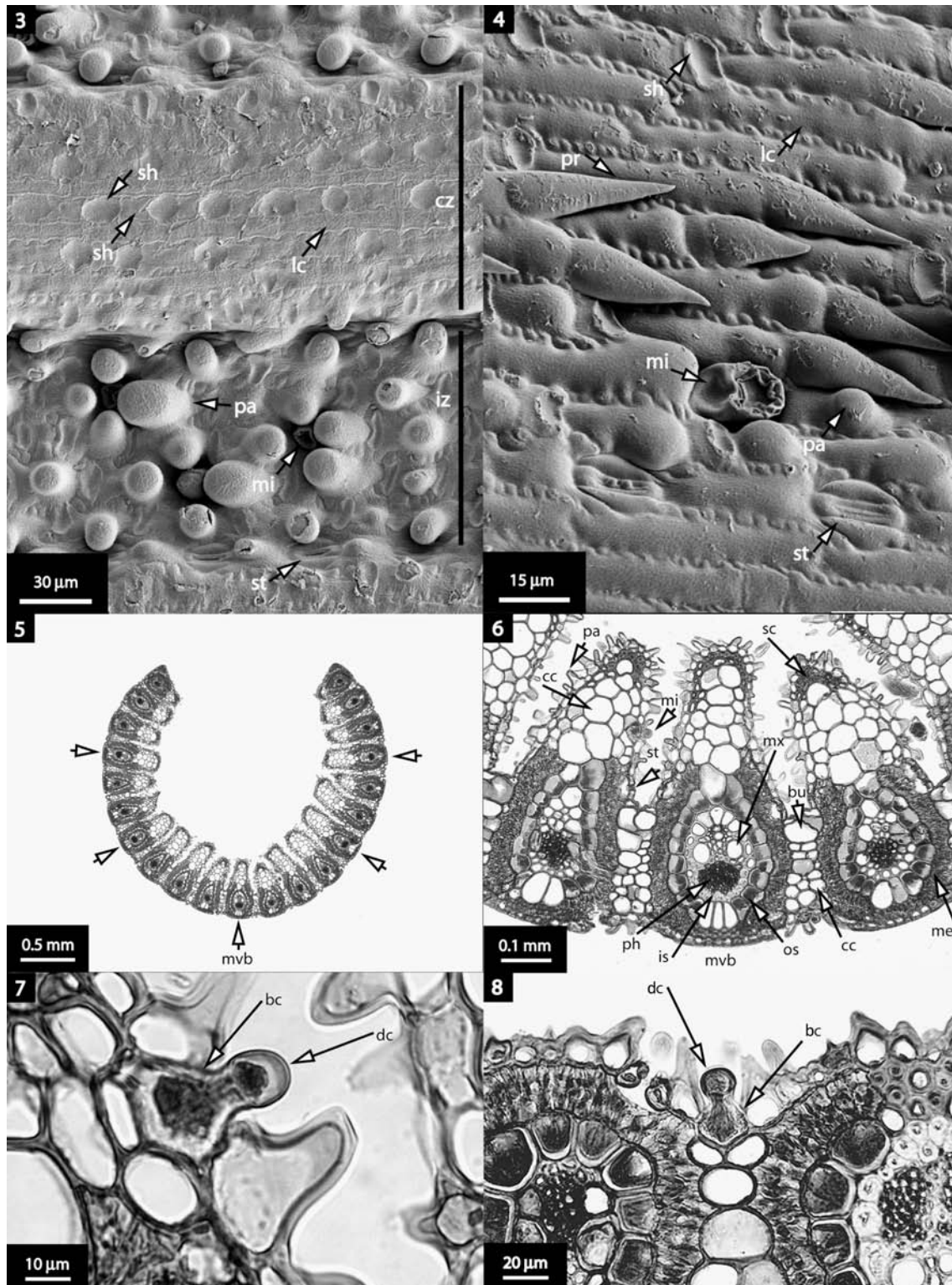


Fig. 3–8. Micromorphology and anatomy.—3. Abaxial surface of leaf blade of *Eragrostis obtusiflora* (Bell 295). Note: some short cells may be silica cells.—4. Abaxial surface of lemma of *E. obtusiflora* (Bell 295).—5. Whole-blade transection of *E. obtusiflora* (Bell 295). Arrows indicate 1st order vascular bundles.—6. Detail of median vascular bundle of leaf blade of *E. obtusiflora* (Bell 295).—7–8. Comparison of microhairs of *E. obtusiflora* (Bell 295-7) and *Distichlis spicata* (Bell 231-8). (bc = basal cell, bu = bulliform cell, cc = colorless cells, cz = costal zone, dc = distal cell, is = inner sheath, iz = intercostal zone, lc = long cell, me = mesophyll, mi = microhair, mvp = median vascular bundle, mx = metaxylem, os = outer sheath, pa = papilla, ph = phloem, pr = prickles, sc = sclerenchyma, sh = short cell, st = stoma).

not been reported for other members of the genus. However, they are strikingly similar to the microhairs found in *Distichlis* (Fig. 8) and other halophytic chloridoideae such as *Aeluropus* Trin., *Cynodon* Rich., *Odyssea* Stapf, *Spartina* Schreb., and *Sporobolus* R.Br. (Levering and Thomson 1971; Liphshitz and Waisel 1974; Oross and Thomson 1982; Amarasinghe and Watson 1988; Somaru et al. 2002; Bell and Columbus 2008).

In addition, *E. obtusiflora* has stomata on its lemmas (Fig. 4), a feature not observed in a small sample of *Eragrostis* species (Liu et al. 2010). In Chloridoideae, stomata on lemmas have been reported in 25 (of ca. 140) genera including *Distichlis* and other related members of Cynodonteae (Columbus 1996; Bell and Columbus 2008; Liu et al. 2010).

Leaf blade anatomy provides additional evidence of the unique nature of *E. obtusiflora*. Four previous studies have presented data on blade transectional anatomy of this species (Ogden 1897; Van den Borre and Watson 1994; Gómez Sánchez and Koch 1998; Bell and Columbus 2008). The conclusion of these studies is that anatomy of *E. obtusiflora* differs from that of other *Eragrostis* species by the presence of papillae in intercostal zones of the abaxial surface and the lack of interruption of the bundle sheath by sclerenchyma (shared only with *E. pergracilis* S.T.Blake). The anatomy of *E. obtusiflora* differs from *Distichlis* in the presence of bundle sheath extensions of colorless cells (absent in *Distichlis*) and the wide diameter of metaxylem cells (narrow in *Distichlis*) (Bell and Columbus 2008). However, the presence of dumbbell or flask-shaped bicellular microhairs with a portion of the basal cell sunken below the epidermis is a character that is shared by *E. obtusiflora* and all members of *Distichlis*, supporting a possible close relationship between these taxa (Fig. 7, 8; Bell and Columbus 2008).

It is clear from analyses of DNA sequence data and from anatomical and morphological evidence that *E. obtusiflora* does not belong in *Eragrostis* and, in fact, is placed in Cynodonteae, but there is no evidence for placing it in any other existing genus. *Distichlis* may be most closely related, but it differs most evidently by its 5–13-nerved lemmas and unisexual flowers. Therefore, we propose a new genus, *Kalinia*, for this species.

TAXONOMIC TREATMENT

Kalinia H.L.Bell & Columbus, gen. nov.—TYPE: *Kalinia obtusiflora* (E.Fourn.) H.L.Bell & Columbus.

Robust perennial with long, glabrous stolons and thick, tan to golden rhizomes with imbricate scales dehiscing to form distinctive scars; ligule a line of short hairs, leaf blades rigid, conspicuously orthodistichous, with markedly pungent tips; inflorescence a narrow to open panicle; spikelets with 5[4?]-12 hermaphroditic florets, the distal floret occasionally reduced, lemmas 3-nerved, glabrous, with an obtuse to slightly pointed tip, sometimes erose, fringed, or mucronate from the central nerve.

Kalinia obtusiflora (E.Fourn.) H.L.Bell & Columbus, comb. nov.

Basionym: *Brizopyrum obtusiflorum* E.Fourn., *Mexic. Pl.* 2: 120 (1886). *Eragrostis obtusiflora* (E.Fourn.) Scribn., *Bull. Div. Agrostol. U.S.D.A.* 8: 10, t. 5 (1897). Type: Mexico. Orizaba, s.d., Émy s.n. (holotype: P!), Fig. 9.

Robust, rhizomatous, and stoloniferous perennial to 50 cm tall, branching from the base; rhizomes stout, to 8 mm thick, tan to golden yellow, with imbricate scales dehiscing to form a

distinctive banding pattern, spiny tipped; stolons branching extravaginally at nodes, internodes to 24 cm long, hollow, nodes distinctly brown; culms erect or ascending, intravaginal from plant base, nodes hollow, pale. Leaf sheaths overlapping, concealing the culm, open, with tufts of villous hairs at distinct collar and ciliate along margin, occasionally sparsely pilose on surface; ligule a short (1–1.5 mm) line of whitish hairs; blades $22 \times 0.3\text{--}0.6\text{ cm}$, conspicuously orthodistichous, ascending to spreading, straight or slightly arcuate, rigid, involute, more tightly so distally, narrowing to a hard, light yellow, markedly pungent tip, abaxial surface glabrous, adaxial surface with deep, narrow furrows, scabrous, margins scaberulous, midrib not prominent. Inflorescence a narrow or open panicle to 20 cm long, exerted or partially included in upper sheath, 1° branches to 3.5 cm long, sometimes with 2° branching, tufts of hairs occasionally observed in branch axils, rachis and branches flattened, scabrous to various degrees, pedicels short (<math><0.5\text{ cm}</math>), appressed to branches. Spikelets 0.8–1.5 \times ca. 0.3 cm, narrowly cylindrical except when the florets spread during anthesis, glabrous, pale or purple-tinged, disarticulation above glumes and between florets, rachilla segment disarticulating with floret below, bracts ovate, usually obtuse; florets 5[4?]-12, terminal floret sometimes reduced; glumes similar, membranous, lower 1-nerved, upper 3-nerved with lateral nerves indistinct, lower 2.5–3.2 mm long, upper 3.2–4.5 mm long; lemmas 3.5–4.5 mm long, chartaceous to apically membranous, tip variable from blunt to slightly pointed (occasionally mucronate from central nerve), frequently erose to fringed with 3 (rarely 5) prominent nerves; palea slightly shorter than lemma, loosely held in lemma, membranous, prominently 2-nerved and 2-keeled, nerves scabridulous, apex obtuse; lodicules 2, broadly cuneate; stamens 3, anthers white to reddish purple, 2.0–2.4 mm long; ovary ca. 1.0–1.2 mm, stigmas 2, plumose, purplish. Caryopses 1.6–2.0 \times 0.8–1.0 mm, narrowly obovate, rounded on side opposite the hilum, with shallow vertical depression on hilum side.

Chromosome number.— $2n = 40$ (Reeder 1977).

Etymology.—The generic name is derived from the Arabic root of alkali, *al qaliy* (ashes of saltwort), in recognition of the habitat preference of this plant.

Common names.—“Zacate amor seco,” “zacate jihuite” (Beetle et al. 1991); “zacahuixtle” (Lleverino González et al. 2000); “carrizillo” (term used in Jalisco, Mexico).

Type locality.—In the *Brizopyrum obtusiflora* protologue, Fournier (1886) indicated “[i]n ora occidentali (Émy in meo herbario).” “Orizaba” is written on the type specimen. Fournier (1878) noted that some specimens collected by members of the French Scientific Commission to Mexico, 1865–1866, did not have detailed collection data. Such specimens were attributed to Captain Émy and to the site of the military encampment, Orizaba, in the state of Veracruz (Hemsley 1882–1886). Fournier mentioned Acapulco (Guerrero) and Mazatlán (Sinaloa) as coastal areas where collections were made by members of the commission; however, *K. obtusiflora* has not been collected from the Pacific (or Gulf) coast of Mexico, including Veracruz. We are not aware of suitable habitat of *K. obtusiflora* near Orizaba. In the region it is known from collections at Laguna Atotonilco (Jalisco), Laguna Cuitzeo (Michoacán), and Lago de Texcoco (México).

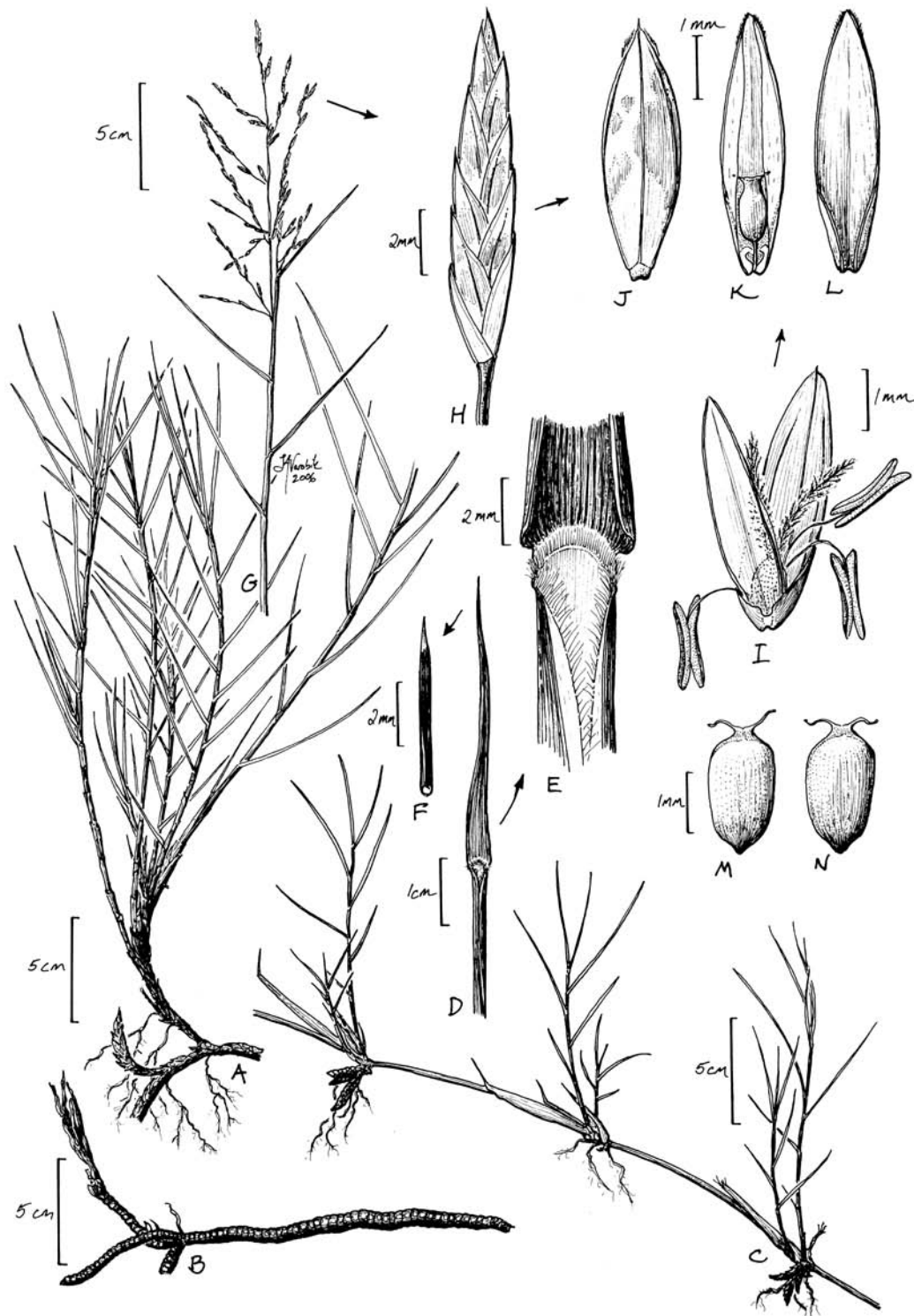


Fig. 9. *Kalina obtusiflora* (E.Fourn.) H.L.Bell & Columbus.—A. Habit.—B. Rhizome with scale scars.—C. Stolon.—D. Leaf.—E. Ligule.—F. Pungent blade tip.—G. Inflorescence.—H. Spikelet.—I. Floret.—J. Lemma abaxial view.—K. Palea, adaxial view, ovary and lodicules.—L. Palea, abaxial view.—M. Caryopsis, hilar view.—N. Caryopsis, scutellar view. (Fig. A from Thornber s.n. (RSA 627597); B–C from Bell 310; D–N from Henrickson 14104). Line drawings by Linda Vorobik.

Distribution and habitat.—*Kalina obtusiflora* occurs in Arizona and New Mexico (USA) and in the Mexican states of Chihuahua, Coahuila, Durango, Guanajuato, Jalisco, México, Michoacán, and San Luis Potosí (Appendix 1; Fig. 10). It is

frequently sympatric with *D. spicata*. A large number of specimens are from Willcox Playa in southern Arizona, and multiple vouchers represent the area around the town of Playas, New Mexico, as well as northern Chihuahua and the

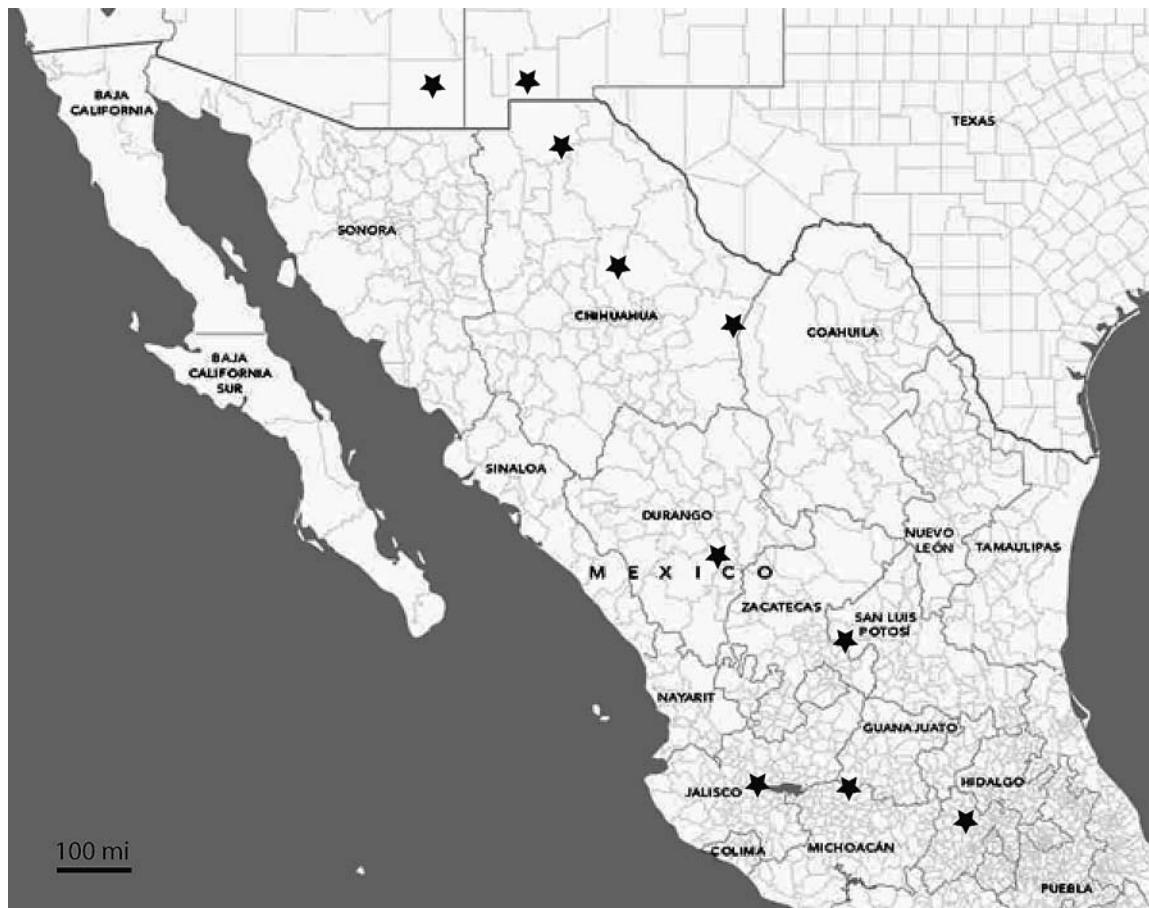


Fig. 10. Distribution of *Kalinia obtusiflora*.

central Mexican states of Jalisco, México, and Michoacán. Throughout its range, *K. obtusiflora* has a patchy distribution on inland saline and alkaline playas.

ACKNOWLEDGMENTS

Linda Vorobik produced the excellent line drawing. David Becker translated portions of E. Fournier's "Sur la distribution géographique des Graminées Mexicaines." Nancy Refulio-Rodriguez facilitated the loan of the type from P and assisted with collecting. Cristina Martínez-Habibe and Jose Zúñiga helped with the translation of the English abstract into Spanish. Jennifer Pilapil assisted with preparation of Fig. 10. Victoria C. Hollowell, Paul M. Peterson, and Isidoro Sánchez Vega reviewed the manuscript. Rancho Santa Ana Botanic Garden and Lon Bell provided support for this project. We thank the curators of ASU, CAS, GH, MEXU, MICH, MO, NMC, NMCR, NY, RSA, TAES, TEX, UNM, US, and WIS for loans of herbarium specimens.

LITERATURE CITED

- AMARASINGHE, V. AND L. WATSON. 1988. Comparative ultrastructure of microhairs in grasses. *J. Linn. Soc. Bot.* **98**: 303–319.
- AND ———. 1990. Taxonomic significance of microhair morphology in the genus *Eragrostis* Beauv. (Poaceae). *Taxon* **39**: 59–65.
- BEEBLE, A. A., E. MANRIQUE F., J. A. MIRANDA S., V. JARAMILLO L., A. CHIMAL H., AND A. M. RODRIGUEZ R. 1991. Las gramíneas de México, Tomo III. Secretaría de Agricultura, Ganadería y Desarrollo Rural, y Recursos Hidráulicos, COTECOCA-SAGAR, Mexico.
- BELL, H. L. AND J. T. COLUMBUS. 2008. Proposal for an expanded *Distichlis* (Poaceae, Chloridoideae): support from molecular, morphological, and anatomical characters. *Syst. Bot.* **33**: 536–551.
- BRIERE, P. R. 2000. Playa, playa lake, sabkha: proposed definitions for old terms. *J. Arid Environm.* **45**: 1–7.
- CALDERÓN DE RZEDOWSKI, G. AND J. RZEDOWSKI. 2001. Flora fanerogámica del Valle de México. 2nd ed. Instituto de Ecología, A. C. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Pátzcuaro (Michoacán), Mexico. 494 p.
- CLAYTON, W. D., K. T. HARMAN, AND H. WILLIAMSON. 2006 onwards. GrassBase—the Online World Grass Flora. <http://www.kew.org/data/grasses-db.html> (May 2012).
- AND S. A. RENVOIZE. 1986. Genera graminum: grasses of the world. *Kew Bull., Addit. Ser.* **13**: 1–389.
- COLUMBUS, J. T. 1996. Lemma micromorphology, leaf blade anatomy, and phylogenetics of *Bouteloua*, *Hilaria*, and relatives (Gramineae: Chloridoideae: Boutelouinae). Dissertation. University of California, Berkeley, USA.
- , R. CERROS-TLATILPA, M. S. KINNEY, M. E. SIQUEIROS-DELGADO, H. L. BELL, M. P. GRIFFITH, AND N. F. REFULIO-RODRIGUEZ. 2007. Phylogenetics of Chloridoideae (Gramineae): a preliminary study based on nuclear ribosomal internal transcribed spacer and chloroplast *trnL-F* sequences. *Aliso* **23**: 565–579.

- ELLIS, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. *Bothalia* **12**: 65–109.
- . 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia* **12**: 641–671.
- FOURNIER, E. 1878. Sur la distribution géographique des Graminées Mexicaines. *Ann. Sci. Nat. (Paris)* **9**: 261–290.
- . 1886. Mexicanas plantas. Pars II. Gramineae. Typographeo Republicae, Paris, France. 160 p.
- GÓMEZ SÁNCHEZ, M. AND S. D. KOCH. 1998. Estudio anatómico comparativo de la lamina foliar de *Eragrostis* (Poaceae: Chloridoideae) de México. *Acta Bot. Mex.* **43**: 33–56.
- GRASS PHYLOGENY WORKING GROUP II [GPWG II]. 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. *New Phytol.* **193**: 304–312.
- HEMSLEY, W. B. 1882–1886. Botany, 136 p. In F. D. Godman and O. Salvin [eds.], *Biologia Centrali-Americana*, contributions to the knowledge of the fauna and flora of Mexico and Central America. R. H. Porter & Dulau & Co., London, UK.
- HITCHCOCK, A. S. 1951. Manual of the grasses of the United States, 2nd ed. (revised by A. Chase). *USDA Misc. Publ.* **200**: 1–1051.
- INGRAM, A. L. AND J. J. DOYLE. 2004. Is *Eragrostis* (Poaceae) monophyletic? Insights from nuclear and plastid sequence data. *Syst. Bot.* **29**: 545–552.
- AND ———. 2007. *Eragrostis* (Poaceae): monophyly and infrageneric classification. *Aliso* **23**: 595–604.
- KISHINO, H. AND M. HASEGAWA. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data and the branching order of hominoidea. *J. Molec. Evol.* **29**: 170–179.
- LEVERING, C. A. AND W. W. THOMSON. 1971. The ultrastructure of the salt gland of *Spartina foliosa*. *Planta* **97**: 183–196.
- LIPHSHITZ, N. AND Y. WAISEL. 1974. Existence of salt glands in various genera of the Gramineae. *New Phytol.* **73**: 507–513.
- LIU, Q., D. X. ZHANG, AND P. M. PETERSON. 2010. Lemma micromorphological characters in the Chloridoideae (Poaceae) optimized on a molecular phylogeny. *S. African J. Bot.* **76**: 196–209.
- LLEVERINO GONZÁLEZ, E., C. A. ORTIZ SOLORIO, AND M. DEL C. GUTIÉRREZ CASTORENA. 2000. Calidad de los mapas de suelos en el ejido de Atenco, Estado de México. *Terra Latinoamericana* **18**: 103–113.
- MCVAUGH, R. 1983. vol. 14. Gramineae. In W. R. Anderson [ed.], *Flora Novo-Galiciana: a descriptive account of the vascular plants of western Mexico*. University of Michigan Press, Ann Arbor, USA.
- OGDEN, E. L. 1897. Studies on American grasses. II. Leaf structure of *Jouvea* and of *Eragrostis obtusiflora*. *Rep. Agrostol. Div. Agrostol. U.S.D.A.* **8**: 12–22, plates VIII, IX.
- CROSS, J. W. AND W. W. THOMSON. 1982. The ultrastructure of the salt glands of *Cynodon* and *Distichlis* (Poaceae). *Amer. J. Bot.* **69**: 939–949.
- PETERSON, P. M., J. T. COLUMBUS, AND S. J. PENNINGTON. 2007. Classification and biogeography of New World grasses: Chloridoideae. *Aliso* **23**: 580–594.
- PRENDERGAST, H. D. V. AND P. W. HATTERSLEY. 1987. Australian C4 grasses (Poaceae): leaf blade anatomical features in relation to C4 acid decarboxylation types. *Austral. J. Bot.* **35**: 355–382.
- REEDER, J. R. 1977. Chromosome numbers in western grasses. *Amer. J. Bot.* **64**: 102–110.
- ROSEN, M. R. 1994. The importance of groundwater in playas: a review of playa classifications and sedimentology and hydrology of playas. Paleoclimate and Basin Evolution of Playa Systems, Geological Society of America Special Paper 289.
- SCRIBNER, F. L. 1897. Studies on American grasses. I. New or little known grasses. *Rep. Agrostol. Div. Agrostol. U.S.D.A.* **8**: 5–11, plates I–VII.
- SOMARU, R., Y. NAIDOO, AND G. NAIDOO. 2002. Morphology and ultrastructure of the leaf salt glands of *Odysea paucinervis* (Stapf) (Poaceae). *Flora* **197**: 67–75.
- SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), vers. 4.0 beta 10. Sinauer Associates, Inc., Sunderland, Washington, USA.
- TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage maps with particular reference to the evolution of humans and apes. *Evolution* **37**: 221–244.
- VAN DEN BORRE, A. AND L. WATSON. 1994. The infrageneric classification of *Eragrostis* (Poaceae). *Taxon* **43**: 383–422.

APPENDIX 1

Representative specimens examined. GenBank numbers for sequences generated during this study are underlined.

MEXICO. CHIHUAHUA: Lake Santa Maria, 20 Apr 1852, *Wright 2035* (GH [2 sheets] (MO)); Laguna Ascencion near La Ascencion, 13 Sep 1939, *Harvey 1750* (CAS, MICH); near Lake Santa Maria, 7 Sep 1899, *Nelson 6413* (MICH); an alkali flat 13 mi N of Parrita, 16 Sep 1960, *Reeder et al. 3489* (UC, UNM); 13 km E of Guzmán on road to Laguna de Santa Maria, 22 Aug 1972, *Chiang et al. 8795* (MEXU, TEX); 6.8 mi N of Guzmán in saline flats of Laguna Guzmán, 14 Sep 1974, *Henrickson 14104* (TEX); Laguna de Guzmán, 17 Sep 2003, *Bell 303* (RSA); 1.6 km N of Galena at km marker 151 along Hwy 10, 18 Sep 2003, *Bell 305* (RSA). COAHUILA: ca. 80 (air) mi E of Saucilla, W side of Laguna Jaco, 21 Sep 1974, *Henrickson 14202* (TEX). DURANGO: intersection of Hwy 40 with road to Carlos Real, 25 Sep 2003, *Bell 310* (RSA). JALISCO: near Km 57, 7–8 mi S of Acatlán de Juárez, alkaline flats bordering Laguna de Atotonilco, 27 Sep 1960, *McVaugh 19461* (MICH); Laguna de Zacoalco, 18 Sep 1980, *Beetle & Guzman M-5331* (MEXU); E of Villa Corona at N end of Laguna Atotonilco, 9 Oct 2003, *Bell 318*

(RSA), ITS = HM152781, *trnL-F* = HM152784. MÉXICO: San Cristobal-Tepexpan, 13–14 Jun 1953, *Matuda 28587* (MEXU); 3 km al N de San Cristobal Ecatepec, 7 Jul 1963, *Rzedowski 16863* (MEXU, MICH, TAES, TEX, WIS [2 sheets]); Km 25 de la carretera México-Pachuca, 3 km al N de El Caracol, mpio. de Ecatepec, 3 Apr 1966, *Cruz 514* (CAS, MICH); Lago de Texcoco, entre Texcoco y México, 17 Apr 1974, *Koch 7456* (CAS, MEXU); sobre la brecha a Netzahualcoyotl, a 7 km al W de Texcoco, 29 Jul 1981, *Guzmán 3841* (MEXU); mpio. Montecillo, al W de los campos del Colegio de Postgraduados, 28 Jun 1990, *Gómez-Sánchez & González 500* (MEXU); Km 12 a la orilla del carril izquierdo de la autopista Méx.-Tex., 28 Jun 1999, *Chavez s.n.* (MEXU 1073963); MICHOACÁN: extremo sur de La Laguna Cuitz[e]o por la carr. Morelia-Salamanca, 1 Sep 1981, *Guzmán 4452* (MEXU); 1 km al N de Cuitzeo, 3 May 1986, *Rzedowski 39649* (MEXU); S end of Laguna Cuitzeo along Hwy 43 between Morelia and Salamanca, 1 Oct 2003, *Bell 314* (RSA). SAN LUIS POTOSÍ: SW edge of Salinas de Hidalgo, 5 Oct 2000, *Columbus 3775* (RSA); W of Hwy 49 b/w San Luis Potosí and Zacatecas at Salinas de Hidalgo, 14 Oct 2001, *Bell 251* (RSA), ITS = HM152782, *trnL-F* = HM152786, *rps16*

intron = HM152787. USA. ARIZONA: Chiricahua Mts, 25 Sep 1896, *Toumey 27* (US); Sulphur Spring Valley, September 1896, *Toumey s.n.* (US 859726); Willcox Playa, August–September 1896, *Toumey s.n.* (US 1723504); 28 Aug 1905, *Thorber s.n.*, (ASU, CAS, GH, MICH, NY, RSA 627597, TAES [2 sheets]), TEX, UNM 90792); 12 Jun 1937, *Goodding s.n.* (MICH, US 1721946, US 1721945); 12 Jun 1937, *Silveus 2169* (TAES, TEX); 12 Apr 1938, *Silveus 2538* (GH, MICH, TEX, US); 19 Sep 1938, *Silveus 5430* (CAS, TAES, TEX); 26 Sep 1938, *Silveus 3502* (CAS, TAES, TEX); 15 Sep 1940, *Shreve 10007* (MICH); 2 Sep 1944, *Pultz et al. 1036* (CAS, GH, MICH, US); 26 Aug 1971, *Reeder & Reeder 5530* (US); 10 Jul 1986, *Reeder & Reeder 7867* (ASU); 23 Jul 1996, *Reeder & Reeder 9411* (ASU); Willcox Playa, 26 Aug 2001, *Bell 239* (RSA); 16 Sep 2003, *Bell 295* (RSA), ITS = HM152783, *trnL-F* = HM152785. CALIFORNIA: Olancha, 29 May 2001, *Bell 231* (RSA) [*Distichlis spicata*]. NEW MEXICO: Las Playas, 23 Jun 1906, *Wootton s.n.* (NMC 690, US 735348); edge of Playa Lake 5 mi N of smelting plant, 9 Jul 1984, *Trent & Allred 111* (NMCR); Playas, 17 Sep 2003, *Bell 297* (RSA).