

CULM ANATOMY OF *BOUTELOUA* AND RELATIVES
(GRAMINEAE: CHLORIDOIDEAE: BOUTELOUINAE)

MA. ELENA SIQUEIROS-DELGADO

Universidad Autónoma de Aguascalientes
Centro de Ciencias Básicas, Departamento de Biología,
Av. Universidad 940, 20100 Aguascalientes, México
masiquei@correo.uaa.mx

ABSTRACT

Transverse sections of mature flowering culms of Boutelouinae were analyzed to explore the usefulness of the culm anatomy to assess phylogenetic relationships. Fifty-five taxa were surveyed from the field and greenhouse collections. Although leaf anatomy in Boutelouinae has been shown to possess systematic utility, culm anatomy has been very little explored. In the Boutelouinae, only few traits of the culm middle internodal region with phylogenetic value, were found. Kranz structures (cells and radial chlorenchyma), number and position of the vascular bundles, and sclerenchyma girders are some culm anatomy characters that can be useful for inferring relationships at higher levels (family, tribes, genera). Culm anatomy suggests close relationships between *B. eriopoda* and *B. eriostachya*, and between *B. ramosa* and *B. breviseta*, and supports the inclusion of the satellite genera into *Bouteloua*. The Kranz structures and chloroplast shape appear to be the most variable features of this region of the culm.

Key words: anatomy, *Bouteloua*, culm, Gramineae.

RESUMEN

Se analizaron cortes transversales de la región media del tallo de 55 taxa de Boutelouinae, con el fin de explorar la utilidad de sus caracteres en el conocimiento de las relaciones filogenéticas del grupo. A pesar de que los caracteres anatómicos de hoja han mostrado ser útiles para inferir relaciones filogenéticas, el examen microscópico del culmo no revela la existencia de muchos rasgos informativos del aspecto evolutivo. Atributos como las estructuras Kranz, el número y posición de los haces vasculares y los anillos de esclerénquima pueden ser caracteres útiles para inferir relaciones filogenéticas a nivel de familia, tribu o género. La anatomía de tallo sugiere una estrecha relación entre *B. eriopoda*

y *B. eriostachya*, así como entre *B. ramosa* y *B. breviseta*, además apoya la inclusión de los géneros satélites dentro de *Bouteloua*. Las estructuras Kranz y la forma de los cloroplastos parecen ser los caracteres más variables de esta región del tallo.

Palabras clave: anatomía, *Bouteloua*, culmo, Gramineae.

INTRODUCTION

Boutelouineae (Gramineae: Chloridoideae) comprise seven genera: *Aegopogon*, *Bouteloua*, *Hilaria*, *Melanocenchrus*, *Neobouteloua*, *Pleuraphis*, and *Schaffnerella* (Columbus, 1999a). This subtribe is characterized by one or more non-digitate inflorescence branches, usually one or more reduced florets, and three-nerved lemmas, each nerve usually terminating in a lobe and/or awn (Columbus, 1996), and its culm anatomy corresponds to the Chloridoideae type (Auquier and Somers, 1967). Most representatives of Boutelouineae are natives of American grasslands (except *Melanocenchrus* from Africa), typically occur in arid or semiarid environments, and their value as forage grass is remarkable. Boutelouineae possess C₄ photosynthesis pathway with the associated characteristic Kranz anatomy (Hattersley and Watson, 1975). Most Boutelouineae have NAD-ME (nicotinamide adenine dinucleotide co-factor to malic enzyme) biochemical pathway, characterized by XyMS+ (mesotome present), centripetal chloroplast with granna, an even Kranz bundle sheath outline and suberised lamella. Some taxa, however, possess PCK (phosphoenolpyruvate carboxykinase), characterized by XyMS+ and centrifugal chloroplasts with granna and an uneven outline. XyMS+ are structural traits characteristic of arid conditions (Prendergast et al., 1987).

Bouteloua is the largest genus with 57 species (Columbus, 1999a), followed by *Hilaria* (9), *Aegopogon* (3), *Melanocenchrus* (3), *Neobouteloua* (1), *Pleuraphis* (3), and *Schaffnerella* (1) (Clayton and Renvoize, 1989). Gould (1980), based on morphology and cytology, recognized 39 species in two subgenera, *Bouteloua* and *Chondrosium*. Based on molecular evidence, Columbus et al. (1998, 2000) and Columbus (1999a), redefined the genus showing that the two subgenera are not monophyletic, and including into *Bouteloua* most of its declinous relatives (*Buchloë*, *Buchlomimus*, *Cathestecum*, *Cyclostachya*, *Griffitsochloa*, *Opizia*, *Pentarrhaphis*, *Pringleochloa* and *Soderstromia*), rendering the genus as monophyletic. These satellite genera were segregated because of their declinous reproductive system (Reeder, 1969). However, molecular data show that they are members of the *Bouteloua* clade.

Leaf anatomy has proved to be a good phylogenetic tool for grass systematics. Many researchers have succeeded in using leaf anatomy to circumscribe species and infer phylogenies (Breakwell, 1914; Brown, 1958, 1975, 1977; Cerros-Tlatilpa, 1999; Columbus, 1996; Ellis, 1987; Fisher, 1939; Morden and Hatch, 1987; Sánchez, 1971). Columbus (1996) evidences the usefulness of leaf anatomy to infer phylogenies in the subtribe Boutelouinae. Based on micromorphology and leaf blade anatomy, he proposed the non-monophyly of *Bouteloua* and *Chondrosium*, the exclusion of *B. juncea* from the *Bouteloua curtispindula* complex, and the close relationship between *B. eriopoda* and *B. aristidoides*, which later were supported by molecular data (Columbus et al., 1998; Columbus et al., 2000; Siqueiros, 2001).

Except in bamboos (Agrasar and Rodríguez, 2002; Grosor and Liese, 1971; Liese 1980, 1998; Londoño et al., 2002; Sekar and Balasubramanian, 1994; Yao et al., 2002), culm anatomy in grasses, has been little explored regarding to the usefulness of its characters in phylogenetics (Cenci et al., 1984; Gasser et al., 1994; Ramos et al., 2002; Siqueiros and Herrera, 1996). Ramos et al. (2002) found that the most important variations in the culm components in *Bromus aleuticus* Trin. ex Ness are the cortical and medular parenchyma, the development and position of the vascular bundles, and the development of the sclerenchyma ring associated with these bundles. Siqueiros and Herrera (1996) found similar results, and pointed out that culm anatomy at the epinodal culm region in *Bouteloua* has restricted phylogenetic value. In *Dasychoa*, *Blepharidachne*, and *Munroa*, however, culm anatomy has shown to be useful to differentiate groups at subfamily or tribal rank (Sánchez, 1983a, 1983b, 1984). In Boutelouinae, culm anatomy corresponds to Chloridoideae type (Auquier and Somers, 1967), and according to De Wet (1960) and Metcalfe (1960), its value in phylogenetics is limited.

Some anatomical characters that have been used in phylogenetic studies are: Kranz sheath (vascular bundle outer sheath), patterns in vascular bundles (Cerros-Tlatilpa, 1999; Columbus, 1996), sclerenchyma patterns (Siqueiros and Herrera, 1996), position and form of the chloroplasts (Columbus, 1996), shape and position of bulliform cells (Cerros-Tlatilpa, 1999; Columbus, 1996). Columbus (1996) pointed out that Kranz sheath is the most useful leaf anatomical character to infer common ancestry in Boutelouinae. In culm anatomy, however, the Kranz cells do not form an outer sheath as in the leaf. The bundle sheath is incomplete, forming an arc external to the vascular bundles. Kranz arc, radial chlorenchyma, culm outline, and chloroplast shape and position, are some of the culm anatomical features suggested to be useful for inferring phylogenies (Siqueiros and Herrera, 1996).

The goal in this study was to characterize the culm anatomy of *Bouteloua* and relatives and to determine its value in phylogenetics.

MATERIALS AND METHODS

Transverse sections of mature flowering culms were obtained from the middle part of the first internode below the inflorescence. This region is usually devoid of leaf sheath. Samples were obtained from plants collected directly in the field or in the RSABG greenhouse. Most field collections were provided by J. T. Columbus, therefore, his collection number is indicated, unless otherwise. Four genera, including 55 taxa within Boutelouinae were surveyed. In addition, permanent slides from the epinodal culm region (above the node) of 49 taxa of Boutelouinae were surveyed in order to examine the chloroplast shape in young tissues. Mature tissue slides of *Bouteloua dactyloides*, *B. johnstonii*, *B. megapotamica*, *B. vaneedenii*, *Melanocenchrus* spp., *Neobouteloua* spp., and *Schaffnerella gracilis* were not obtained due to collecting and technical difficulties. For widely distributed species three or more samples from different geographical locations were studied, while for endemic or restricted taxa such as *B. pedicellata*, and *B. reflexa*, only one sample was studied (Appendix).

Samples were fixed in FPA and desilicificated with hydroxyfluoric acid. Tissues were dehydrated in ethanol series of 2 hs each (Ruzin, 1993) and embedded in paraplast. Before sectioning, the blocks were exposed and soaked in softening solution (Schmid and Turner, 1977), then rinsed in acetic acid. The tissues were sectioned and stained following Sharman (1943) protocol. The slides and the specimens are deposited at Rancho Santa Ana Botanic Garden, Claremont CA. Analyzed characters are shown in Table 1.

RESULTS

The analyses of the middle internode region of the flowering mature culms show a similar anatomical pattern in most Boutelouinae. However, variation among some taxa was observed. A brief description of the tissues and their position in the culm, the anatomical patterns of the genera, and the relationships among taxa inferred from culm anatomy is provided.

Table 1. Culm anatomy characters analyzed in this study.

Transection outline	Smooth, undulate
Epidermic cells	Presence/absence of cuticule Presence/absence of silica cells
Sclerenchyma patterns	Forming a girder/not forming a girder Forming a ring
Kranz structures	Shape and position of radial chlorenchyma Shape of the Kranz arc: straight, horseshoe, or half circle Number, shape, and position of Kranz cells Shape and position of Kranz cells chloroplasts
Mestome	Number of mestome layers Thickness of mestoma cell walls
Vascular bundles	Kind of vascular bundles: I°, II°, or III° Position Number

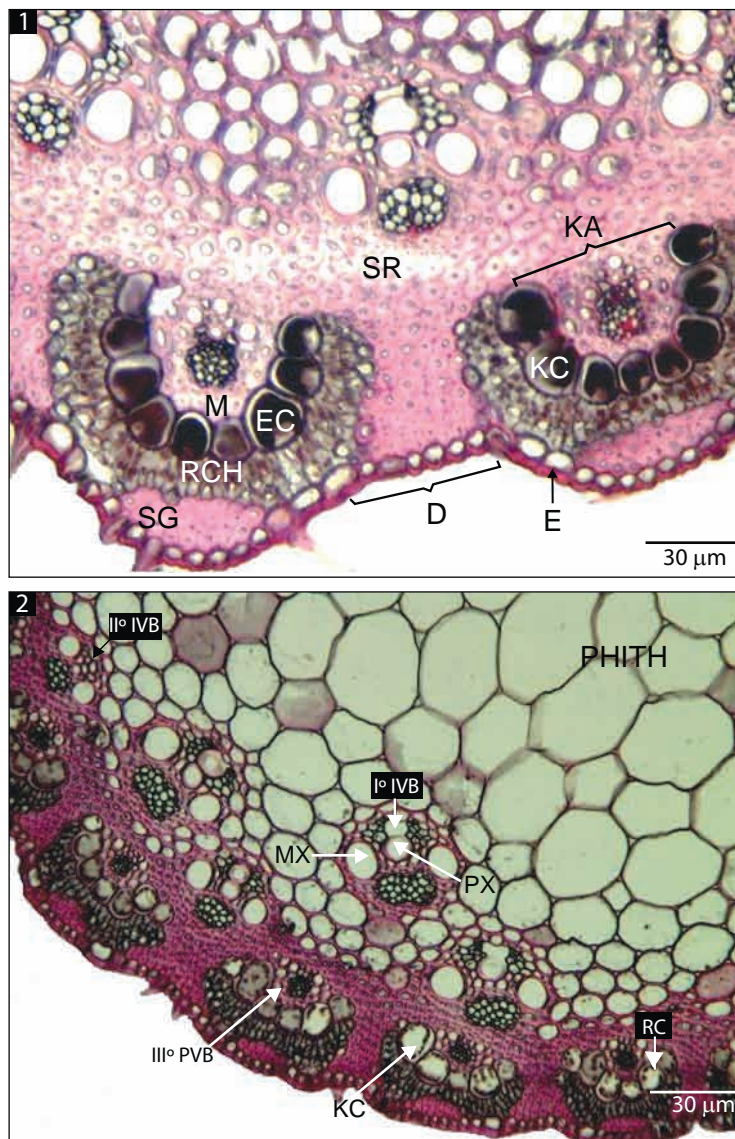
Tissues description in *Boutelouinae*

Epidermis. The single-layered epidermis is composed of round to square cells surrounded by a cutin layer. Trichomes, stomata and silica bodies are usually present (Fig. 1E).

Sclerenchyma. Cells with thick secondary walls and a small lumen, are observed. They form a subepidermal ring variable in thickness (Fig. 1SR), and interrupted by peripheral vascular bundles (PVB). In cross-section outline, sclerenchyma forms a girder, usually yielding conspicuous crests (Fig. 1SG).

Parenchyma. Parenchymatous cells are thin walled, and can be tubular or isodiametric, forming the radial chlorenchyma and the culm pith. Radial chlorenchyma cells are usually small, tubular, and perpendicular to the epidermis surface, following the curvature of the Kranz arc (Fig. 1RCH). The culm pith is located in the center of the culm, and it is constituted by large, isodiametric, thin walled, rounded cells (Fig. 2). Sometimes internal vascular bundles (IVB) are embedded within the pith.

Kranz cells. In leaves, Kranz cells form a perivascular bundle sheath. However, in culms this bundle sheath is incomplete, giving an aspect of arc or crown, variable in size and number of cells. This incomplete bundle sheath is called Kranz arc (Fig. 1KA). Kranz arc curvature varies from almost straight (Fig. 6KA) to half circle (Figs. 1, 4) or horseshoe (Fig. 7), always bordered by radial chlorenchyma.



Figs. 1 y 2. Culm cross-section of *Bouteloua chihuahuana* (Columbus 2824), and *B. curtipendula* (Columbus 2573) showing some of the main features of the culm anatomy. D. Culm depressions. EC. Elongated centripetal chloroplasts. E. Epidermis. KA. Kranz arc. KC. Kranz cells. M. Mestome. MX. Metaxylem cells. PX. Protoxylem cells. RCH. Radial chlorenchyma. SR. Sclerenchyma ring. SG. Sclerenchyma girder. RC. Round centrifugal chloroplasts. I°IVB. First order internal vascular bundles. II°IVB. Second order internal vascular bundles. III°PVB. Third order peripheral vascular bundles.

Kranz cells may be regular to irregular, even to uneven, and their shape can vary from round to oval (Fig. 2kC), square or trapezoid (Fig. 1kC). The cells number is usually correlated with its size. According to our observations, Kranz cells are found only on the exposed mature zone of the internode and they hold elongate or round chloroplasts.

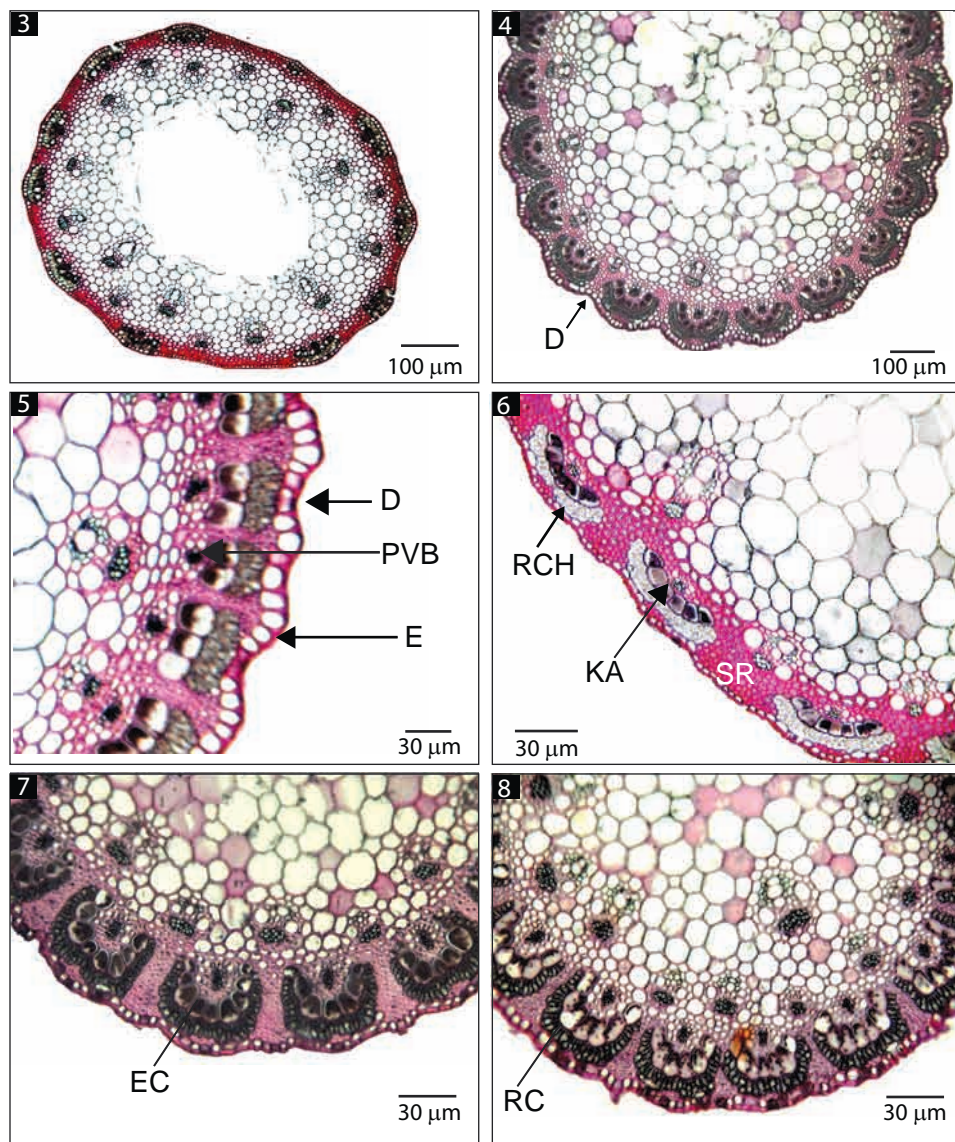
Mestome. It is formed by small, thick walled cells, similar to the sclerenchyma, surrounding the vascular bundles and occurring usually in a single layer. Mestome cells constitute the internal bundle sheath, and their size and shape are variable (Fig. 1M).

Vascular bundles. The vascular bundles are peripheral (PVB) or internal (IVB), and can be I° (proto and metaxylem cells well developed [Fig. 2MX, PX]), II° (only metaxylem cells developed), or III° (inconspicuous proto and metaxylem cells) order (Ellis, 1976; Fig. 2). The peripheral vascular bundles are associated to Kranz cells, and most of them are III° order. The IVB are I° order or II° order, and are organized in one to three concentric circles. The number of PVB, as well as IVB is variable.

Patterns of culm anatomy in *Boutelouinae*

Aegopogon. Culms are round to oval in cross-section, with a smoothly undulate outline (Fig. 3). Small and round epidermis cells are observed. The ones adjacent to radial chlorenchyma are larger than the rest of epidermis cells. Silica bodies and stomata are present. The sclerenchyma ring is formed by three to five layers of cells with evident lumen and surrounding 11 PVB in *A. cenchroides*, and one or none in *A. tenellus*. The Kranz arc is slightly curved with six to eight round, uneven cells with round chloroplasts. Sclerenchyma girder is missing. Seven to 17 IVB are embedded in the parenchymatous pith in two concentric circles, the outermost are II° and the internal ones are I° (Fig. 3).

Bouteloua. Culms are round to oval in cross-section, with a smooth to strongly undulate outline (Fig. 4). The epidermis cells usually are small, round, and regular to irregular. Some taxa, however, display larger, square, and regular cells (*B. eriopoda* [Fig. 5E]). Trichomes, stomata and silica bodies are always present. The subepidermal zone displays a continuous sclerenchymatous ring (Fig. 6SR), 3 to 15 cells thick, interrupted by PVB with associated Kranz structures (Kranz cells and radial chlorenchyma). The sclerenchymatous ring completely surrounds the PVB and joins the IVB by their apexes. The PVB are usually II° and their number ranges from 6 to 40. In undulated cross-sections PVB usually alternate with the culm de-



Figs. 3-8. Culm anatomy cross-sections of *Aegopogon* and *Bouteloua*, showing some features of the culm anatomy. Fig. 3. *Aegopogon cenchroides* (Columbus 2629). Fig. 4. *Bouteloua hirsuta* (Columbus 2713). Fig. 5. *B. eriopoda* (Columbus 2806). Fig. 6. *B. quiriegoensis* (Herrera & Siqueiros 1320). Fig. 7. *B. ramosa* (Columbus 2486). Fig. 8. *B. ramosa* (Columbus 2807). D. Culm depressions. E. Epidermis. EC. Elongated centripetal chloroplasts. KA: Kranz arc. PVB. Third order peripheral vascular bundles. RC. Round centrifugal chloroplasts. RCH. Radial chlorenchyma. SR. Sclerenchyma ring.

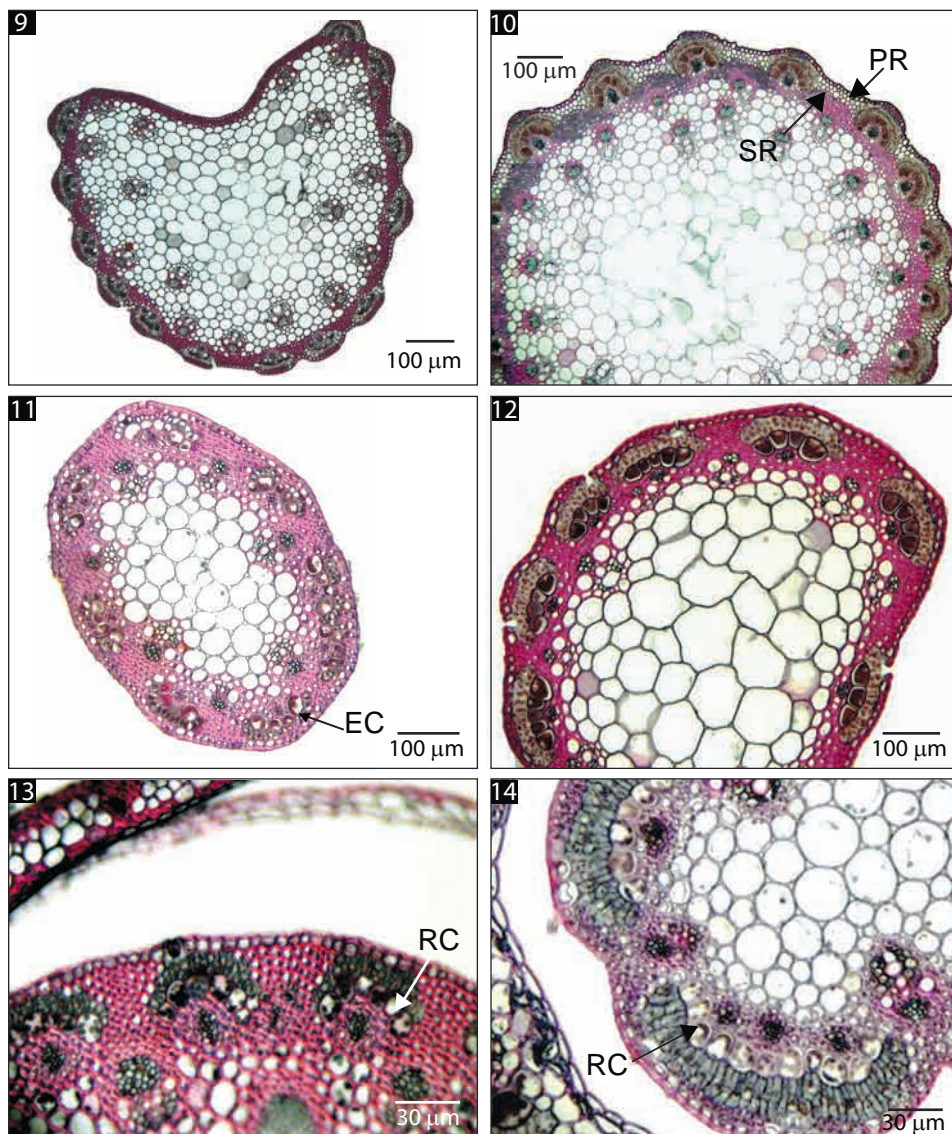
pressions (Fig. 4D), however, in *B. eriopoda* and *B. eriostachya*, PVB are opposite to culm depressions (Fig. 5D). Each PVB holds up an arc of Kranz cells of variable size, shape, curvature, and number. Some taxa show from 4 to 10 small, round, and uneven Kranz cells (*B. curtispindula* complex [Table 1, Fig. 2KC]); other show large square to oval, uniform cells (*B. chihuahuana*, *B. eriopoda*, *B. hirsuta*, and *B. ramosa* [Figs. 1KC, 5, 4, and 7, respectively]). The number of Kranz cells varies from 3 to 12 (usually 4 to 7), and the arc curvature varies from almost straight (*B. aristidoides* [Fig. 6KA] and the *B. curtispindula* complex taxa [Fig. 2]) to half circle (*B. chihuahuana* [Fig. 1KA], *B. hirsuta* [Fig. 4]), or horseshoe (*B. ramosa* [Fig. 7]). The chloroplasts of the Kranz cells are elongated (most *Bouteloua* taxa [Fig. 1EC, 7 EC, 11EC]) or round (*B. curtispindula* complex [Fig. 2RC]). The radial chlorenchyma is variable in shape, always following the Kranz arc curvature (Fig. 1, 6RCH). Frequently, it possesses a depression in the central part, which is filled by the sclerenchyma girder (Fig. 1SG). The IVB vary from 12 to 40, and they are arranged in one to three concentric circles.

Hilaria. The culm is a half circle in cross-section, with a slightly to evidently undulated surface (Fig. 9). Small epidermal cells with thick cutin layer, silica cells, trichomes, and stomata are present. The sclerenchyma ring is formed by five layers of compact cells, surrounding eight to 13 PVB distributed mostly along the curved side. Kranz arc is slightly curved, formed by four to six round, uneven cells with round chloroplasts. Radial chlorenchyma is conspicuous, bordering the Kranz cells. Eleven to 17 I° order IVB in two concentric circles are found.

Pleuraphis. The culm is round to slightly oval, with an undulated margin in cross-section (Fig. 10). Epidermal cells are round and small. Silica cells, trichomes and stomata are present. Below the epidermis, there is a parenchyma ring of two or three layers (Fig. 10PR), interrupted by 17 to 24 PVB. Under the parenchyma ring, the sclerenchyma ring is located (Fig. 10SR). The Kranz arc is conspicuously curved in a half circle, with seven to eight squared, compact cells with elongate chloroplasts. Twenty-two I° order IVB, in two concentric circles are found. The most external ones are attached on their apexes to the sclerenchyma ring.

Relationships among taxa inferred by culm anatomy

Although culm anatomy characters have restricted value to infer phylogenetic relationships, several culm features may provide evidence of common ancestry. Most of the *Boutelouinae* taxa share a similar culm anatomy pattern. Undulated outline, sclerenchyma ring with PVB within, Kranz cells forming an arc, and IVB embed-



Figs. 9-14. Culm anatomy cross-section of *Bouteloua*, *Hilaria* and *Pleuraphis* showing some features of the culm anatomy. Fig. 9. *Hilaria cenchroides* (Columbus 2605). Fig. 10. *Pleuraphis mutica* (Columbus 2803). Fig. 11. *Bouteloua juncea* (Axelrod 8856). Fig. 12. *B. aristidoides* (Columbus 2801). Fig. 13. Immature culm cross-section of *B. breviseta* (Columbus 2280). Fig. 14. Immature culm cross-section of *B. simplex* (Columbus 2570). EC. Elongated centripetal chloroplasts. PR. Parenchyma ring. RC. Round centrifugal chloroplasts. SR: Sclerenchyma ring.

ded in parenchymatic pith are the constant characters of this group (Fig. 1). Some related species, however, display few traits that allow inference of relationships. From all culm anatomy characters studied (Table 2), the Kranz structures (cells and radial chlorenchyma [Figs. 1KC, RCH]) and sclerenchyma ring (Fig. 1SR) apparently are the most useful. The Kranz cells, when mature, are the most conspicuous elements on the culm anatomy. The size, shape and uniformity of Kranz cells, the curvature the Kranz arc, the shape and size of radial chlorenchyma, the sclerenchyma girders and the position of sclerenchyma ring are the most variable traits. Also, the chloroplast shape of the Kranz cells may be an important trait for inferring relationships at higher taxonomical levels.

The taxa of the *B. curtispindula* complex display a pattern somewhat different from most of the remaining *Boutelouinae*. It shows a slightly curved Kranz arc with 4 to 8 round and irregular cells, and an inconspicuous to evident sclerenchyma girder (Fig. 2). However, the most compelling features that define the group is the presence of round, small, peripheral and centrifugal chloroplasts in the Kranz cells (Fig. 2RC). Centripetal chloroplasts are typical of NAD-ME type, and centrifugal ones are observed in NADP-ME type and some species of PCK type (Prendergast et al., 1987). Small, centrifugal chloroplasts plus other structural traits in leaves (suberized lamella, uneven bundle sheath) have been associated to PCK pathway of C_4 photosynthesis (Hattersley and Watson, 1975). The PCK pathway has been documented in *B. curtispindula* (Gutiérrez et al., 1974; Prendergast et al., 1987), and in *Hilaria belangeri* (Brown, 1977). Chapman and Peat (1992) pointed out that *B. curtispindula* may have both PCK and NAD-ME C_4 photosynthetic mechanisms, however, Prendergast et al. (1987) state that *B. curtispindula*, may be biochemically and structurally intermediate between NAD-ME/PCK, since this species, unlike the “classical” PCK species (Hattersley and Browning, 1981), lacks suberized lamella and uneven bundle sheath outline. It has been suggested that PCK type species evolved from NAD-ME type (Hattersely and Watson, 1992; and Clayton and Renvoize, 1989). Columbus et al. (1998, 2000), based on molecular data, showed that *Aegopogon*, *Hilaria* and *B. curtispindula* do not descend from the same most recent ancestor, suggesting that chloroplast shape evolved independently from different NAD-ME ancestors. Although it has not been previously proposed, the rest of the taxa of the *B. curtispindula* complex (Appendix) likely exhibit the same photosynthesis pathway, since they share the same chloroplast features.

Gould and Kapadia (1964) recognized 12 species in the *B. curtispindula* complex (Appendix). Columbus (1996) based on leaf anatomy and micromorphology, pointed out that *B. juncea* was not a member of the complex. Molecular data (Co-

lumbus et al., 1998; Columbus et al., 2000; Siqueiros, 2001) further support the exclusion of *B. juncea* from the *B. curtipendula* complex. Elongated centripetal chloroplasts of the Kranz cells, supports the exclusion of *B. juncea* from the complex (Fig. 11EC).

Except taxa of the *B. curtipendula* complex, most *Bouteloua* species, typically display elongated centripetal chloroplasts in leaves and culms. Noteworthy is the presence of round, peripheral chloroplasts in the culm Kranz cells in *B. americana* (Worthington 22775), *B. barbata* (2289), *B. breviseta* (2280 [Fig. 13RC], 2908), *B. dimorpha* (2373, 2593, 2647), *B. nervata* (2343), *B. radicata* (2341, 2462), *B. ramosa* (2807 [Fig. 8RC], 2846), *B. repens* (2332, 2425), *B. simplex* (2579 [Fig. 14RC]), and *B. williamsii* (2357), which typically display elongate and centripetal chloroplasts. Several populations of *B. repens* complex, sister group of *B. curtipendula* complex (Columbus et al., 1998), exhibit round chloroplasts, rather than elongated ones in culm Kranz cells. In fact, several taxa in Boutelouinae possess round chloroplasts in juvenile stages of culm development, while the culm Kranz cells are not well differentiated yet (Figs. 13, 14RC). This could indicate that round chloroplasts may be the ancestral shape in Boutelouinae, which later in their evolution have changed to elongate in the NAD-ME type in most taxa.

Bouteloua eriopoda and *B. eriostachya* share the same unique pattern, particularly with respect to the position of the PVB, which are opposite to the culm depressions. Also, the Kranz arc is nearly straight, formed by oval to rectangular and regular cells. The radial chlorenchyma is conspicuous, and lies along the upper surface of the arc, not bordering the sides of the ending cells, as found in the other taxa (Fig. 6). Anatomical, molecular, and morphological evidence (Columbus, 1996; Columbus et al., 1998; and Columbus, 1999b, respectively) show that *B. eriopoda* and *B. eriostachya* are closely related. In fact, Swallen (1939) recognized them as a single species.

Columbus et al. (1998) and Columbus (1999b), show evidence of a close relationship among *B. eriopoda*, *B. eriostachya*, *B. annua* and *B. aristidoides*. Similarities between *B. eriopoda* and *B. eriostachya*, and also between *B. annua* and *B. aristidoides* were found, but not between the two pairs of clades. The clade *B. eriopoda*-*B. eriostachya* differs from *B. annua*-*B. aristidoides* clade in the presence of highest number of PVB, the shape of radial chlorenchyma, and by the absence of sclerenchyma girder. *Bouteloua aristidoides* and *B. quiriegoensis* also share a similar pattern, with square and regular cells, forming nearly a straight arc (Figs. 6 and 12, respectively). *Bouteloua hirsuta* displays similar features; however, it differs in

its Kranz arc, which is conspicuously curved (Fig. 4). In the *Boutelouinae* phylogeny (Columbus et al., 1998, 2000), these taxa are closely related forming sister clades.

Bouteloua ramosa and *B. breviseta* share also similar features in culm anatomy, particularly with respect to Kranz structures. The most distinct feature characterizing these two species is an angular Kranz arc with large and elongated cells, bordered by an angular radial chlorenchyma (Fig. 7). *Bouteloua ramosa* differs in its horseshoe shaped arc, while *B. breviseta* has a less curved arc. Both also share round chloroplasts in immature developmental stages (Fig. 8, 13RC). *Bouteloua ramosa* and *B. breviseta* have been suggested to be closely related to *B. chasei* and *B. karwinskii*, however, the two latter do not exhibit the angular arc, and their Kranz cells are rounded but not elongated.

Culm anatomy also supports the inclusion of the satellite genera (*Buchloë*, *Buchlomimus*, *Cathestecum*, *Cyclostachya*, *Griffitsochloa*, *Opizia*, *Pentarrhaphis*, *Pringleochloa* and *Soderstromia*) within *Bouteloua* (Columbus, 1999a), as all of them possess almost the same basic anatomical pattern of *Bouteloua*.

CONCLUSIONS

Although culm anatomy does not display the same degree of variation as leaf anatomy does, there are several culm anatomy characters that can be useful for inferring relationships at higher levels (family, tribes, genera). The most important phylogenetic culm anatomy features are Kranz structures (cells and radial chlorenchyma), number and position of the vascular bundles, and sclerenchyma girders. *Bouteloua eriopoda* and *B. eriostachya* share similar anatomical structure, as *B. breviseta* and *B. ramosa* do. Culm anatomy also supports the inclusion of satellite genera in *Bouteloua*. In general culm anatomy has valuable, but a restricted systematic value.

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Appendix. Taxa, collections/vouchers, and origin of slides made for this study. Specimens and slides are deposited at RSA. *Denotes *Bouteloua curtispindula* complex representatives.

Taxon	Collection/Voucher	Origin
<i>Aegopogon cenchroides</i> Humb. & Bonpl. ex Willd.	<i>Columbus</i> 2629	México: Michoacán
	<i>Columbus</i> 2740	México: Sonora
<i>Aegopogon tenellus</i> (DC.) Trin.	<i>Columbus</i> 2415	México: Oaxaca
	<i>Columbus</i> 2720	México: Sonora
<i>Bouteloua dactyloides</i> (Nutt.) J. T. Columbus	<i>Columbus</i> 2565	México: Hidalgo
	<i>Columbus</i> 25689	México: Querétaro
	<i>Columbus</i> 2602	México: San Luis Potosí
<i>Bouteloua alamosana</i> Vasey	<i>Columbus</i> 2418	México: Oaxaca
	Herrera & <i>Siqueiros</i> 1319	México: Sonora
<i>Bouteloua annua</i> Swallen	<i>Columbus</i> 2433	México: Baja California Sur
	<i>Columbus</i> 2434	México: Baja California Sur
<i>Bouteloua americana</i> (L.) Scribn.	<i>Worthington</i> 22775	Grenada: St. George
<i>Bouteloua aristidoides</i> (Kunth) Griseb.	<i>Columbus</i> 2644	México: Oaxaca
	<i>Columbus</i> 2692	México: Sonora
	<i>Columbus</i> 2788	México: Chihuahua
	<i>Columbus</i> 2801	México: Chihuahua
<i>Bouteloua barbata</i> Lag.	<i>Columbus</i> 2454	U.S.A.: Arizona
	<i>Columbus</i> 2646	México: Oaxaca
	<i>Columbus</i> 2693	México: Sonora
	<i>Columbus</i> 2799	México: Chihuahua
	<i>Columbus</i> 2800	México: Chihuahua
	<i>Columbus</i> 2811	México: Chihuahua
	<i>Columbus</i> 2829	México: Durango
	<i>Columbus</i> 2837	México: Coahuila
	<i>Columbus</i> 2844	México: Coahuila
	<i>Columbus</i> 2576	México: Hidalgo
<i>Bouteloua bracteata</i> (McVaugh) J. T. Columbus	<i>Columbus</i> 2373	México: Michoacán
<i>Bouteloua breviseta</i> Vasey	<i>Columbus</i> 2530	U.S.A.: Arizona
	<i>Columbus</i> 2279	U.S.A.: Texas
	<i>Columbus</i> 2280	México: Tamaulipas
	<i>Columbus</i> 2908	U.S.A.: New Mexico
<i>Bouteloua chasei</i> Swallen	<i>Columbus</i> 2328	México: San Luis Potosí
<i>Bouteloua chihuahuana</i> (M. C. Johnst.) J. T. Columbus	<i>Columbus</i> 2824	México: Chihuahua
<i>Bouteloua chondrosioides</i> (Kunth) Benth. ex S. Watson	<i>Columbus</i> 2451	U.S.A.: Arizona
	<i>Columbus</i> 2609	México: Jalisco
	<i>Columbus</i> 2622	México: Michoacán
	<i>Columbus</i> 2791	México: Chihuahua

Appendix. Continuation

Taxon	Collection/Voucher	Origin
	<i>Herrera & Siqueiros 1301</i>	México: Aguascalientes
* <i>Bouteloua curtispicula</i> (Michx.) Torr.	<i>Columbus 2191</i> <i>Columbus 2124</i> <i>Columbus 2213</i> <i>Columbus 2331</i> <i>Columbus 2449</i> <i>Columbus 2549</i> <i>Columbus 2572</i> <i>Columbus 2573</i> <i>Columbus 2574</i> <i>Columbus 2592</i> <i>Columbus 2596</i> <i>Columbus 2604</i> <i>Columbus 2606</i> <i>Columbus 2610</i> <i>Columbus 2620</i> <i>Columbus 2790</i> <i>Columbus 2809</i> <i>Columbus 2817</i> <i>Columbus 2823</i> <i>Columbus 2834</i> <i>Columbus 2845</i> <i>Columbus 2857</i> <i>Columbus 2868</i> <i>Herrera & Siqueiros 1458</i>	México: Coahuila U.S.A.: Texas U.S.A.: New Mexico México: Hidalgo U.S.A.: Arizona México: México México: Hidalgo México: Hidalgo México: Sonora México: Querétaro México: San Luis Potosí México: San Luis Potosí México: San Luis Potosí México: Jalisco México: Michoacán México: Chihuahua México: Chihuahua México: Chihuahua México: Chihuahua México: Coahuila México: Coahuila México: Nuevo León México: Tamaulipas México: Coahuila
<i>Bouteloua dimorpha</i> J. T. Columbus	<i>Columbus 2375</i> <i>Columbus 2589</i> <i>Columbus 2593</i> <i>Columbus 2633</i> <i>Columbus 2647</i>	México: Michoacán México: Querétaro México: Querétaro México: Puebla México: Puebla
* <i>Bouteloua distans</i> Swallen	<i>Siqueiros 4449</i> <i>Siqueiros 4454</i>	México: Oaxaca México: Puebla
* <i>Bouteloua disticha</i> (Kunth) Benth.	<i>Columbus 2376</i> <i>Columbus 2693</i>	México: Michoacán México: Guerrero
<i>Bouteloua diversispicula</i> J. T. Columbus	<i>Columbus 2598</i> <i>Columbus 2694</i> <i>Columbus 2904</i>	México: San Luis Potosí México: Sonora U.S.A.: Texas
<i>Bouteloua elata</i> Reeder & C. Reeder	<i>Columbus 2358</i>	México: Jalisco

Appendix. Continuation

Taxon	Collection/Voucher	Origin
<i>Bouteloua eludens</i> Griffiths	<i>Columbus</i> 2272 <i>Columbus</i> 2452	U.S.A.: Arizona U.S.A.: Arizona
<i>Bouteloua eriopoda</i> (Torr.) Torr.	<i>Columbus</i> 2267 <i>Columbus</i> 2461 <i>Columbus</i> 280 <i>Herrera & Siqueiros</i> 1340	U.S.A.: California U.S.A.: Arizona México: Chihuahua México: Chihuahua
<i>Bouteloua eriostachya</i> (Swallen) Reeder	<i>Columbus</i> 2843	México: Coahuila
<i>Bouteloua gracilis</i> (Kunth) Lag. ex Griffiths	<i>Columbus</i> 2460 <i>Columbus</i> 2559 <i>Columbus</i> 2574 <i>Columbus</i> 2603 <i>Columbus</i> 2608 <i>Columbus</i> 2612 <i>Columbus</i> 2640 <i>Columbus</i> 2718 <i>Columbus</i> 2793 <i>Columbus</i> 2804 <i>Columbus</i> 2832 <i>Columbus</i> 2863	U.S.A.: Arizona México: México México: Hidalgo México: San Luis Potosí México: Aguascalientes México: Jalisco México: Puebla México: Sonora México: Chihuahua México: Chihuahua México: Coahuila México: Nuevo León
<i>Bouteloua hirsuta</i> Lag.	<i>Columbus</i> 2342 <i>Columbus</i> 2284 <i>Columbus</i> 2558 <i>Columbus</i> 2611 <i>Columbus</i> 2713 <i>Columbus</i> 2792 <i>Columbus</i> 2808 <i>Columbus</i> 2860 <i>Columbus</i> 2894	México: México México: Coahuila México: México México: Jalisco México: Sonora México: Chihuahua México: Chihuahua México: Nuevo León U.S.A.: Texas
<i>Bouteloua johnstonii</i> Swallen	<i>Columbus</i> 2851	México: Coahuila
<i>Bouteloua juncea</i> (Desv. ex P. Beauv.) Hitchc.	<i>Axelrod</i> 8856 <i>Axelrod</i> 8862	Grenada: St. George Grenada: St. George
<i>Bouteloua kayi</i> Warnock	<i>Columbus</i> 2281	U.S.A.: Texas
* <i>Bouteloua media</i> (E. Fourn.) Griffiths	<i>Columbus</i> 2420 <i>Columbus</i> 2632	México: Oaxaca México: Puebla
<i>Bouteloua mexicana</i> (Scribn.) J. T. Columbus	<i>Columbus</i> 2398	México: Guerrero
<i>Bouteloua multifida</i> (Griffiths) J. T. Columbus	<i>Columbus</i> 2617	México: Oaxaca

Appendix. Continuation

Taxon	Collection/Voucher	Origin
<i>Bouteloua nervata</i> Swallen	<i>Columbus</i> 2334	México: Hidalgo
<i>Bouteloua parryi</i> (E. Fourn.) Griffiths	<i>Columbus</i> 2299 <i>Columbus</i> 2351	México: Sonora México: Jalisco
<i>Bouteloua pectinata</i> Feath.	<i>Columbus</i> 2899	U.S.A.: Texas
* <i>Bouteloua pedicellata</i> Swallen	<i>Columbus</i> 2408 <i>Columbus</i> 2634	México: Tlaxcala México: Puebla
* <i>Bouteloua purpurea</i> Gould & Kapadia	<i>Columbus</i> 2337 <i>Columbus</i> 2563	México: México México: México
<i>Bouteloua quiriegoensis</i> A. Beetle	<i>Herrera &</i> <i>Siqueiros</i> 1320	México: Sonora
<i>Bouteloua radicata</i> (E. Fourn.) Griffiths	<i>Columbus</i> 2341 <i>Columbus</i> 2462 <i>Columbus</i> 2714 <i>Columbus</i> 2872 <i>Herrera &</i> <i>Siqueiros</i> 1300	México: México U.S.A.: Arizona México: Sonora México: Tamaulipas México: Aguascalientes
<i>Bouteloua ramosa</i> Scribn. ex Vasey	<i>Columbus</i> 2287 <i>Columbus</i> 2290 <i>Columbus</i> 2807 <i>Columbus</i> 2826 <i>Columbus</i> 2835 <i>Columbus</i> 2846	México: Coahuila México: Chihuahua México: Chihuahua México: Chihuahua México: Coahuila México: Coahuila
<i>Bouteloua reederorum</i> J. T. Columbus	<i>Columbus</i> 2642 <i>Columbus</i> 2648	México: Puebla México: Puebla
* <i>Bouteloua reflexa</i> Swallen	<i>Siqueiros</i> 4394 <i>Siqueiros</i> 4401 <i>Siqueiros</i> 4404 <i>Herrera &</i> <i>Siqueiros</i> 1311	México: Sonora México: Sinaloa México: Sinaloa México: Sinaloa
<i>Bouteloua repens</i> (Kunth) Scribn. & Merr.	<i>Columbus</i> 2350 <i>Columbus</i> 2425 <i>Columbus</i> 2569 <i>Columbus</i> 2607 <i>Columbus</i> 2613 <i>Columbus</i> 2618 <i>Columbus</i> 2621 <i>Columbus</i> 2705 <i>Columbus</i> 2865 <i>Columbus</i> 2879	México: Jalisco México: Yucatán México: Querétaro México: San Luis Potosí México: Jalisco México: Jalisco México: Michoacán México: Sonora México: Nuevo León México: Tamaulipas
<i>Bouteloua rigidiseta</i> (Steud.) Hitchc.	<i>Columbus</i> 2231 <i>Columbus</i> 2233	U.S.A.: Texas U.S.A.: Texas

Appendix. Continuation

Taxon	Collection/Voucher	Origin
<i>Bouteloua scabra</i> (Kunth) J. T. Columbus	<i>Columbus</i> 2395	México: Guerrero
<i>Bouteloua scorpioides</i> Lag.	<i>Columbus</i> 2200 <i>Columbus</i> 2344 <i>Columbus</i> 2547 <i>Columbus</i> 2635	México: Nuevo León México: México México: México México: Puebla
<i>Bouteloua simplex</i> Lag.	<i>Columbus</i> 2554 <i>Columbus</i> 2570 <i>Columbus</i> 2615 <i>Columbus</i> 2643 <i>Columbus</i> 2798 <i>Columbus</i> 2854	México: México México: Hidalgo México: Jalisco México: Puebla México: Chihuahua México: Nuevo León
* <i>Bouteloua triaena</i> (Trin.) Scribn.	<i>Columbus</i> 2338 <i>Columbus</i> 2357 <i>Columbus</i> 2566 <i>Columbus</i> 2649	México: México México: Jalisco México: Hidalgo México: Puebla
<i>Bouteloua trifida</i> Thurb. ex S. Watson	<i>Columbus</i> 2126 <i>Columbus</i> 2269 <i>Columbus</i> 2805 <i>Columbus</i> 2849 <i>Columbus</i> 2864 <i>Columbus</i> 2882 <i>Columbus</i> 2902	U.S.A.: Texas U.S.A.: Arizona México: Chihuahua México: Coahuila México: Nuevo León México: Tamaulipas U.S.A.: Texas
* <i>Bouteloua uniflora</i> Vasey	<i>Columbus</i> 2190 <i>Columbus</i> 2319 <i>Columbus</i> 2833 <i>Columbus</i> 2855 <i>Columbus</i> 2901	México: Coahuila México: Zacatecas México: Coahuila México: Nuevo León U.S.A.: Texas
<i>Bouteloua varia</i> (Swallen) J. T. Columbus	<i>Columbus</i> 2645	México: Oaxaca
* <i>Bouteloua warnockii</i> Gould & Kapadia	<i>Columbus</i> 2907	U.S.A.: Texas
<i>Bouteloua williamsii</i> Swallen	<i>Columbus</i> 2353	México: Jalisco
<i>Hilaria cenchroides</i> Kunth	<i>Columbus</i> 2605 <i>Columbus</i> 2571 <i>Columbus</i> 2654	México: San Luis Potosí México: Hidalgo México: Hidalgo
<i>Hilaria ciliata</i> (Scribn.) Nash	<i>Columbus</i> 2599	México: San Luis Potosí
<i>Pleuraphis mutica</i> Buckley	<i>Columbus</i> 2803 <i>Columbus</i> 2810	México: Chihuahua México: Chihuahua