

## A REVISION OF *CHABOISSAEA* (POACEAE: ERAGROSTIDEAE)

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### ABSTRACT

*Chaboissaea* is a New World genus of open, marshy meadows that includes four species, three ranging from northwestern Chihuahua to Distrito Federal, Mexico, and one endemic to Jujuy and Salta, Argentina. It is characterized by gray to grayish-yellow spikelets with one, two, or occasionally three florets per spikelet, the lower floret perfect and the upper pedicelled floret often staminate or sterile; and a base chromosome number of  $x = 8$ . The revision includes a key, descriptions of morphology and anatomy, a hypothesized phylogeny, distribution maps, and illustrations for each species. *Chaboissaea atacamensis* represents a transfer from *Muhlenbergia*. A key distinguishing *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Muhlenbergia*, and *Sporobolus* is presented.

### RESUMEN

*Chaboissaea* es un género del Nuevo Mundo, de praderas cenagosas, con especies, de las cuales tres se encuentran en México, en la región del nordeste de Chihuahua hasta el Distrito Federal y una es endémica de Jujuy y Salta, Argentina. El género se caracteriza por la presencia de espiguillas grisáceas o amarillo cenizo, con uno, dos y ocasionalmente tres flósculos por espiguilla; los flósculos basales son perfectos y los distales generalmente estaminados o estériles; el género tiene un número cromosómico básico  $x = 8$ . Esta revisión incluye una clave, descripciones morfológicas y anatómicas, mapas de distribución, ilustra cada una de las especies y postula una hipótesis filogenética. *Chaboissaea atacamensis* es transferida del género *Muhlenbergia*. El presente artículo provee una clave para los géneros *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Muhlenbergia* y *Sporobolus*.

Historically, *Chaboissaea* Fourn., s. str., contained a single species, *C. ligulata* Fourn., that ranged from northern Chihuahua to Distrito Federal, Mexico. It differs from other eragrostoid genera in having gray to grayish-yellow spikelets with one, two, or occasionally three florets per spikelet, the lowermost perfect and the upper pedicelled florets usually staminate or reduced and sterile; and a base chromosome number of  $x = 8$ . *Chaboissaea ligulata* is rather scantily distributed in Mexico and is restricted to blackish clay soil in meadows, drainage ditches, and irrigation canals.

Based on specimens collected in San Luis Potosi by Virlet d'Aoust, the genus *Chaboissaea* was first recognized by Fournier (1886) as containing a single perennial species, *C. ligulata*. In his generic description, Fournier stressed that *Chaboissaea* has 2-flowered spikelets containing a lower fertile floret and a pedicelled, upper sterile



floret, and an entire or toothless palea. Lamson-Scribner and Merrill (1901) legitimately transferred *C. ligulata* to *Muhlenbergia* Schreb. but did not see the type, basing their decision on two collections from Durango (Palmer 731 & 948) which they incorrectly assumed were the same species. Hitchcock (1935) later recognized the Durango collections as belonging to a separate annual species, *M. subbiflora*, and designated Palmer 948 as the type. Even before these specimens from Durango were appropriately named, Lamson-Scribner and Merrill thought these collections were conspecific with *C. ligulata*.

Although the transfer of *C. ligulata* to *Muhlenbergia* was based on *M. subbiflora* its use as *M. ligulata* was accepted by Hitchcock (1913), Bews (1929), Conzatti (1946), and more recently Watson et al. (1985) and Clayton and Renvoize (1986). Conzatti (1946) placed *Chaboissaea* in the unnatural and no longer recognized tribe, Agrostideae, and Sohns (1953) placed it in the Festuceae (=Pooideae).

In the southern hemisphere, Parodi (1948) described an annual species, *M. atacamensis*, from Jujuy, Argentina, designating one of his own collections as the type (Parodi 9656). In his observations he notes, "La especie [*M. atacamensis*] mas emparentada es *M. ligulata* [= *C. ligulata*] de Mexico." Therefore, he viewed the closest relative to be *C. ligulata*, which he included in *Muhlenbergia*.

Based on collections from Chihuahua by Hernandez X. and Tapia J., Swallen (1958) described another annual species, *M. decumbens*, which he stated was "closely related to *Muhlenbergia subbiflora* Hitchc." More recently Reeder and Reeder (1988) transferred *M. decumbens* and *M. subbiflora* to *Chaboissaea*.

In the Eragrostideae (sensu Clayton and Renvoize 1986) the base chromosome number is generally 10 and only *Bealia* Scribner in Hackel, *Blepharoneuron* Nash, *Chaboissaea*, *Dasyochloa* Willdenow ex Rydberg, *Erioneuron* Nash, and *Munroa* Torrey have a base number of 8 (Gould 1958; Peterson 1988b, 1989; Peterson and Annable 1990; Reeder 1967, 1968, 1971, 1977; Reeder and Reeder 1988; Tateoka 1961). Reported chromosome counts for *C. ligulata* and *C. subbiflora* indicate these species are diploid ( $2n=16$ ), although the latter possesses an aneuploid series of  $2n=14, 16, 18$  (Reeder 1967, 1968; Reeder and Reeder 1988). *Chaboissaea decumbens* is a tetraploid ( $2n=32$ ) with all counts being made from individuals of a single population in two successive years (Reeder and Reeder 1988).

While working on a revision of the annual species of *Muhlenbergia* Schreb. (Peterson and Annable 1991) and collecting throughout Mexico in 1985 and 1986, we recognized the morphological similarities among *M. decumbens* Swallen, *M. subbiflora* Hitchc., and *C. ligulata*. Reeder and Reeder (1975) suggested that *M. decumbens* and *M. subbiflora* should be placed in *Chaboissaea*. Subsequently,



Peterson (June, 1988a) stated in an abstract that he would be transferring these two annual species into *Chaboissaea*. Later that year, Reeder and Reeder (June, 1988) published the new combinations of *C. decumbens* (Swallen) J. & C. Reeder and *C. subbiflora* (Hitchc.) J. & C. Reeder. Even though *C. decumbens* and *C. subbiflora* are allopatric, they occur in similar habitats, i.e., cienagas or marshy meadows in clayish soils, and are sometimes associated with *C. ligulata*.

After reviewing type specimens of *Muhlenbergia* at United States National Herbarium (US) we became aware that *M. atacamensis* Parodi, a regional endemic from Jujuy and Salta, Argentina, also belonged in *Chaboissaea*. Parodi (1948) suggested this affinity but did not place this species in *Chaboissaea* because he treated this genus as a synonym of *Muhlenbergia*. This species occurs in cienagas, muddy sumps, ephemeral pools along roadside ditches in clayish soil, and sandy margins surrounding lagoons.

The need for a revision of this genus is apparent, since it was treated as monotypic from its inception and more recently by Sohns (1953), McVaugh (1983), and Beetle (1987). There is no treatment of *Chaboissaea* containing keys to the species, adequate descriptions comparing the four species, and citations of recent collections. Nor has there been a thorough anatomical examination comparing the four species (Schwabe 1948; Decker 1964; Peterson et al. 1989). The present revision is based on field work, combined with laboratory and herbarium studies of morphology, anatomy, and chromosome numbers. In the present study we examine the phylogenetic relationships of the four species within *Chaboissaea* through cladistic analyses of morphological attributes.

## METHODS

The external morphology of the study group was examined by observing living plants in the field and in culture, and by examining herbarium specimens. A complete set of vouchers has been deposited in the US and duplicates have been distributed to various herbaria (see specimen citations).

For the anatomical studies field-collected leaf blades from the mid-culm region were fixed in FAA. In *C. atacamensis*, the leaf blades from an herbarium specimen were soaked for 24 hours in a solution of water and tween 20 before dehydration in alcohol. After dehydration in an increasing ethanol series, the leaves were embedded in paraffin, sectioned at 8–10  $\mu\text{m}$  thickness, and stained with safranin/fast green (Berlyn and Miksche 1976). Leaf scrapes were prepared in alcohol and stained with safranin and celestine blue B. Samples were examined and photographed on an Olympus BH-2 photomicroscope using Kodak Technical Pan film. Anatomical de-



TABLE 1. DATA SET AND CHARACTERS USED IN THE CLADISTIC ANALYSES OF *CHABOISSAEA*. 1—duration: annual (1), perennial (2); 2—number of florets: one (1), two to three (2); 3—ligule length: less than 3.5 mm (1), 6–10 mm long (2); 4—palea awns: present (1), absent (2); 5—awn-tipped glumes: absent (1), present (2); 6—rooting at lower nodes: present (1), absent (2); 7—lemma length: less than 3 mm (1), more than 3 mm (2); 8—anther length: less than 1.2 mm (1), more than 1.2 mm (2); 9—anther color: olivaceous or greenish (1), purplish (2); 10—chromosome base ( $x$ ): eight (1), ten (2); 11—adaxial furrow of leaf blade: rounded (1), cleft (2); 12—walls of intercostal long cell: sinuous (1), straight (2); 13—walls of costal short cells: straight (1), sinuous (2).

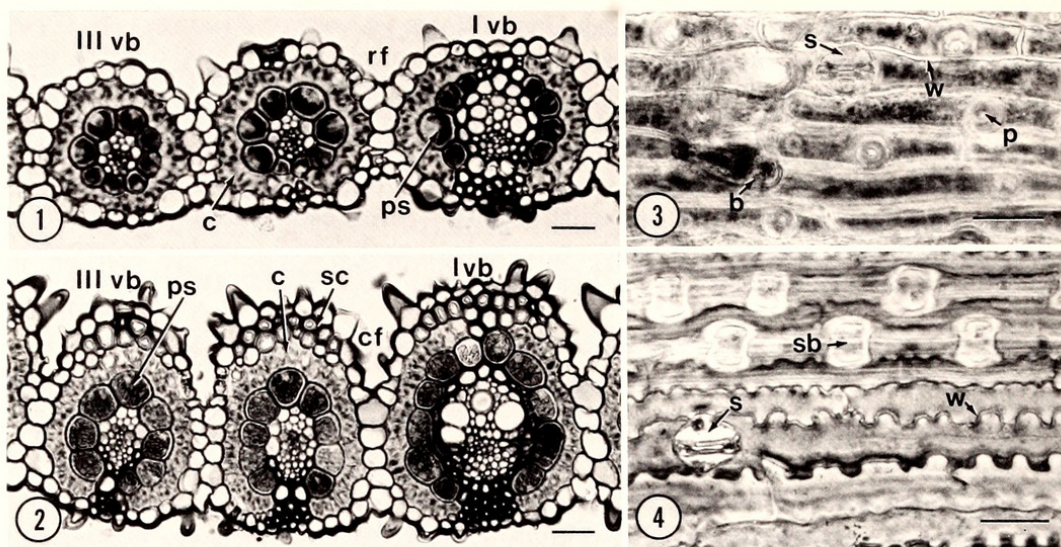
<i>C. atacamensis</i>	1	2	1	1	2	2	1	1	1	1	1	1	2
<i>C. decumbens</i>	1	2	1	1	2	1	2	1	1	1	1	1	2
<i>C. ligulata</i>	2	2	2	2	2	2	2	2	2	1	2	1	1
<i>C. subbiflora</i>	1	2	1	1	2	2	1	2	2	1	1	2	1
<i>Bealia mexicana</i>	1	1	1	2	1	2	2	2	2	1	1	2	1
<i>Muhlenbergia richardsonis</i>	2	1	1	2	1	2	1	2	2	2	1	1	2

scriptions were completed following the procedure for standardizing comparative leaf anatomy as outlined by Ellis (1976, 1979). For purposes of comparison and standardization, primary, I° vascular bundles (first order) are defined as those containing large metaxylem vessels on either side of the protoxylem elements and usually associated with sclerenchyma girders or strands (Ellis 1976). All other vascular bundles are considered as tertiary, III° (third order), and contain indistinguishable xylem and phloem elements.

Floral buds were field collected and fixed in ethanol-acetic acid (3:1, V:V) prior to storage under refrigeration in 70% ethanol. Meiotic chromosome counts were obtained from aceto-carmines squashes of pollen mother cells. Representative cells were photographed using Kodak Technical Pan film and interpretations were based on 20 or more cells.

*Cladistics.* A total of thirteen morphological attributes were scored for each species and used in the cladistic analyses (Table 1). Phylogenetic analyses were conducted on an IBM-model 80 computer using version 2.4 of phylogenetic analysis using parsimony (PAUP) written by Swofford (1985). In addition to the four species of *Chaboissaea*, *Bealia mexicana* Scribn. in Beal, a closely allied annual with a similar base chromosome number, and *Muhlenbergia richardsonis* (Trin.) Rydb., a low, mat-forming, rhizomatous perennial of similar habitats and spikelet characteristics, were used as outgroups to determine character polarities. For all analyses, the ALLTREES option, was employed and all character transformations were unordered. With *Bealia mexicana* as the designated outgroup, character 10 was invariant and therefore deleted from the cladistic analysis.





FIGS. 1-4. Leaf anatomy of *Chaboissaea*, adaxial surface uppermost in Figs. 1 and 2. 1. *C. decumbens* with rounded adaxial furrows. 2. *C. ligulata* with cleft adaxial furrows and well developed sclerenchyma just below the adaxial epidermis of each vascular bundle. 3. *C. subbiflora* in abaxial view with straight intercostal long cell walls and prominent papillae. 4. *C. ligulata* in abaxial view with sinuous intercostal long cell walls and saddle shaped silica bodies. Scales = 25  $\mu$ m. b = bicellular microhair; c = chlorenchyma; cf = cleft furrows; p = papillae; ps = parenchyma bundle sheath; rf = rounded furrow; s = stomata; sb = silica body; sc = sclerenchyma; w = intercostal long cell wall; I vb = primary vascular bundle; III vb = tertiary vascular bundle.

### LEAF ANATOMY

*Chaboissaea* is a typical  $c_4$  chloridoid that exhibits kranz leaf anatomy, particularly the P.S., XyMS+ subtype where the perivascular sheath is composed of an inner mestome sheath and an outer parenchymatous bundle sheath (Brown 1977; Hattersley and Watson 1976). A cursory survey of the leaf anatomy reported that *C. ligulata* exhibits eragrostoid structure, oval-shaped stomata, bulbous bicellular microhairs, and saddle-shaped siliceous cells (Decker 1964). An excellent illustration of the transection of *C. atacamensis* is given in the treatment of the leaf anatomy of some Agrostideae (Schwabe 1948). The following descriptions refer to all four species unless otherwise noted.

*Leaf blade in transverse section (Figs. 1 and 2).* The lamina is flat to outwardly bowed near the margins with shallow (less than  $\frac{1}{4}$  blade thickness) to medium ( $\frac{1}{3}$  to  $\frac{1}{2}$  blade thickness), rounded adaxial furrows whereas the adaxial furrows in *C. ligulata* are cleft shaped. The abaxial ribs are much smaller than the adaxial ribs. The abaxial projection of the midrib or keel is comprised of a single vascular bundle that is very inconspicuous and flat with a small girder of sclerenchyma one to six cell layers thick. There are two tertiary (III°) vascular bundles between each primary (I°) vascular bundle. Primary



(I°) and tertiary (III°) vascular bundles are circular and the phloem without sclerenchyma tissue adjoins the mestome sheath. The parenchyma sheath of each primary (I°) vascular bundle is interrupted on the abaxial surface and sometimes the adaxial surface by a narrow to broad, often triangular girder (less than four fibers deep) of sclerenchyma. The parenchyma sheath of the tertiary (III°) vascular bundle is complete on the abaxial and adaxial surface and interrupted on the abaxial surface by a narrow girder of sclerenchyma in *C. ligulata*. A small strand (2–4 fibers wide) to a well developed (wider than deep) band of adaxial sclerenchyma is located between the chlorenchyma and the epidermis just above the vascular bundle. It is always a well developed band in *C. ligulata*. A sclerenchyma cap varying from a few fibers deep to wider than the tertiary (III°) vascular bundle is present at the margin of the leaf. The chlorenchyma tissue is composed of a single radiate layer of tightly packed tabular cells that surround each vascular bundle, commonly interrupted on the abaxial surface and occasionally interrupted on the adaxial surface. Each vascular bundle is separated by a group of colorless cells interspersed with larger, more inflated bulliform cells. These bulliform cells and colorless cells form a 1, 2, or occasionally 3 cell wide column that extends from the abaxial to the adaxial epidermis. Macrohairs have a sunken, nonconstricted base and are embedded between bulliform/colorless cells.

*Leaf epidermis in abaxial view (Figs. 3 and 4).* The intercostal long cells are three times or more longer than wide with moderately thickened walls. The walls are sinuous except in *C. subbiflora* where they are straight to slightly undulating. The intercostal short cells are tall and narrow with smooth to slightly undulating walls. These cells are more numerous in *C. ligulata* than the other species. Dome-shaped stomata are common and occur in two bands, one band on each side of the costal zone, each band with one, occasionally two rows of stomata. One distally positioned, dome-shaped papilla with unthickened walls per epidermal long cell. In *C. subbiflora* the papillae are large and conspicuous. Chloridoid-type (clavate) bicellular microhairs are attached to short cells in a single row in the middle of furrow. Prickle hairs are restricted to the leaf margins and macrohairs are absent. One or two rows of silica cells are located in the costal zone. The silica bodies are saddle-shaped to cuboid, sometimes elongate. Silica cells alternate with rectangular short cells that are less than three times longer than wide. In *C. atacamensis* and *C. decumbens*, the walls of the short cells are sinuous whereas in *C. ligulata* and *C. subbiflora* the walls are straight or only slightly undulate.

*Leaf epidermis in adaxial view.* Unicellular macrohairs and prickle hairs occur sporadically on the costal zone and papillae are



prominent and generally larger than on the abaxial surface. Other characters are similar to the abaxial surface.

### PHYLOGENY

A recent classification places *Chaboissaea* as a synonym of *Muhlenbergia* in the subtribe Sporobolinae which includes *Crypsis* Aiton, *Lycurus* Kunth, *Muhlenbergia*, and *Sporobolus* R. Brown (Clayton and Renvoize 1986). On the basis of cork and silica cell distribution on the surface of the lemma, Valdes-Reyna and Hatch (in manuscript) suggested that *Blepharoneuron* is also closely related to *Chaboissaea*. Additional data from restriction site variation of chloroplast genomes and gross morphology may help in discerning the relationship of this genus within the Eragrostideae (Duvall and Peterson in preparation).

At two locations (*Peterson & Annable 10319, 10323*) individuals of *C. atacamensis* were found to be diploid at  $2n=16$  (Fig. 5). This lends karyological evidence that the morphological similarity of *C. atacamensis* with other members of the genus is a consequence of common ancestry. At present morphological traits are the only suitable characters available for evaluating the relationship among the four species of *Chaboissaea*.

*Cladistics.* Using *Muhlenbergia richardsonis* as the designated outgroup produced a single tree of 15 steps with a consistency index of 0.87 (Fig. 6). *Chaboissaea ligulata* is the most basal member of the group suggesting that the annual species of *Chaboissaea* were probably derived from perennial ancestors very similar to *C. ligulata*. Two synapomorphies, the annual habit (1) and the possession of awned paleas (4), support the clade of *C. atacamensis*, *C. decumbens*, and *C. subbiflora*. *Chaboissaea atacamensis* and *C. decumbens* form a closely related couplet supported by two synapomorphies, small, greenish or olivaceous anthers (8, 9) and a reversal involving the walls of the costal short cells (13), also shared by *M. richardsonis*. Three synapomorphies support the monophyly of the ingroup: possession of two or three florets (2), awn-tipped glumes (5), and a base chromosome number of  $x = 8$ . While none of these characters are unique in the Eragrostideae, in combination they strongly suggest that these four species are monophyletic.

When *Bealia mexicana* is used as the designated outgroup two equally parsimonious trees are produced, each with 14 steps and a consistency index of 0.86. One tree has the same topography as the tree derived from using *M. richardsonis* as the outgroup (Fig. 6) and will not be discussed further. In the second tree, *C. subbiflora* is the most basal member of the group, supported by the parallel derivation of a short lemma (7), a very plastic character (Fig. 7). Since *Bealia mexicana* is an annual, an additional autapomorphy (1) is added to



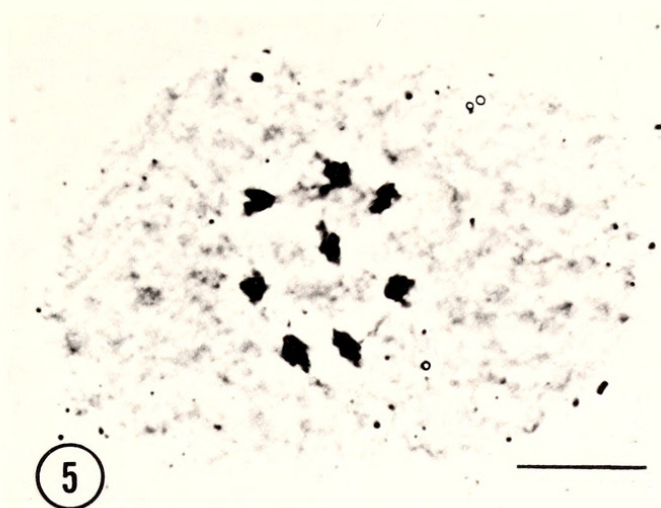


FIG. 5. Photomicrograph of meiotic chromosomes of *Chaboissaea atacamensis* in diakinesis,  $n = 8$ , Peterson & Annable 10319. Line scale = 5  $\mu\text{m}$ .

the *C. ligulata* branch, thereby inverting the position of the latter taxon with *C. subbiflora*. The possession of awned paleas (4) in relation to *Bealia mexicana* is reversed and lost in *C. ligulata* but still found in the other three species of *Chaboissaea*.

The first cladogram (Fig. 6) seems to represent a more parsimonious explanation of the phylogenetic history of the genus and can perhaps be used to postulate the geographic origin. There are many cases of North/South American amphotropical disjunctions occurring within the same species of Eragrostideae, i.e., *Eragrostis lugens* Nees, *Erioneuron avenaceum* (Kunth) Tateoka, *E. pilosum* (Buckl.)

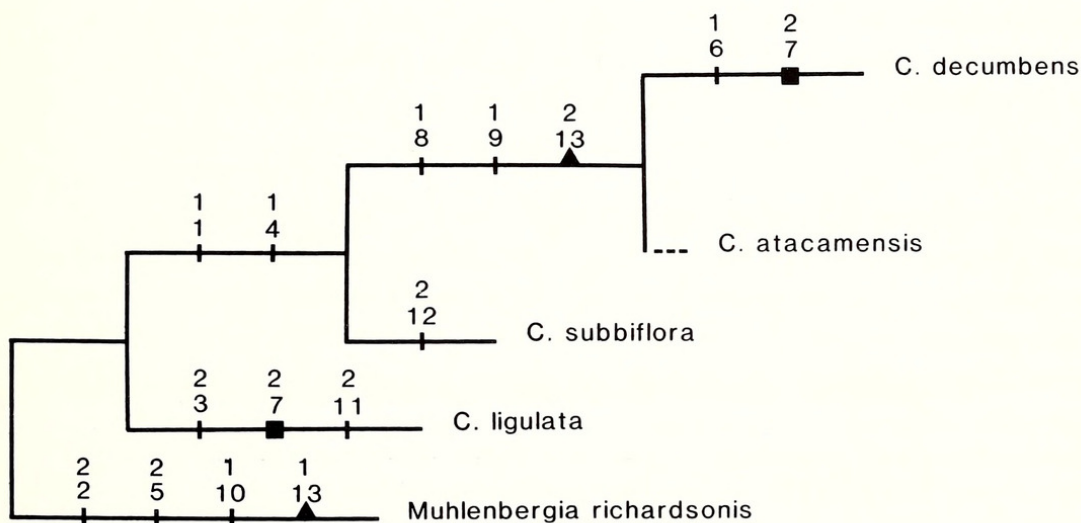


FIG. 6. Cladogram of the four species of *Chaboissaea* rooted with *Muhlenbergia richardsonis* (cf. Table 1). Lower numbers along branches refer to characters, upper numbers refer to character states, squares indicate parallelisms, and triangles indicate reversals. Length = 15, consistency index = 0.87.



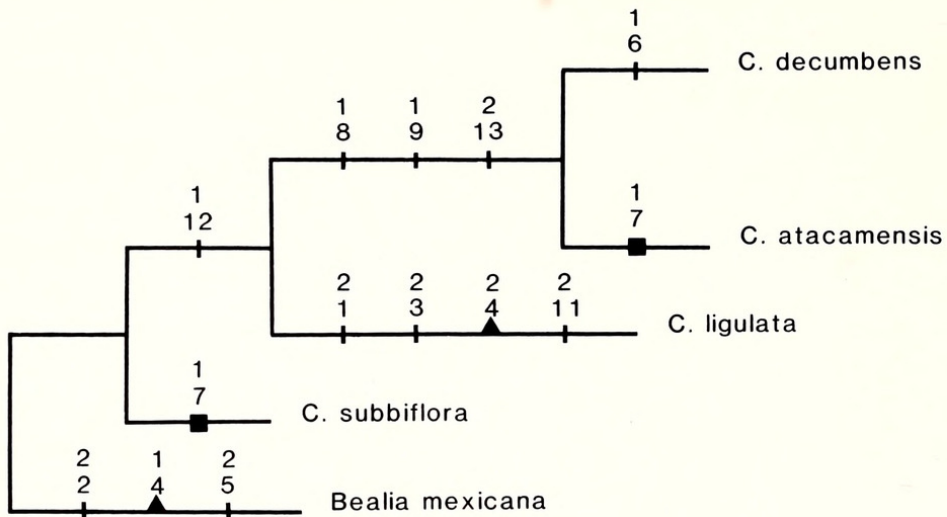


FIG. 7. Cladogram of the four species of *Chaboissaea* rooted with *Bealia mexicana* (cf. Table 1). Lower numbers along branches refer to characters, upper numbers refer to character states, squares indicate parallelisms, and triangles indicate reversals. Length = 14, consistency index = 0.86.

Nash, *Leptochloa dubia* (Kunth) Nees, *L. filiformis* (Lam.) Beauv., *L. uninervia* (Presl) Hitchc., *L. virgata* (L.) Beauv., *Lycurus setosus* (Nutt.) C. Reeder, *Muhlenbergia asperifolia* (Nees & Meyen) Parodi, *M. ramulosa* (Kunth) Kunth, *M. peruviana* (Beauv.) Steud., *M. tenuifolia* (Kunth) Kunth, *M. torreyi* (Kunth) Hitchc. ex Bush, *Scleropogon brevifolius* Philippi, and *Tripogon spicatus* (Nees) E. Ekman. Our evidence from morphology and biogeography suggests that the genus arose in northcentral Mexico where three species still exist (Fig. 8) and migrated to Argentina via long distance dispersal by a chance event or more probably by jumping from "islands" of similar habitats (Raven 1963; Thorne 1972). There is very little morphological divergence among all three annual species of *Chaboissaea* which suggests the migration event could be very recent. Preliminary data from enzyme electrophoresis of the North American species indicate that *C. decumbens* and *C. subbiflora* are more similar in their allozymic phenotypes than either is to *C. ligulata* (Peterson and Duvall unpublished data). It appears that the widespread perennial, *C. ligulata*, gave rise to the rather narrowly distributed annual endemics by sympatric speciation, followed by subsequent radiation.

The unusual morphological characters in *Chaboissaea* of spikelets with one, two, or occasionally three florets per spikelet, the lower floret perfect and the upper pedicelled floret often staminate; and a base chromosome number of  $x = 8$  support the hypothesized monophyly of these four species. The following key is provided to distinguish among *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Muhlenbergia*, and *Sporobolus* using gross morphological features.



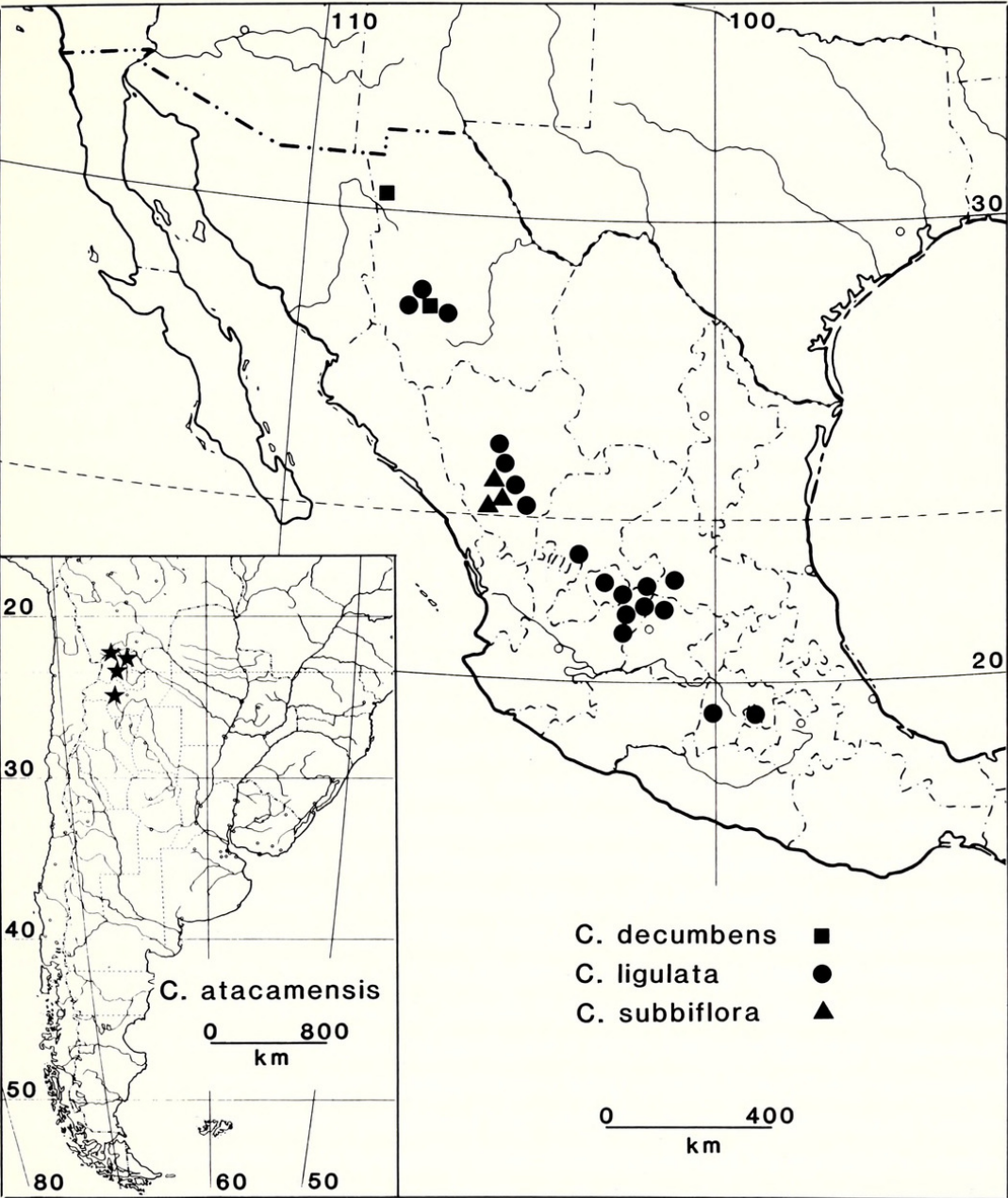


FIG. 8. Distribution of *Chaboissaea atacamensis*, *C. decumbens*, *C. ligulata*, and *C. subbiflora*.

KEY TO RELATED GENERA

- a. Lemma 1-nerved; ligule a short fringe of hairs or ciliate membrane; fruit with a seed coat remaining separate from the pericarp (a true achene), the seed usually falling free from the lemma and the palea at maturity ..... *Sporobolus*
- a'. Lemma 3-nerved; ligule usually membranous, occasionally ciliate, but never hairy; fruit a caryopsis with an attached, hardened pericarp, the seed usually tightly enclosed by the lemma and palea at maturity.
  - b. Lemma with densely appressed to spreading, silky, whitish hairs on the midnerve and margins, these hairs often appearing as ridges on the surface at 20×; paleas densely silky-villous between the two nerves. .... *Blepharoneuron*
  - b.' Lemma glabrous or with appressed to spreading hairs on the midnerve and



margins, but without silky, whitish hairs that appear as ridges on the surface at 20 $\times$ ; palea glabrous, occasionally with appressed to spreading hairs between the two nerves.

- c. Spikelet with one, two, or occasionally three florets, the lowermost perfect, the upper pedicelled florets usually staminate, reduced, and/or sterile. . . . . *Chaboissaea*
- c'. Spikelet with one floret, or when occasionally two-flowered the upper floret usually fertile.
- d. Lemma deeply bilobed, the lobes 1–1.4 mm long, rounded to obtuse; awn crisped-curved to flexuous, borne between the lobes; a single annual species in Chihuahua and Durango, Mexico. . . . . *Bealia*
- d'. Lemma not deeply bilobed (except in the perennial, *M. argentea* Vasey), sometimes minutely bifid, then the teeth less than 1 mm long, usually acuminate to aristate; awn straight to flexuous; wide ranging in North and South America to SE Asia. . . . . *Muhlenbergia*

### SYSTEMATIC TREATMENT

CHABOISSAEA Fournier, Mex. Pl. 2:112. 1886.—TYPE: *Chaboissaea ligulata* Fournier.

Tufted perennials with slender upright stems or decumbent annuals sometimes rooting at the lower nodes. Culms glabrous, hollow. Sheaths open, glabrous, usually shorter than the internodes. Ligules hyaline often scarious, truncate to acute-acuminate. Blades flat to loosely involute, scaberulous above and along margins, glabrous to scaberulous below. Inflorescence a terminal narrow panicle, with distant, alternate, subdivided, strongly appressed branches. Spikelets mostly appressed along secondary branches, dark gray or plumbeous to grayish-yellow, 1- or 2-flowered, occasionally 3-flowered, when 2-flowered the lower floret perfect and the upper usually staminate or neuter, articulation above the glumes. Glumes subequal, mostly shorter than the florets, acute or acuminate, often awn-tipped, 1-nerved, sometimes obscurely so. Lemmas chartaceous, obscurely 3-nerved, lanceolate, mottled, somewhat compressed keeled, awned or unawned, minute appressed hairs along the margins and midnerve below; apex long acuminate to acute. Paleas lanceolate, usually shorter than the lemmas, glabrous, strongly 2-nerved, often extending into short awns. Lodicules two, short, fleshy, truncate, lateral margins thin. Ovary glabrous; styles not all united at the base, the two stigmas plumose, dark gray. Anthers three. Caryopses fusiform, brownish, usually not falling free from the lemma and the palea. Embryo large, with an epiblast, scutellar tail, and elongated mesocotyl internode; embryonic leaf margins meeting, endosperm hard.  $x = 8$ .

Four species, three in Mexico and one in northern Argentina.

### KEY TO THE SPECIES OF *CHABOISSAEA*

- a. Tufted perennials; ligules 6–10 m long; nerves of palea not extending into awns. . . . . 3. *C. ligulata*



- a'. Erect or decumbent annuals; ligules 1.6–3.2 mm long; nerves of palea usually extending into awns 0.3–1.2 mm long.
- b. Lemmas 3.0–3.8 mm long; plants commonly rooting at the lower nodes; north-central Chihuahua, Mexico. . . . . 2. *C. decumbens*
- b'. Lemmas 1.8–2.9 mm long; plants not rooting at the lower nodes; Durango, Mexico or Jujuy and Salta, Argentina.
- c. Plants (3)5–10(15) cm tall; anthers 0.9–1.1 mm long, olivaceous; inflorescence 1–5.4 cm long; northern Argentina. . . . . 1. *C. atacamensis*
- c'. Plants 20–50 cm tall; anthers 1.4–2.0 mm long, purplish to grayish; inflorescence 7–12 cm long; southwestern Durango, Mexico. . . . . 4. *C. subbiflora*

1. ***Chaboissaea atacamensis*** (Parodi) Peterson & Annable, comb. nov.—(Fig. 9). *Muhlenbergia atacamensis* Parodi, Rev. Argentina Agron. 15:248. 1948.—TYPE: Argentina, Provincia de Jujuy, La Quiaca, 15 Feb 1931, *Parodi 9656* (holotype: BAA!; isotype: BAA! US!).

*Muhlenbergia atacamensis* Parodi var. *brachyanthera* Parodi, Rev. Argentina Agron. 15:250. 1948.—TYPE: Argentina, Provincia de Jujuy, Departamento de Cochinoca, Puesto del Marques, 30 Jan 1943, *Cabrera 7785* (holotype: BAA!)

Slender, weak annuals. Culms (3)5–10(15) cm tall, upright, sometimes spreading and sprawling, freely branching below, glabrous below the nodes, 0.3–0.4 mm diam. just below the inflorescence. Sheaths 1.0–2.4 mm long, glabrous, sometimes keeled, shorter than the internodes, margins hyaline. Ligule 1.5–3.2 mm long, hyaline, the apex acuminate, entire, the margins entire, decurrent. Blades 1.2–7.0 cm long, 0.7–3.0 mm wide, flat, lax, scaberulous, the margins scabrous especially towards apex. Inflorescence 1.0–5.4 cm long, 0.4–2.4 cm wide, a narrow panicle with ascending primary branches appressed or spreading 0–80° from the culm axis, the secondary branches appressed; the pedicels 1–3 mm long, stiff, scabrous; nodes per inflorescence 6–10; usually one inflorescence branch per node, 0.3–1.8 cm long. Spikelets erect, 1- or 2-flowered, grayish-yellow to grayish-green. Glumes 1–2.0 mm long, subequal, yellowish to greenish with gray mottles, glabrous and scabrous along the midnerve, acute to obtuse, the first 1–1.7 mm long, the second 1.3–2.0 mm long. Lemmas 1.8–2.9 mm long, lanceolate, unawned or awned, compressed-keeled towards the apex, with appressed hairs on the midnerve and margins on the proximal  $\frac{2}{3}$ , the hairs up to 0.2 mm long, scabrous along the midnerve and up the awn; yellow to greenish with gray mottles, and sometimes purplish near the apex; apex acuminate to acute, the awn up to 2 mm long. Paleas 1.7–2.8 mm long, narrowly lanceolate to lanceolate, the scabrous nerves usually extending into short awns; yellow to greenish with gray mottles; apex acute, the awns 0–0.3 mm long. Anthers 0.9–1.1 mm long, olivaceous. Caryopsis 1.3–1.5 mm long, fusiform, brownish. Chromosome number,  $n = 8$ .



*Phenology and distribution* (Fig. 8). Flowering January and February. Seasonally wet marshes, meadows, moist clay flats, gravelly roadside pools, margins of ephemeral pools, and sandy margins of lagoons in the Atacama Puna, associated with *Bouteloua simplex* Lag., *Poa annua* L., *Muhlenbergia fastigiata* (Presl) Henr., *Distichlis*, *Festuca*, *Eleocharis*, *Polypogon*, *Cynodon*, *Eragrostis*, and *Marsilea*; known from the Provincias de Jujuy and Salta, Argentina, but suspected to occur just north of La Quiaca in Potosi, Bolivia; 2900–3700 m.

*Specimens examined*. ARGENTINA. Jujuy: Santa Catalina, 5 km de Santa Catalina camino a oratorio, 8 Feb 1978, *Okada, Montes & Clausen* 6707 1/2 (SI); Cochinoca, campos algo huinedos, 1959, *Cabezas* 23168 (SI); 2 km W of Abra Pampa on road to Cochinoca at the Rio Miraflores Puente, 14 Feb 1991, *Peterson & Annable* 10294 (US); 34 km S of La Quiaca on Ruta Nacional 9 towards Abra Pampa, at "Demostrativo La Intermedia," 15 Feb 1991, *Peterson & Annable* 10300 (US); 29 km W of La Quiaca and 7.5 km E of Cieneguillas on Hwy 5, at Toquero, 16 Feb 1991, *Peterson & Annable* 10319 (US),  $n = 8$ ; 2.4 km NW of Cieneguillas at Junction of road to Santa Catalina and Casira/Piscuno, 16 Feb 1991, *Peterson & Annable* 10323 (US),  $n = 8$ ; 14 km S of Cieneguillas on road to Abra Pampa, just E of Lago Pozuelos, 16 Feb 1991, *Peterson & Annable* 10327 (US); 36 km S of Cieneguillas and 57 km NW of Abra Pampa, just E of Lago Pozuelos, 17 Feb 1991, *Peterson & Annable* 10337 (US). Salta: Depto. Cachi, Las Pailas, 24 Feb 1987, *Nicora et al.* 9125 (SI); Nevado de Cachi, 15 km NW of Cachi just below the Ruinas Las Pailas, 10 Feb 1991, *Peterson et al.* 10183 (US).

2. CHABOISSAEA DECUMBENS (Swallen) J. & C. Reeder, *Phytologia* 65:156. 1988.—(Fig. 10). *Muhlenbergia decumbens* Swallen, *Bol. Soc. Bot. Mexico* 23:30. 1958.—TYPE: Mexico, Chihuahua, road between Cuauhtémoc and V. Guerrero, 27 Oct 1954, *Hernandez X. & Tania J.* N-359 (holotype: US!).

Slender, weak annuals. Culms 12–30 cm tall, decumbent spreading below freely branching, rooting at the lower nodes, glabrous below the nodes, 0.4–0.7 mm diam. just below the inflorescence. Sheaths 1.2–4.6 cm long, glabrous, usually about half as long as the internodes, margins hyaline. Ligules 1.6–2.5 mm long, hyaline, the apex truncate to broadly rounded, entire, the margins entire, decurrent. Blades, 2.5–8.0 cm long, 0.8–1.4 mm wide, flat, scaberulous, the margins scabrous especially towards apex. Inflorescence (4.5)8–11 cm long, 1.5–4.5 cm wide, a narrow panicle with ascending primary branches appressed or spreading 0–80° from the culm axis, the secondary branches appressed; the pedicels 1–3 mm long, stiff, scabrous;





FIG. 9. *Chaboissaea atacemensis*, Jujuy, Argentina (Parodi 9656). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Two florets. G. Upper floret. H. Lower floret. I. Upper palea, ventral view. J. Lower palea, ventral view. K. Stamens, pistil, and lodicules.





FIG. 10. *Chaboissaea decumbens*, Chihuahua, Mexico (Peterson & Annable 4533). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Two florets. G. Lower floret. H. Upper floret. I. Lemma. J. Lower palea, dorsal view. K. Lower palea, ventral view. L. Lower palea, side view. M. Stamens, pistil, and lodicules.



nodes per inflorescence 6–10; usually a single primary inflorescence branch per node, 2.5–4.8 cm long. Spikelets erect, 1- or 2-flowered, plumbeous. Glumes 1.8–3.2 mm long, subequal, grayish, glabrous and scabrous along the midnerve, the apex acuminate sometimes awn-tipped, the awn up to 0.6 mm long, the first 1.8–2.5 cm long, the second 2.4–3.2 mm long, broader than the first. Lemmas 3.0–3.8 mm long, lanceolate, compressed-keeled towards apex, awned or unawned, with appressed hairs on the margins and lower third, the hairs up to 0.2 mm long, scabrous along the midnerve continuing up the awn; dark-green to gray with lighter greenish-white areas; apex long acuminate to acuminate, the awn 0.2–3 mm long. Paleas 3.0–3.7 mm long, narrowly lanceolate, glabrous, the scabrous nerves extending into short awns; dark green to gray with lighter greenish-white areas; apex acute, the awns 0.3–0.6 mm long. Anthers 0.9–1.1 mm long, greenish. Caryopsis 2–2.3 mm long, fusiform brownish. Chromosome number  $n = 16$ .

*Phenology and distribution* (Fig. 8). Flowering September and October. Sandy clay loam to dark clay soil along slough and wet sticky depressions in black soil in pine–oak–juniper woodlands; known only from two or three locations in northwestern Chihuahua, Mexico; 2200 m.

*Specimens examined*. MEXICO. Chihuahua: W of Casas Grandes, 5 mi S of Hernandez, 18 Sep 1960, *Reeder et al.* 3510 (US); about 11 mi W of Cuauhtémoc, 5 Oct 1966, *Reeder & Reeder* 4593 (ARIZ, MICH, US), *Reeder & Reeder* 4601 (ARIZ, MICH, UC, US); 4 Sep 1967, *Reeder & Reeder* 4848 (ARIZ, US); 13 mi W of Cuauhtémoc on Hwy 16, 21 Sep 1986, *Peterson & Annable* 4533 (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 23 Sep 1988, *Peterson & Annable* 5820 (US); 9 Sep 1989, *Peterson & Annable* 7983 (US); 23 Aug 1990, *Peterson* 9587 (US).

3. *CHABOISSAEA LIGULATA* Fournier, Mex. Pl. 2:112. 1886.—(Fig. 11). *Muhlenbergia ligulata* (Fournier) Scribner & Merrill, U.S.D.A. Div. Agrostol. Bull. 24:19. 1901.—TYPE: Mexico, San Luis Potosi, 1851, *Virlet d'Aoust s.n.* (holotype: P, fragment US!).

Tufted perennials. Culms (10)20–70(90) cm tall, upright, leafy below, glabrous and sometimes purplish below the nodes, 0.5–1.1 mm diam. just below the inflorescence. Sheaths (0.8)2.5–11(13) cm long, glabrous, keeled, usually shorter than the internodes, margins hyaline. Ligule 6–10 mm long, hyaline, the apex acuminate, lacerate, the margins entire, decurrent. Blades (3)5–15(20) cm long, 1–2.5 mm wide, flat to conduplicate or involute, glabrous above and scaberulous below, the margins scabrous especially towards apex. In-



florescence 6–28 cm long, 1–10 cm wide, a somewhat narrow panicle with ascending primary branches 10–70° from the culm axis, the secondary branches appressed or narrowly spreading; the pedicels 0.2–3 mm long, stiff, scabrous; nodes per inflorescence 9–12; usually one inflorescence branch per node, 0.5–10 cm long. Spikelets erect, 1-, 2-, or occasionally 3-flowered plumbeous. Glumes 1.0–4.0 mm long, subequal in length, grayish, glabrous and scabrous along the midnerve, the apex acute to acuminate, sometimes awn-tipped, the awn up to 0.5 mm long, the first 1.0–3.2 mm long, the second 1.2–4.0 mm long. Lemmas (2.0)2.4–3.5(4.0) mm long, lanceolate, unawned or awned, compressed-keeled towards the apex, with appressed hairs on the midnerve and margins of the proximal ½, the hairs up to 0.2 mm long, scabrous along the midnerve and up the awn; greenish-yellow with dark-gray mottles, sometimes purplish near apex; apex acuminate to acute, the awn up to 2 mm long. Palea (1.9)2.4–3.3(3.8) mm long, lanceolate, unawned; greenish-yellow with dark gray mottles; apex acute or obtuse. Anthers 1.4–1.8 mm long, yellowish to purplish. Caryopsis 1.1–1.3 mm long, fusiform, brownish. Chromosome number  $n = 8$ .

*Phenology and distribution* (Fig. 8). Flowering mid August to mid November. Drainage ditches, irrigation canals, and meadows in blackish clay soil often in muddy water, associated *Acacia* and *Prosopis* grasslands with *Cyperus*, *Juncus*, *Leptochloa*, and occasionally *Chaboissaea subbiflora* and *C. decumbens*; Chihuahua, Durango, Zacatecas, Aguascalientes, San Luis Potosi, Jalisco, Guanajuato, Mexico, and Distrito Federal, Mexico; 1900–2500 m.

*Specimens examined*. MEXICO. Aguascalientes: La Congoja, municipio de San José de Gracia, 17 Oct 1973, *McVaugh* 850 (MICH), *McVaugh* 851 (MICH, MO). Chihuahua: Sanchez, 12 Oct 1910, *Hitchcock* 7693 (US); 13 mi W of Cuauhtémoc on Hwy 16, 21 Sep 1986, *Peterson & Annable* 4532 (GH, MO, NY, RSA, US, WS); 11.5 mi W of Cuauhtémoc on Hwy 16, 23 Sep 1988, *Peterson & Annable* 5819 (US); 54.4 mi N of Parral on MEX 24 to Chihuahua, 14 Sep 1989, *Peterson & Annable* 8111 (US). Distrito Federal: 3.5 km SE of Ixtapalapa, on road to Los Reyes, 17 Aug 1960, *Iltis & Koeppen* 1302 (US). Durango: 36 mi N of Durango, 9 Oct 1966, *Reeder & Reeder* 4638 (MEXU, RSA, US); 29 mi N of Durango, 9 Oct 1966, *Reeder & Reeder* 4641 (US); about 41 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder* 6480 (US); about 34 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder* 6486 (RSA, US); ca. 8 km E of Durango, 6 Sep 1984, *Herrera* 427 (ANSM, MEXU); Rancho El Tamascal, municipio de Suchil, 25 Oct 1984, *Acevedo* 147 (GUADA, MEXU); 66 km N of Durango on Hwy 45, 27 Sep 1988, *Peterson & Annable* 5989 (US); 55 km N of Durango on Mex 45, S of turnoff to Canatlan (Hwy 26), 26 Aug 1990, *Peterson* 9635 (US); 6 mi E of Durango on Mex 45 to Zacatecas, 27 Aug 1990, *Peterson*





FIG. 11. *Chaboissaea ligulata*, Zacatecas, Mexico (Peterson & Annable 6198). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Glumes. F. Lower floret. G. Lemma, ventral view. H. Lower palea, dorsal view. I. Lower palea, ventral view. J. Upper palea. K. Upper palea, ventral view. L. Stamens, pistil, and lodicules.



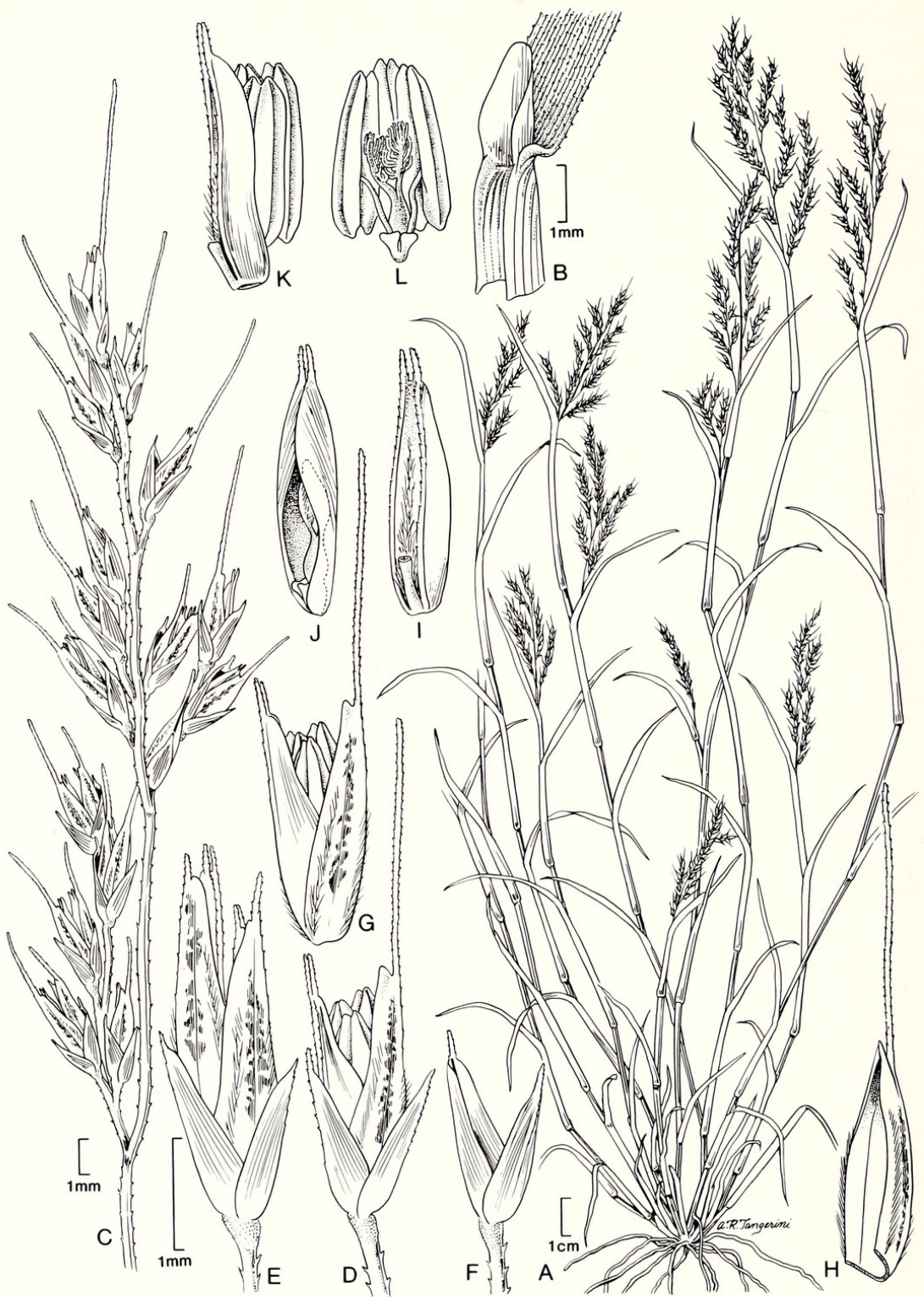


FIG. 12. *Chaboissaea subbiflora*, Durango, Mexico (Reeder & Reeder 6481). A. Habit. B. Ligule. C. Inflorescence. D. Spikelet. E. Spikelet from Reeder & Reeder 6488a. F. Glumes. G. Lower spikelet. H. Lemma, ventral view. I. Lower palea, dorsal view. J. Lower palea, ventral view. K. Lower palea, side view. L. Stamens, pistil, and lodicules.



9650 (US). Jalisco: along the Ojuelos-Aguascalientes highway, about 1.5 km E of state line, 17 Aug 1958, *McVaugh 17058* (MICH, TAES, US); 14–15 km E of Arandas, 14 Nov 1970, *McVaugh 24376* (MICH); Presa El Cuarenta, entre Lagos de moreno y ojuelos, municipio de Lagos de Moreno, 30 Jul 1985, *Santana Michel 1596* (GUADA); 14.5 mi E of Aguascalientes on Hwy 70 towards San Luis Potosi, 7 Oct 1988, *Peterson & Annable 6185* (US); 29 Aug 1990, *Peterson 9680* (US). Guanajuato: about 6 km E of San Felipe, 24 Oct 1952, *Sohns 398, 411* (US); 26 Oct 1952, *Sohns 446* (MICH, MO, US); 10 mi SE of Ojuelos de Jalisco on Hwy 51 towards Ocampo, 29 Aug 1990, *Peterson 9682* (US); 1.4 mi SE of San Felipe on Mex 37 to Leon, 30 Aug 1990, *Peterson 9685* (US); 24.1 mi SE of San Felipe and 28.5 mi NE of Leon on Mex 37, 30 Aug 1990, *Peterson 9697* (US). Mexico: Villa de Allende, 5 Oct 1952, *Matuda et al. 27664* (MEXU, US). Zacatecas: about 1 mi E of Ojuelos, Jalisco, 18 Nov 1964, *Reeder & Reeder 4183* (RSA, US); about 13 mi W of Huejucar, 3 Oct 1974, *Reeder & Reeder 6459* (RSA, US); 3 mi E of Ojuelos de Jalisco on Hwy 70 to San Luis Potosi, 7 Oct 1988, *Peterson & Annable 6198* (US); 2.5 mi E of Ojuelos de Jalisco on Hwy 80 towards San Luis Potosi, 29 Aug 1990, *Peterson 9681* (US).

4. *CHABOISSAEA SUBBIFLORA* (Hitchcock) J. & C. Reeder, *Phytologia* 65:156. 1988.—(Fig. 12). *Muhlenbergia subbiflora* Hitchcock, *North Amer. Flora* 17:437. 1935.—TYPE: Mexico, Durango, City of Durango and vicinity, Nov 1896, *Palmer 948* (holotype: US!; isotypes: MEXU! MO! US!).

Slender, weak annuals. Culms 20–50 cm tall, upright, sometimes spreading and sprawling, freely branching below, glabrous below the nodes, 0.4–0.6 mm diameter just below the inflorescence. Sheaths 1.5–4.5 cm long, glabrous, usually about half as long as the internodes, the margins hyaline. Ligules 2.0–3.0 mm long, membranous to hyaline, the apex acute to obtuse, entire, the margins decurrent. Blades 2–8 cm long, 0.8–1.4 mm wide, flat, scaberulous above and along margins, glabrous below. Inflorescence 7–12 cm long, 1.8–5.5 cm wide, a narrow panicle sometimes included in the sheath below and appearing axillary with ascending primary branches appressed or spreading 0–70° from the culm axis, the secondary branches appressed or narrowly spreading; the pedicels 1–3 mm long, stiff, scabrous; nodes per inflorescence 8–15; usually a single primary inflorescence branch per node, 2.0–5.5 cm long. Spikelets erect on stout pedicels, 1- or 2-flowered, grayish. Glumes 1.0–2.2 mm long, subequal, grayish, glabrous and scabrous along the midnerve, the apex acute to acuminate, occasionally obtuse, sometimes awn-tipped, the awn up to 0.3 mm long, the first 1.0–2.0 mm long, the second 1.2–2.2 mm long, broader than the first. Lemmas 2.2–2.9 mm long, lanceolate, awned, occasionally unawned, somewhat compressed-



keeled towards apex, with appressed hairs along the midnerve and margins on the proximal  $\frac{2}{3}$ , the hairs up to 0.2 mm long; greenish-yellow with dark greenish-gray mottles, sometimes purplish near apex; apex acuminate or acute, sometimes minutely bifid, the awn 1–6 mm long, straight or flexuous. Paleas 2.1–2.9 mm long, lanceolate, awned, occasionally unawned, the nerves extending into short awns; greenish-yellow, occasionally with greenish-gray mottles; apex obtuse to rounded, the awns 0.3–1.2 mm long. Anthers 1.4–2.0 mm long, purplish to grayish. Caryopsis 1.0–2.5 mm long, fusiform, brownish. Chromosome number  $n = 7, 8, 9$ .

*Phenology and distribution* (Fig. 8). Flowering September through November. Gravelly, alkaline flats and open bottomlands with clay loam soils often growing in standing water in gramma (*Bouteloua*) grasslands with *Prosopis* and *Acacia*; known only from in and around the city of Durango, Mexico; 1900–2000 m.

*Specimens examined*. MEXICO: Durango: city of Durango and vicinity, Sep 1896, *Palmer 731* (GH, MEXU, MO, NY, US); 6 mi SE of Ciudad Durango near Rio Mesquital, 1 Oct 1948, *Gentry 8436* (GH, MICH, MO, US); 40 mi N of Ciudad Durango, 3 Oct 1948, *Gentry 8589* (GH, MEXU, MICH, US); 10.4 mi NE of Durango, 30 Sep 1959, *Soderstrom 804* (US); 27 Aug 1990, *Peterson 9651* (US); 4 mi E of Cd. Durango, 26 Sep 1963, *Reeder & Reeder 3828* (ARIZ); 40 mi N of Cd. Durango, 1 Sep 1965, *Reeder & Reeder 4485* (ARIZ); 39 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4636* (ARIZ, US); 29 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4640* (ARIZ, US); 22 mi N of Durango, 9 Oct 1966, *Reeder & Reeder 4642*, (ARIZ, US); 4 mi E of Durango, 9 Oct 1966, *Reeder & Reeder 4643* (ARIZ, US); 41 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6479, 6481* (ARIZ, US); 34 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6485* (ARIZ, US); 26 mi N of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6487* (ARIZ, US); 4 mi E of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6488, 6488a* (ARIZ, US); 10 mi NE of Cd. Durango, 5 Oct 1974, *Reeder & Reeder 6491* (ARIZ, US); 66 km N of Durango on Hwy 45, 8 Sep 1985, *Peterson & Annable 4086* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 27 Sep 1988, *Peterson & Annable 5988* (US); 3 Oct 1989, *Peterson & King 8266* (US); 25 Aug 1990, *Peterson 9619* (US); 26 Aug 1990, *Peterson 9630* (US); 64 km N of Durango on Hwy 45, 8 Sep 1985, *Peterson & Annable 4087* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 27 Sep 1986, *Peterson & Annable 4580* (ARIZ, ENCB, GH, MEXU, MICH, MO, NMC, NY, RSA, TAES, UC, UNLV, US, UTC, WIS, WS); 55 km N of Durango on Mex 45, just S of the turnoff to Canatlan (Hwy



26), 26 Aug 1990, *Peterson 9637* (US); 2.5 mi S of Durango on road to Ferreria, just before crossing rio, 27 Aug 1990, *Peterson 9652* (US).

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