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AN EXPANDED CIRCUMSCRIPTION OF *BOUTELOUA* (GRAMINEAE: CHLORIDOIDEAE): NEW COMBINATIONS AND NAMES

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ABSTRACT

Cladistic analysis of nuclear ribosomal and chloroplast DNA sequences has revealed that the New World grass genus Bouteloua (Chloridoideae) is not monophyletic. Indeed, some species of Bouteloua are more closely related to species in other genera than to congeners. The problem was dealt with by expanding the circumscription of Bouteloua to include species formerly positioned in the satellite genera Buchloë (1 species), Buchlomimus (1), Cathestecum (4), Cyclostachya (1), Griffithsochloa (1), Opizia (2), Pentarrhaphis (3), Pringleochloa (1), and Soderstromia (1). Thirteen new combinations and names were necessary. As here circumscribed, Bouteloua is monophyletic and comprises 57 species.

Key words: *Bouteloua*, Chloridoideae, classification, generic circumscription, Gramineae, new combinations, new names, nomenclature, sexual dimorphism, taxonomy.

Until recently, little was known about the phylogeny of the New World grass genus Bouteloua Lag. and relatives (Chloridoideae). The first significant contribution came only last year with publication of a cladistic parsimony analysis of nuclear ribosomal internal transcribed spacer (ITS) region DNA sequences (Columbus et al. 1998). Prior to this study, insights into possible relationships were largely confined to remarks concerning a few taxa. Although Bouteloua and both subgenera proved not to be monophyletic, Columbus et al. (1998) proposed no new circumscriptions in lieu of additional phylogenetic estimates, particularly from the nonrecombining chloroplast genome. The trnLtrnF region of chloroplast DNA has since been sequenced and analyzed (Columbus et al., in press, in prep.). Although differences exist between the ITS and trnL-F strict consensus trees, there is much agreement, and nearly all of the discordance involves poorly supported nodes. Figure 1 is the strict consensus of six most parsimonious trees resulting from an analysis of the two data sets combined (Columbus et al., in press). Bullets denote clades having the same composition of taxa in all minimum-length trees from the ITS, trnL-F, and combined analyses. Most of these clades are supported by high bootstrap percentages and decay indices. When the data are subjected to other kinds of analyses such as neighbor joining and UPGMA, these same groupings of taxa result (Fig. 2). Hence, because ITS and trnL-F are located in distinct genomes, characterized by different modes of inheritance, their phylogenetic concordance provides solid ground upon which to base taxonomic decisions.

In contrast to *Bouteloua* (42 spp.), species in the satellite genera *Buchloë* Engelm. (1 sp.), *Buchlomimus* Reeder, C. Reeder, & Rzed. (1 sp.), *Cathestecum* J. Presl (4 spp.), *Cyclostachya* Reeder & C. Reeder (1 sp.), *Griffithsochloa* G. J. Pierce (1 sp.), *Opizia* J. Presl (2 spp.), *Pringleochloa* Scribn. (1 sp.), and *Soderstromia* C. V. Morton (1 sp.) possess dimorphic spikelets, some or all of which are unisexual. Historically, taxonomists have segregated sexually dimorphic grasses from their hermaphroditic relatives, placing them in different genera. The following excerpt from Reeder and Reeder (1963), justifying their description of a new genus, *Cyclostachya*, to accommodate a dioecious and dimorphic species, illustrates well this traditional practice:

With the discovery that [Bouteloua stolonifera Scribn.] is dioecious, a re-evaluation of its generic position seems pertinent. Dioeciousness per se would not appear to be sufficient grounds to exclude a species from an otherwise hermaphroditic genus. Both Poa and Eragrostis, for example, contain dioecious members, even though in the majority of the included species the florets are bisexual. In these cases, however, δ and φ spikelets are essentially alike morphologically, any differences being largely those of size, and the fact that organs of only one sex are developed.

In the case under discussion, the staminate and pistillate plants differ to such a degree that they have been considered to represent different species. This would suggest that this grass has undergone a long evolutionary history from the time unisexuality first appeared. To retain it within a genus in which no dicliny has been reported thus far would seem to be at variance with accepted practice.

Later, Reeder and Reeder (1966) reported "dioecy (or gynodioecy)" in some populations of *Bouteloua*

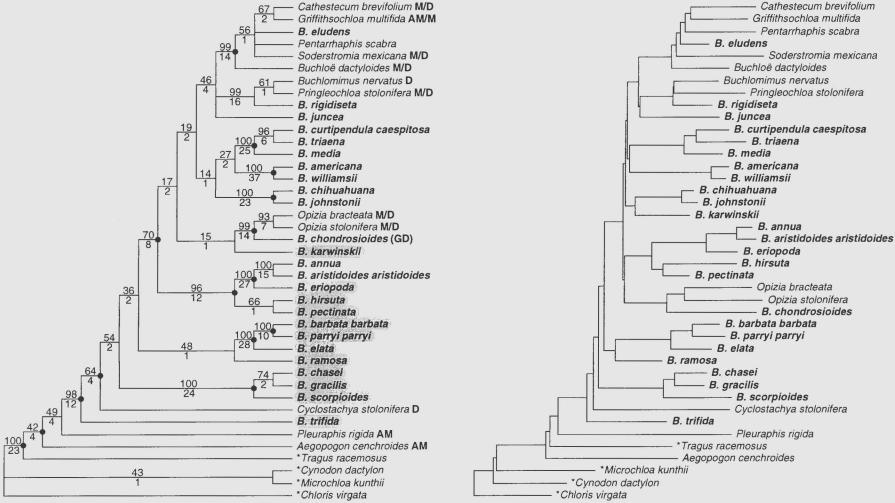


Fig. 1. Strict consensus of six most parsimonious trees resulting from a PAUP* version 4.0 beta 1 (Swofford 1998) analysis of combined ITS and trnL-F sequences of representatives of Bouteloua and related and outgroup genera (Columbus et al., in press). Asterisks denote outgroup taxa. In bold are members of Bouteloua. Shaded are members of Bouteloua subg. Chondrosium (Desv.) Gould. Numbers above and below branches are bootstrap percentages and decay indices, respectively. Bullets denote clades having the same composition of taxa in all minimum-length trees from separate and combined analyses of ITS and trnL-F. AM = andromonoecious, D = dioecious, (GD) = facultatively gynodioecious, M = monoecious. Tree length = 2001, consistency index = 0.51, retention index = 0.59.

Fig. 2. Neighbor-joining tree computed by PAUP* version 4.0 beta 1 using uncorrected ("p") distances and combined ITS and trnL-F sequences of representatives of Bouteloua and related and outgroup genera. Asterisks denote outgroup taxa. In bold are members of Bouteloua.

chondrosioides (Kunth) Benth. ex S. Watson, but refrained from erecting a new genus because the requisite dimorphic features were not evidenced. (Reeder [1969] subsequently indicated that the populations are likely gynodioecious, a conclusion confirmed by H. E. Conner [pers. comm. in Columbus et al., in press].)

Given the greater insight into the phylogeny of Bouteloua and related genera afforded by these molecular data, a reconsideration of generic circumscriptions is in order. A major problem with the present classification is that some species of Bouteloua, namely B. chondrosioides, B. eludens Griffiths, and B. rigidiseta (Steud.) Hitchc., are more closely related to species in other genera than to congeneric species (Fig. 1). All taxonomic solutions, therefore, necessarily involve changes in the circumscription of Bouteloua. In order to maintain all of the satellite genera, Bouteloua would have to be diminished in size, beginning with the removal of B. chondrosioides (to Opizia or a new genus), B. eludens (to a new genus), and B. rigidiseta (to a new genus). Removal of these species, however, would not render Bouteloua monophyletic. To achieve a system of monophyletic genera, further fragmentation of Bouteloua would be necessary. Because the relationships among a number of the terminal taxa and clades remains uncertain, as is evident from those nodes in the ITS + trnL-F strict consensus tree having low bootstrap percentages and decay indices (Fig. 1), the establishment of unequivocally monophyletic genera would result in more than double the number of genera currently recognized. Such a classification would have limited practical utility, as morphologically similar pairs of species such as B. chondrosioides-B. eludens and B. chasei Swallen-B. karwinskii (E. Fourn.) Griffiths would be positioned in different gen-

An alternate solution, and the one I advocate, is to expand the circumscription of *Bouteloua* to include the aforementioned genera and *Pentarrhaphis* Kunth (3 spp.). Dating from 1805, *Bouteloua* has priority over the other generic names (see Clayton and Renvoize 1986). Monophyly of *Bouteloua* in this expanded sense has strong support (bootstrap 98%, decay index 12; Fig. 1) and, by accenting the morphological similarities among the species, the new generic circumscription has a practical advantage over the current classification: species can be more readily and accurately determined to genus, especially in the field, by persons not expert in the group. The following new combinations and names are thereby necessary:

Bouteloua bracteata (McVaugh) J. T. Columbus, comb. nov.

Basionym: *Opizia bracteata* McVaugh. Fl. Novo-Galiciana, vol. 14, pp. 269–271. 1983.

Bouteloua dactyloides (Nutt.) J. T. Columbus, comb. nov.

Basionym: Sesleria dactyloides Nutt. Gen. N. Amer. pl., vol. 1, p. 65. 1818.

Bouteloua dimorpha J. T. Columbus, nom. nov.

Replaced name: Opizia stolonifera J. Presl. Reliq. Haenk., vol. 1, pp. 293-294, pl. 41, figs. 1-11. 1830.

Notes.—A new specific epithet is necessary due to (1) the existence of the validly published *Bouteloua stolonifera* Scribn. and (2) the absence of taxonomic synonyms. The epithet refers to the sexually dimorphic inflorescences and spikelets.

Bouteloua diversispicula J. T. Columbus, nom. nov.

Replaced name: Cathestecum brevifolium Swallen. J. Wash. Acad. Sci. 27: 500–501. 1937.

Notes.—A new specific epithet is necessary due to (1) the existence of the validly published Bouteloua brevifolia Buckley and (2) the absence of taxonomic synonyms (Pierce 1979). The epithet refers to the polymorphic spikelets, which vary according to position and sex.

Bouteloua erecta (Vasey & Hack.) J. T. Columbus, comb. nov.

Basionym: Cathestecum erectum Vasey & Hack. Bull. Torrey Bot. Club 11: 37-38, pl. 45. 1884.

Bouteloua griffithsii J. T. Columbus, nom. nov.

Replaced name: Cathestecum prostratum J. Presl. Reliq. Haenk., vol. 1, p. 295, pl. 42. 1830.

Notes.—A new specific epithet is designated on account of (1) the validly published Bouteloua prostrata Lag. and (2) the validly published B. annua Swallen, which precludes the transfer to Bouteloua of Cathestecum annuum Swallen, the sole taxonomic synonym of C. prostratum (Pierce 1979). The epithet commemorates David Griffiths, who in 1912 authored a revision of Bouteloua and relatives.

Bouteloua mexicana (Scribn.) J. T. Columbus, comb. nov.

Basionym: Fourniera mexicana Scribn. U. S. D. A. Div. Agrostol. Bull. 4: 8-9. 1897.

Bouteloua multifida (Griffiths) J. T. Columbus, comb. nov.

Basionym: Cathestecum multifidum Griffiths. Contr. U. S. Natl. Herb. 14: 360-361. 1912.

Bouteloua polymorpha (E. Fourn.) J. T. Columbus, comb. nov.

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Table 1. Corresponding species names under the former (e.g., Pierce 1979; McVaugh 1983; Clayton and Renvoize 1986) and new treatments.

Former treatment	New treatment
Buchloë dactyloides (Nutt.) Engelm.	Bouteloua dactyloides (Nutt.) J. T. Columbus
Buchlomimus nervatus (Swallen) Reeder, C. Reeder, & Rzed.	Bouteloua nervata Swallen
Cathestecum brevifolium Swallen	Bouteloua diversispicula J. T. Columbus
Cathestecum erectum Vasey & Hack.	Bouteloua erecta (Vasey & Hack.) J. T. Columbus
Cathestecum prostratum J. Presl	Bouteloua griffithsii J. T. Columbus
Cathestecum varium Swallen	Bouteloua varia (Swallen) J. T. Columbus
Cyclostachya stolonifera (Scribn.) Reeder & C. Reeder	Bouteloua stolonifera Scribn.
Griffithsochloa multifida (Griffiths) G. J. Pierce	Bouteloua multifida (Griffiths) J. T. Columbus
Opizia bracteata McVaugh	Bouteloua bracteata (McVaugh) J. T. Columbus
Opizia stolonifera J. Presl	Bouteloua dimorpha J. T. Columbus
Pentarrhaphis annua Swallen	Bouteloua swallenii J. T. Columbus
Pentarrhaphis polymorpha (E. Fourn.) Griffiths	Bouteloua polymorpha (E. Fourn.) J. T. Columbus
Pentarrhaphis scabra Kunth	Bouteloua scabra (Kunth) J. T. Columbus
Pringleochloa stolonifera (E. Fourn.) Scribn.	Bouteloua reederorum J. T. Columbus
Soderstromia mexicana (Scribn.) C. V. Morton	Bouteloua mexicana (Scribn.) J. T. Columbus

Basionym: Atheropogon polymorphus E. Fourn. Mexic. pl., vol. 2, p. 141. 1886.

Bouteloua reederorum J. T. Columbus, nom. nov.

Replaced name: Atheropogon stolonifer E. Fourn. Mexic. pl., vol. 2, pp. 140–141. 1886.

Notes.—A new specific epithet is necessary on account of (1) the validly published Bouteloua stolonifera Scribn., (2) the validly published B. pringlei Scribn., which rules out the transfer to Bouteloua of Opizia pringlei Hack., a nomenclatural synonym of Atheropogon stolonifer, and (3) the absence of taxonomic synonyms. The epithet honors John R. Reeder and Charlotte O. Goodding Reeder, who have contributed much to our understanding of Bouteloua, including the discovery of dioecism in two species.

Bouteloua scabra (Kunth) J. T. Columbus, comb. nov.

Basionym: *Pentarrhaphis scabra* Kunth. Nov. gen. sp., vol. 1, p. 178, pl. 60. 1816.

Bouteloua swallenii J. T. Columbus, nom. nov.

Replaced name: *Pentarrhaphis annua* Swallen. *Ceiba* 4: 286–287. 1955.

Notes.—A new specific epithet is designated on account of (1) the validly published Bouteloua annua Swallen and (2) the absence of taxonomic synonyms. The epithet honors Jason R. Swallen, who described a number of species belonging to Bouteloua.

Bouteloua varia (Swallen) J. T. Columbus, comb.

Basionym: Cathestecum varium Swallen. J. Wash. Acad. Sci. 27: 498-499. 1937.

The change in generic circumscription affects the

names of 15 species. Listed in Table 1 are the binomials as employed under the former treatment and the corresponding names under the new treatment. Adding these species to the 39 recognized in Gould's (1980) treatment and three later additions (Reeder and Reeder 1981; Beetle 1986; Columbus 1996), *Bouteloua* now comprises 57 species.

I propose no subgeneric or sectional names at this time, pending additional sampling of taxa and greater knowledge of relationships (discussed above). The key remaining species of *Bouteloua* to be sequenced for ITS or *trnL-F* is *Bouteloua megapotamica* (Spreng.) Kuntze. Genera believed to be related to *Bouteloua* (e.g., Lamson-Scribner 1890; Clayton and Richardson 1973; Clayton and Renvoize 1986) and hence in need of sampling include *Melanocenchris* Nees (2 spp.), *Neobouteloua* Gould (2 spp.), and *Schaffnerella* Nash (1 sp.). *Neobouteloua lophostachya* (Griseb.) Gould was first described as a species of *Bouteloua* and treated as such in Griffiths' (1912) revision of the genus.

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- P. 106, Fig. 4, Aegopogon and Pleuraphis: AM, not A/M
- P. 111, col. 1, line 24: decay index of 1, not 1.0
- P. 112, col. 2, line 2: Pentarrhaphis, not Pentar rhaphis
- P. 121, Appendix 1: scale (·) and indel (+) markers should be shifted one nucleotide to the left
- P. 122, Appendix 1: scale 560 marker (·) should be moved one nucleotide to the right