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Delimiting species boundaries within the *Bothriochloa saccharoides* complex (Poaceae) through morphometric analysis

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Abstract

The *Bothriochloa saccharoides* complex is one of the most interesting groups within the genus *Bothriochloa* (Poaceae). The plants inhabit grasslands of tropical and subtropical regions from the Americas. Principal components analysis (PCA) and discriminant analysis (DA) were employed to evaluate the morphological variation among 60 herbarium specimens tentatively identified as *B. imperatoides*, *B. laguroides*, *B. longipaniculata*, *B. saccharoides* and *B. torreyana*. Twenty-three morphological characters were included in the analysis in order to clarify problematic species boundaries. Chemical data was incorporated to improve the resolution on delimitation of the species complex. Taxa were delimited according to the observed clustering of specimens in the PCA plots and discriminant analysis, and diagnostic characters were identified. The results showed that five taxa could be distinguished on the basis of morphological characters and chemical data. Two new subspecies are described: *B. saccharoides* subsp. *americana* and *B. saccharoides* subsp. *australis*. An identification key and a taxonomic synopsis are provided.

Key words: American grasses, Gramineae, geographical distribution, multivariate analysis, new subspecies, numerical taxonomy, species complex, species delimitation

Introduction

Bothriochloa Kuntze (1891: 762) (Poaceae: Andropogoneae) occurs mostly in tropical and subtropical regions of Africa, America, Asia and Australia, and comprises 35 to 40 species (Clayton & Renvoize 1986, Nicora & Rúgolo de Agrasar 1987, Watson & Dallwitz 1992). In America, 12 native taxa show a disjunct distribution in North and South America (De Wet 1968, Allred 1981, Allred & Gould 1983, Vega 2000), and are important components of grasslands and savannas in those areas. According to their morphological and cytological characteristics, the American species belong to two complexes. In the *Bothriochloa barbinodis* (Lagasca 1816: 3) Herter (1940: 135) complex, the spikelets have a glandular pit in the first glume, spikelets are longer than 5 mm with a long awn, and the chromosome complement is 2n=180 or 220. The species of the *B. saccharoides* (Swartz 1788: 26) Rydberg (1931: 81) complex have the lower glume lacking a glandular pit, spikelets usually less than 5 mm, short awns, and a chromosome complement of 2n=60 or 120. Nevertheless, polymorphic species of difficult circumscription exist in both complexes (De Wet 1968, Allred & Gould 1983).

Bothriochloa saccharoides s.l. is an American perennial grass mainly distributed in two disjunct regions: a) southern United States, Mexico and West Indies, b) southern Brazil, Uruguay, Paraguay and Argentina. It has never been the subject of an adequate comparative study. There is high morphological diversity of specimens and still much uncertainty about the circumscription of especially the entities around *B. saccharoides*. For example, there are doubts if plants from the North and South America, assigned to *B.*

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saccharoides, really belong to this species (Allred, pers. comm.). Indeed, preliminary examination of herbarium specimens as well as live plants has suggested overlapping variation in most characters within the "*B. saccharoides* complex", i.e. the complex tentatively comprising *B. imperatoides* (Hackel 1883: 293) Herter (1940: 135), *B. laguroides* (Candolle 1813: 78) Herter (1940: 135), *B. torreyana* (Steudel 1840: 93) Scrivanti & Anton (2011: 156), *B. longipaniculata* (Gould 1955: 18) Allred & Gould (1983: 180) and *B. saccharoides*.

The taxonomy of this group of species has been controversial with different treatments by diverse authors (Hackel 1883, 1889, Hitchcock 1927, 1930, Cabrera 1953, 1970, Gould 1957, 1975, Acevedo 1968, De Wet 1968, Burkart 1969, Rosengurtt *et al.* 1970, Allred & Gould 1983, Marchi & Longhi-Wagner 1998, Vega 2000, Scrivanti *et al*. 2009). Some characters employed in the treatments are not easy to use in species identification because they are hardly perceptible and overlapping to some extent or with similar variation ranges in the dichotomy. Recently, *B. laguroides* and *B. torreyana* have been accepted at the species level by chemical and morphological data (Scrivanti & Anton 2011).

The objective of the present work is to assess the morphological variation to clarify the identity of taxa related to the *Bothriochloa saccharoides* complex, including several characters which had not been considered in other treatments. In the present study, the morphological variation within the *B. saccharoides* complex is analysed by multivariate statistical analysis.

Materials and methods

Sixty herbarium specimens from CORD, ICN, LSU, MO, NY, S, UNAH, US and W (Holmgren *et al.* 1990) were tentatively identified: six as *Bothriochloa imperatoides*, 12 as *B. laguroides*, five as *B. torreyana*, four as *B. longipaniculata* and 33 as *B. saccharoides* (Appendix 1). The tentative identifications were based on regional treatments according to the geographic origin of the material. These specimens were selected to cover the geographic range and the morphological variability of each species. Vegetative traits were measured on fertile innovations. For each specimen, the mean of the blade length and width was obtained from measurements of three leaves of the middle portion of the culm. The reproductive traits (panicles, rachis, fertile and sterile spikelets) were measured in complete mature racemes. The analysis of the spikelet features was conducted in the middle portion of the panicle. Forty-two morphological characters were analyzed to detect variable characters; however, only twenty-three were informative (Table 1). The distribution of each variable in the different groups was analyzed using diagram boxes. The mean, standard deviation, 75th percentiles and range of variation were calculated for each quantitative variable. One-way ANOVA at a significance level of 5% ($\alpha = 0.05$) was made to evaluate the existence of significant differences for each trait among the taxa analyzed. Duncan's ($p \leq 0.05$) test was carried out to test differences between each pair of means.

Multivariate analysis including principal component analysis (PCA) and discriminant analysis (DA) were conducted on the data sets. The clustering method used was average linkage (UPGMA) with Euclidean distance measure. Principal components analysis based on correlation matrices was used to evaluate the morphological variation amongst specimens. Principal components analysis has previously proved useful in morphometric studies of the genus *Bothriochloa* (Allred & Gould 1983). Discriminant analysis was performed to examine multivariate differentiation among a priori designated groups and to identify which quantitative characters were more useful in detecting these differences. First, analysis incorporating all tentative species was performed. Subsequently, separate analysis was made on specimens of *B. saccharoides s.l.* in order to enhance resolution within this group and in relation to geographical distribution. Specimens with missing values were excluded. The data were standardized and analysed using INFOSTAT statistical program version 1.1 (Group InfoStat 2002).

A dichotomous key was prepared, together with brief morphological descriptions in which variation in all measured characters was indicated as the interquartile range, with minimum and maximum values added in

parentheses. In addition, the geographic distribution was characterized based on collection data from herbarium specimens included in the study.

TABLE 1. List of the seven binary or multistate characters (marked with asterisks) and the sixteen quantitative characters measured in the study.

1	Culm length (mm)
2	Culm thickness (mm)
3*	Node pubescense: glabrous or pilose
4*	Ligular region: glabrous, sparsely pilose or pilose
5	Ligule length (mm)
6	Blade length (mm)
7	Blade width (mm)
8*	Adaxial blade pubescense: glabrous, sparsely pilose or pilose
9*	Abaxial blade pubescense: glabrous, sparsely pilose or pilose
10	Panicle length (mm)
11	Rachis length (mm)
12	Rachis hair length (mm)
13	Sessile spikelet length (mm)
14	Sessile spikelet width (mm)
15	Awn length (mm)
16	Callus hair length (mm)
17	Hair at the lower glume sessile spikelet length (mm)
18	Pedicellate spikelet length (mm)
19	Pedicel length (mm)
20	Pedicel hair length (mm)
21*	Groove: narrow or wide
22*	Ramification: basal or cauline
23*	Violet stains: absent or present

Results

The distribution of the average values and standard deviation of the quantitative traits and one-way analysis of variance is showed in box plots (Fig. 1).

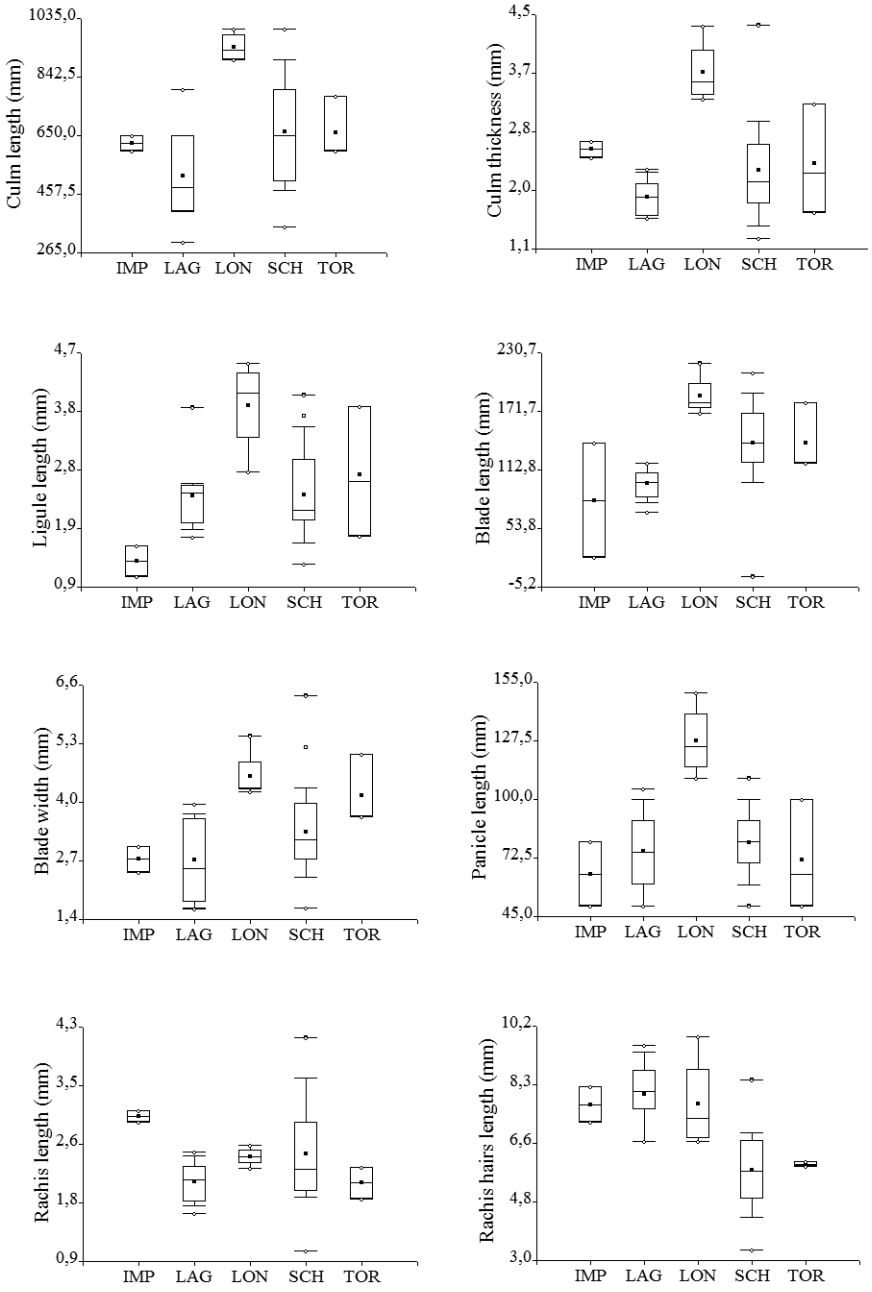
Principal components analysis including all species

Variation along the first three axes from the PCA incorporating all tentative species of the *B. saccharoides* complex is illustrated in Figure 2. Table 2 shows the three main components that explain 56% (24, 19 and 13%, respectively) of the total variation. The cophenetic correlation is r=0.87, indicating a good fit between the euclidean distance among OTUs in two dimensional plot. Loading on the first component was contributed mainly by the following characters: sessile spikelet length and width, pedicellate spikelet length, pedicel length, awn length, culm length and thickness, presence or absence of hairs at the nodes, and blade length. Almost all populations of *B. saccharoides* showed a continuous morphological variability for this component. Loading on the second component was contributed mainly by the type of ramification, blades length and width, presence or absence of hairs at the ligular zone and adaxial blade, hair at the lower glume of sessile spikelets, callus hairs length, and rachis length. Plotting on components 1 and 2 showed an overlap among populations of *B. saccharoides* and *B. torreyana*. Populations of *B. longipaniculata*, *B. imperatoides* and *B.*

laguroides were differentiated. Loading on the third component was contributed mainly by the pedicel hairs length, rachis hairs length, panicle length, pedicel length, callus hair length and presence or absence of hairs at the nodes. Plotting on components 1 and 3 showed an overlap among *B. saccharoides* populations and *B. imperatoides* population. The populations of *B. longipaniculata*, *B. torreyana* and *B. laguroides* were differentiated from other populations of the complex. Components 1, 2 and 3 separated clearly the populations of *B. laguroides* from all the other species of *B. saccharoides* complex (Fig. 2).

Discriminant analysis including all species

Discriminant analysis correctly classified specimens with 98.04% success in the classification matrix (Fig. 3), coinciding with the results obtained by means of PCA. The absolute values of the coefficients of the first two standardized discriminant functions are shown in Table 3. The first canonical axis explained 61.19% of the morphometric variation and the second canonical axis explained 25.29%. The specimens of *B. saccharoides* had positive canonical coefficients for the first axis and the characters that best discriminate are



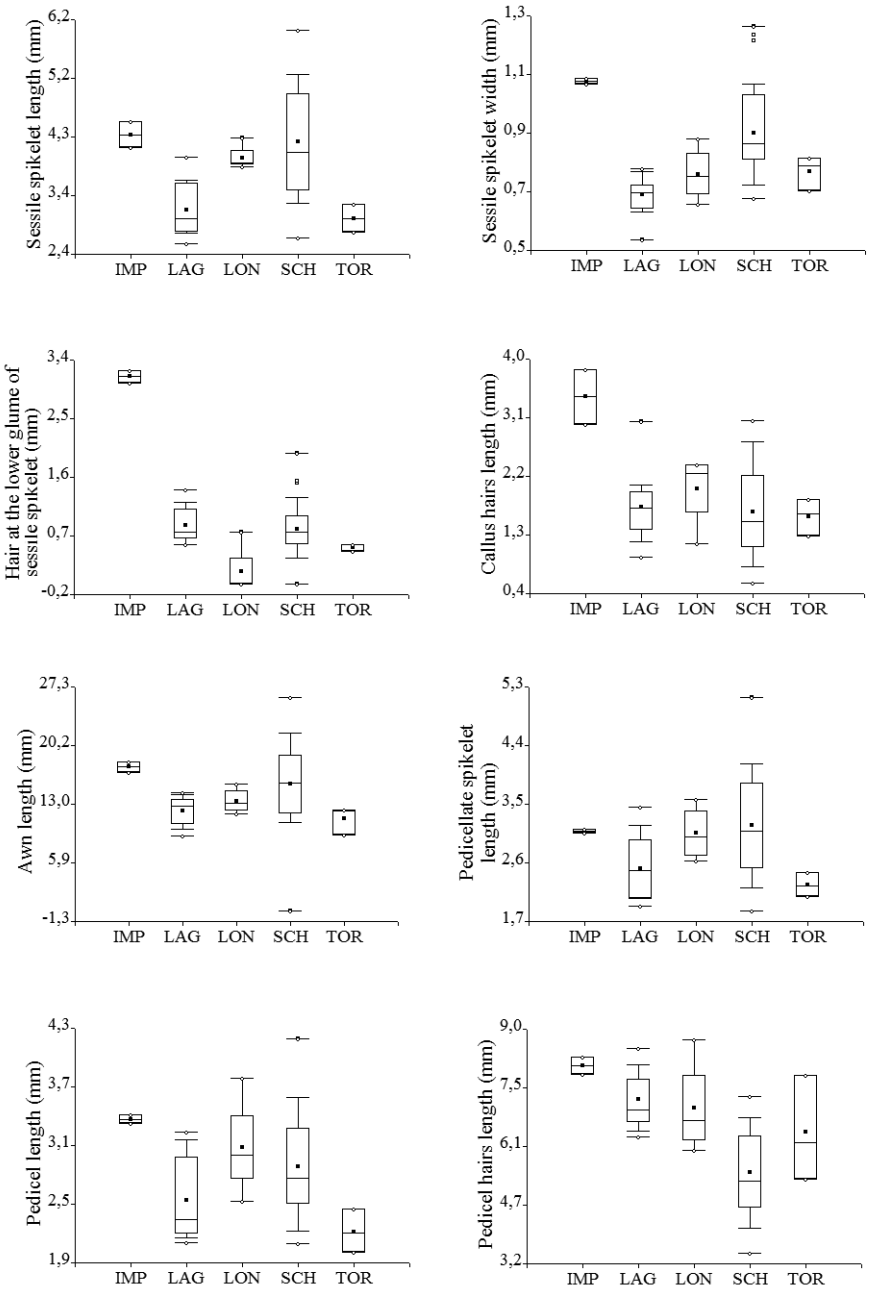


FIGURE 1. Box plots representing the mean, median, interquartile range, adjacent values (lines), and outliers (dots) of some exomorphological characters in each species analyzed. IMP: *B. imperatoides*, LAG: *B. laguroides*, LON: *B. longipaniculata*, SCH: *B. saccharoides*, TOR: *B. torreyana*.

the pedicellate spikelet length, the sessile spikelet width, blade width, panicle length and ligule length (Fig. 3). High negative values on first axis are mainly determined by the culm thickness, rachis length, rachis hairs length, pedicel length, hair at the lower glume sessile spikelets length and hairs pedicel length. The specimens of *B. imperatoides*, *B. longipaniculata* and *B. laguroides* were grouped in the left of the graph. Populations of *B. torreyana* were grouped in the middle portion of the graph. High positive value on the second canonical axis corresponded to pedicellate spikelet length, hair at the lower glume sessile spikelets length, and sessile spikelet width, which aligns to specimens of *B. imperatoides*, while high negative values on the second canonical axis are characterized by pedicel length, ligule length, and panicle length, which align to specimens of *B. longipaniculata* (Fig. 3). According to quantitative characters, the specimens of *B. imperatoides* can be identified by the mean values of the callus hairs length and sessile spikelet width (see Fig. 1), and the specimens of *B. longipaniculata* by the mean values of the culm thickness and length, as well as blade and

panicle length (see Fig. 1). The specimens of *B. laguroides*, *B. torreyana* and *B. saccharoides* were grouped in the middle portion of the graph. *B. laguroides* differs from the other two taxa by having leaf blades shorter than 120 mm and rachis hairs length exceeding 9 mm (see Fig. 1). *Bothriochloa torreyana* has leaf blade width of about 4.12 mm and qualitative characters such as glabrous ligular region and cauline ramification. *Bothriochloa saccharoides* differs from the other taxa by its spikelet sessile length exceeding 6 mm and 1.25 mm width, the pedicellate spikelet longer than 5.15 mm and the pedicel length not exceeding 7.32 mm (see Fig. 1).

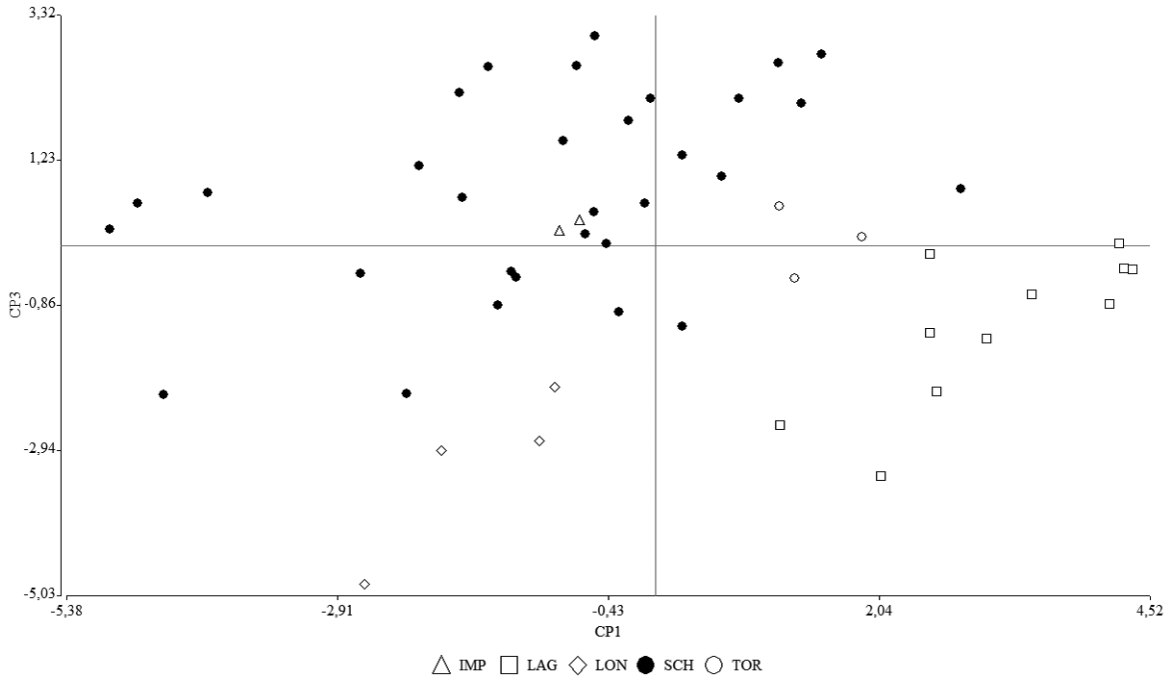


FIGURE 2. Plot from the first three principal components of the principal components analysis (PCA) that incorporated all tentative species in the study. IMP: *B. imperatoides*; LAG: *B. laguroides*; LON: *B. longipaniculata*; SCH: *B. saccharoides*; TOR: *B. torreyana*.

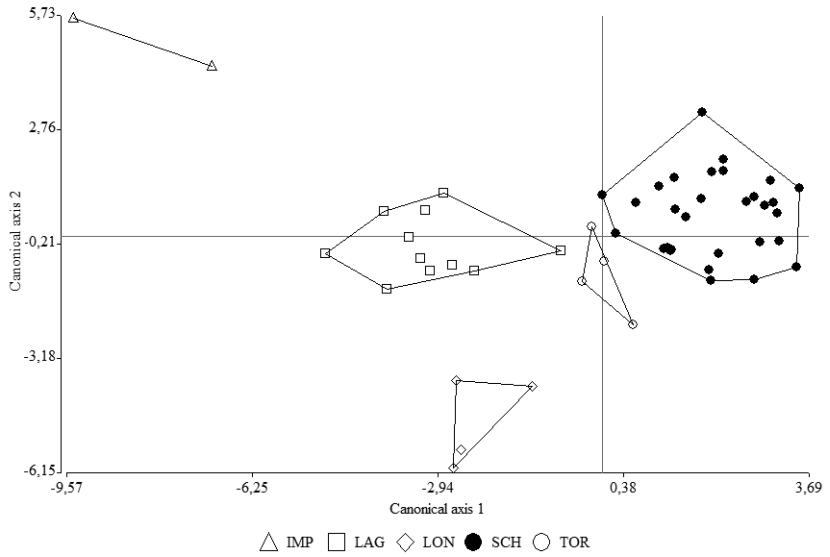


FIGURE 3. Plot of discriminant analysis (DA) along the first two discriminat axes obtained from all populations of *B. saccharoides* complex pertaining to the priori defined groups. IMP: *B. imperatoides*; LAG: *B. laguroides*; LON: *B. longipaniculata*; SCH: *B. saccharoides*; TOR: *B. torreyana*.

TABLE 2. Contributions of individual characters to the first three multivariate axes of the principal components analysis (PCA) incorporating all tentative taxa of the *Bothriochloa saccharoides* complex and *B. saccharoides* subgroups only. Characters are numbered according to Table 1.

Character	All taxa			*B. saccharoides*	
	PC1	PC2	PC3	PC1	PC2
1	-0.26	0.20	-0.08	-0.02	0.38
2	-0.24	0.21	-0.12	-0.06	0.37
3	-0.24	-0.10	0.35	0	0
4	0.17	-0.28	-0.15	-0.24	-0.03
5	-0.11	0.20	-0.19	-0.13	0.27
6	-0.25	0.25	-0.05	-0.07	0.30
7	-0.11	0.28	-0.14	0.12	-0.06
8	0.07	-0.30	0.04	-0.07	0.19
9	-0.08	-0.18	0.19	0.08	0.25
10	-0.14	0.20	-0.34	-0.02	-0.09
11	-0.22	-0.23	-0.15	-0.32	-0.17
12	0.15	-0.11	-0.47	-0.17	-0.36
13	-0.36	-0.16	-0.03	-0.36	0.11
14	-0.29	-0.21	0.12	-0.29	0.08
15	-0.26	-0.21	0.03	-0.29	0.16
16	-0.12	-0.27	-0.23	-0.33	0
17	-0.01	-0.28	0.16	-0.06	0,18
18	-0.32	-0.16	-0.19	-0.39	-0.01
19	-0.27	-0.20	-0.25	-0.36	-0.17
20	0.13	-0.15	-0.40	-0,17	-0.20
21	-0.12	0.06	0.03	0.01	0.04
22	-0.22	0.25	0.10	0.13	0.17
23	-0.22	-0.04	0.16	-0.12	0.32

TABLE 3. Contribution of the quantitative variables to the first two canonical axes of the discriminant analysis (DA) incorporatingall tentaive taxa of the *Bothriochloa saccharoides* complex and *B. saccharoides* subgroups only. Characters are numbered according to Table 1.

Character	All taxa		*B. saccharoides*	
	C1	C2	C1	C2
1	-0.21	-0,24	0	0.38
2	-1.47	-0.28	0.05	-0.08
5	0.42	0.58	0.66	-1.03
6	-0.08	-0.03	-0.08	0.19
7	0.53	0.15	-0.86	0.05
10	0.75	-0.33	0.70	-1.35
11	-0.83	-0.22	-0.64	0.89
12	-1.12	0.05	-1.34	0.72
13	-0.04	0.13	1.28	-0.78
14	1.09	0.39	-0.96	-0.40
15	0.11	-0.28	-0,05	-0.38
16	-0.36	-0.27	1,11	0.47
17	-0.59	0.86	-0.74	0.47
18	1.66	1.14	2.12	1.92
19	-0.76	-0.62	-1.80	-1.95
20	-0.47	-0.09	-0.60	0.34

Principal components analysis including the specimens of *B. saccharoides*

The PCA (cophenetic coefficient of correlation=0.78) conducted on the *B. saccharoides* specimens in relation to geographical distribution shows the specimens from North America, West Indies and South America to form discrete groups (Fig. 4). Table 2 shows the two main components that explain 40% (23 and 17%, respectively) of the total variation. The West Indies and North American specimens exhibit some overlapping. Brazilian populations were closest to West Indian and North American populations (see arrows, Fig. 4). Loading on the first component was contributed mainly by the sessile and pedicellate spikelet length, pedicel length, rachis length, callus hairs length, sessile spikelet width and awn length. Loading on the second component was contributed mainly by culm length and thickness, presence of violet spots on lower glume of sessile spikelets, rachis hairs length, blade length, ligule length, and presence or absence of hairs at the abaxial surface blade.

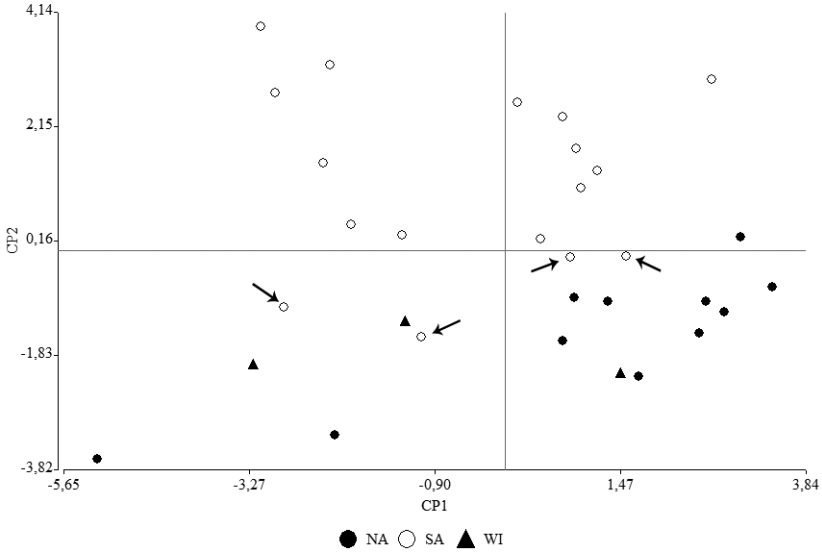


FIGURE 4. Plot from the first two principal components of the principal components analysis (PCA) that incorporated all tentative American *B. saccharoides* specimens. NA: specimens from North American; SA: specimens from South America; WI: specimens from West Indies. The arrows indicate Brazilian populations.

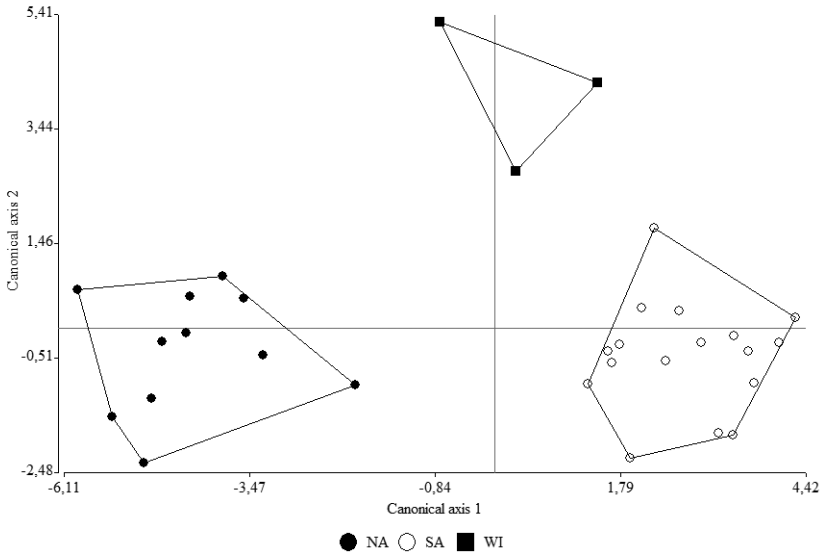
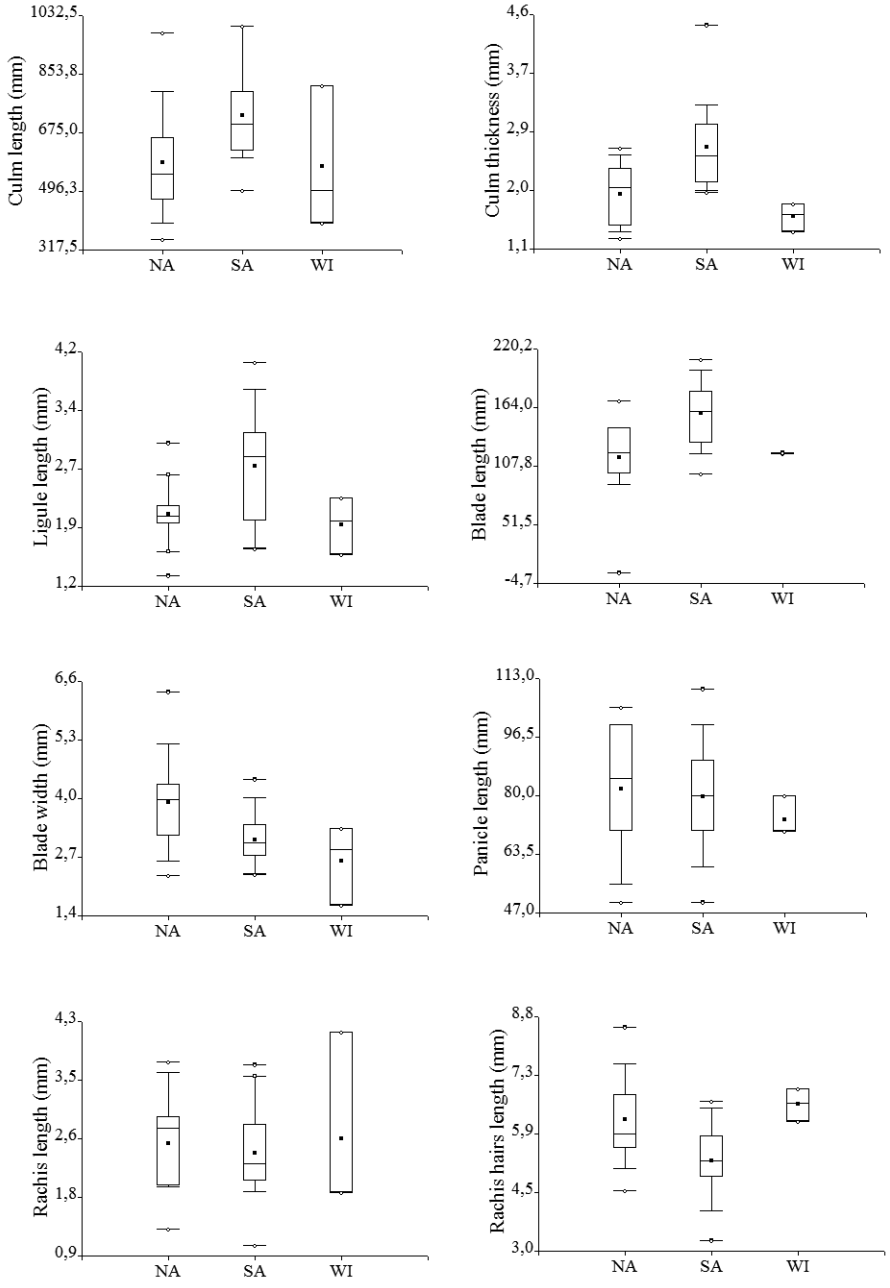


FIGURE 5. Plot of discriminant analysis (DA) along the first two discriminat axes obtained from all tentative American *B. saccharoides* specimens. NA: specimens from North American; SA: specimens from South America; WI: specimens from West Indies.

Discriminant analysis including the specimens of *B. saccharoides*

Discriminant analysis of all specimens of *Bothriochloa saccharoides* correctly classified specimens with 100% success in the classification matrix (Fig. 5), coinciding with the results obtained by means of PCA. The absolute values of the coefficients of the first two standardized discriminant functions are shown in Table 3. The first canonical axis expressed 85.62% of the morphometric variation and the second canonical axis explained 14.38%. The specimens of *B. saccharoides* from North America had negative canonical coefficients for the first axis and the characters that best discriminate are the pedicel length, sessile spikelets width, blade width, rachis hairs length, hair at the lower glume sessile spikelets length and pedicel hairs length (Fig. 5). High positive values on first axis are mainly determined by the sessile and pedicellate spikelet length, callus hairs length, and panicle length. The specimens of *B. saccharoides* from West Indies and South America are grouped to the right of the graph. High positive value on the second canonical axis corresponded to the pedicellate spikelet length, rachis length, rachis hairs length, callus hairs length, and the length of hairs on the



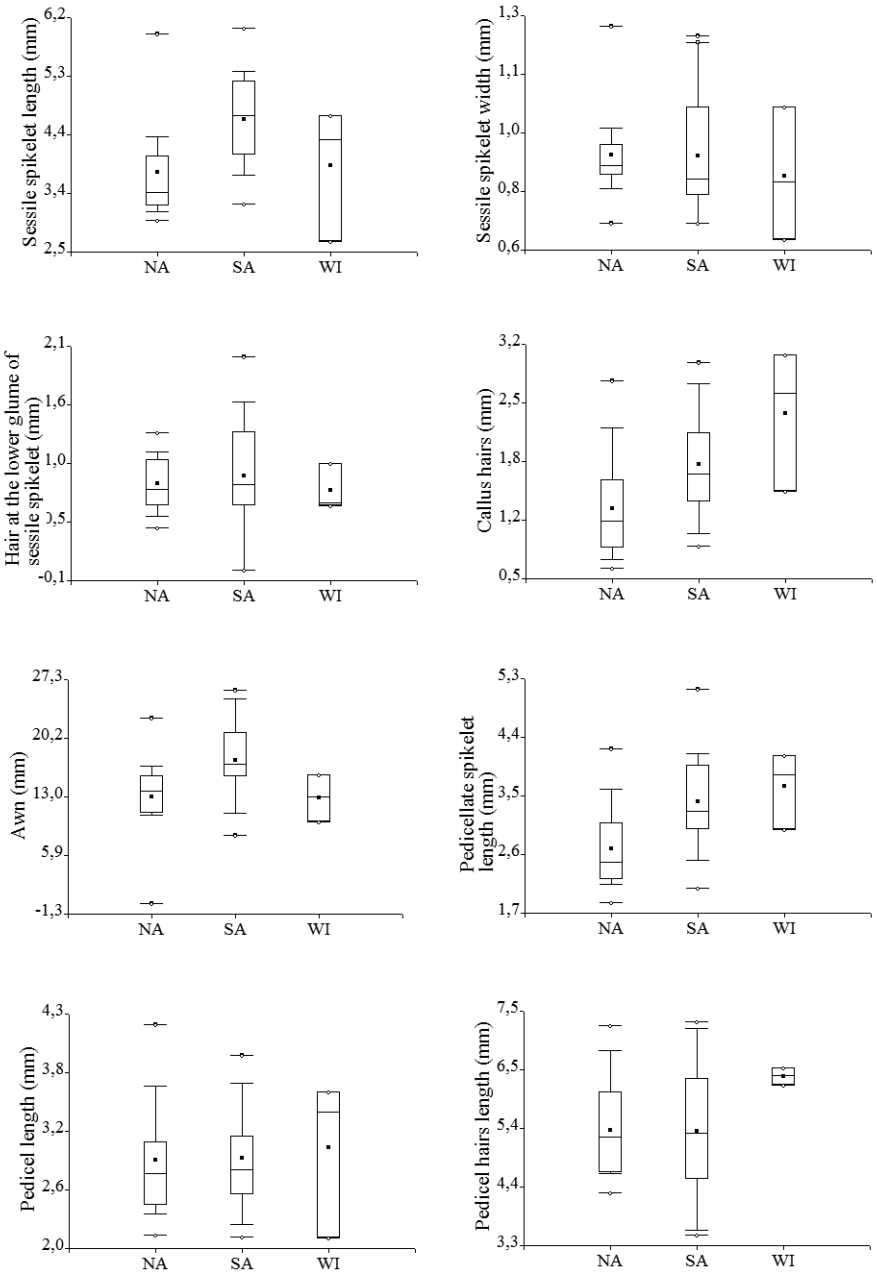


FIGURE 6. Box plots representing the mean, median, interquartile range, adjacent values (lines), and outliers (dots) of some quantitative morphological characters in populations of *B. saccharoides* according to their grographic distribution. NA: North America, SA: South America, WI: West Indies.

lower glume sessile spikelets, which mainly groups to specimens of *B. saccharoides* from the West Indies, while high negative values on the second canonical axis are characterized by lengths of pedicel, panicle and ligule, and sessile spikelet length and width, which align to the specimens from North America and South America (Fig. 5). However, quantitative characters such as culm thickness and blade length, and qualitative traits such as the abaxial surface of the blades being sparsely pilose and the groove being wide, distinguish specimens from South America from North American and West Indies specimens (Fig. 6).

Principal components analysis incorporating chemical data from all species

On the other hand, when adding essential oil composition provided by Scrivanti *et al.* (2009) to the morphological matrix, all the groups show better resolution (cophenetic coefficient of correlation=0.84) (Fig.

7). The *B. imperatoides*, *B. torreyana*, *B. longipaniculata* and *B. laguroides* specimens are well defined and separated from the *B. saccharoides* specimens from South America. Unfortunately, there are no studies on the chemical composition of essential oils of *B. saccharoides* specimens from North America and West Indies, therefore they were not included in this analysis. The PCA analysis based on the combination of morphological and chemical data clearly distinguished the populations of *B. imperatoides, B. laguroides, B. longipaniculata, B. saccharoides* and *B. torreyana* (Fig. 7). Loading on the first component was contributed mainly by sessile spikelets length, presence of γ-gurjunene and *E*-β-fernasene, presence or absence of hair at the nodes, presence or absence of 1-tetradecane, n-dodecane and hexadecene. Loading on the second component was contributed mainly by blade width, presence or absence of hairs at the abaxial and adaxial surface blades, hair at the lower glume sessile spikelets length, presence or absence of 1-tetradecene and *E,E*-farnesol, alloaromadendrene and dedecanoic acid.

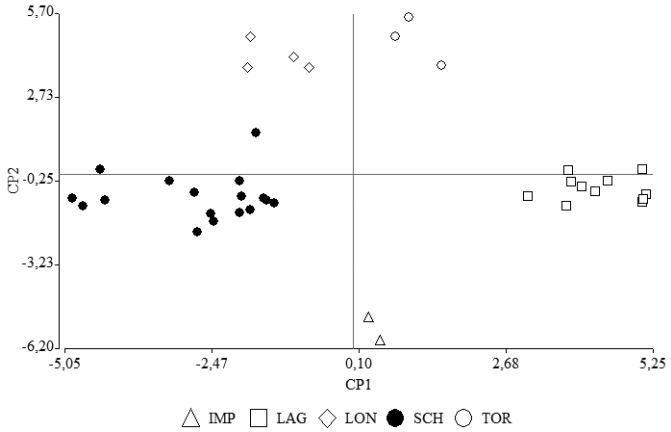


FIGURE 7. Plot from the first two principal components of the principal components analysis (PCA) evaluated for morphological and chemical characters that incorporated all tentative species. IMP: *B. imperatoides*; LAG: *B. laguroides*; LON: *B. longipaniculata*; SCH: *B. saccharoides*; TOR: *B. torreyana*.

Discussion

Our results show that multivariate methods based on quantitative and qualitative morphological traits allow the differentiation of five related species within of *B. saccharoides* complex. The populations recognized as *B. saccharoides* differ among themselves according to their geographic region.

The PCA analysis incorporating all tentative species of the *B. saccharoides* complex distinguished five groups in their natural habitats (Fig. 2). It is clearly shown that *B. imperatoides, B. laguroides, B. torreyana* and *B. longipaniculata*, as traditionally circumscribed, are morphologically and chemically distinct from the *B. saccharoides* forms, and these results are consistent with previous reports from Allred & Gould (1983) and Scrivanti *et al*. (2011). The PCA and DA analysis demonstrate clear and substantial morphometric differences among the five species of the *B. saccharoides* complex. Several quantitative and qualitative morphological measurements distinguished members of the complex. The incorporation of chemical markers in this study, from the work of Scrivanti *et al*. (2009), contributed to a better discrimination of the taxa.

B. imperatoides is characterized by the combination of pilose adaxial and abaxial leaf blade surface; sparsely pilose ligular region; callus hairs 3–3.9 mm long; hair at the lower glume sessile spikelets 3.1–3.3 mm long; sessile spikelet ca. 1 mm wide; awn 16.9–18.1 mm long. In addition, the South American specimens are distinguished by the presence of chemical compounds such as 2-*E*-hexenyl butanoate, damascone (*E*)-β and *E,E*-farnesol.

B. laguroides is characterized by the combination of glabrous nodes; pilose ligular region; pilose adaxial surface blades; rachis hairs 6.6–9.6 mm long; pedicel hairs 6.3–8.5 mm long. In addition, the South American specimens are distinguished by the presence of chemical compounds such as 1-tetradecene, hexadecene and *E,E*-farnesol.

B. longipaniculata is characterized by the combination of panicle 11–15 cm long; blades 17–22 × 0.4–0.5 cm; ligule 2.8–4.6 mm long; culms ca. 90–100 × 0.3–0.4 cm; ramification cauline; callus hairs 1.2–2.4 mm long; pedicel hairs 2.5–3.8 mm long; nodes glabrous. In addition, the South American specimens are distinguished by the presence of chemical compounds such as farnesyl acetate, dodecanoic acid and *E,E*-farnesol.

B. torreyana is characterized by sessile spikelets 2.8–3.2 × 0.7–0.8 mm in size; pedicellate spikelets 2.1–2.5 mm long; pedicel 2–2.4 mm long; glabrous nodes; glabrous ligular region; rachis hairs 5.8–6 mm long, hairs at the lower glume sessile spikelets 0.5–0.6 mm long. In addition, the South American specimens are distinguished by the presence of chemical compounds such as alloaromadendrene, 1-tetradecene and farnesyl acetate.

B. saccharoides is characterized mainly by the combination of sessile spikelet 2.7–6 × 0.6–1.3 mm in size; pedicellate spikelet 1.9–5.2 mm long; pedicel 2.1–4.2 mm long; awn up to 26 mm long; pilose nodes; rachis 1.1–4.2 mm long; ramification cauline; blades 10–21 × 0.16–0.63 cm; culms 35–100 × 0.1–0.4 cm; sparsely pilose abaxial surface blade; hair at the lower glume sessile spikelets 0.6–2 mm long. In addition, the South American specimens are distinguished by the presence of chemical compounds such as γ-gurjunene and E-β-farnesene.

When populations of *B. saccharoides* are analysed at a geographical scale, patterns of variation become much more obvious, giving a general picture of morphological variation of the typical species. The South American populations differ from North American and West Indian mainly by their abaxial surface blade sparsely pilose, narrow groove, rachis hairs shorter, violet stained at the apex of the spikelets, culm and blades wider and longer, respectively. The North American populations differ from West Indian mainly by wider blades and callus hairs shorter. The presence of wider groove observed in specimens from North America and West Indies studied do not agree with Allred & Gould (1983) observations since they observed the opposite in their materials. This character does not contribute to delimitation of the taxa in our analysis. Nevertheless, other quantitatives morphological traits mentioned above allow the separation of the South American populations from those of North America and West Indies. The results obtained do not provide statistical support for considering them as independent species. However, a distinction at subspecies level is possible due to their different geographic ranges (Luckow 1995) and to the significant differences of some morphological characters. Taking into account their current geographical distribution and spatial isolation and their morphological peculiarities, it can be suggested that their morphological distinction is being formed through an incipient process of allopatric speciation.

Summing up, the results of the multivariate analysis based on morphological traits support the identity of five species, one of them with three subspecies. Based upon the information obtained, a new identification key for these taxa is proposed.

Taxonomic treatment

Key to the species of *Bothriochloa saccharoides* complex

1. Nodes glabrous 2
- Nodes pilose..... 3
2. Culms longer than 90 cm. Blades 18–22 cm long. Ligule longer than 2.8 mm. Panicle 11–15 cm long. Farnesyl acetate, dodecanoic acid and *E,E*-farnesol present ..... 3. *B. longipaniculata*
- Culms not more 85 cm long. Blades 7–18 cm long. Ligule less than 2.8 mm long. Panicle 5–10 cm long 4
3. Adaxial and abaxial surface blade abundantly pilose. Sessile spikelet more than 1 mm wide. Callus hairs longer than 3 mm. Hair at the lower glume sessile spikelet up 3 mm long. Pedicel hairs 7.8–8.3 mm long. 2-*E*-hexenyl butanoate, damascone (*E*)-β and *E,E*-farnesol present ..... 1. *B. imperatoides*
- Adaxial and abaxial surface blade usually glabrous. Sessile spikelet less than 1 mm wide. Callus hairs less than 3 mm long. Hair at the lower glume of sessile spikelets less than 2 mm long. Pedicel hairs 3.5–7.3 mm long. γ-gurjunene and E-β-farnesene present (in South American specimens) 5

4. Ramification basal. Blades 7–12 cm long. Ligular region pilose. Rachis hairs 6.6–9.5 mm long. Hair at the lower glume of sessile spikelets 0.6–1.45 mm long. E,E-farnesol and hexadecene present .....2. *B. laguroides*
- Ramification cauline. Blades 12–18 cm long. Ligular region glabrous. Rachis hairs 5.8–6.0 mm long. Hair at the lower glume of sessile spikelets 0.5–0.6 mm long. Alloaromadendrene, 1-tetradecene and farnesyl acetate present .. ..7. *B. torreyana*
5. Abaxial surface blade sparsely pilose. Groove narrow. Rachis hairs about 5 mm long. Violet stains usually on apex of the spikelets. Culm longer than 80 cm. Blades exceed 15 cm long .....6. *B. saccharoides* subsp. *australis*
- Abaxial surface blade usually glabrous. Groove wide. Rachis hairs up 6 mm long. Violet stains absent. Culm rarely exceed 70 cm long. Blades shorter than 12 cm long 6
6. Blades about 2.6 mm width. Callus hairs 2.0–2.5 mm long. Ligular region pilose. Pedicellate spikelet usually longer than 3 mm long .....4. *B. saccharoides* subsp. *saccharoides*
- Blades usually about 4 mm width. Callus hairs 1.0–1.5 mm long. Ligular region glabrous. Pedicellate spikelet usually less than 2.9 mm long..... 5. *B. saccharoides* subsp. *americana*

1. *Bothriochloa imperatoides* (Hack.) Herter (1940: 135)

Andropogon saccharoides var. *imperatoides* Hackel (1883: 293). *Andropogon imperatoides* (Hack.) Lillo (1916: 20). Type:—BRAZIL. Habitat in Brasilia australi, no date, *Sello s.n.* (holotype B!).

Bothriochloa springfieldii var. *australis* de Wet (1968: 1249). Type:—URUGUAY. Maldonado: 50 km E of Montevideo, *De Wet Okla 11577* (holotype CEL).

Culms 60–65 cm tall, ca. 3 mm diameter, ramification usually basal, nodes densely pilose; ligule 1.1–1.6 mm long, ligular region sparsely pilose; blades 2.5–14 × 0.2–0.3 cm, adaxial and abaxial blades pilose. Panicle 5–8 cm long, lanceolate, densely pilose. Rachis 2.9–3.1 mm long; rachis hairs 7.2–8.3 mm long. Groove wide. Sessile spikelet 4.1–4.6 × 1.1 mm; lower glume hairs 3.1–3.3 mm long, densely pilose, not pitted; callus hairs 3.0–3.9 mm long; awn 16.9–18.1 mm long; chasmogamous. Pedicellate spikelet ca. 3.1 mm long; pedicel ca. 3.4 mm long, pedicel hairs 7.9–8.3 mm long. No violet stains on the spikelets.

Distribution:—South American native grasses from Argentina, Brazil and Uruguay. Inhabits plains or grasslands of dry climate.

2. *Bothriochloa laguroides* (DC.) Herter (1940: 135)

Andropogon laguroides Candolle (1813: 78). *Trachypogon laguroides* (DC.) Nees von Esenbeck (1829: 349). *Andropogon saccharoides* var. *laguroides* (DC.) Hackel (1883: 293). *Andropogon saccharoides* subsp. *laguroides* (DC.) Hackel (1889: 495). *Sorghum saccharoides* var. *laguroides* (DC.) Kuntze (1898: 368). *Holcus saccharoides* var. *laguroides* (DC.) Hackel (1904: 48). *Bothriochloa laguroides* (DC.) Pilger (1940: 160). *Dichanthium saccharoides* subvar. *laguroides* (DC.) Roberty (1960: 168). *Bothriochloa saccharoides* var. *laguroides* (DC.) Beetle (1975: 344). Type:—MEXICO. Province unknown, no date, “Hab. in Nova Hispania” (not located).

Deyeuxia megapotamica Sprengel (1827: 30). Type:—Brazil. Rio Grande do Sul: Rio Grande, *Sellow* (holotype B!, isotype US-75645!).

Andropogon laguriformis Grisebach (1879: 309). Type:—ARGENTINA. Córdoba, no date, *P.G. Lorentz 176* (holotype GOET-6187!).

Andropogon tenuirachis Fournier (1886: 58). Type:—MÉXICO. San Luis Potosí, *Virlet 1357* (ST).

Culms 30–80 cm tall, 2 mm diameter, ramification basal, nodes glabrous, dark; ligule 1.7–3.8 mm long, ligular region pilose; blades 7–12 × 0.2–0.4 cm, adaxial and abaxial blades usually glabrous. Panicle 5–10.5 cm long, lanceolate. Rachis 1.6–2.5 mm long, rachis hairs 6.6–9.6 mm long. Groove wide. Sessile spikelet 2.6–4 × 0.5–0.8 mm; lower glume hairs on lower half 0.6–1.5 mm long, not pitted; callus hairs 1–3.1 mm long; awn 9.1–14.4 mm long; chasmogamous. Pedicellate spikelet 1.9–3.5 mm long; pedicel 2.1–3.3 mm long, pedicel hairs 6.3–8.5 mm long. No violet stains on the spikelets.

Distribution:—American native grasses from Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Panama and United States. Inhabits grasslands and roadsides up to 2600 m elevation.

3. *Bothriochloa longipaniculata* (Gould) Allred & Gould (1983: 180).

Andropogon saccharoides var. *longipaniculatus* Gould (1955: 18). *Bothriochloa saccharoides* var. *longipaniculata* (Gould) Gould (1959: 212). Type:—UNITED STATES. Texas: Brazos Co., southwestern limits of Collage Station, near Consolidated School, *Gould 6670* (holotype TAES!, isotype MO!).

Culms 90–100 cm tall, 3–4 mm diameter, ramification cauline, nodes glabrous; ligule 2.8–4.6 mm long, ligular region glabrous; blades 17–22 × 0.4–0.5 cm, adaxial and abaxial blades glabrous. Panicle 11–15 cm long, lanceolate. Rachis 2.3–2.6 mm long, rachis hairs 6.6–9.8 mm long. Groove wide. Sessile spikelet 3.8–4.3 × 0.6–0.9 mm; lower glume usually glabrous or pilose on middle low (0-)0.2–0.8 mm long, not pitted; callus hairs 1.2–2.4 mm long; awn 11.8–15.5 mm long; chasmogamous. Pedicellate spikelet 2.7–3.6 mm long; pedicel 2.5–3.8 mm long, pedicel hairs 6–8.7 mm long. Rarely violet stains on the spikelets.

Distribution:— American native grasses, distributed in two disjunct regions North and South America from Argentina, Brazil, Guatemala, Mexico, Panama, Paraguay and United States. Inhabits sandy soils near rivers and water sources between 100 and 2250 m elevation.

4. *Bothriochloa saccharoides* (Sw.) Rydberg (1931: 81) subsp. *saccharoides*.

Andropogon saccharoides Swartz (1788: 26). *Andropogon saccharoides* subsp. *genuinus* Hackel (1889: 493), *nom. inval*. *Sorghum saccharoides* (Sw.) Kuntze (1891: 792). *Holcus saccharoides* (Sw.) Stuckert (1904: 48). *Amphilophis saccharoides* (Sw.) Nash (1912: 125). *Bothriochloa saccharoides* (Sw.) Rydberg (1931: 81). *Dichanthium saccharoides* (Sw.) Roberty (1960: 168). Type:—JAMAICA. Province unknown, no date, *Swartz s.n.* (holotype S!).
Andropogon berteronianus Steudel (1854: 380). Type:—CHILE. In pascuis saxosis praeruptis maritimis loco dicto: "la plaga ancha" et in fruticetis rupestribus Valparaiso, *Bertero 799* (holotype NY-38429!; isotypes MO-2523209!, US-1063655!).
Andropogon kunthii Fournier (1886: 59). Type:—MEXICO. *Sesse s.n.* (*BAA-1422!*)
Andropogon saccharoides var. *surius* Krause (1914: 334). Type:—BARBADOS. *Wiegand 2085* (not traced).

Culms 40–82 cm tall, 1–2 mm diameter, ramification usually basal, nodes pilose; ligule 1.6–2.3 mm long, ligular region pilose; blades 12–12.5 × 0.2–0.3 cm, abaxial and adaxial blade glabrous, adaxial blades rarely hirsute. Panicle 7–8 cm long, lanceolate, densely pilose. Rachis 1.8–4.2 mm long, rachis hairs 6.2–7 mm long. Groove wide. Sessile spikelet 2.7–4.7 × 0.7–1 mm; lower glume hairs 0.6–1 mm long, not pitted; callus hairs 1.5–3.1 mm long; awn 10–15.7 mm long; chasmogamous. Pedicellate spikelet 3–4.1 mm long; pedicel 2.1–3.6 mm long, pedicel hairs 6.2–6.5 mm long. Usually no violet stains on the spikelets.

Distribution:—Native from Central America: Cuba, El Salvador, Guatemala, Haiti, Honduras, Jamaica, Nicaragua, Panama and the Dominican Republic. Inhabits grasslands.

Subspecific variation:—The illustration can be found in Swallen & McClure (1955: 25).

5. ***Bothriochloa saccharoides*** subsp. *americana* Scrivanti, *subsp. nov.*

It differs from the typical subspecies by the ramification usually cauline, wider blades, adaxial surface of the blades usually hirsute, ligular region glabrous, panicle scarcely hairy, callus hairs and pedicellate spikelet shorter.

Type:—UNITED STATES. Texas: Pecos County, 7 January 1943, *Tharp 43 a 92* (holotype LSU 58501!).

Culms 35–98 cm tall, 1–3 mm diameter, ramification usually cauline, nodes pilose; ligule 1.3–3 mm long, ligular region usually glabrous; blades 5.5–17 × 0.2–0.6 cm, adaxial blades occasionally hirsute, abaxial blade glabrous. Panicle 5–10.5 cm long, lanceolate, scarcely hairy. Rachis 1.3–3.7 mm long, rachis hairs 4.5–8.5 mm long. Groove wide. Sessile spikelet 3–5.9 × 0.7–1.3 mm; lower glume hairs 0.4–1.3 mm long, not pitted; callus hairs 0.6–2.8 mm long; awn 0.5–22.7 mm long; chasmogamous. Pedicellate spikelet 1.9–4.2 mm long; pedicel 2.1–4.2 mm long, pedicel hairs 4.3–7.3 mm long. Usually no violet stains on the spikelets.

Distribution:—North American native grass from United Stated and México. Inhabits grasslands.

Subspecific variation: The illustration can be found in Britton & Brown (1913: 119).

6. *Bothriochloa saccharoides* subsp. *australis* Scrivanti, *subsp. nov.*

It differs from the typical subspecies by the more culm thicker, ramification usually cauline, ligule longer, blades usually longer, abaxial surface of the blades pilose, panicle usually longer than 8 cm and generally dark green in living plants, rachis hairs generally shorter than 6 mm, exceptionally exceed 6.5 mm, sessile spikelet longer than 4.5 mm, lower glume usually glabrous, narrower groove and awn usually exceed 25 mm.

Type:—ARGENTINA. Córdoba: Copina, 15 April 2003, *Scrivanti 76* (holotype CORD!).

Culms 50–100 cm tall, 2–4 mm diameter, ramification usually cauline, nodes pilose; ligule 1.6–4 mm long, ligular region usually pilose, blades 10–21 × 0.2–0.4 mm, adaxial and abaxial blade usually pilose. Panicle 5–11 cm long, lanceolate, abundantly hairy. Rachis 1.1–3.7 mm long, rachis hairs 3.3–6.7 mm long. Groove usually narrow. Sessile spikelet 3.3–6 × 0.7–1.3 mm; lower glume occasionally glabrous or pilose on lower half 0.5–2 mm long, no pitted; callus hairs 0.9–3 mm long; awn 8.4–26 mm long; chasmogamous. Pedicellate spikelet 2.1–5.2 mm long; pedicel 2.1–3.9 mm long, pedicel hairs 3.5–7.3 mm long. Usually with violet stains on the spikelets.

Distribution:—South American native grass from Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Peru, Uruguay and Venezuela. Inhabits clay limestone soils in grasslands up 2600 m elevation.

Subspecific variation:—The illustration can be found in Vega & Scrivanti (2012: 509)

7. ***Bothriochloa torreyana*** (Steud.) Scrivanti & Anton (2011: 156).

Andropogon torreyanus Steudel (1840: 93). *Andropogon saccharoides* var. *torreyanus* (Steud.) Hackel (1889: 495). *Amphilophis torreyanus* (Steud.) Nash (1901: 71). *Bothriochloa saccharoides* var. *torreyana* (Steud.) Gould (1959: 212). *Dichanthium saccharoides* subvar. *torreyanum* (Steud.) Roberty (1960: 168). *Bothriochloa laguroides* subsp. *torreyana* (Steud.) Allred & Gould (1983: 179). Type:—UNITED STATES. Oklahoma: Indian Territory, Canadian River, *James s.n.* (holotype NY!).

Andropogon hassleri var. *aristatus* Hackel (1909: 341). Type:—PARAGUAY. Province unknown, in campis in regione fluminis Pilcomayo, *Rojas 448a* (fragment US).

Andropogon saccharoides var. *pulvinatus* Gould (1957: 25). *Bothriochloa saccharoides* var. *pulvinata* (Gould) Gould (1959: 212). Type:—MÉXICO. Coahuila: Rancho Sierra Hermosa, 40 miles west of Monclava, *Gould 6467* (holotype TAES!, isotype US!).

Culms 60–78 cm tall, 2–3 mm diameter, ramification cauline, nodes glabrous; ligule 1.8–3.9 mm long, ligular region glabrous; blades 12–18 × 0.4–0.5 cm, adaxial and abaxial blades usually glabrous. Panicle 5–10 cm long, lanceolate, hairs small. Rachis 1.8–2.3 mm long, rachis hairs 5.8–6 mm long. Groove wide. Sessile spikelet 2.8–3.2 × 0.7–0.8 mm; lower glume usually glabrous or pilose on lower half 0.5–0.6 mm long, not pitted; callus hairs 1.3–1.9 mm long; awn 9.3–12.3 mm long; chasmogamous. Pedicellate spikelet 2.1–2.5 mm long; pedicel 2–2.5 mm long, pedicel hairs 5.3–7.8 mm long. No violet stains on the spikelets.

Distribution:— American native grasses, distributed in two disjunct regions North and South America from Argentina, Brazil, Chile, Honduras, Mexico, Panama and United States. Inhabits sandy, calcareous and rocky soils between 350–1900 m elevation.

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Appendix 1. Vouchers and specimens examined

Bothriochloa imperatoides:—ARGENTINA. Buenos Aires: La Plata, around La Plata, SE grassland, 21 December 1922, *Cabrera 2660* (NY). Entre Ríos: Federación, route 14 intersection with Río Mandisoví Grande towards Federación, 30°56´39´´S 58°03´29´´W, 25 March 2010, *Scrivanti 353* (CORD). La Paz, to 3 km access on route 12, 30°46´03´´S, 58°35´19´´W, 15 March 2005, *Scrivanti 321* (CORD). URUGUAY. Lavalleja: route 8 82 km from Solís de Mataojo towards Minas, 34°34´56´´S 55°27´53´´W, 13 March 2005, *Scrivanti 239* (CORD). Maldonado: route 8 km 90 access to Piriápolis, 10 June 1990, *Marchi 103* (ICN), *104* (ICN).

Bothriochloa laguroides:—ARGENTINA. Córdoba: Colón, La Cumbre, Av. San Martín 700-800, road to route 38, 26 April 2004, *Scrivanti 178* (CORD). In the fields of lavender, on road La Madrid crossing the rails, 20 January 2004, *Scrivanti 109* (CORD). Punilla, Cosquín, 20 January 2004, *Scrivanti 107* (CORD). San Justo, 16 December 1970, *Ariza Espinar 2475* (CORD). Santa María, 08 February, *Anton 341* (CORD). Río Segundo, road from Pilar to Villa del Rosario, 200 m entrance to Costa Sacate, 31°39´S 63°46´15´´W, 26 December 2003, *Scrivanti 94* (CORD). Catamarca: Ancasti, 02 December 1960, *Hunziker 15681* (CORD). Corrientes: Mercedes, access to Mercedes, 29°10´42´´S 58°06´W, 3 March 2004, *Scrivanti 131* (CORD). Entre Ríos: Paraná, access to Hasemkamp, 31°34´40´´S 59°52´54´´W, 2 March 2004, *Scrivanti 121* (CORD). BRAZIL. Rio Grande do Sul: Sananduba, towards Cacique Doble, 24 March 2004, *Scrivanti 162* (CORD).

Bothriochloa longipaniculata:—ARGENTINA. Chaco: 1° de Mayo, access to Colonia Benitez, 27°18´54´´S 58°59´01´´W, 6 March 2004, *Scrivanti 147* (CORD). San Fernando, route 16 towards Resistencia, 6 March 2004, *Scrivanti 146* (CORD). Entre Ríos: Federación, route 14, crossing with the Mandisoví Grande river, 30°56´28´´S 58°03´25´´W, 15 March 2005, *Scrivanti 242* (CORD). Federal, route 127, 212 km from Conquistadores towards Federal, 30°51´57´´S 58°42´28´´W, 29 March 2004, *Scrivanti 171* (CORD). Paraná, route 12, on entrance to access to Aldea Santa María, 31°35´09´´S 60°00´41´´W, 29 March 2004, *Scrivanti 172* (CORD). Misiones: General Manuel Belgrano, 51.7 km from Bernardo de Irigoyen towards Eldorado, 26°20´17´´S 54°02´45´´W, 27 March 2004, *Scrivanti 166* (CORD). Santa Fe: General Obligado, on route 11 from Resistencia towards Reconquista, 27°37´09´´S 59°11´03´´W, 08 March 2004, *Scrivanti 158* (CORD).

Bothriochloa saccharoides subsp. *saccharoides:*—HONDURAS. Choluteca: San Marcos de Colón, El Aguacate, road to Las Delicias, ca. 3 airline mi directly S of San Franciso, 13°21'26"N 86°54'22"W, 17 June 1994, *Davidse 35073* (MO). Olancho: La Unión, 5 mi E of La Unión along road to Olanchito. Pine forest with a well-developed herbaceous understory dominated by grasses and with broad-leaved forest along the quebrada, 15°03'37"N 86°35'54"W, 1 July 1994, *Davidse 35447* (MO). GUATEMALA. San Marcos: San Miguel Ixtahuacan, La Hamaca, Al. El Salitre, San Miguel Ixtahuacan, 15°16'31"N 91°41'16"W, 13 December 2004, *Morales 3085* (MO).

Bothriochloa saccharoides subsp. *americana:*—. MEXICO. Nuevo León: General Zaragoza, El Salto, located in the municipality of Zaragoza, pine and oak forest, litosol soil, 23°56'39"N 99°45'47"W, 30 June 1994, *Noe Bazualdo 192* (MO). Oaxaca: Teotitlan, locality of Xiquila River (Big Earth) collected along the river, deciduous forest with shrubs, 18°02'N 97°11'W, 22 July 1990, *Sánchez-Ken 60* (MO). UNITED STATES. Louisiana: Cameron Parish, Holleyman Bird Sanctuary at Peveto Beach ca. 8 mi W of Holly Beach, 27 September 1986, *Negron 129* (LSU). Hackberry, Along Hwy. 27 S of Hackberry within the boundaries of Sabine Refuge, *Materne s.n.* (LSU 31947). Oklahoma: Oklahoma County, Village, cleared area for housing developement beside Okla. 74, 10 October 1970, *Rupley 21966* (LSU). Texas: Austin County, Industry, 1 January 1904, *Wurzlow s.n.* (LSU 85986). Dallas County, SMU campus, disturbed ground, blackland clay, unshaded, 15 September 1950, *Storm 1104* (LSU). Lampasas County, Lampasas, about 5 mi. W of Lampasas on Hwy 190 within 1.2 mi. E and W of the Carrol Ranch main gate along side of the road, 11 May 1989, *Namken 5*, (LSU). Roadside ditches and moist valleys, 1 July 1943, *Tharp 43a92* (LSU). Travis County, Tom Miller Dam, water filtration plant area above Tom Miller Dam on Colorado River, 10 June 1975, *Urbatsch 1651* (LSU). Pecos County, Tom Green County, San Angelo, in the vacant lot on the corner of Oregon St. and Foster St, in San Angelo, 11 May 1989, *Manken 20* (LSU).

Bothriochloa saccharoides subsp. *australis:*—ARGENTINA. Catamarca: Ambato, 9 April 1974, *Hunziker 21191* (CORD). Córdoba: Colón, La Cumbre, in the fields of lavender, on road La Madrid and Vélez Sarsfield, 30°52´32´´S 64°30´12´´W, 10 May 2004, *Scrivanti 191* (CORD). On La Madrid street crossing the rails, 20 January 2004, *Scrivanti*

108 (CORD). Road from Ascochinga to 17 km of La Cumbre, 30°56´33´´S 64°22´26´´W, 26 April 2004, *Scrivanti 176* (CORD). Cruz del Eje, 24 March 1970, *Hunziker 20587* (CORD). 11 March 1986, *Astegiano 133* (CORD). Punilla, from Copina towards Mina Clavero, 15 April 2003, *Scrivanti 73* (CORD), *75* (CORD), *76* (CORD). 1 km before the Copina bus stop, 31°34´39´´S 64°39´22´´W, 10 May 2004, *Scrivanti 183* (CORD). Corrientes: Curuzú Cuatiá, route 12 towards Aguay, 29°20´17´´S 58°32´39´´W, 3 March 2004, *Scrivanti 129* (CORD). Mercedes, towards Felipe Yofre, 29°08´41´´S 58°07´54´´W, 3 March 2004, *Scrivanti 133* (CORD). Santa Fe: Vera, on route 11 towards Vera, 29°16´22´´S 59°45´52´´W, 8 March 2004, *Scrivanti 159* (CORD). BRAZIL. Mato Grosso do Sul: 42.5 km SW of Morro do Azeite, access for Carandàzal, 30 October 1985, *Valls 9490* (ICN). Corumbá, 20 km S from entrance Carandàzal, 28 October 1986, *Valls 10365* (ICN). Río Grande do Sul: Porto Alegre, Morro da Policía, 28 March 1990, *Marchi 79* (ICN).Uruguaiana, BR-472, 24 November 1972, *Valls & Barcellos 2503* (ICN).

Bothriochloa torreyana:—ARGENTINA. Corrientes: Paso de Los Libres, route 14, 510-511 km, towards Tapebicua, 29°35´27´´S 57°12´20´´W, 15 March 2006, *Scrivanti 263* (CORD). Santo Tomé, route 94, from Santo Tomé towards Garruchos, 5 March 2010, *Scrivanti 341* (CORD), *343* (CORD), *344* (CORD). Formosa: Formosa, route 11, 1200 km from Clorinda towards Formosa, 25°28´22´´S 58°09´01´´W, 07 March 2004, *Scrivanti 157* (CORD). Misiones: Eldorado, 11 km from Eldorado towards Berbardo de Irigoyen, 26°24´07´´S 54°28´11´´W, 28 March 2004, *Scrivanti 167* (CORD). URUGUAY. Maldonado: Punta del Este, del Mar Avenue and Costanera, 34°36´39´´S 54°55´16´´W, 13 March 2005, *Scrivanti 237* (CORD).