Systematic Botany (2014), 39(3): pp. 804–813

DOI 10.1600/036364414X681509
Date of publication 05/27/2014

Taxon Delimitation in the *Andropogon lateralis* Complex (Poaceae) in Southern South America based on Morphometrical Analyses

Nicolás Nagahama,[1,3] Ana M. Anton,[1] and Guillermo A. Norrmann[2]

[1]Instituto Multidisciplinario de Biología Vegetal (Universidad Nacional de Córdoba / Consejo Nacional de Investigaciones Científicas y Técnicas), Casilla de correo 495, X5000JJC, Córdoba, Argentina.
[2]Facultad de Ciencias Agrarias, Instituto de Botánica del Nordeste (Universidad Nacional del Nordeste / Consejo Nacional de Investigaciones Científicas y Técnicas), casilla de correo 209, 3400, Corrientes, Argentina.
[3]Author for correspondence (nagahama@imbiv.unc.edu.ar)

Communicating Editor: Victoria Sosa

Abstract—In the tribe Andropogoneae, morphological variation is remarkable, mainly in the inflorescence on the pair of spikelets which are the core elements of the inflorescence. The genus *Andropogon* includes the *Andropogon lateralis* complex, which is distributed primarily in South and Central America, comprising approximately twelve taxa and inter-specific hybrids. The aim of this study was to assess morphological variation in the *A. lateralis* complex through morphometric analyses of specimens from natural populations. For this purpose, univariate ANOVA, as well as principal component analysis and discriminant analysis of 19 morphological variables of synflorescences were performed, revealing differences between species and interspecific hybrids. The selected diagnostic traits of species and hybrids based on quantitative characters of the synflorescences provided a valuable tool for taxonomic studies in the genus. The results obtained made it possible to generate the first identification key that includes both species and hybrids of the *A. lateralis* complex for South America.

Keywords—Andropogoneae, ANOVA, canonical discriminant analysis, interspecific hybrids, morphology, principal component analysis.

Andropogon L. is a pantropical genus of grasses with approximately 110 species in grasslands of Africa and America (Clayton and Renvoize 1986; Campbell and Windisch 1986). African species are mainly diploids or tetraploids (Campbell 1983a) while in the New World they are usually diploid or hexaploid (Gould 1967; Norrmann 1985; Campbell and Windisch 1986; Galdeano and Norrmann 2000; Norrmann and Scarel 2000; Norrmann et al. 2004; Nagahama and Norrmann 2012).

Four sections are recognized in the genus, three of which are distributed both in Africa and in the New World (*Andropogon* Stapf, *Leptopogon* Stapf, and *Notosolen* Stapf) while Sect *Piestium* Stapf is restricted to Africa (Stapf 1919; Gould 1967). Species of Section *Leptopogon* are either diploids or hexaploids, and there are three complexes in America: *A. virginicus* L., distributed in North America (Campbell 1983a), while the *A. selloanus* (Hack.) Hack. and *A. lateralis* Nees complexes are mainly distributed in South America (Campbell and Windisch 1986; Norrmann 2009; Nagahama et al. 2013).

The *Andropogon lateralis* complex is considered to be a group of seven allohexaploid species ($2n = 6x = 60$) (Campbell and Windisch 1986; Norrmann et al. 2004; Nagahama et al. 2012), in which anther size and the number of pollen grains in the fertile sessile spikelets are greatly reduced compared with those of the pedicellate spikelets. This diagnostic character (dimorphism of anthers) defines the complex (Campbell 1983a; Campbell and Windisch 1986), which is composed entirely of New World species: (1) *Andropogon arenarius* Hack. is an aggressive sand colonizer of the Atlantic coasts growing in a narrow area near the Atlantic Ocean, from São Paulo state in southeastern Brazil to Uruguay (Zanin 2001; Norrmann 2009). Two species of the *A. lateralis* complex are sympatric with *A. arenarius* (*Andropogon bicornis* L. and *Andropogon lateralis* Nees) and interspecific hybridization occurs among these (Campbell and Windisch 1986; Norrmann 2009). (2) *Andropogon bicornis* is the most invasive species in the complex, is widespread from Argentina to North America (Campbell 1983b), and hybridizes with most species of the *A. lateralis* complex (*A. arenarius*, *A. glaziovii* Hack., and *A. lateralis*). (3) *Andropogon glaziovii* occurs in swamps of Paraguay, Bolivia, and Brazil. So far, natural hybridization has been observed only between *A. glaziovii* and *A. bicornis* at two sites in Paraguay and one in Brazil (Norrmann 2009). (4) *Andropogon hypogynus* Hack. occurs in dense, humid soils of sedimentary origin of northeastern Argentina, Brazil, Bolivia, Colombia, and Paraguay. This species commonly hybridizes with *A. lateralis* in Paraguay and northeastern Argentina, producing fertile progeny. In contrast to *A. lateralis*, *A. hypogynus* does not seem to hybridize with other species that might be sympatric, such as *A. bicornis* (Norrmann 2009). (5) *Andropogon lateralis* is distributed from northeastern Argentina to Brazil and Peru, with scattered populations in Central America and Cuba. This species hybridizes with *A. arenarius* in southeast Brazil and Uruguay, with *A. bicornis* wherever parental species grow together (recorded for Argentina, Brazil, and Paraguay), and with *A. hypogynus*. Only two members of this complex (*A. canaliglumis* Norrmann, Swenson & Caponio and *A. ekmanii* Norrmann, Swenson & Caponio) are endemic to the West Indies (Norrmann et al. 2008).

Zanin and Longhi-Wagner (2006) developed a taxonomic identification key for species of *Andropogon* for Brazil, including *A.* × *lindmanii* Hack. (pro. sp.) [*arenarius* × *lateralis*]; later, Norrmann (2009) proposed the names *A.* × *subtilior* Hack. and *A.* × *coloratus* Hack. for the hybrid combinations *A. bicornis* × *A. lateralis* and *A. hypogynus* × *A. lateralis*, respectively. Nagahama et al. (2012) described *A.* × *catarinensis* Norrmann & Nagahama (*A. arenarius* × *A. bicornis*) and *A.* × *velutinus* Norrmann & Nagahama (*A. bicornis* × *A. glaziovii*) as names for these interspecific hybrids belonging to the *A. lateralis* complex. Thus, the *A. lateralis* complex in southern South America so far comprises five species (*A. arenarius*, *A. bicornis*, *A. glaziovii*, *A. hypogynus*, and *A. lateralis*) and five interspecific hybrids (*A.* × *catarinensis*, *A.* × *coloratus*, *A.* × *lindmanii*, *A.* × *subtilior*,

Table 1. Hybrid combinations among *Andropogon* species studied and taxonomic names used in type collections. The hybrid combination marked with a superscript 1 has not been reported in the wild, and no detailed cytogenetic and fertility analyses have been conducted. Only two herbarium specimens have been located that could represent this hybrid combination, therefore in this study *A.* × *multiflorus* was excluded from the analysis.

Parental species	*A. bicornis*	*A. hypogynus*	*A. lateralis*
A. arenarius	*A.* × *catarinensis*	Not sympatric	*A. lindmanii* *A.* × *lindmanii*
A. bicornis		*A. incanus* var. *bogotensis* *A. lateralis* var. *bogotensis* *A. multiflorus* *A. bogotensis* *A.* × *multiflorus*[1]	*A. incanus* var. *subtilior* *A. lateralis* var. *subtilior* *A.* × *subtilior*
A. hypogynus			*A. coloratus* *A.* × *coloratus*
A. glaziovii	*A.* × *velutinus*	Not found yet	Not found yet

and *A.* × *velutinus*), increasing the taxonomic complexity of this group. Table 1 shows information about the synonymy of hybrids.

The *A. lateralis* complex was originally described by Campbell (1983a) for southern South America. Since then, one of us (G. N.) studied the complex in the region, visiting many herbaria (BAA, CEN, CORD, CTES, FL, G, GH, ICN, K, L, LE, LIL, M, NY, P, RB, S, SI, UB, US, and W) looking for old collections of natural hybrids from the rest of the Americas. Based on these surveys, Norrmann (2009) recognized five hybrid combinations and proposed three main hybridization areas for the *Andropogon lateralis* complex: (1) The Corrientes–Chaco–Misiones (Argentina) area includes combinations involving *A. bicornis*, *A. hypogynus*, and *A. lateralis*. This region contains the boundaries of the Chaco and Amazonic phytogeographical domains. The Paraná River divides the two, leaving the heavy sedimentary soils to the west (*A. hypogynus*), while the east is the most suitable habitat for *A. lateralis*. (2) The Itapirubá site (Brazil, Santa Catarina State) contains combinations involving *A. arenarius*, *A. bicornis,* and *A. lateralis*. All necessary ecotones for each species and the hybrids are present there: moving dunes (*A. arenarius*); fertile, damp soil, generally used for forage (*A. lateralis*); and wet roadsides and swamps (*A. bicornis*). (3) The Paraguayan area holds the restricted combination *A. bicornis* × *A. glaziovii*, and is the southeastern limit of *A. glaziovii*. Norrmann (2009) did not find natural hybrids beyond the area studied in this work. Thus, up to now, most natural hybrids are found in southern South America.

Male and female complete sterility is almost a rule in hybrids within the complex. *Andropogon lateralis* and *A. hypogynus* appear to be the only pair of species whose hybrids show a relatively high level of fertility (Norrmann 2009). In spite of such closeness, both species deserve to remain taxonomically separate because of morphological and ecological features. *Andropogon coloratus* includes variants (F1, F2, and backcrosses) generated through these crosses. Fertility lower than 0.01% has been detected in *A. lindmanii* (Campbell and Windisch 1987; Norrmann 2009).

Morphometric studies provide tools for establishing taxonomic limits when simple qualitative analyses are insufficient (Giussani 2000; Pelser and Houchin 2004; Woods et al. 2005). This is especially remarkable in cases where plant populations are composed of morphologically similar species and/or interspecific hybrids (Denham et al. 2006; Peichoto et al. 2008; Da Costa et al. 2009; Nagahama et al. 2012; Nagahama et al. 2013). Multivariate analyses have been performed for several families of angiosperms, with the aim of elucidating the difficulties involving species complexes (e.g. Eckenwalder 1996; Negrón-Ortiz and Hickey 1996; Oyama 1996; Compton and Hedderson 1997; Bottini et al. 1998; Chandler and Crisp 1998; Hess and Stoynoff 1998; Henderson 2005; Leonard et al. 2005). Particularly in Poaceae, these methods have been used to circumscribe species in *Poa* L. (Giussani 2000), *Deschampsia* P. Beauv. (Chiapella 2000; Chiapella et al. 2011), and *Andropogon* (Nagahama et al. 2013).

In the present study, univariate analysis of variance (one-way ANOVA) and multivariate morphometric analyses such as principal component analysis (PCA) and canonical discriminant analysis (CDA) were performed in an attempt to clarify the taxonomic boundaries within the *A. lateralis* complex in southern South America. The objectives of this work were: (1) to identify quantitative morphological traits with discriminant value that could be used in future cladistic studies and (2) to generate a novel identification key to the *A. lateralis* complex, providing new tools for identifying hybrids that are not easily recognizable by traditional means.

Materials and Methods

***Plant Material*—**The living collection of *Andropogon* species held at the Instituto de Botánica del Nordeste (IBONE), Corrientes, Argentina was used. Additionally, collection trips were undertaken from April 2007–2012, covering northeastern Argentina (Chaco, Corrientes, Formosa, Misiones, and Santa Fe), southeastern Brazil (Rio Grande do Sul and Santa Catarina), and Paraguay (Fig. 1). Each field collection included live samples and synflorescences in full bloom; specimens were identified as natural hybrids only if the putative parents were present at the collection sites. Voucher specimens have been deposited at CORD and CTES. Herbarium material from CTES, ICN, LIL, MBM, MO, SI, US, and W was analyzed. The following taxa were studied: *Andropogon lateralis*, *A. hypogynus*, *A. glaziovii*, *A. bicornis*, *A. arenarius*, *A.* × *lindmanii* (*A. lateralis* × *A. arenarius*), *A.* × *coloratus* (*A. lateralis* × *A. hypogynus*), *A.* × *subtilior* (*A. lateralis* × *A. bicornis*), *A* × *velutinus* (*A. bicornis* × *A. glaziovii*), and *A.* × *catarinensis* (*A. arenarius* × *A. bicornis*). Samples were identified on the basis of morphological and ecological characters listed in Zanin (2001), Norrmann (2009), and Nagahama et al. (2013). Several plants of each population were collected for measurements. A full list of the accessions is given in Appendix 1. Further details of the species and hybrids can be found in Norrmann (2009) and Nagahama et al. (2012).

***Morphological Data Set*—**Morphological characters included in this study are those traditionally used for the delimitation of species in *Andropogon* (Campbell 1983a; Campbell and Windisch 1986; Zanin 2001; Zanin and Longhi-Wagner 2006; Norrmann 2009; Nagahama et al. 2012; Nagahama et al. 2013). We focused particularly on characters of the synflorescences. We excluded vegetative characters from the analysis as in previous analyses because these characters usually show low variability among the species within the complex (Nagahama et al. 2012; Nagahama et al. 2013). In the *A. lateralis* complex, few vegetative characters are variable, i.e. the junciform blade (in contrast to the flat blade in the rest of species) is useful for identifying *A. arenarius* and this character was included in the identification key. The plant height is also useful for the identification of *A. arenarius* and is incorporated in the study character "synflorescence length," SL). For the selection of variables to be measured, the inflorescences were interpreted according to Vegetti and Müller-Doblies (2004), Tivano and Vegetti (2010), and Nagahama et al. (2013). The term "axillary fascicle" (AF) was used to describe the full proximal set of branches originating from the prophylls and the proximal bract. We excluded both the first pair of spikelets and the terminal sessile spikelet of each unit of inflorescence

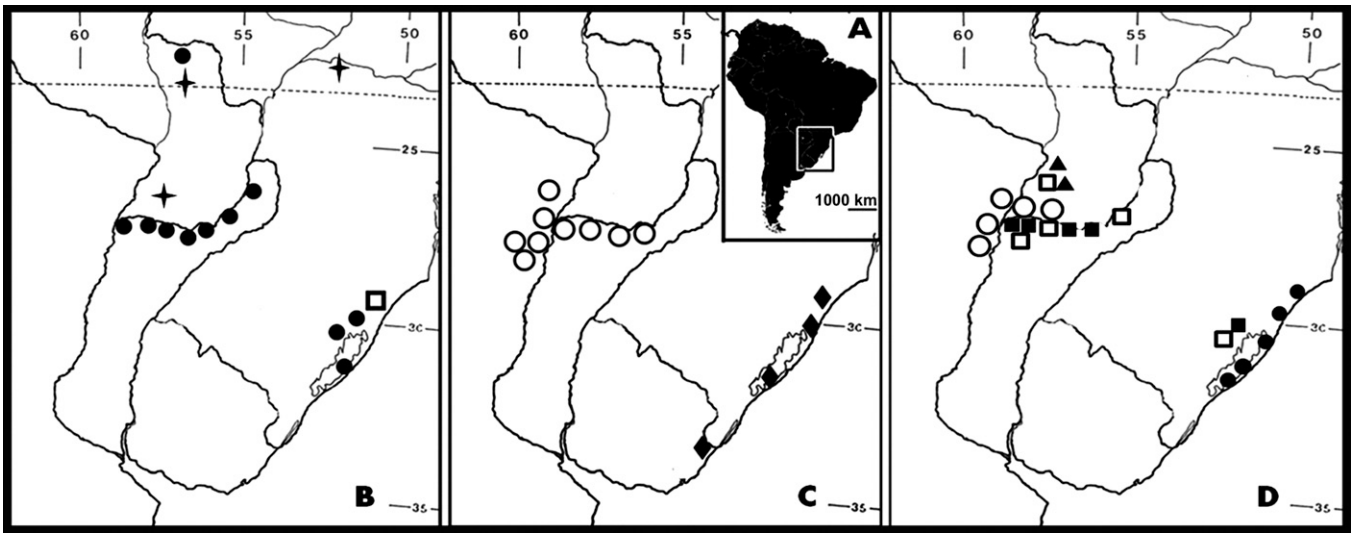

FIG. 1. Distribution of the species and natural hybrids in *Andropogon*. A. (inset) Location of the surveyed area. B. *Andropogon* × *subtilior* (solid circles), *A.* × *velutinus* (stars), *A.* × *catarinensis* (open squares). C. *A.* × *coloratus* (open circles), *A.* × *lindmanii* (solid diamonds). D. *A. arenarius* (solid circles), *A. bicornis* (open squares), *A. glaziovii* (solid triangles), *A. hypogynus* (open circles) *A. lateralis* (solid squares).

(UIF) from the analyses, due to the variability of the first pair and the truncation of the last pair (Vegetti 1999).

Thirteen quantitative and six semi-quantitative characters of the synflorescence were measured or scored on each herbarium specimen (operational taxonomic units, OTUs; Table 2). Some selected morphological characters are illustrated in Fig. 2. A total of 288 OTUs (24–30 individuals per taxon; see Tables 3 and 4) were analyzed using a stereoscopic microscope and measured using a digital caliper (Electronic IP65, 797B Series, Starrett®).

One-way ANOVA—All the variables were tested for normality with the Shapiro-Wilks test (Mahibbur and Govindarajulu 1997), as well as using diagram boxes (see Fig. 3). Homogeneity of variance was tested with Bartlett's test. To evaluate the significance of differences for each trait among the taxa analyzed, one-way ANOVA at a significance level of 5% ($\alpha = 0.05$) was performed and Tukey's test (5%) was carried out for a posteriori comparison of each pair of means. For the analysis of the variable awn length (AL), *A. bicornis* and *A. hypogynus* were excluded because these species lack awns in the fertile lemma of the sessile spikelet.

Multivariate Analyses—Pearson and Spearman correlation coefficients (Michener and Sokal 1957; Conover 1999) were estimated to identify pairs of highly correlated characters that may distort multivariate analyses. The Kaiser–Meyer–Olkin (KMO) analysis was performed to determine the adequacy of *Andropogon* sampling. The data set (see morphological data set section) was analyzed by both PCA and CDA; represented by mean values of each character. Morphological character values were standardized and semi-quantitative characters log-transformed prior to use in the multivariate analysis. Multivariate normal distribution of the characters was tested by the Bartlett test. Principal component analysis was performed, based on individual means (288 OTUs) from field-collected plants and herbarium specimens, and the correlation matrix of all 19 characters. The aim was to identify the morphological traits that most contribute to the separation between taxa. Canonical discriminant analysis was performed using the same data matrix to explore a better morphological differentiation between species. For this purpose, each specimen was assigned to an a priori group based on morphological characters. The analyses were performed using Infostat v. 2010 program (Di Rienzo et al. 2010).

TABLE 2. Characters for morphologic analyses. Characters with an asterisk are illustrated in Fig. 1.

1. SL: Synflorescence length (cm). 2. IEZ: Number of internodes of enrichment zone axis. 3. BEZ: Number of branches in axillary fascicles on the enrichment zone axis. 4. FBL: First branch length (cm). 5. IFB: Number of internodes of first branch. 6. BFB: Number of branches in axillary fascicles on first branch. 7. SBL: Second branch length (cm). 8. ISB: Number of internodes of second branch. 9. SPL: Spatheole length (cm). 10. NFB: Number of floriferous branches per unit of inflorescence. 11. FLL: Floriferous branch length (cm)*. 12. RIL: Rachis internode length (cm). 13. RIH: Length of rachis internode hairs (cm). 14. SSL: Sessile spikelet length (cm)*. 15. SSW: Sessile spikelet width (cm)*. 16. AL: Awn length (cm)*. 17. PSL: Pedicellate spikelet length (cm)*. 18. PL: Pedicel length (cm)*. 19. Pedicel hair length (cm)*.

RESULTS

One-way ANOVA—All the variables analyzed showed significant differences between two or more taxa when submitted to the a posteriori test (Tables 3 and 4); these characters may therefore be used for taxon delimitation. The average values and standard deviation of the quantitative traits analyzed, as well as the results of the a posteriori test, are summarized in Tables 3 and 4.

Multivariate Analyses—The value of KMO analysis performed for the variation of *Andropogon* accessions was 0.837, which indicates an adequate plant sampling and enabled us to perform multivariate analyses. In the PCA (Fig. 4), the first three components accounted for 75% of the total variance (38.5%, 22.3%, and 14%, respectively; Table 5). The cophenetic correlation is high (0.926), indicating a good fit between the euclidean distance between OTUs in the two dimensional plot and the distance in the original multidimensional space. In the PCA analysis, all species were clearly discriminated when the first two principal components (PCs) were plotted. All inter-specific hybrids were clustered between their parental species. *Andropogon* × *catarinensis*, *A.* × *velutinus* and *A.* × *subtilior* were well separated from their parental species, whereas *A.* × *lindmanii* was not clearly separated from *A. lateralis* or *A.* × *coloratus* from *A. lateralis* and *A. hypogynus* (see Fig. 4).

The variables that contribute most to PC1 are the number of internodes of second branch (ISB), number of branches in axillary fascicles on first branch (BFB), number of internodes of first branch (IFB), number of branches in axillary fascicles on the enrichment zone axis (BEZ), number of

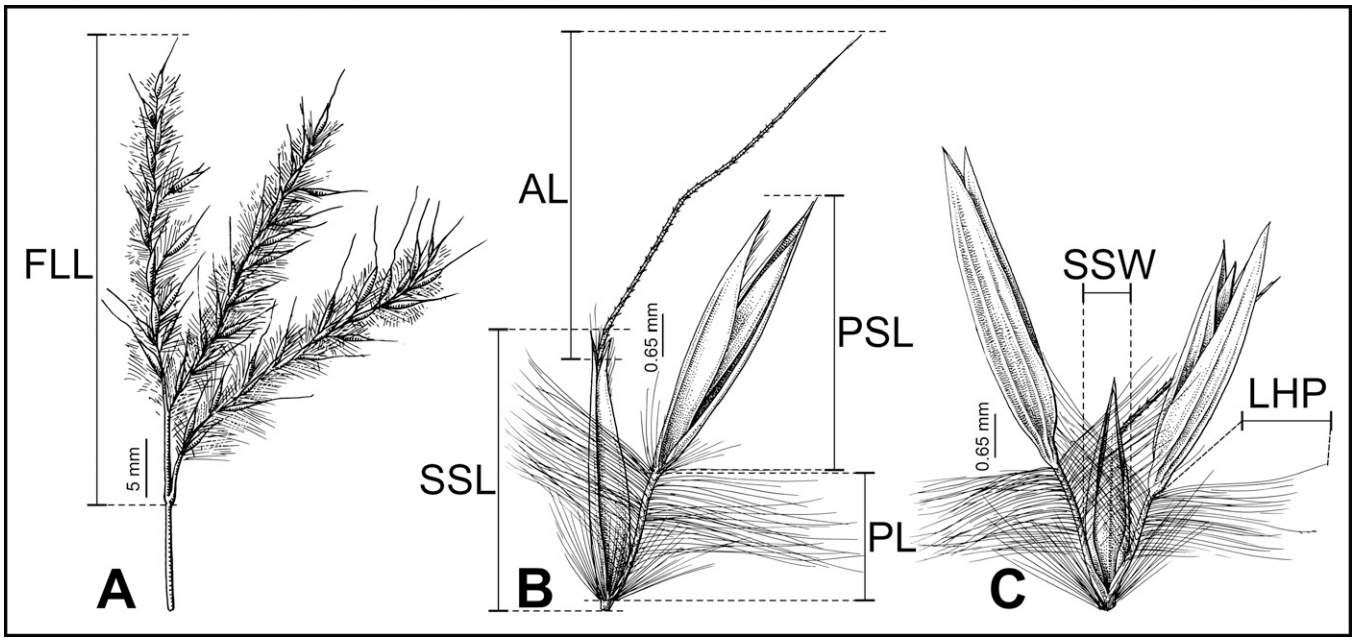

FIG. 2. *Andropogon lindmanii*. Definition of characters used in the morphological analysis. A. Unit of inflorescence. B. Middle or proximal pair of spikelets. C. Distal pair of spikelets. Characters: FLL: Floriferous branch length. SSL: Sessile spikelet length. AL: Awn length. PL: Pedicel length. PSL: Pedicellate spikelet length. SSW: Sessile spikelet width. LHP: Pedicel hair length. A–C (*Norrmann 341*).

internodes of the enrichment zone axis (IEZ), and pedicellate spikelet length (PSL), while length of rachis internode hairs (RIH), synflorescence length (SL), first branch length (FBL), number of floriferous branches per unit of inflorescence (NFB), sessile spikelet width (SSW), and second branch length (SBL) contribute to the second component (PC2, see Table 5).

The CDA results in a reliable classification of specimens of the different taxa (Fig. 5), in agreement with the results obtained by the PCA. Species and inter-specific hybrids were clearly discriminated, except for some specimens of *A. lateralis* and *A.* × *coloratus* showing partial overlapping in the CDA scatter plot (see Fig. 5). The first two axes accounted for 75% of the variation. The absolute values of the coefficients of the standardized discriminant functions are shown in Table 6. The variables that contributed most to the first canonical axis (54% of the variation) were the length of rachis internode hairs (RIH), first branch length (FBL), pedicellate spikelet length (PSL), pedicel hair length (LHP), number of branches in axillary fascicles on first branch (BFB), pedicel length (PL), and number of internodes of second branch (ISB). Characters that best discriminate along canonical axis two (21% of the variation) were the length of the first branch (FBL), number of branches in axillary fascicles on the first branch (BFB), number of branches in axillary fascicles on the enrichment zone axis (BEZ), length of rachis internode hairs (RIH), pedicel hair length (LHP), and the length of the spatheole (SPL). No case

TABLE 3. Summary of morphometric variables in ten taxa of the *Andropogon lateralis* complex. * *A. bicornis* and *A. hypogynus* lack awn in the upper lemma of the sessile spikelet and these were not considered in the analysis for this character. Different letters means significant differences among taxa.

Variables/Taxa	*A. arenarius* (N = 30)	*A. bicornis* (N = 30)	*A. hypogynus* (N = 24)	*A. lateralis* (N = 30)	*A. glaziovii* (N = 30)	*F*	*p*
1. Synflorescence length (cm)	42.82 ± 19.60^{a}	155.65 ± 16.93^{de}	160.3 ± 42.96^{ef}	120.44 ± 36.23^{bc}	201.52 ± 31.12^{g}	65.91	< 0.0001
2. Number of internodes of EZ axis	5.53 ± 1.07^{a}	13.13 ± 1.59^{e}	8.63 ± 1.01^{c}	5.00 ± 1.11^{a}	11.10 ± 1.40^{d}	140.78	< 0.0001
3. Number of branches on EZ axis	7.13 ± 1.36^{a}	34.87 ± 7.19^{e}	13.21 ± 4.24^{b}	12.00 ± 2.59^{b}	26.30 ± 5.47^{d}	238.55	< 0.0001
4. First branch length (cm)	17.59 ± 2.94^{a}	40.53 ± 2.65^{bc}	50.98 ± 14.14^{d}	34.21 ± 7.45^{b}	46.50 ± 14.36^{cd}	91.28	< 0.0001
5. Number of internodes of first branch	3.27 ± 0.69^{ab}	9.17 ± 1.72^{f}	4.88 ± 1.62^{d}	2.20 ± 0.66^{a}	7.03 ± 1.35^{e}	105.9	< 0.0001
6. Number of branches on first branch	3.40 ± 1.13^{ab}	24.37 ± 4.56^{e}	4.67 ± 1.66^{ab}	2.73 ± 1.01^{a}	19.77 ± 7.46^{d}	327.41	< 0.0001
7. Second branch length (cm)	10.62 ± 1.83^{a}	37.82 ± 5.52^{d}	43.88 ± 11.23^{d}	38.14 ± 14.33^{d}	22.83 ± 1.99^{b}	78.64	< 0.0001
8. Number of internodes of second branch	2.47 ± 0.51^{ab}	8.37 ± 1.25^{g}	4.08 ± 1.38^{cd}	1.83 ± 0.79^{a}	4.90 ± 0.84^{de}	160.12	< 0.0001
9. Spatheole length	7.52 ± 1.51^{c}	4.16 ± 0.60^{a}	7.19 ± 2.04^{bc}	6.57 ± 1.53^{bc}	3.68 ± 0.87^{a}	38.53	< 0.0001
10. Number of floriferous branches per UIF	2.43 ± 0.68^{ab}	2.37 ± 0.49^{ab}	14.17 ± 4.78^{d}	2.63 ± 0.72^{ab}	3.67 ± 1.15^{b}	137.65	< 0.0001
11. Floriferous branch length (cm)	3.73 ± 0.77^{bcd}	3.10 ± 0.65^{abc}	10.69 ± 3.33^{f}	3.92 ± 1.05^{cd}	2.48 ± 0.69^{a}	94.73	< 0.0001
12. Rachis internode length (cm)	0.31 ± 0.03^{cd}	0.27 ± 0.02^{bc}	0.46 ± 0.22^{e}	0.35 ± 0.06^{d}	0.16 ± 0.01^{a}	40.82	< 0.0001
13. Length of rachis internode hairs (cm)	0.97 ± 0.13^{g}	0.82 ± 0.03^{f}	0.03 ± 0.02^{a}	0.22 ± 0.02^{b}	0.30 ± 0.02^{c}	669.09	< 0.0001
14. Sessile spikelet length (cm)	0.42 ± 0.04^{d}	0.34 ± 0.02^{b}	0.39 ± 0.02^{c}	0.41 ± 0.03^{d}	0.33 ± 0.02^{ab}	55.62	< 0.0001
15. Sessile spikelet width (cm)	$0.05 \pm 3.6E\text{-}03^{c}$	0.03 ± 0.01^{a}	0.09 ± 0.01^{f}	0.05 ± 0.01^{b}	0.06 ± 0.01^{d}	187.52	< 0.0001
16. Awn length (cm)	0.47 ± 0.08^{c}	~*	~*	0.65 ± 0.06^{d}	0.92 ± 0.20^{f}	262.61	< 0.0001
17. Pedicellate spikelet length (cm)	0.37 ± 0.07^{cd}	0.10 ± 0.03^{a}	0.47 ± 0.03^{f}	0.52 ± 0.03^{g}	0.34 ± 0.03^{c}	496.08	< 0.0001
18. Pedicel length (cm)	0.26 ± 0.03^{d}	0.35 ± 0.03^{f}	0.18 ± 0.04^{a}	0.22 ± 0.02^{bc}	0.20 ± 0.01^{ab}	85.17	< 0.0001
19. Pedicel hair length (cm)	0.83 ± 0.06^{f}	0.66 ± 0.10^{e}	0.13 ± 0.03^{a}	0.26 ± 0.08^{b}	0.28 ± 0.03^{b}	611.9	< 0.0001

Table 4. Summary of morphometric variables in ten taxa of the *Andropogon lateralis* complex (continued).

Variables/Taxa	*A. catarinensis* (N = 30)	*A. coloratus* (N = 25)	*A. lindmanii* (N = 29)	*A. subtilior* (N = 30)	*A. velutinus* (N = 30)	*F*	*p*
1. Synflorescence length (cm)	101.79 ± 7.96^{b}	136.49 ± 42.02^{cde}	114.35 ± 26.68^{bc}	131.86 ± 35.14^{cd}	182.46 ± 28.14^{fg}	65.91	< 0.0001
2. Number of internodes of EZ axis	9.47 ± 0.94^{c}	5.48 ± 1.05^{a}	7.21 ± 0.98^{b}	11.17 ± 2.09^{d}	12.97 ± 2.06^{e}	140.78	< 0.0001
3. Number of branches on EZ axis	20.13 ± 3.75^{c}	13.20 ± 2.55^{b}	16.31 ± 2.69^{bc}	43.40 ± 7.01^{f}	54.70 ± 10.27^{g}	238.55	< 0.0001
4. First branch length (cm)	34.88 ± 7.30^{b}	36.40 ± 9.06^{b}	32.80 ± 9.23^{b}	86.74 ± 18.39^{e}	52.28 ± 8.39^{d}	91.28	< 0.0001
5. Number of internodes of first branch	6.03 ± 0.85^{e}	3.60 ± 1.04^{bc}	4.59 ± 1.05^{cd}	8.43 ± 2.46^{f}	9.23 ± 0.82^{f}	105.9	< 0.0001
6. Number of branches on first branch	13.00 ± 3.21^{c}	5.00 ± 2.20^{ab}	6.45 ± 3.48^{b}	28.83 ± 5.11^{f}	41.97 ± 4.33^{g}	327.41	< 0.0001
7. Second branch length (cm)	29.14 ± 5.69^{b}	29.53 ± 11.06^{bc}	25.70 ± 5.45^{b}	67.25 ± 15.81^{e}	37.36 ± 7.72^{cd}	78.64	< 0.0001
8. Number of internodes of second branch	5.17 ± 0.75^{e}	1.64 ± 0.49^{a}	3.17 ± 1.00^{bc}	6.73 ± 2.24^{f}	9.13 ± 0.86^{g}	160.12	< 0.0001
9. Spatheole length	6.72 ± 1.50^{bc}	6.67 ± 1.97^{bc}	7.46 ± 1.38^{bc}	6.33 ± 1.15^{b}	3.46 ± 0.74^{a}	38.53	< 0.0001
10. Number of floriferous branches per UIF	2.57 ± 0.77^{ab}	6.24 ± 1.09^{c}	2.41 ± 0.50^{ab}	3.03 ± 1.03^{ab}	2.27 ± 0.45^{a}	137.65	< 0.0001
11. Floriferous branch length (cm)	3.75 ± 0.65^{bcd}	6.69 ± 1.72^{e}	4.43 ± 0.89^{d}	3.97 ± 0.35^{cd}	2.78 ± 0.38^{ab}	94.73	< 0.0001
12. Rachis internode length (cm)	0.23 ± 0.02^{ab}	0.50 ± 0.17^{e}	0.28 ± 0.05^{bcd}	0.35 ± 0.05^{d}	0.21 ± 0.01^{ab}	40.82	< 0.0001
13. Length of rachis internode hairs (cm)	1.05 ± 0.10^{h}	0.24 ± 0.04^{bc}	0.60 ± 0.06^{d}	0.68 ± 0.10^{e}	0.54 ± 0.05^{d}	669.09	< 0.0001
14. Sessile spikelet length (cm)	0.33 ± 0.03^{ab}	0.38 ± 0.04^{c}	0.39 ± 0.01^{c}	0.38 ± 0.02^{c}	0.32 ± 0.01^{a}	55.62	< 0.0001
15. Sessile spikelet width (cm)	0.04 ± 0.01^{a}	0.07 ± 0.01^{e}	0.05 ± 0.01^{c}	0.04 ± 0.01^{b}	0.05 ± 3.9E-03^{c}	187.52	< 0.0001
16. Awn length (cm)	0.29 ± 0.10^{b}	0.38 ± 0.18^{c}	0.57 ± 0.07^{d}	0.05 ± 0.01^{a}	0.75 ± 0.10^{e}	262.61	< 0.0001
17. Pedicellate spikelet length (cm)	0.15 ± 0.03^{b}	0.43 ± 0.02^{e}	0.46 ± 0.04^{ef}	0.38 ± 0.03^{d}	0.13 ± 0.02^{ab}	496.08	<0.0001
18. Pedicel length (cm)	0.27 ± 0.02^{de}	0.21 ± 0.04^{bc}	0.23 ± 0.05^{c}	0.29 ± 0.02^{e}	0.26 ± 0.02^{d}	85.17	<0.0001
19. Pedicel hair length (cm)	0.86 ± 0.08^{f}	0.13 ± 0.02^{a}	0.53 ± 0.05^{d}	0.33 ± 0.03^{c}	0.49 ± 0.02^{d}	611.9	<0.0001

was erroneously classified in the classification function of discriminant analysis.

Discussion

To resolve taxonomic limits in the *Andropogon lateralis* complex, morphometrical analyses were carried out based on synflorescence traits. Results showed that these methods (PCA and CDA) enable the recognition of species and interspecific hybrids within the complex. Most taxa form clearly defined groups, and hybrid combinations are positioned between the parental species (see Figs. 4 and 5). Norrmann (2009) suggested that, in *Andropogon* hybrids, the synflorescence in the interspecific hybrids share characteristics from both parents. This is true for most hybrids, with the exception of some specimens of *A.* × *coloratus* that overlap with the group constituted by *A. lateralis*. The explanation for this may be the fact that these hybrids (*A.* × *coloratus*) are fertile and backcrossing occurs within these populations (Norrmann 2009).

Although differences between species in the *A. lateralis* complex (species and most hybrids) are clearly seen and they were recognized as different taxa in the past, the taxonomic complexity is generated by one hybrid, (*A. coloratus*, i.e. *A. lateralis* × *A. hypogynus*) in which the morphological limits are not clearly defined by traditional methods (analyzing only qualitative characters). Zanin and Longhi-Wagner (2006) distinguished *A. arenarius* from *A.* × *lindmanii* by the shape of the inflorescence, the sessile and pedicellate spikelet size, and the length of hairs in the pedicels and rachis internodes in relation to the sessile spikelet. Norrmann (2009) suggested that these two taxa were differentiated by the sessile spikelet size, the hair length of the sessile spikelet callus and the awn length of the sessile spikelet. Our results show that these taxa are better distinguished by means of the length of synflorescence, branches and rachis internodes, hairs in the pedicels, rachis internodes, and pedicellate spikelets. The number of internodes developed in the enrichment zone axis and in the first and second branches, the number of branches in the axillary fascicles on the enrichment zone axis and first branches are also important. In addition, for *A. arenarius* the junciform leaf blade is a diagnostic character.

Andropogon × *catarinensis* was recognized from *A. arenarius* and *A. bicornis* by the length of the synflorescence, number of internodes of EZ axis, number of branches on EZ axis, number of internodes of first branch, number of branches on first branch, second branch length, number of internodes of second branch, length of rachis internode hairs, awn length, and pedicellate spikelet length.

Andropogon × *coloratus* was distinguished from *A. hypogynus* and *A. lateralis* by the number of internodes of first branch, second branch length, number of floriferous branch per UIF, floriferous branch length, sessile spikelet width, awn length, and pedicellate spikelet length. However, due to hybrid combinations between *A. hypogynus* and *A. lateralis* that are completely fertile, only the F1 can be effectively identified as *A.* × *coloratus*. Norrmann (2009) suggests that *A. lateralis* and *A. hypogynus* are morphologically the most similar species in the complex, being different mainly at the ecological level. These species can be recognized by the number of racemes per inflorescence unit, size of spikelets, hairiness of pedicels, and presence of awn in sessile spikelet. Our results showed that the length of pedicel, rachis internodes, rachis internode hairs, branches, and floriferous branches, as well as the sessile spikelet width, number of internodes in the enrichment zone axis, and the number of internodes in lateral branches are also worth considering.

Andropogon × *subtilior* shows significant differences from *A. bicornis* and *A. lateralis* in the number of internodes of EZ axis, number of branches on EZ axis, first branch length, number of branches on first branch, second branch length, number of internodes of second branch, length of rachis internode hairs, sessile spikelet length, awn length, pedicellate spikelet length, pedicel length, and pedicel hair length.

Andropogon × *velutinus* was differentiated from *A. bicornis* and *A. glaziovii* by means of the number of branches on EZ axis, number of branches on first branch, length of rachis internode hairs, sessile spikelet width, awn length, pedicel length, and pedicel hair length.

Considering that the morphological species concept is that most used in plant taxonomy because of the availability of data for analysis (Cronquist 1988), our study provides a practical taxonomic tool for the recognition of members of the *A. lateralis* complex.

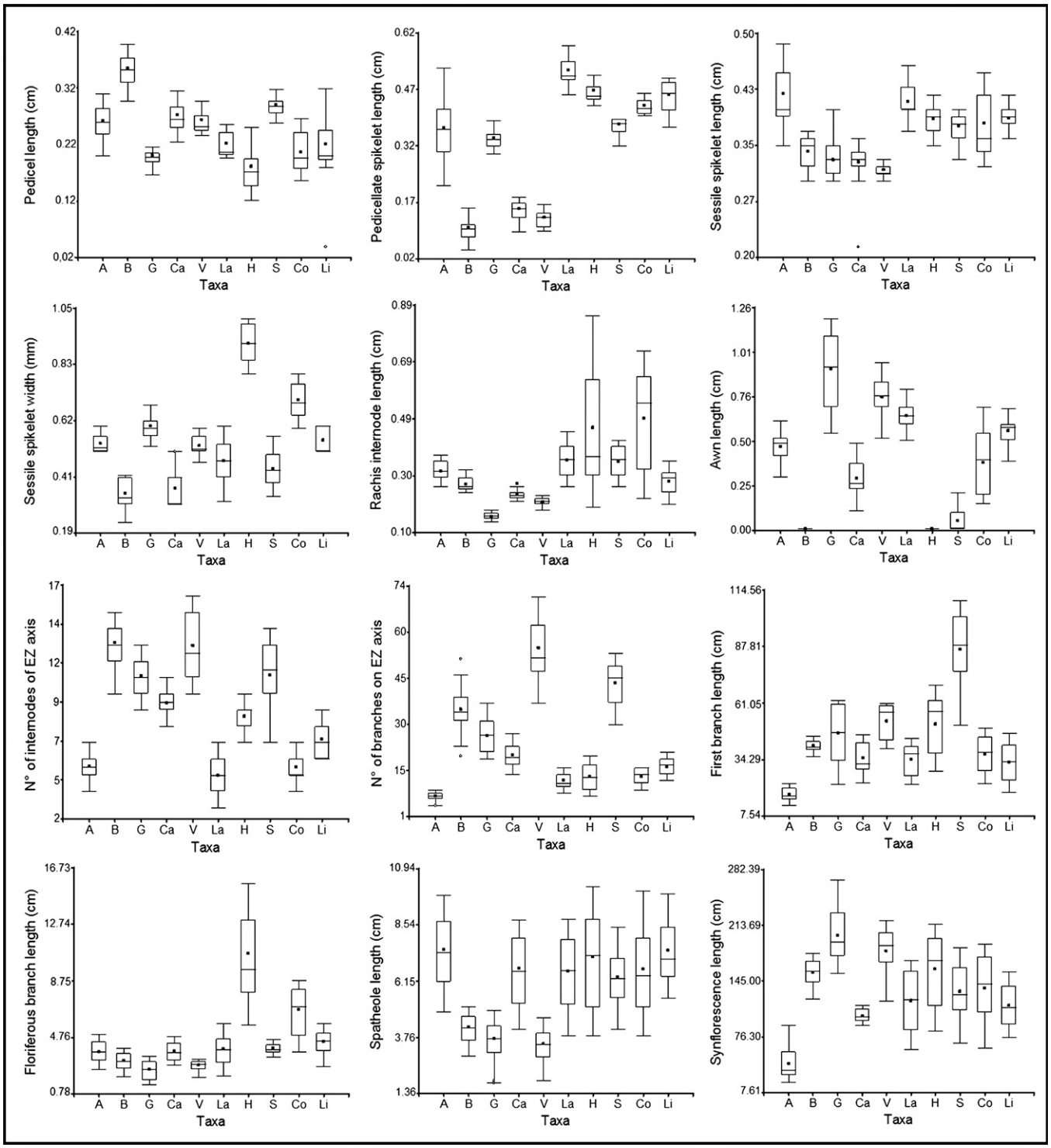

FIG. 3. Variation in selected morphological characters of the *A. lateralis* complex. Box = interquartile range. Squares inside the boxes = mean value. Circles outside of the boxes = outlier; *n* = 288. A. *A. arenarius*. B. *A. bicornis*. G. *A. glaziovii*. H. *A. hypogynus*. La. *A. lateralis*. Ca. *A.* × *catarinensis*. Co. *A.* × *coloratus*. Li. *A.* × *lindmanii*. S. *A.* × *subtilior*. V. *A.* × *velutinus*.

KEY TO TAXA OF THE *ANDROPOGON LATERALIS* COMPLEX IN SOUTH AMERICA

1. Leaf blade junciform. Synflorescences 20.1–90 cm long. Number of branches in axillary fascicles on the enrichment zone axis 4–9. ..... *A. arenarius*
1. Leaf blade flat. Synflorescence length usually more than 95 cm. Number of branches in axillary fascicles on the enrichment zone axis usually more than 9 2
   2. Inflorescences highly branched, distally dense. Usually more than 9 internodes in the enrichment zone axis. Number of branches in axillary fascicles on the enrichment zone axis more than 20. Usually more than 5 internodes in the first branch. Usually more than 10 branches in axillary fascicles on the first branch 3

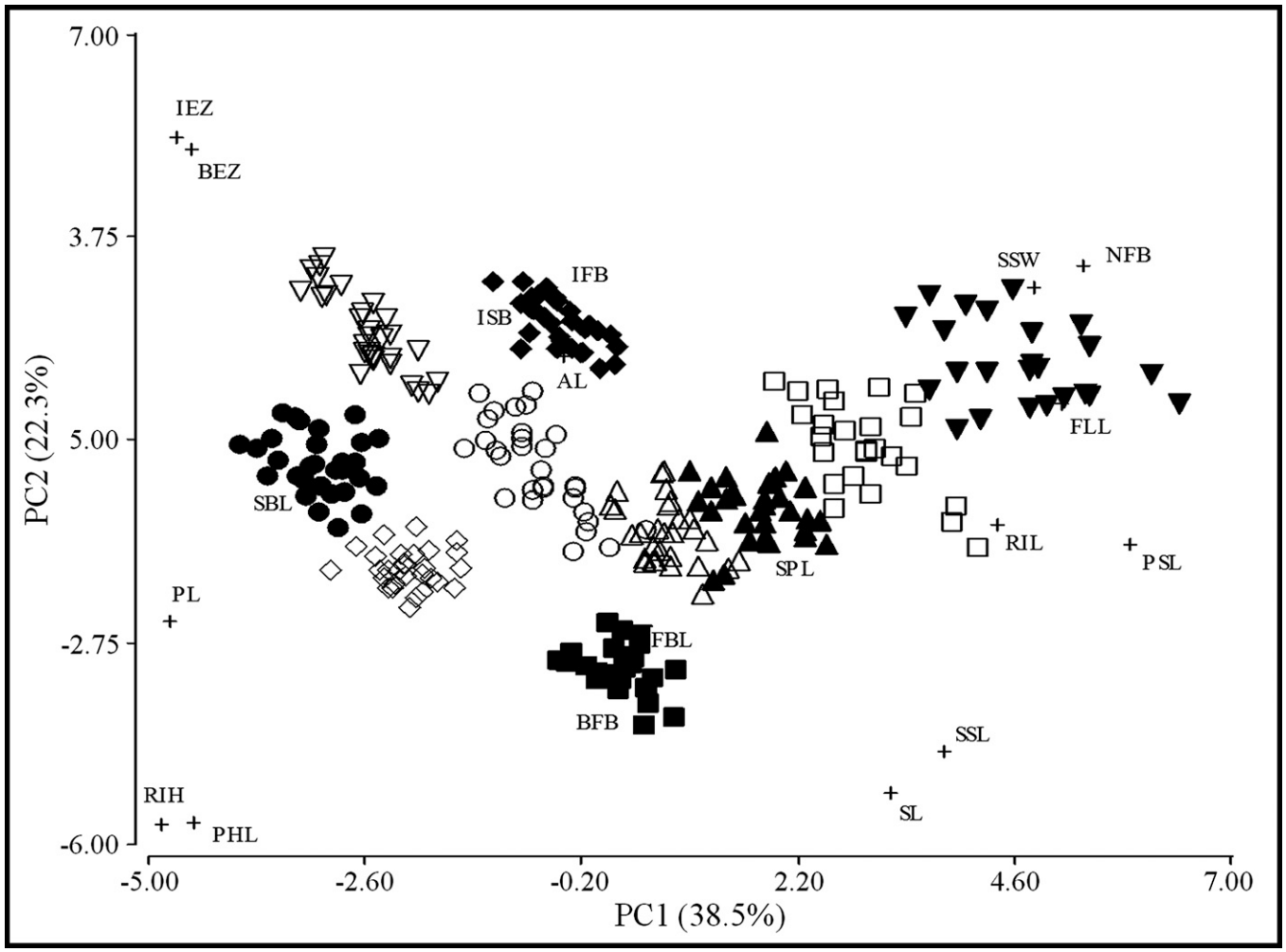

FIG. 4. Multivariate analysis. Plot of mean value of 288 OTUs on the first two principal components. *A. arenarius* (solid squares), *A. bicornis* (solid circles), *A. glaziovii* (solid diamonds), *A. hypogynus* (solid inverted triangles), *A. lateralis* (solid triangles), *A.* × *catarinensis* (open diamonds), *A.* × *coloratus* (open squares), *A.* × *lindmanii* (open triangles), *A.* × *subtilior* (open circles), and *A.* × *velutinus* (open inverted triangles). PC1 = 38.5%, PC2 = 22.3%, PC3 = 13.1%. Crosses represent the variables with their acronyms (see Table 1).

3. Synflorescence length usually less than 115 cm long. Pedicel hair length more than 8 mm. Length of rachis internodes hairs usually more than 1 cm ..... *A.* × *catarinensis*
3. Synflorescence length usually more than 115 cm. Pedicel hair length less than 8 mm. Length of rachis internode hairs less than 9 mm 4
4. Sessile spikelets always awnless or awnless and awned at the same inflorescences; when awned, awns less than 2 mm long 5
5. Sessile spikelets awnless, the pedicellate usually reduced to the pedicel; when developed, 0.5–2 mm long. Pedicels 3.1–4.5 mm long. Pedicel long-haired, hairs 6.5–7.5 mm long. ..... *A. bicornis*
5. Sessile spikelets awnless and awned in the same inflorescences, awns less than 2 mm long, the pedicellate developed 2.2–4 mm long. Pedicels 2.5–3.5 mm long. Pedicel hairs 2.8–4 mm long ..... *A.* × *subtilior*
4. Sessile spikelets awned, awns more than 5 mm long 6
6. Spatheoles as long as or longer than the corresponding inflorescence units, these sometimes completely (rarely partially) hidden inside the bract. Pedicel hairs less than 3 mm long. Pedicellate spikelets 2.5–4.1 mm long. Number of branches in axillary fascicles on the enrichment zone axis 19–36 ..... *A. glaziovii*
6. Spatheoles shorter than the inflorescence units, this exserted (rarely partially hidden in the bract). Pedicel hairs longer than 4 mm. Pedicellate spikelets 1–2.3 mm long. Number of branches in axillary fascicles on the enrichment zone axis 37–71 ..... *A.* × *velutinus*

2. Inflorescences less branched. Usually less than 9 internodes in the enrichment zone axis. Number of branches in axillary fascicles on the enrichment zone axis less than 20. Usually less than 5 internodes in the first branch. Usually less than 10 branches in axillary fascicles on the first branch 7
7. Usually more than 4 racemes per inflorescence unit. Sessile spikelet width 0.6–1 mm 8
8. Usually more than 8 racemes per inflorescence unit, 6–16 cm long. Sessile spikelets awnless. Pedicel hairs 0.1–0.7 mm long ..... *A. hypogynus*
8. Usually less than 8 racemes per inflorescence unit, 3.9–9 cm long. Sessile spikelets awned, awn 1.5–7 mm long. Pedicel hairs 1.8–3 mm long ..... *A.* × *coloratus*
7. Usually less than 4 racemes per inflorescence unit. Sessile spikelet width 0.3–0.6 mm 9
9. Number of branches in axillary fascicles on the first branch 1–4. Pedicel hairs 1–4 mm long. Rachis internode hairs 1.9–2.5 mm long ..... *A. lateralis*
9. Number of branches in axillary fascicles on the first branch usually more than 4, (3–) 4–12. Pedicel hairs 4.2–6 mm long. Rachis internode hairs 5.1–7 mm long ..... *A.* × *lindmanii*

TABLE 5. PCA results. Factor loadings and percentage of variance for the three principal components obtained from the 19 characters analyzed. Numbers in bold font indicate the higher values.

Variables	Principal Components 1	2	3
Pedicel length	0.21	0.19	**–0.32**
Pedicellate spikelet length	**–0.28**	–0.15	0.02
Sessile spikelet length	–0.22	0.02	–0.21
Pedicel hair length	0.11	0.4	–0.14
Awn length	–0.01	0.06	**0.59**
Sessile spikelet width	–0.19	**–0.3**	0.09
Rachis internode length	–0.18	–0.17	**–0.29**
Length of rachis internodes hairs	0.14	**0.38**	–0.24
Synflorescence length	0.18	**–0.32**	0.24
Number of internodes of EZ axis	**0.32**	–0.12	–0.01
Number of branches in AFs on EZ axis	**0.32**	–0.13	0.01
First branch length	0.19	**–0.31**	–0.18
Number of internodes of first branch	**0.33**	–0.12	–0.06
Number of branches in AFs on first branch	**0.33**	–0.1	0.05
Second branch length	0.15	**–0.29**	**–0.31**
Number of internodes of second branch	**0.34**	–0.09	–0.08
Floriferous branch length	–0.19	–0.25	–0.21
Number of floriferous branch per UIF	–0.15	**–0.31**	–0.13
Spatheole length	–0.2	0.06	**–0.28**
Variation explained (%)	38.5	22.3	14

TABLE 6. CDA. Standardized coefficients for canonical variables derived from discriminant function analysis of the *Andropogon lateralis* complex. Numbers in bold font indicate the higher values.

Variables	Axis1	Axis2
Pedicel length	**–0.31**	–0.11
Pedicellate spikelet length	**0.48**	–0.28
Sessile spikelet length	0.07	–0.24
Pedicel hair length	**–0.43**	**–0.35**
Awn length	0.11	0.08
Sessile spikelet width	0.28	0.27
Rachis internode length	0.06	–0.13
Length of rachis internode hairs	**–0.54**	**–0.4**
Synflorescence length	0.07	0.15
Number of internodes of EZ axis	–0.01	0.01
Number of branches in AFs on EZ axis	–0.29	**0.4**
First branch length	**0.51**	**–0.83**
Number of internodes of first branch	–0.2	–0.01
Number of branches in AFs on first branch	**–0.32**	**0.71**
Second branch length	0.25	–0.1
Number of internodes of second branch	**–0.31**	0.3
Floriferous branch length	0.11	–0.05
Number of floriferous branches per UIF	0.16	0.18
Spatheole length	–0.02	**–0.33**
Cumulative proportion %	54.06	75

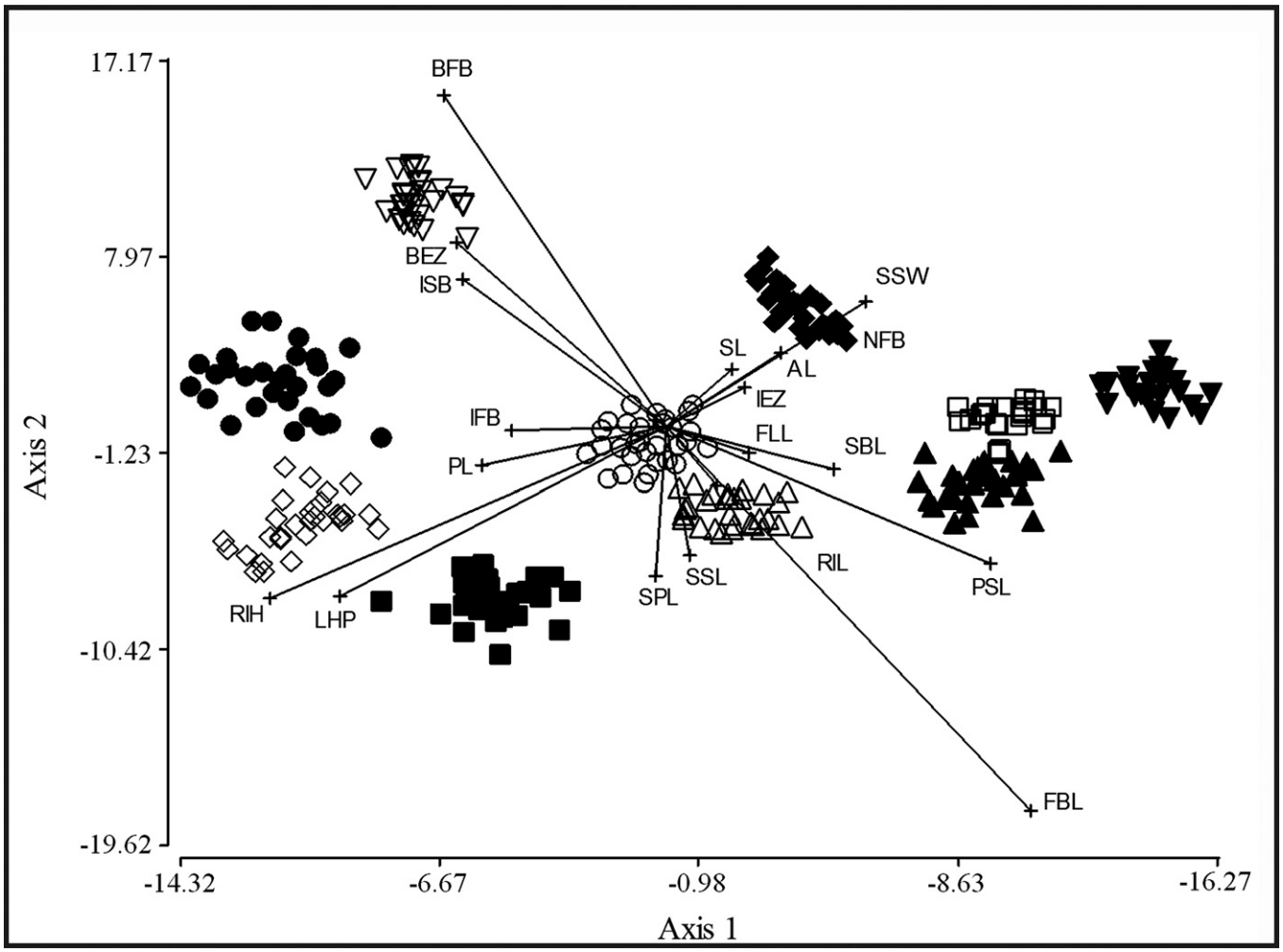

FIG. 5. Scatterplot of scores derived from discriminant functions Axis 1 vs. Axis 2 produced by discriminant analysis applied to 19 morphological characters for ten taxa of the *Andropogon lateralis* complex. *A. arenarius* (solid squares), *A. bicornis* (solid circles), *A. glaziovii* (solid diamonds), *A. hypogynus* (solid inverted triangles), *A. lateralis* (solid triangles), *A.* × *catarinensis* (open diamonds), *A.* × *coloratus* (open squares), *A.* × *lindmanii* (open triangles), *A.* × *subtilior* (open circles), and *A.* × *velutinus* (open inverted triangles). Crosses represent the variables with their acronyms (see Table 1).

Acknowledgments. This work was supported by CONICET (PIP 112-200801-01557 and Doctoral fellowship), SECyT-UNC and SGCyT-UNNE. We thank the curators of CORD and CTES for loans of herbarium specimens. We are grateful to Laura Ribulgo for the illustrations and Joss Heywood for correcting the English version.

Literature Cited

Bottini, M. C. J., M. C. Orsi, E. J. Greizerstein, and L. Poggio. 1998. Relaciones fenéticas entre las especies de *Berberis* (Berberidaceae) del nordeste de la región patagónica. *Darwiniana* 35: 115–129.

Campbell, C. S. 1983a. Systematics of the *Andropogon virginicus* complex (Gramineae). *Journal of the Arnold Arboretum* 64: 171–254.

Campbell, C. S. 1983b. Wind dispersal of some North American species of *Andropogon* (Gramineae). *Rhodora* 85: 65–72.

Campbell, C. S. and P. Windisch. 1986. Chromosome numbers and their taxonomic implications for eight Brazilian *Andropogon* (Poaceae). *Brittonia* 38: 411–414.

Campbell, C. S. and P. Windisch. 1987. Hybridization among three species of *Andropogon* (Poaceae: Andropogoneae) in southern Brazil. *Bulletin of the Torrey Botanical Club* 114: 402–406.

Chandler, G. T. and M. D. Crisp. 1998. Morphometric and phylogenetic analysis of the *Daviesia ulicifolia* complex (Fabaceae, Mirbelieae). *Plant Systematics and Evolution* 209: 93–122.

Chiapella, J. O. 2000. The *Deschampsia cespitosa* complex in central and northern Europe: A morphological analysis. *Botanical Journal of the Linnean Society* 134: 495–512.

Chiapella, J. O., V. L. DeBoer, G. C. Amico, and J. C. Kuhl. 2011. A morphological and molecular study in the *Deschampsia cespitosa* complex (Poaceae; Poeae; Airinae) in northern North America. *American Journal of Botany* 98: 1366–1380.

Clayton, W. D. and S. A. Renvoize. 1986. Genera graminum: Grasses of the world. *Kew Bulletin Additional Series* 13: 349–351.

Compton, J. A. and T. A. J. Hedderson. 1997. A morphometric analysis of the *Cimicifuga foetida* L. complex (Ranunculaceae). *Botanical Journal of the Linnean Society* 123: 1–23.

Conover, W. J. 1999. *Practical nonparametric statistics*. New York: John Wiley and Sons, Inc.

Cronquist, A. 1988. *The evolution and classification of flowering plants*. Ed. 2. New York: The New York Botanical Garden.

Da Costa, A. F., P. J. F. P. Rodrigues, and M. D. G. L. Wanderley. 2009. Morphometric analysis and taxonomic revision of the *Vriesea paraibica* complex (Bromeliaceae). *Botanical Journal of the Linnean Society* 159: 163–181.

Denham, S., M. E. Múlgura de Romero, A. Slanis, and E. Bulacio. 2006. *Lippia integrifolia* versus *L. boliviana* (Verbenaceae). *Darwiniana* 44: 363–374.

Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, and C. W. Robledo. 2010. InfoStat v. 2010. Córdoba: Grupo InfoStat, FCA, Universidad Nacional de Córdoba.

Eckenwalder, J. E. 1996. Taxonomic signal and noise in multivariate interpopulational relationships in *Populus mexicana* (Salicaceae). *Systematic Botany* 21: 261–271.

Galdeano, F. and G. A. Norrmann. 2000. Natural hybridization between two South American diploid species of *Andropogon* (Gramineae). *The Journal of the Torrey Botanical Society* 127: 101–106.

Giussani, L. M. 2000. Phenetic similarity patterns of dioecious species of *Poa* from Argentina and neighboring countries. *Annals of the Missouri Botanical Garden* 87: 203–233.

Gould, F. W. 1967. The genus *Andropogon* in the United States. *Brittonia* 19: 70–76.

Henderson, A. 2005. A multivariate study of *Calyptrogyne* (Palmae). *Systematic Botany* 30: 60–83.

Hess, W. J. and N. A. Stoynoff. 1998. Taxonomic status of *Quercus acerifolia* (Fagaceae) and a morphological comparison of four members of the *Quercus schumardii* complex. *Systematic Botany* 23: 89–100.

Leonard, M. R., R. E. Cook, and J. C. Semple. 2005. A multivariate morphometric study of the aster genus *Sericocarpus* (Asteraceae: Astereae). *Sida* 21: 1471–1505.

Mahibbur, R. M. and Z. Govindarajulu. 1997. A modification of the test of Shapiro and Wilks for normality. *Journal of Applied Statistics* 24: 219–235.

Michener, C. D. and R. R. Sokal. 1957. A quantitative approach to a problem in classification. *Evolution* 11: 130–162.

Nagahama, N. and G. A. Norrmann. 2012. Review of the genus *Andropogon* (Poaceae: Andropogoneae) in America based on cytogenetic studies. *Journal of Botany* 2012: 1–9.

Nagahama, N., A. M. Anton, M. I. Hidalgo, and G. A. Norrmann. 2012. Naming hybrids in the *Andropogon lateralis* complex (Andropogoneae, Poaceae) after multivariate analysis. *Darwiniana* 50: 114–123.

Nagahama, N., A. M. Anton, A. C. Vegetti, and G. A. Norrmann. 2013. Synflorescence analysis in South American species of *Andropogon* section *Leptopogon* (Andropogoneae, Poaceae): A tool to identify different ploidy levels. *Phytotaxa* 82: 45–63.

Negron-Ortiz, V. and R. J. Hickey. 1996. The genus *Ernodea* (Rubiaceae) in the Caribbean Basin. II. Morphological analysis and systematics. *Systematic Botany* 21: 445–458.

Norrmann, G. A. 1985. Estudios citogenéticos en especies argentinas de *Andropogon* (Gramineae). *Boletín de la Sociedad Argentina de Botánica* 24: 137–149.

Norrmann, G. A. 2009. Natural hybridization in the *Andropogon lateralis* complex (Andropogoneae, Poaceae) and its impact on taxonomic literature. *Botanical Journal of the Linnean Society* 159: 136–154.

Norrmann, G. A. and F. Scarel. 2000. Biología reproductiva de cuatro especies sudamericanas hexaploides de *Andropogon* L. (Gramineae, Andropogoneae). *Kurtziana* 28: 173–180.

Norrmann, G. A., L. Hanson, S. Renvoize, and I. J. Leitch. 2004. Genomic relationships among diploid and hexaploid species of *Andropogon* (Poaceae). *Genome* 47: 1220–1224.

Norrmann, G. A., U. Swenson, and I. Caponio. 2008. Two new species of *Andropogon* (Poaceae, Panicoideae) from Cuba. *Darwiniana* 46: 328–334.

Oyama, K. 1996. Quantitative variation within and among populations of *Arabis serrata* Fr. & Sav. (Brassicaceae). *Botanical Journal of the Linnean Society* 120: 243–256.

Peichoto, M. C., S. M. Mazza, and V. G. Solís Neffa. 2008. Morphometric analysis of *Schizachyrium condensatum* (Poaceae) and related species. *Plant Systematics and Evolution* 276: 177–189.

Pelser, P. B. and R. Houchin. 2004. Taxonomic studies on *Senecio aquaticus* (Asteraceae). A recommendation for the taxonomic status of Aquaticus and Barbareifolius. *Botanical Journal of the Linnean Society* 145: 489–498.

Stapf, O. 1919. Gramineae, *Andropogon*. Pp. 208–265 in *Flora of tropical Africa 9*, ed. Prain D.. London: Reeve.

Tivano, J. C. and A. C. Vegetti. 2010. Growth forms in Pappophoreae (Poaceae). *Flora* 205: 291–301.

Vegetti, A. C. 1999. Typology of synflorescence of Andropogoneae (Poaceae), additional comments. *Feddes Repertorium* 110: 111–126.

Vegetti, A. C. and D. Müller-Doblies. 2004. Inhibition areas within the synflorescences of Poaceae. *Beiträge zur Biologie der Pflanzen* 73: 51–74.

Woods, K., K. W. Hilu, J. H. Wiersema, and T. Borsch. 2005. Pattern of variation and systematics of *Nymphaea odorata*: I. Evidence from morphology and inter-simple sequence repeats (ISSRs). *Systematic Botany* 30: 471–480.

Zanin, A. 2001. *Revisão de Andropogon L. (Poaceae - Panicoideae - Andropogoneae) no Brasil*. Doctoral thesis. São Paulo: Universidade de São Paulo.

Zanin, A. and H. M. Longhi-Wagner. 2006. Sinopse do gênero *Andropogon* L. (Poaceae - Andropogoneae) no Brasil. *Revista Brasilera de Botânica* 29: 289–299.

Appendix 1. Origin and identification of the *Andropogon* material cited in this investigation.

A. arenarius Hack. BRAZIL. Rio Grande do Sul: Osorio, praia Atlántida, 2 Feb 1971, *Valls 1468* (CTES); Osorio, em campo de dunas móveis, 10 Oct 1972, *Valls 2146* (CTES); Torres, beira da Praia, próximo ao Morro do Farol, 28 Feb 1970, *Valls 1116* (CTES); Capão da Canoa, 4 Mar 1992, *Norrmann 104* (BAA, CTES, CEN, US). Santa Catarina: Imbituba, Itapirubá, 22 Feb 2008, *Nagahama & Norrmann 29, 30, 31, 32, 33* (CORD); 2 Jan 1994, *Norrmann 139* (CTES, MBM, SI, K); Laguna, en dunas, 2 Jan 1994, *Norrmann 224* (CTES, MBM, US).

A. bicornis L. ARGENTINA. Chaco: 1 de Mayo, Colonia Benítez, 20 Apr 1965, *Schulz 15022* (CTES); s. d., 21 Apr 1965, *Schulz 15024* (CTES). Corrientes: Bella Vista, 15 km N of Bella Vista, 16 May 1983, *Norrmann & Quarín 89* (CTES); Capital, 18 km SE of Corrientes, Ruta 5, 25 Mar 1982, *Norrmann 51* (CTES, LIL); Riachuelo, 7 Apr 1974, *Quarín 2344* (CTES); Campus Universitario, *Schinini 34389* (CTES); General Alvear, ruta 14 y Río Aguapey, 17 May 1983, *Norrmann & Quarín 91* (CTES, BAA, US); Itatí, ruta 12, 47 km E of Itatí, *Ahumada 775* (CTES).

Ituzaingó, ruta 12 y ruta 38, 24 Jun 1990, *Schinini 26868* (CTES); desembocadura del Arroyo Garapé en el Río Paraná, 24 Apr 1975, *Schinini 11093* (CTES); Isla Apipé Grande, Puerto San Antonio, 10 Dec 1973, *Krapovickas 24122* (CTES); Santo Tomé, Laguna la Luna, Galarza, en embalsado, Jul 1995, *Schinini 6596* (CTES). Formosa: Bermejo, Puerto Bermejo, 2 Mar 1901, *Kermes 634* (CTES); Pilcomayo, Estero Isla Leona, ruta 86, 22 Mar 1979, *Piccinini & Petetin 3674* (CTES); San Pedro, ruta 20 y Arroyo Piray Guazú, 21 Mar 1997, *Tressens 5704* (CTES); Monte Carlo, 22 May 1951, *Montes 15388* (SI, BAA). Misiones: Capital, Posadas, 11 Jun 1912, *Ekman 549*, *550* (CORD); El Dorado, ruta provincial 17, Pozo Azul, 27 May 2002, *Keller 1832* (CTES). BRAZIL. Minas Gerais: Ouro Preto, 22 Jan 1984, *Schinini & Ferrucci 24590* (CTES). Paraná: s. d., 11 Feb 1974, *Anderson, W. 10784* (CTES). Rio Grande do Sul: Gramado, estrada Taquara, 7 Apr 1971, *Valls 11486* (CTES); Ijuí, km 346 da BR 285, 24 Jul 1973, *Valls 2682* (CTES); Torres, colonia Sao Pedro, 28 Mar 1970, *Valls 1102* (CTES). Rondônia: Porto Velho, Estrada Manaus, Castanho Tupana, 7 Jul 1972, *Silva 184* (CTES). PARAGUAY. Alto Paraná: Estancia Santa Elena, 5 km N of Hernandarias, s. d., *Schinini & Caballero 27414* (CTES). Asunción: Jardín Botánico, en terrenos modificados, s. d., *Schinini 6230* (CTES). Cordillera: Cordillera de Altos, Cerro Tobatí, s. d., *Schinini 24050* (CTES). Misiones: Santiago, Estancia La Soledad, s. d., *Pedersen 5941* (CTES). Paraguarí: Pirayú, en esteros, s. d., *Mereles 234* (CTES). Presidente Hayes: Ruta Trans, Chaco, km 120, s. d., *Mereles 3019* (CTES).

A.* × *catarinensis Norrmann & Nagahama **(= *A. arenarius* × *A. bicornis*).** BRAZIL. Santa Catarina: Itapirubá, 22 Feb 2008, *Nagahama & Norrmann 48*, *49*, *50*, *58*, *67* (CORD); *Norrmann 331, 332* (CTES).

A.* × *coloratus Hack. **(*pro. sp.*) (= *A. hypogynus* × *A. lateralis*).** ARGENTINA. Chaco: Primero de Mayo, Colonia Benitez, leg. Nic. Rojas Acosta 2 Sep 1909, *Stuckert 20275* (CORD, as *A. coloratus*); *Norrmann 340* (CTES); Rinconada Lag. Pereira-Irupé, 8 Mar 1942, *A. G. Schulz 3276*, *3726a* (CTES, CORD). Corrientes: controlled hybrid between *A. hypogynus* N36 × *A. lateralis* N72, Feb 1991, *Norrmann 109* (CTES); Ea. Las Tres Marías, flooded land by the Paraná, 15 Mar 1967, *Pedersen 8095* (CTES); Rincón de Sta. María, Ea. Abelenda, 9 Jul 1955, *Carnevali 506* (CTES); Villa Ocampo, 17 Dec 1980, *Pire 739* (CTES). Santa Fe: Florencia, 25 Apr 2001, *Norrmann & Scarel 333* (CTES).

A. glaziovii Hack. BRAZIL. Goiás: 70 km SE of Jataí, 17° 52′ S, 51° 42′ W, 12 Apr 1988, *Valls 11712* (CTES); 39 km SW of Gacu, 12 Apr 1988, *Valls 11720* (CTES). Mato Grosso do Sul: 5 km W of Ribas ao Rio Pardo, 14 Apr 1988, *Valls 11765* (CTES); Campo Grande, s. d., *Norrmann 311* (CTES). São Paulo: Guzolandia, Route SP 310, km 574, 12 Jun 1999, *Zanin 793* (SPF). PARAGUAY. Amambay: Parque Nacional Cerro Corá, ruta 5, 18 Apr 1995, *Norrmann 163* (CTES). Concepción: Ruta 5, 32 km noreste of Concepción, 20 Apr 1995, *Norrmann 196* (CTES). Misiones: 2 km E of San Juan Bautista por ruta 1, 21 Apr 1995, *Norrmann 75*, *217*, *222* (CTES, CORD); 14 April 2010, *Nagahama & Norrmann 133*, *134*, *135*, *137* (CORD); 2.1 km E of San Juan Bautista por ruta 1, 16 Apr 2009, *Nagahama 87*, *88*, *89* (CTES); *Norrmann 175* (CORD). San Pedro: Ayo. Ipané y ruta 3, 20 Apr 1995, *Norrmann 203* (CTES).

A. hypogynus Hack. ARGENTINA. Chaco: 1 de Mayo, Colonia Benítez, s. d., *Norrmann 342* (CTES); San Fernando, Colonia Florencia, SW of Basail, 23 Mar 1965, *Schulz 14837* (CTES). Corrientes: Ituzaingó, 40 km E of Ituzaingó, s. d., *Norrmann 117* (CTES); 36 km E of Ituzaingó, por ruta 12, 29 Mar 1982, *Norrmann 36* (CTES); ruta 12, 35 km W of border with Misiones, 26 Mar 1970, *Krapovickas et al. 15703* (CTES). Misiones: Candelaria, Cerro Corá, en campos bajos, 8 Jan 1946, *Bertoni 2599* (LIL); San Ignacio, Ayo. Yabebirí, 16 Jan 1966, *Krapovickas 12081* (CTES). BOLIVIA. La Paz: Abel Iturralde, Lousita, 28 Aug 1985, *Haase 653* (W). BRAZIL. Mato Grosso do Sul: Aquidauana, Fazenda Río Negro, 31 Oct 1978, *Allem et al. 2309* (CTES); Poconé, Corumbá, Fazenda Bodoquena, Carandazal, 28 Oct 1978, *Allem et al. 2240* (CTES); Fazenda Ipiranga, km 10 MT3, 12 Feb 1978, *Allem & Vieira 1692* (CTES). PARAGUAY. Itapuá: Ruta 1, 6 km E of Gral. Delgado, 20 Apr 1995, *Norrmann et al. 223* (CTES); Isla Talavera, 10 Apr 1992, *Quintana et al. 38* (PY); Sierra de Amambay, s. d., 1907 *E. Hassler 9994* (W).

A. lateralis Nees. ARGENTINA. Corrientes: Berón de Astrada, ruta 12 y desvío a Berón de Astrada, 24 Feb 1993, *Arbo et al. 6027* (CTES); Capital, Barrio Dr. Montaña, s. d., *Norrmann 111* (CTES). Concepción, Estancia Tranquera de Hierro, 66 km noroeste de Chavarria, camino de Concepción, 3 Dec 1996, *Arbo et al. 6950* (CTES); Paso Crucesita, 20 Apr 1974, *Arbo et al. 631* (CTES); Tabay, 30 Jan 1971, *Arbo 308* (CTES); General Paz, 29 km S de Caa Catí, ruta 13, 17 Mar 1978, *Ahumada 1998* (CTES); Goya, Paso Tala, 16 Dec 1948, *Cabrera 10542* (CTES); Ituzaingó, 20 km NW of Virasoro, ruta 38, 3 Mar 1982, *Norrmann 71* (CTES); Estancia San José del Boquerón, 25 km NE de Playadito, 12 Dec 1981, *Carnevali 5005* (CTES); Estancia Abelenda, Rincón de Santa María, 9 Jul 1955, *Carnevali 506* (CTES); La Cruz, costa del Río Uruguay, 20 Dec 1944, *Ibarrola 1759* (LIL); Mocoretá, 20 Feb 1945, *Ibarrola 2467* (LIL); Monte Caseros, 8 km S de Labougle, costa río Uruguay, 22 Feb 1979, *Ahumada 2661* (CTES); Paso de los Libres, Bondpland, 17 Jan 1945, *Ibarrola 2113* (LIL); San Cosme, 25 km E Corrientes, ruta 12, 25 Feb 1978, *Ahumada 1573* (CTES); 28 km E de Corrientes, ruta 12, 26 Feb 1978, *Ahumada 1635* (CTES); San Martín, 8 Feb 1979, *Schinini et al. 16842* (CEN); Estancia Itá Berá, 25 km N de Carlos Pellegrini, ruta 14, 22 Feb 1976, *Irigoyen 320* (CTES); San Roque, 1 km de Cañada Mala, sobre camino, 30 Jun 1980, *Carnevali 6286* (CTES); Santo Tomé, 17 km S of Santo Tomé, ruta 40, 3 Mar 1982, *Norrmann 72* (CTES). Misiones: Capital, 11 Jun 1912, *Ekman 552*, *554* (CORD); Pantanos del Arroyo Zaimán, 15 Oct 1995, *Norrmann 46* (MNES). Formosa: Laishi, Reserva El Bagual, 15 May 2002, *Di Giacomo 576* (CTES). BOLIVIA. Santa Cruz: Andrés Ibanez, 1 km E of Intern. Airport Viru Viru, 17° 40′ S, 63° 10′W, 1 Jan 1986, *Killeen 1550* (CTES); Barrio Florida, zona sur de Santa Cruz, 8 km del centro, 17° 46′ S, 63° 11′ W, 400 m, 13 Feb 1992, *Mostacedo 246* (CTES). BRAZIL. Mato Grosso do Sul: Corumbá, Nhecolandia, Fazenda Cáceres, 28 Nov 1979, *Filho 30* (CTES). Paraná: Sierra de Sao Luis, Br 277, 19 Jan 1985, *Ferrucci et al. 217* (CTES). Rio Grande do Sul: Dos Irmaos, Santa María do Herval, 26 Jan 1983, *Bueno et al. 3639* (CTES). PARAGUAY. Caaguazú: sur les collines incultes, 19 Nov 1874, *Balansa 226* (K, SI, as var. *trichocoleus*). Itapuá: Isla Yacyreta, 18 Mar 1992, *Pin et al.* 170 (CTES).

A.* × *lindmanii Hack. **(*pro. sp.*) (= *A. arenarius* × *A. lateralis*).** BRAZIL. Santa Catarina: Itapirubá, 22 Feb 2008, *Nagahama 33*, *34*, *35*, *36*, *37*, *41*, *42*, *43*, *44*, *45*, *46* (CORD); *Norrmann 327, 328, 329, 330* (CTES).

A.* × *subtilior (Hack.) Norrmann **(*pro. sp.*) (= *A. bicornis* × *A. lateralis*).** ARGENTINA. Corrientes: Capital, Ciudad de Corrientes, 1 Jun 1996, *Norrmann 142* (CTES); Ituzaingó, 36 km E de Ituzaingó, 29 Mar 1982, *Norrmann 34* (CTES); Estancia La Negra sobre ruta 12, 11 Feb 2010, *Nagahama* & *Norrmann 152* (CORD). Misiones: Capital. 12 km W de Posadas, 19 Feb 1991, *Norrmann 108*, *108a* (CTES); Santo Tomé, ruta 94 camino a Garruchos, 28° 21′ 28″ S 55° 57′ 19″ W, *Nagahama 143*, *144* (CORD). BRAZIL. Rio Grande do Sul: entre Porto Alegre y Guaiba, 28 Jan 1983, *Norrmann et al. 88* (CTES); Estación Experimental Guaiba, 28 Jan 1983, *Norrmann et al. 87* (CTES); 60 km E de Santa María, Jan 1992, *Norrmann et al. 313* (CTES); Santa Catarina, Itapirubá, 23 Feb 2008, *Nagahama* 76 (CORD). PARAGUAY. Amambay: 5 km N del Río Aquidabán, *Norrmann et al. 175*, *176* (CTES, CORD). Concepción: 13 km NW de Horqueta a Loreto, Apr 1995, *Norrmann et al. 177* (CTES).

A.* × *velutinus Norrmann & Nagahama **(= *A. bicornis* × *A. glaziovii*).** BRAZIL. São Paulo: Auriflama, SP 310, km 570, 27 Dec 1984, *C.S. Campbell 4704* (SP); Pereira Barreto, 27 Dec 1984, *C. S. Campbell 4705* (SP); s. d., 27 Dec 1984, *C. S. Campbell 4706* (SP). PARAGUAY. Concepción: 38 km E de Concepción por ruta 5, 20 Apr 1995, *Norrmann 199* (CTES). Misiones: 2 km E de San Juan Bautista por ruta 1, 21 Apr 1995, *Norrmann 218*, *219*, *222* (CTES). San Pedro: Ipane y ruta 3, 43 km S de Iba Biyu, 20 Apr 1995, *Norrmann et al. 203* (CTES).