Species delimitation in the *Sporobolus aeneus* complex (Zoysieae, Chloridoideae, Poaceae) using the phylogenetic species concept

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Abstract The "*Sporobolus aeneus* complex" constitutes a morphologically well-defined group of species with lax, exerted, pyramidal panicles with verticillate branches, and comprises 14 species and six infraspecific taxa in southern South America (eastern Bolivia, eastern Paraguay, Uruguay, southern Brazil, northeastern Argentina). Species delimitation in the complex remains unresolved. To clarify the taxonomy of the group, multivariate analyses of qualitative and quantitative characters from herbaria specimens were performed. We applied the phylogenetic species concept and we used a modified "population aggregation analysis." Five species (*S. aeneus*, *S. cubensis*, *S. linearifolius*, *S. multinodis*, *S. recurvatus*) are recognized by unique combinations of qualitative character states, and three varieties based on significant mean value differences of quantitative characters. We conclude that leaf blade pilosity, widely used as a diagnostic character in the complex, is affected by external conditions like fire or blade age and is taxonomically unreliable. Two new cominations, *Sporobolus aeneus* var. *angustifolia* (Döll) S. Denham & Aliscioni and *S. aeneus* var. *eximius* (Nees ex Trin.) S. Denham & Aliscioni are made. *Vilfa acuminata* Trin. and *Vilfa eximia* Nees ex Trin. are lectotypified.

Keywords multivariate analyses, phylogenetic species concept, population aggregation analysis, South America, *Sporobolus*

Supplementary Material Table S1 is available in the free Electronic Supplement to the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

■ INTRODUCTION

The genus *Sporobolus* R. Br. belongs to the subfamily Chloridoideae, tribe Zoysieae, subtribe Sporobolinae (Peterson & al., 2007), and contains more than 160 species in the tropics, subtropics and temperate regions of both hemispheres (Clayton & Renvoize, 1986; Peterson & al., 1997). In the New World it includes more than 70 species, of which 72% are endemic and 90% are native (Peterson & al., 2007).

Sporobolus has been studied in regional floras and systematic revisions are available for Argentina (Parodi, 1928), Malaysia (Baaijens & Veldkamp, 1991), Brazil (Boechat & Longhi-Wagner, 1995), Australia (Simon & Jacobs, 1999), United States and Canada (Peterson & al., 2003), northeastern Mexico (Peterson & al., 2004), and northwestern South America (Giraldo-Cañas & Peterson, 2009). A complete revision or treatment of all American species is lacking, however. Phylogenetically, *Sporobolus* appears to be non-monophyletic, including *Calamovilfa* (A. Gray) Hack. ex Scribn. & Southw., *Spartina* Schreb., *Crypsis* Aiton, *Pogoneura* Napper, and *Zoysia* Willd. (Ortiz-Diaz & Culham, 2000; Hilu & Alice, 2001; Columbus & al., 2007; Peterson & al., 2010).

The *Sporobolus aeneus* complex constitutes a morphologically well-defined group of species with lax, exerted, pyramidal panicles with verticillate branches, spikelets more than 2.5 mm long, with the upper glume as long as the spikelet, and plants that are commonly tufted. This complex includes *S. acuminatus* (Trin.) Hack., *S. adustus* (Trin.) Roseng., B.R. Arril. & Izag., *S. aeneus* (Trin.) Kunth, *S. camporum* Swallen, *S. cubensis* Hitchc., *S. eximius* (Nees ex Trin.) Ekman, *S. linearifolius* Nicora, *S. minarum* Boechat & Longhi-Wagner, *S. multinodis* Hack., *S. nudiramus* Boechat & Longhi-Wagner, *S. paucifolius* Boechat & Longhi-Wagner, *S. recurvatus* Boechat & Longhi-Wagner, *S. reflexus* Boechat & Longhi-Wagner, *S. sprengelii* Kunth, *S. subbulbosum* Arechav., and many infraspecific taxa. Except for *S. cubensis* (distributed from Mexico to Bolivia and Brazil) all species occur in a limited region in southern South America, including eastern Bolivia, eastern Paraguay, Uruguay, southern Brazil, and northeastern Argentina.

Many authors recognized the affinity among species of the complex but, as having been studied only partially in regional floras, species delimitation has remained unresolved. Also, distributional data could not be correctly established because of lack of agreement as to species delimitation.

Within the complex, species concepts are dissimilar and incongruent; different authors use different characters to define species and, as a result, we found many specimens which are identified as different species by different authors, and even, by the same author in the same publication. Diagnostic characters most used for separating species of this complex are: sheath pubescence, blade pubescence and form, inflorescence length, and distribution of spikelets along the inflorescence branches (e.g., the naked basal portion of the branches).

Hitchcock (1927), in his study of the grasses of Ecuador, Peru, and Bolivia, circumscribed *S. aeneus* to have felty, involute or folded blades, and inflorescence branches with spikelets near the base, and *S. eximius* to have flat blades and naked branch bases. He also mentioned that in *S. aeneus* new innovations are more pilose than older ones. Parodi (1928) studied Argentinean species of *Sporobolus* and included in this treatment *S. acuminatus*, *S. eximius*, *S. aeneus*, and *S. multinodis*. This author used leaf pilosity to segregate *S. eximius*, and blade form to separate the remaining species. He established two varieties in *S. aeneus* based on glume length, relating them to *S. adustus*. Rosengurtt & al. (1970) considered *S. multinodis* and *S. adustus* for Uruguay and separated them by inflorescence length, glume and palea surface. Smith & al. (1981), for Flora Catarinense, lumped *S. eximius*, *S. adustus*, and *S. camporum* under *S. aeneus* and considered this to be a very variable species. Renvoize (1984) considered only *S. aeneus* growing in the state of Bahia, Brazil, and he related it with *S. sprengelii*, *S. adustus*, and *S. eximius*; characters used to distinguish between species were: leaf form and pubescence, panicle length, the naked portion of inflorescence branches and spikelet surface. Later, Renvoize (1988) studying Hatschbach's Paraná grasses, treated *S. exilis* (= *S. linearifolium*), *S. camporum*, *S. aeneus*, and *S. eximius*, and did not use blade pilosity to distinguish them but used culms and inflorescences length and blade form. Renvoize (1998) described *S. cubensis* and *S. aeneus* for Bolivia, as plants having inflorescence branches with spikelets all along it. Killeen (1990) considered *S. sprengelii* and *S. cubensis* from Santa Cruz (Bolivia), including them as an intergrading species complex with *S. adustus*, *S. acuminatus*, and *S. eximius*. Boechat & Valls (1991) discussed the difficulty in defining *S. adustus*, *S. aeneus*, and *S. eximius*, and considered species growing in Rio Grande do Sul (Brazil) such as *S. camporum*, distinct from *S. multinodis*. For the Argentinean flora Astegiano (1996) distinguished *S. eximius* by blade pilosity, and *S. acuminatus* and *S. aeneus* by blade form, plant length, and inflorescence length. Boechat and Longhi-Wagner (1995) studied the genus *Sporobolus* in Brazil including 30 species. This is the only work where all species of the complex are included and some new varieties are proposed. All species of the complex are considered as valid, but many overlapping quantitative characters are used, and qualitative characters are frequently ambiguous. Intermediate specimens are mentioned and others are simultaneously placed in more than one species, showing that the complex is not easy to resolve.

A more rigorous approach is needed to clarify the taxonomy of the *Sporobolus aeneus* complex. In order to delimit the species of the complex, we following Henderson (2004, 2005) who proposed to use a modified "population aggregation analysis" (PAA) of Davis and Nixon (1992) for the identification of phylogenetic species. The phylogenetic species concept (PSC) defines species as "the smallest aggregation of population (sexual) or linage (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon & Wheeler, 1990: 218). The PSC proceeds by looking for constant characters within and among populations, considering that constancy of characters is evidence of fixation and lack of reticulation, while traits that vary are considered to provide evidence of intersection and lack of hierarchy (Luckow, 1995). Only characters or character states (not traits) are used to distinguish species. Because the PSC-PAA approach requires placement, a priori, of specimens in a population, Henderson (2004, 2005) introduced some operational modifications to warrant applicability to herbaria material, which usually includes specimens collected from scattered localities and not on a population basis. He proposed to score specimens (instead of populations) for all attributes (traits and characters) and to use successive cluster analyses to distinguish traits from characters at the same time that groups of specimens are delimited. Finally, groups of specimens with unique combinations of character states are discovered.

Luckow (1995) discussed the extention of the PSC to the subspecific level and stated that "groups of populations that differ not by fixed characters but by differences in mean value would be recognized as subspecies or varieties". We followed Luckow's taxonomic concept in recognition of infraspecific taxa but considering groups of specimens instead of populations.

The aim of this work is to resolve the taxonomy of the *Sporobolus aeneus* complex by applying the phylogenetic species concept by means of the modified PSC-PAA method.

■ MATERIALS AND METHODS

Specimens. — Most herbaria with significant grass collections from the distribution area of the species complex were consulted (BA, BAA, BAB, CORD, LIL, LP, MVFA, MVM, SI, US). Also, collection trips were carried out in Argentina and Uruguay, in sites from where relatively few collections were available. Type material was searched for in herbaria worldwide and many digital photos were studied. Geographical and ecological data were recorded from specimen labels.

Morphological and anatomical studies. — Measurements of spikelets were made using an ocular micrometer. In order to describe leaf blade outlines, transverse sections were made from the middle segments of leaf blades of herbarium specimens. The samples were re-hydrated in water for 24 h in a heater at 42°C, afterwards in ethyleneglycol 50% at the same temperature for 24 h. Previous to infiltration, fragments were pretreated with 10% fluorhydric acid to remove silica cells. The material was dehydrated in an ethanol-alcohol series, embedded in paraffin, and sectioned on a rotary microtome at 10 μm thickness. Histological samples were stained with safranin-fast green and mounted in Canada balsam (D'Ambrogio de Argüeso, 1986). Photomicrographs were taken by a digital camera Nikon E5400 linked to the optical microscope. For anatomical descriptions we followed the terminology proposed by Ellis (1976).

Data matrix and analysis. — More than 250 specimens were studied; incomplete or not fully developed plants were excluded from the analyses, as well as specimens suspected to be isolated new innovations of a larger plant. Qualitative and quantitative characters were explored from the entire plant. No

Table 1. List of morphological attributes.

1. Sheath margins with long, straight, silky, white or yellow hairs that continue at base blade for a distance: absent (0), present (1)
2. Sheath margins with caducous, woolly hairs: absent (0), present (1)
3. Sheath margins glabrous or glabrescent: absent (0), present (1). Some specimens with pubescent sheaths, but with hairs not like those described in character 1 and 2, were included in this character.
4. Abaxial blade surface (basal blades): glabrous (0), pubescent (1)
5. Adaxial blade surface (basal blades): glabrous (0), pubescent (1)
6. Blade margins with tuberculate hairs: absent (0), present (1)
7. Flabelate basal blades: absent (0), present (1)
8. Blades strongly narrower than sheaths: absent (0), present (1)
9. Blades filiform: absent (0), present (1). When not filiform blades are externally convolute, involute or planar; these states were not scored because they may vary with state of plant humidity when collected or among blades of the same sample. Nevertheless, the filiform state was checked anatomically (Figure 4).
10. Blade width (mm). The middle portion of the broader basal blade was used to score this character.
11. Inflorescence length (cm)
12. Solitary basal branch: absent (0), present (1)
13. First verticil: an imperfect whorl (0), a perfect whorl (1)
14. Basal branch length (average from 3 branches, cm)
15. Naked portion of basal branch (average from 3 branches, cm)
16. Naked portion of basal branch/basal branch length ratio
17. Relative length of glume and lemma: G<L (0), G = L (1), G>L (2)
18. Spikelet length (mm)
19. Pilose pedicels: absent (0), present (1)
20. Prickles on pedicels: absent (0), present (1)
21. Pilose lower glume: absent (0), present (1)
22. Prickles on lower glume: absent (0), present (1)
23. Upper glume long acuminate, with short hairs: absent (0), present (1)
24. Prickles on upper glume: absent (0), present (1).

quantitative character presented gaps in the complete matrix to allow delimitation of discrete character states. Finally, 18 qualitative and 6 quantitative attributes were scored for 127 specimens with no missing values, and type material was included when possible (Table 1; Table S1; and Specimens examined). Multivariate methods of analysis were performed using the program NTSYSpc v.2.02h (Rohlf, 1986–1998) and InfoStat (Di Rienzo & al., 2009). Cluster analysis (CA) with square-root transformed qualitative variables (for all specimens) were carried out based on a similarity matrix obtained with the simple matching coefficient and using the UPMGA clustering algorithm. Standardized quantitative variables (for a subgroup of specimens, see above) were examined with principal component analysis (PCA), using the product-moment correlation coefficient to compute the correlation matrix from which eigenvectors were extracted. Discriminant analysis (DA) was performed on the same quantitative characters and specimens of PCA. For PCA and DA, characters were assumed to be multivariate normal considering both procedures relatively insensitive to deviations from normality; nevertheless, results are viewed as approximate. To avoid logically correlated characters (14–16), character 15 was not used in the PCA and DA. One-way ANOVA on $\log_{10}$ transformed variables and Bonferroni pairwise procedure was used to see pairs of means differing significantly at $P < 0.01$.

Delimitation of specimens groups and taxonomic status. — Qualitative attributes were divided into characters and traits using successive rounds of CA. All attributes were used in the first CA, then, suspected traits (high polymorphic attributes within a cluster) were removed and not used in the following CA, until a suite of characters was discovered which, when analyzed, gave clusters of specimens with unique combinations of states. These groups of specimens with unique combinations of character states were considered as species under PSC.

Within discovered species, quantitative characters were analyzed by PCA in order to detect internal consistency or the presence of specimen subgroups that could be considered as varieties. The DA of pre-classified subgroups of specimens (those obtained by PCA) was used to analyze most discriminant characters and the percentage of classification success. When subgroups could be distinguished by one ore more significant different mean values of a character, they were recognized as varieties (Luckow, 1995).

Biogeographical provinces (Cabrera & Willink, 1973) were used to help delimit subgroups.

In order to identify the correct names, and to construct synonymies, the morphology of each finally accepted taxon was compared with protologues and all available type specimens or digital imagines. Traditional descriptions are given under the Taxonomy section, considering new taxa circumscription, their synonymies and distributional data. Ranges (min-max) are given for plant structures, while character statistics are shown by box-plots.

■ RESULTS

Six out of the 18 qualitative attributes were detected as characters by successive rounds of cluster analysis. The achieved dendogram (not shown) established five major clusters, each characterized by a unique combination of six qualitative characters (Table 2), which are assigned to species level (see Discussion).

When each group was examined for internal consistency by PCA, only Group 5 could be further subdivided based on quantitative characters (Fig. 1). Eigenvalues of the three first

Table 2. Major groups found by cluster analysis and their combination of character states.

	Sheaths margins with long, straight, silky, white or yellow hairs that continue at base blade for a distance: absent (0), present (1)	Sheaths margins with caducous, woolly hairs: absent (0), present (1)	Sheaths margins glabrous or glabrescent: absent (0), present (1)	Blades strongly narrower than sheaths: absent (0), present (1)	Blades filiform: absent (0), present (1)	Upper glume long acuminate with short hairs absent (0), present (1)
Group 1 (*S. cubensis*)	1	0	0	0	0	0
Group 2 (*S. linearifolius*)	0	0	0	0	1	0
Group 3 (*S. multinodis*)	0	0	0	1	0	1
Group 4 (*S. recurvatus*)	0	1	0	0	0	0
Group 5 (*S. aeneus*)	0	0	1	0	0	0

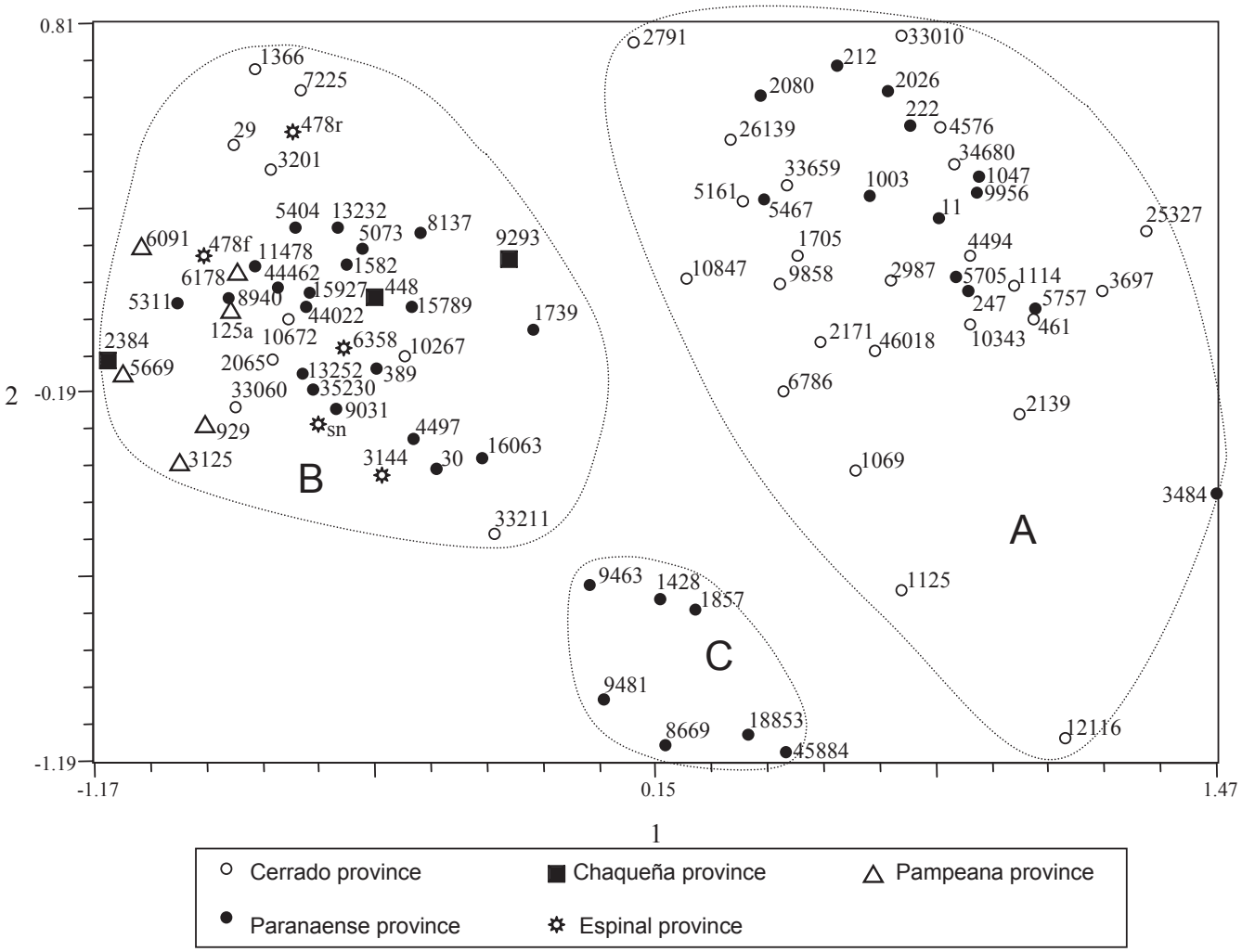

Fig. 1. Scatter-plots of the the first two components from Principal Component Analysis based on five quantitative characters and 87 specimens from *Sporobolus aeneus*. Biogeographic provinces (Cabrera & Willink, 1973) are indicated for each specimen.

components represent 90.8% of the total variation. Among the characters that better explain the variation in the first component are inflorescence length (eigenvector 0.87), blade width (0.85), and basal branch length (0.80). The character best explaining the second component is naked portion of basal branch/basal branch length ratio (–0.67). Spikelet length (0.90) is the character that contributes most to component 3. The PCA plot (Fig. 1) shows three subgroups (A–C) defined by components 1 and 2. No significant resolution could be observed along the third axis (not shown). Discriminant analysis separates the three subgroups with 97.70% success and blade width is the most discriminating character. ANOVA shows that all subgroups differ in 1 or 2 mean values; all characters present significant differences in mean values for some pairs of subgroups, although no character differs among all subgroups (Table 3).

■ DISCUSSION

Groups 1 to 5, each with a unique combination of character states, are considered as species under the PSC. Quantitative characters for species are shown in Fig. 2. Subgroups A, B and C (from Group 5) are considered as varieties because of significant differences in character mean values. Groups and subgroups were compared with type material and original descriptions in order to assign a name (see Taxonomy; Table 4 on p. 1780).

Group 1. — Group 1 (23 specimens) corresponds to *Sporobolus cubensis*. In our analysis this group of specimens is distinguished by the following character state combination: sheaths with long, straight, silky white or yellow hairs that continue at base of the blade (Fig. 3A), hairs not caducous and woolly, blades not strongly narrower than sheaths, blades convolute to planar, and upper glumes glabrous, apices acute. This species can be well described by inflorescence quantitative characters which are not very variable, such as inflorescence length and basal branch length (Fig. 2). Hitchcock (1909) mentioned in the protologue the "copiously felty-ciliate basal sheaths" as being characteristic of the species. Most qualitative and quantitative characters of the 23 specimens match the original description of *S. cubensis* (blade form, inflorescence length, smooth spikelets, spikelet length). Moreover, characters are generally constant along the large distributional range of the species. Recognition of the species has been unproblematic in the northernportion of its range, but within the geographical region of the analyzed complex it has been frequently confused with *S. aeneus*.

Group 2. — Group 2 (5 specimens) corresponds to *Sporobolus linearifolius*. The combination of character states that distinguish this group are: sheaths glabrous, blades not strongly narrower than sheaths, blades filiform, and upper glumes glabrous and acuminate. Apart from the blade width, considering quantitative characters, this taxon can be recognized by the shortest inflorescences in the complex (Fig. 2). The filiform (thread-like) external morphology of the leaf blade corresponds anatomically to a permanently infolded blade (Ellis, 1976), nearly circular in transverse section, with 3–5 first order vascular bundles. The remaining species have inrolled or V-shaped blades, not permanently infolded; these are broad with more than five first order vascular bundles (Fig. 4).

The specimens of group 2, all from southern Brazil and including type material, match the diagnostic characters of *S. linearifolius* as described by Renvoize (1987, as *S. exilis*, *nom. illeg.*). Specimen labels show that this species has in the past been confused with *S. cubensis* and *S. aeneus*.

Group 3. — Group 3 (7 specimens) corresponds to *Sporobolus multinodis*. The combination of character states for that group is: sheaths glabrous or glabrescent, blades much narrower than sheaths (Fig. 7D), blades conduplicate to planar, and upper glumes with long acuminate apex and pilose with short hairs. Inflorescence length also characterizes this species (Fig. 2). Hackel (1909) pointed out the presence of pilose glumes, and blades narrower than the sheaths are evident in the type specimen. All specimens are from southern Brazil and northern Uruguay. Type material of *S. multinodis* var. *exasperatus* agrees with characters of this group and this variety is therefore considered a synonym. Our concept of *S. multinodis* agrees with Parodi (1928) and Boechat & Longhi-Wagner (1995). Authors that consider blade pilosity as a diagnostic character place some of these specimens under *S. eximius* as revealed by specimen labels.

Group 4. — Group 4 (5 specimens) corresponds to *Sporobolus recurvatus.* This group of specimens is distinguished by the combination of the following character states: sheath margins with caducous, woolly hairs (Fig. 3B), blades not strongly narrower than sheaths, convolute blades, and upper glumes

Table 3. Results from ANOVA analysis. Different symbols within a column represent significant differences in mean value; first number is the mean value, second number is the standard deviation.

	Blade width *P*-value < 0.0001	Inflorescence length *P*-value < 0.0001	Basal branch length *P*-value < 0.0001	Naked portion of basal branch *P*-value < 0.0001	Naked portion of basal branch / basal branch length ratio *P*-value < 0.0001	Spikelet length *P*-value = 0.0026
Subgroup A (var. *aeneus*)	# 8.32, 1.84	* 27.58, 5.48	* 5.67, 1.70	* 1.38, 0.71	# 0.24, 0.10	* 3.30, 038
Subgroup B (var. *angustifolia*)	* 2.65, 1.07	# 14.17, 4.74	# 3.13, 0.77	* 1.36, 0.45	* 0.43, 0.07	* # 3.69, 0.62
Subgroup C (var. *eximius*)	* 3.51, 1.33	* 31.29, 3.15	* 6.84, 0.91	# 3.74, 0.72	* 0.55, 0.09	# 3.37, 0.75

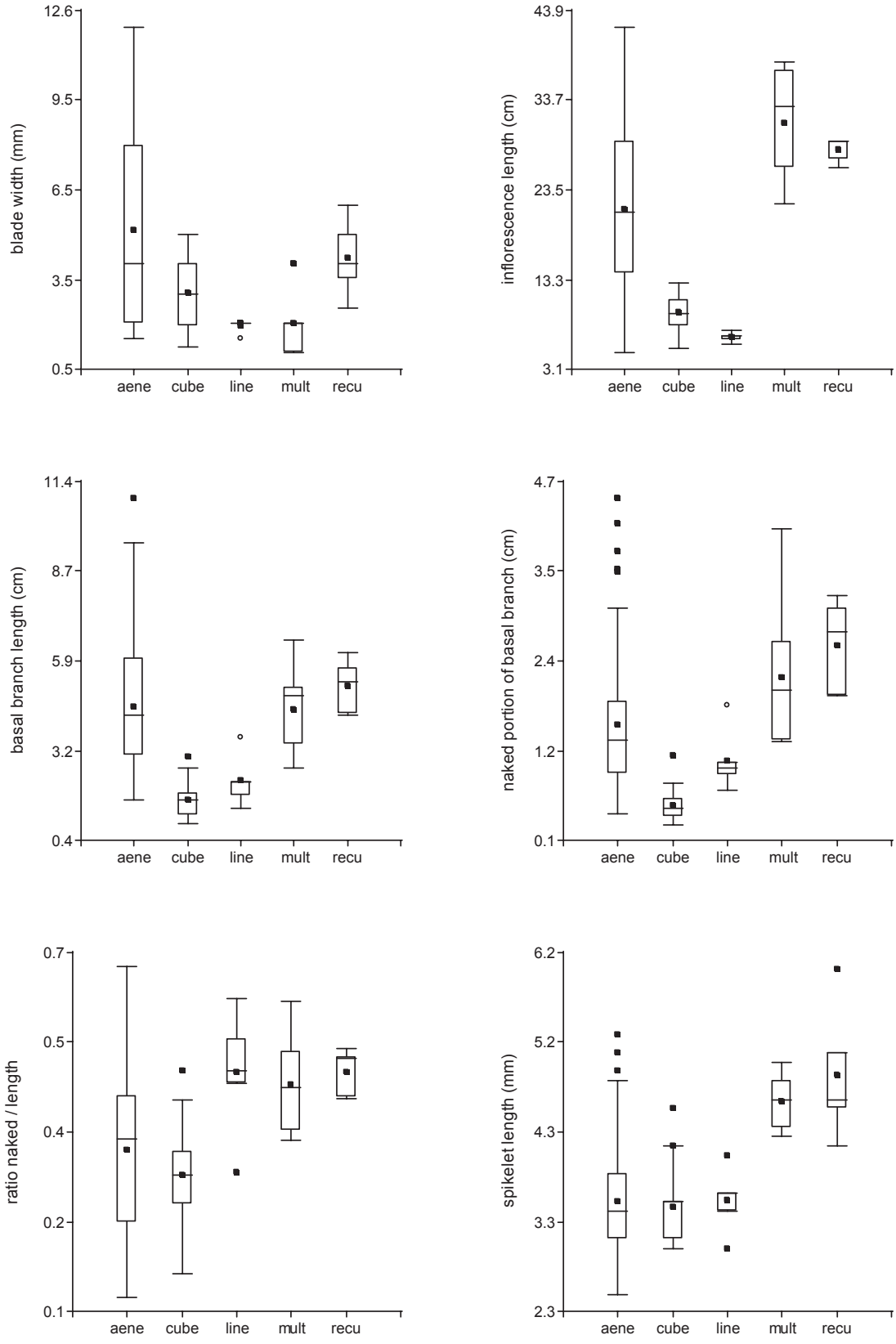

Fig. 2. Box-plots of quantitative characters of species in the *Sporobolus aeneus* complex. Boxes incorporate 50% of values; horizontal line in box indicates median value; dark points within vertical line indicate mean value; dark points outside vertical line indicate outside values; open circles indicate far outside values.

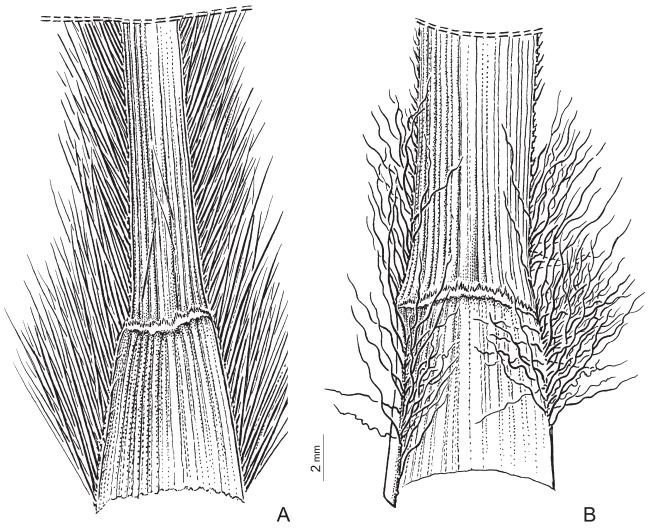

Fig. 3. Ligule zone. **A,** *Sporobolus cubensis* showing sheaths margins with long straight hairs that continue at the base of the blade for a distance, from *Zuloaga 4786* (SI); **B,** *Sporobolus recurvatus* showing sheath margins with woolly hairs, from *Irwin 17840* (CTES).

glabrous. Long basal branches lacking spikelets for a long portion is a good character for this species, as shown in Fig. 2. The holotype and one isotype of *S. recurvatus* were included in the analysis and cluster in this group. All specimens are from Brazil (Mato Grosso, Goias). Without considering the typical woolly sheaths, large inflorescences, and tall culms, some herbaria specimens have been identified as *S. aeneus* or *S. multinodis*.

Group 5. — Group 5 (87 specimens) corresponds to *Sporobolus aeneus*. The character states that distinguish this group are: sheath margins glabrous or glabrescent, blades not strongly narrower than sheaths, convolute to planar blades, and upper glumes glabrous. This group is the largest one and also has the most variable traits and quantitative characters (Figs. 2 and 5). It includes many taxa described in the complex that are here considered as synonyms because no exclusive combination of character states was recovered for them: *S. adustus, S. acuminatus, S. camporum, S. eximius, S. minarum, S. nudiramus, S. paucifolius, S. subbulbosus, S. reflexus*, *S. aeneus* var. *barbicollis, S. acuminatus* var. *longispiculus, S. aeneus* fo. *parviflora, S. eximius* var. *latifolius*. The binomial *S. aeneus*, based on *Vilfa aenea*, has priority and must be selected for this group (see also *S. sprengelii* under Doubtful names).

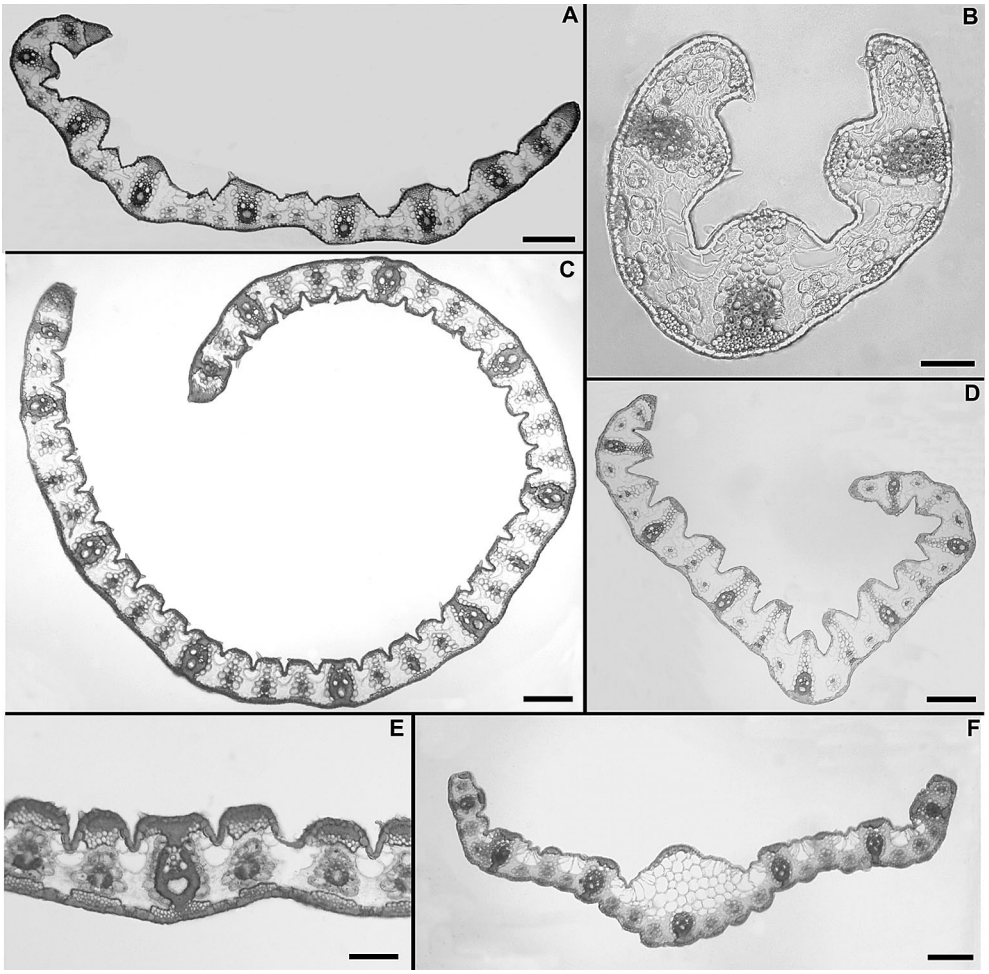

Fig. 4. Blade cross sections. **A,** *Sporobolus cubensis*, from *Renvoize 5405* (US); **B,** *Sporobolus linearifolius*, from *Dombrowski 6540* (CTES); **C,** *Sporobolus aeneus* var. *aeneus*, from *Nicora 9858* (SI); **D,** *Sporobolus aeneus* var. *angustifolia*, from *Montoro Guarch 3125* (BAA); **E,** *Sporobolus recurvatus*, from *Chase 11887* (isotype SI); **F,** *Sporobolus multinodis*, from *Rosengurtt 7033* (US). Scale bars: A, C–E = 123.5 μm; B = 136 μm; F = 111 μm.

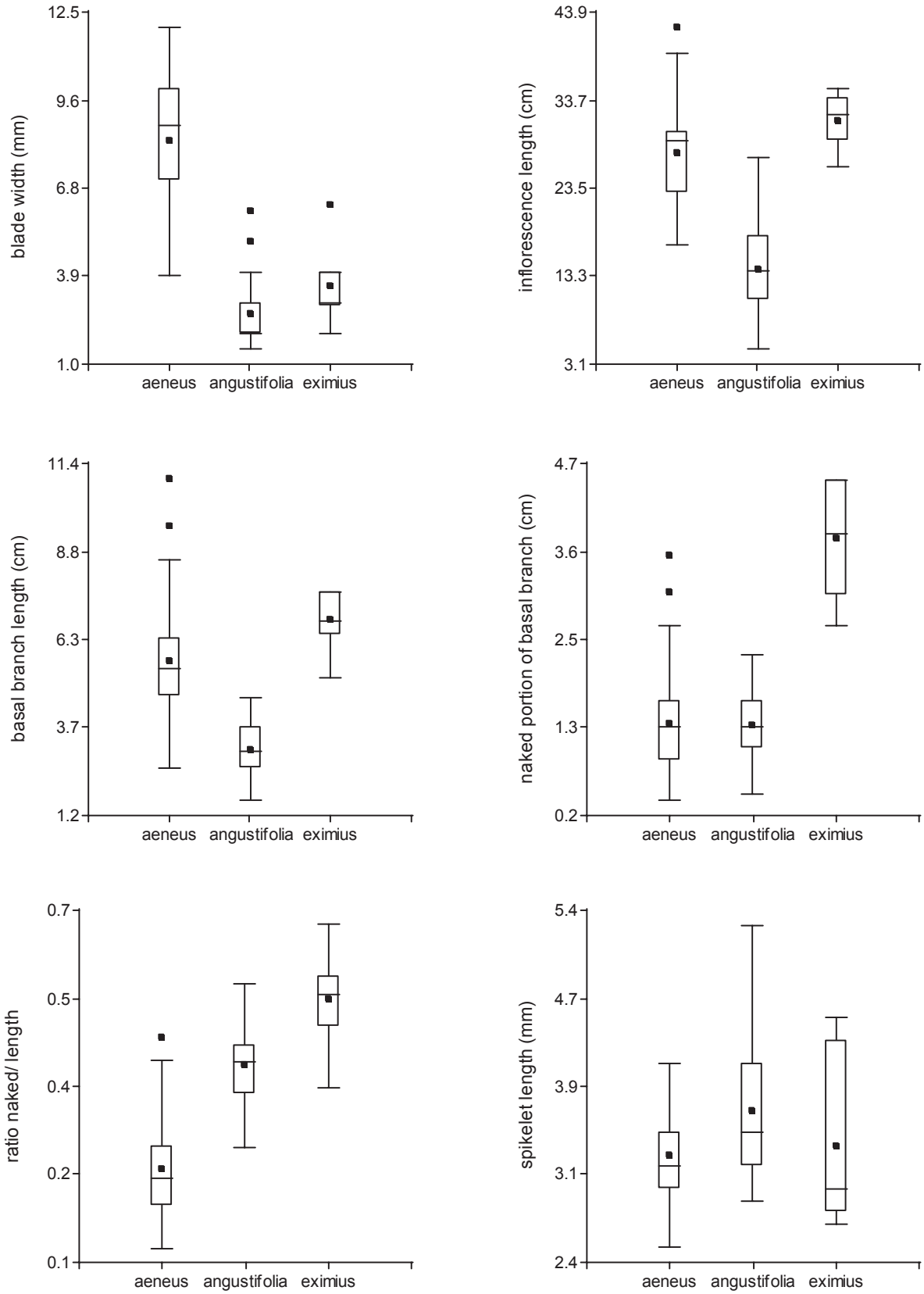

Fig. 5. Box-plots of quantitative characters of varieties in *Sporobolus aeneus*. Boxes incorporate 50% of values; horizontal line in box indicates median value; dark points within vertical line indicate mean value; dark points outside vertical line indicate outside values.

Within Group 5, three subgroups were recognized by PCA (Fig. 1), which are considered as varieties:

Subgroup A. — Subgroup A (37 specimens) corresponds to *S. aeneus* var. *aeneus*. Mean values of blade width and the naked portion of basal branch/basal branch length ratios differ significantly from the other two subgroups (Table 3). It includes specimens with long inflorescences (17–42 cm long), long basal branches (2.6–11.0 cm long), broad leaf blade (3.9–12.0 mm wide), and inflorescences branches with spikelets near the base (the lower 0.4–3.6 cm of the branch is naked and generally less than 1/3 the entire length of the branch is naked) (Fig. 5). This subgroup occurs in the Cerrado and Paranaense biogeographical provinces; all specimens from the latter province are from one locality in Misiones (Argentina). When considering mean values of quantitative characters from these two geographical sets no significant differences were found (*P*-value 0.32, 0.24, 0.74, 0.25, 0.07, 0.36 for characters 10, 11, 14, 15, 16 and 18, respectively).

Considering the long inflorescences, broad leaves, and spikelets all along the inflorescence branches of the type material (*Vilfa aenea*), we relegate this name to the typical variety, and include these as synonyms: *S. acuminatus* (based on *Vilfa acuminata*), *S. aeneus* var. *barbicollis*, *S. eximius* var. *latifolius*, and *S. acuminatus* var. *longispiculus*.

Specimens of this group have previously been identified as *S. acuminatus*, *S. camporum*, or *S. eximius*, the later name usually used for plants with pilose blades.

Subgroup B. — Subgroup B (43 specimens) corresponds to *S. aeneus* var. *angustifolia*. Inflorescence length and basal branch length mean values in subgroup B are significantly different from subgroup A and C (Table 3). It includes specimens with shorter inflorescences than the previous one (5–27 cm long), and shorter basal branches (1.6–4.6 cm long), narrow blades (1.5–6.0 mm wide), and inflorescences branches without spikelets in the basal portion (branches 0.4–2.2 cm long near base naked, corresponding to 1/3–1/2 or more the length of the branch naked) (Fig. 5). Specimens are distributed through NE Argentina, Paraguay, Uruguay, Bolivia, and southern Brazil without geographical discontinuity, including many different biogeographical provinces (Cerrado, Chaqueña, Espinal, Paranense, Pampeana).

Type material of *Vilfa adusta*, *S. subbulbosus*, *S. aeneus* f. *parviflora*, *S. camporum*, *S. minarum*, *S. paucifolius*, and *S. reflexus* match subgroup B characteristics. Specimens with pilose blades included in this group have been identified as *S. eximius*; other samples have been assigned to *S. multinodis* when not considering the inflorescence length and blade form.

Subgroup C. — Subgroup C (7 specimens) corresponds to *S. aeneus* var. *eximius*. The mean value of the length of the naked portion of basal branch differs significantly from the others two subgroups (Table 3). This group comprises plants with long inflorescences (26–35 cm long) and somewhat broad blades (2.0–6.2 mm wide) but with inflorescences branches longer (5.1–7.6 cm) and naked at the base (branches 2.6–4.5 cm long near the base naked, usually more than 1/2 the length of the branch naked) (Fig. 5). Specimens are from the Paranaense biogeographical province.

The original description under *Vilfa eximia*, indicates that plants are taller than *Vilfa adusta* with longer inflorescences and branches, the branches naked on the proximal 1/2, and blades "patenti-hirsuta" which may refer to patent tuberculate hairs on blade margins or to conspicuous pubescence on blade surface. Later authors recognized *V. eximia* by its long inflorescences and convolute and hirsute blades (Steudel, 1855; Döll, 1878). There is no illustration with the original description but when Ekman transferred *V. eximia* to *Sporobolus* he included a plate which shows the long inflorescence with long and basally naked branches. In our analysis, specimens of subgroup C equal this "*V. eximia* inflorescence type" and present mostly convolute, glabrous or abaxially pilose blades.

Specimens of this group have been identified as *S. camporum*, *S. eximius* or *S. acuminatus*.

Blade pilosity. — Most authors use blade pilosity as a diagnostic character when delimiting species of the complex. We scored pilosity on both abaxial and adaxial blade surfaces. In the cluster analysis these characters came out as traits, i.e., occurring in some but not all representatives of a group, and also in other groups. When eliminating other attributes from the matrix to permit blade pilosity to form groups based on glabrous or pubescent specimens, we found that those groups were highly inconsistent in many aspects. Blade pilosity seems to be affected by external conditions like fire or organ age and thus taxonomically unreliable. We found that blades from new innovations may be pubescent while blades of fertile culms are glabrescent (*S. multinodis*: *Sacco 97*). Within a single culm external (old) blades may be glabrous and internal (new) ones pubescent (*S. aeneus* var. *adusta: Hatschbach 33060*). Rosengurtt & al. (1960) indicated that foliar pubescence in grasses should be examined on young leaves due to caducous hairs. In some samples, hairs were easily removed and it was easy to find loose hair masses inside a convolute blade. Finally, we observed specimens with burned sheaths that had pubescent blades on the basal portion and were glabrous elsewhere (*Sporobolus cubensis*: *Smith 3209*, *Eiten 9123*, *S. aeneus* var. *angustifolia*: *Dusén 13232*, *13252*), indicating that pilosity may be modified after fire. All this confirms that blade pilosity is not a good character to delimit species in this complex. In contrast, sheath pilosity was a reliable character, especially in differentiating *S. cubensis* from *S. recurvatus*. In *S. cubensis* fire affected blade pilosity but sheath pilosity remained constant. Fixed characters from basal organs, like sheath pilosity or presence of glands, have been reported to be a fire adaptation in grasses from Cerrado Province (Vega & al., 2008).

■ TAXONOMY

Key to the species

1. Blades strongly narrower than sheaths, upper glume apices long acuminate, glumes with short hairs . . ***S. multinodis***
1. Blades not strongly narrower than sheaths, upper glume apices acute to acuminate, glumes smooth or with prickles, but glabrous. **2**

2. Sheath margins with long, straight, silky, white or yellow hairs that continue at base blade for a distance . . . . . ***S. cubensis***
2. Sheath margins glabrous, glabrescent or pilose, but hairs different from *S. cubensis* **3**
3. Sheaths margins with caducous, woolly hairs at margins . . . . . ***S. recurvatus***
3. Sheaths margins glabrous, glabrescent or pilose **4**
4. Blades filiform; culms with 1–2 observable nodes . . . . . ***S. linearifolius***
4. Blades not filiform; culms with 3–8 observable nodes . . **5**
5. Panicles 5–27 cm long, basal branches 1.6–4.6 cm long, culms (30–)65–80 cm tall. . . ***S. aeneus*** var. ***angustifolia***
5. Panicles 17–42 cm long, basal branches 2.6–11.0 cm long, culms 70–120 cm tall **6**
6. Branches of the first whorl 2.6–11.0 cm long, with spikelets all along the branches or mostly less than 1/3 the length of the branch naked; blades 3.9–12.0 mm wide . . . . . ***S. aeneus* var. *aeneus***
6. Branches of the first whorl 5.1–7.6 cm long, more than 1/2 the length of the branch naked; blades 2.0–6.2 mm wide . . . . . ***S. aeneus*** var. ***eximius***

1. *Sporobolus cubensis* Hitchc. in Contr. U.S. Natl. Herb. 12: 237. 1909 – Type: Cuba, Isle of Pines, *A.H. Curtiss 392* (holotype, US-522010 [photo seen]; isotype, MO [photo seen]).

Iconography: Giraldo-Cañas & Peterson, 2009: 53; Judziewicz, 1990: 609.

Plants perennial, cespitose; culms 40–65 cm long, 1.0–1.3 mm diam., hollow, slender, erect, simple; nodes (3)4–6, glabrous; basal sheaths strongly striate, usually reddish and shiny, with long, straight, silky, white or yellow hairs which continue upward along blade margins for a short distance; culm sheaths 4–6 cm long, glabrous, shorter than internodes; ligules with a short line of hairs, ligule lobules with hairs 3 mm long; blades 6–20 cm long, 1.2–5.0 mm wide, striate, glabrous except at basal margins, mostly flat or convolute, upper ones shorter. Panicles 5–13 cm long, narrowly pyramidal, branches 3–10 in the first whorl, divergent or reclinate when mature, branches 0.7–3.1 cm long without spikelets in the lower 1/5–1/3–(1/2), with an elongated gland at the base; pedicels glabrous. Spikelets 3.0–4.5 mm long, brownish or purplish, glabrous; lower glumes 1/3–1/2 as long as the spikelet, apex acute or acuminate, 0−1-nerved, upper glumes usually as long as the floret, 1-nerved, apex acute; lemma as long or slightly shorter than the palea. Stamens 3, anthers 2 mm long, dark purple. Fruit 2.0–2.1 mm long, obovoid, embryo 1/3–1/2 the length of the fruit.

Notes. – This species can be easily recognized by the basal sheaths usually reddish and shiny, with long, straight, silky, white or yellow hairs that continue upward along the blade margins of 1–2 cm. Panicles are short, up to 13 cm long and are narrowly pyramidal.

Distribution and habitat. – *Sporobolus cubensis* is the most widespread species of the complex, ranging from Mexico, Central America, Cuba, Colombia, Venezuela, Suriname, French Guiana, Guyana, Bolivia to Brazil; in grassland, savanna, and cerrado of Brazil; on rocky or sandy soil, from sea level to 1000 m or up to 1850 m in La Paz, Bolivia. Persistent burned sheaths indicate that the species flowers after fires.

Specimens examined. – BOLIVIA. Beni: Prov. Vaca Diez, Riberalta, 18 Oct 1991, *Beck 20551* (SI). La Paz: Prov. Franz Tamayo, 28 Nov 2002, *Miranda 181* (CTES). Santa Cruz: Velasco, 22 Oct 1987, *Killeen 2826* (US); Velasco, Parque Nacional Noel Kempff, 15 Oct 1993, *Killeen 5493* (SI). BRAZIL. Bahia: Palmeiras, 11 Feb 1994, *Zuloaga 4786* (SI). Goias: Municipio de Flores de Goiás, 10 Oct 1997, *da Silva 3389* (IBGE); Serra do Caiapó, 18 Oct 1964, *Irwin 7027* (SI); Municipio de Campos Belos, 1 Nov 2000, *Oliveira 1177* (IBGE); Niquelandia, 7 Nov 1994, *Filgueiras 3037* (SI). Mato Grosso: Serra do Roncador, Municipio de Barra do Garças, 6 Oct 1968, *Eiten 9123* (US); vicinity of Xavantina, 9 Oct 1964, *Irwin 6684*, *Irwin 6699* (SI); Expedition Base Camp, 07 Sep 1968, *Richards 6859* (US). Minas Gerais: Municipio de Formoso, Parque Nacional Grande Sertão Veredas, 3 Dec 1997, *da Silva 3687* (IBGE). Roraima: Serra do Sol, 18 Dec 1954, *Maguire 40350* (US); rodovia BR 174 a 7 km de Santa Helena, 19 Jun 1974, *Pires 14568* (US). Without locality, "campos", without collector (SI). COLOMBIA. Meta: Carimagua, 18 Sep 1992, *Renvoize 5405* (US). GUYANA. Rupununi Northern Savanna: Marakanata Old Village, 13 Oct 1963, *Goodland 986* (US). FRENCH GUIANA. Berbice Corentyne Region: Canje River, 15 Apr 1987, *Pipoly 11602* (US). Savanna between Takutu River and Kanaku Mountains, 22 Mar 1938, *Smith 3209* (LIL). SURINAME. Distr. Brokopondo: E of railroad km 106, 13 Dec 1965, *Donselaar 2737* (US). VENEZUELA. Bolívar: Gran Sabana, San Ignacio de Yuruaní, 4 May 1988, *Liesner 24212* (SI).

2. *Sporobolus linearifolius* Nicora in Hickenia 2(19): 90. 1993 ≡ *Sporobolus exilis* Renvoize in Kew Bull. 42(4): 923. 1987, non *Sporobolus exilis* (Trin.) Balansa – Type: Brazil, Paraná, *Dombrowski 6520* (holotype, PKDC; isotype, K [photo seen]). Figure 6.

Plants perennial, cespitose; culms 20–60 cm long, 1.0–1.5 mm diam., hollow, slender, erect, simple; nodes 1–2 observable, glabrous; sheaths 2–5 cm long, rounded, glabrous, basal ones densely arranged and shorter; culm sheaths 7–13 cm long, shorter than the internodes; ligule with a short line of hairs, ligule lobules with hairs 2–3 mm long; blades 1–2 mm wide, filiform, glabrous, with tuberculate hairs on margins, basal blades 7–13 cm long, culm blades 2–4 cm long. Panicles 4–7 cm long, short pyramidal, branches 4–9 in the first whorl, divergent or erect-patent, branches 1.2–3.7 cm long, without spikelets in the lower 1/3–1/2, usually with a solitary branch under the first whorl; pedicels glabrous. Spikelets 3–4 mm long, plumbeous, glabrous; lower glumes up to 1/2 as long as the spikelet, apex acuminate, 0–1-nerved; upper glumes nearly as long as the lemma, 1-nerved; lemma as long as the palea. Stamens 3, anthers 2.1 mm long, dark brownish. Fruit 1.8–2.0 mm long, obovoid, embryo 1/2 the length of the fruit.

Notes. – This species includes small plants with culms that have only one or two elongated internodes and filiform, short blades.

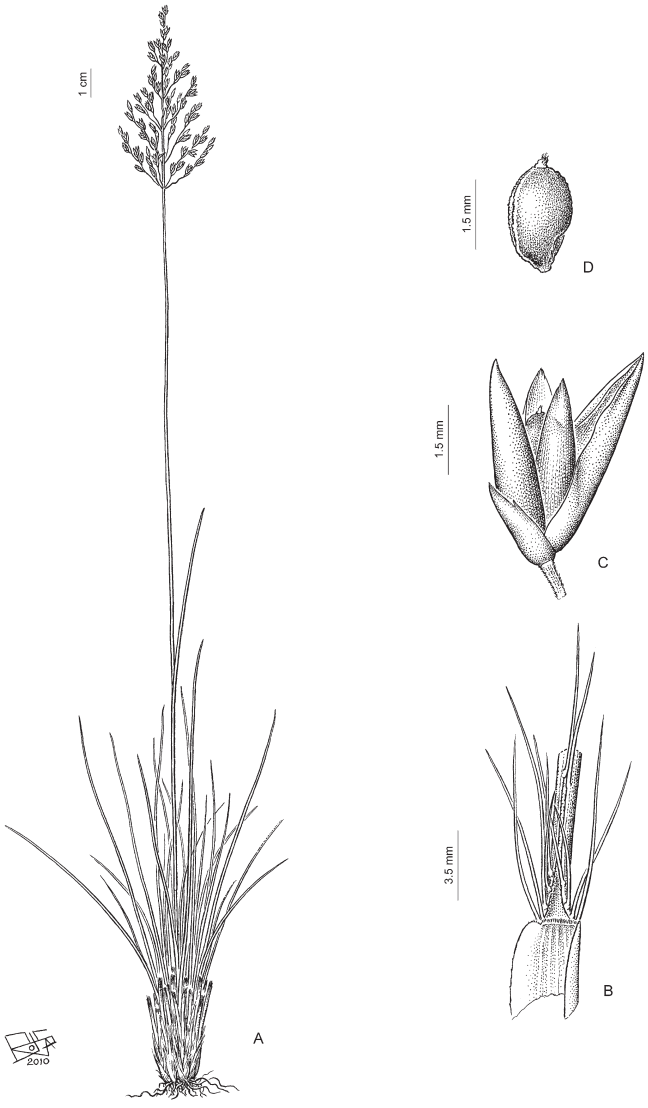

Fig. 6. *Sporobolus linearifolius*. **A,** Habit; **B,** detail of ligule; **C,** spikelet; **D,** fruit. From *Araujo 178* (BAA).

Distribution and habitat. – Endemic to Brazil, growing in Paraná and Santa Catarina states and probably Rio Grande do Sul (Boechat & Longhi-Wagner, 1995); in rocky or sandy campos; 800–1300 m; in distrito de los Campos of the southern Paranense province (Cabrera and Willink, 1973). Burned sheaths are common in herbaria material indicating this species flowers after fire. Nicora (1993) mentioned this species as growing in Paraguay, and probably in Argentina; she was surely considering specimens of *S. aeneus* var. *angustifolia*, although no specimens were cited by Nicora.

Specimens examined. – BRAZIL. Paraná: Desvio Ribas, Dec 1952, *Araujo 178* (BAA); Ponta Grossa, 15 Mar 1946, *Swallen 8769* (US); Santa Rita, Mun. Palmeiras, 26 Oct 1982, *Hatschbach 45699* (CTES); without locality, *Dombrowski 6540* (CTES). Santa Catarina: Mun. Campo Alegre, 08 Nov 1956, *Smith 7443* (US).

3. *Sporobolus multinodis* Hack. in Repert. Spec. Nov. Regni Veg. 7: 316. 1909 – Type: Brazil, Rio Grande do Sul, Rio Pardo Mun., X-1905, *C. Juergens G153* (holotype, W [photo seen]; isotypes, BAA-2912 not located, US-1127181 [photo seen], US-81957 [photo seen]). Figure 7.

= *Sporobolus multinodis* var. *exasperatus* Hack., Repert. Spec. Nov. Regni Veg. 7: 317. 1909 – Type: Brazil, Rio Grande do Sul, Campo de St. Angelo, Municipio de St. Angelo dos Missioes, alt. 400 m.s.m., II-1906, *C. Juergens G259* (holotype, W [photo seen]; isotypes, US-1127180 [photo seen], US-81958 [photo seen]).

Plants perennial, cespitose; culms 90–115 cm long, 3.5–4.5 mm diam., fistulous to hollow, erect, simple; nodes 8–12, glabrous; sheaths 4–8 cm long, rounded, grabrous to glabrescent on surface or margins, longer than internodes; ligule with a short line of hairs, ligule lobules glabrous or with few hairs 1–2 mm long; blades 10–19 cm long, 1–4 mm wide, strongly narrower than sheaths, conduplicate to planar, abaxial surface glabrous or pilose, adaxial surface mostly pilose, with tuberculate hairs on margins, blades of innovations densely pilose and narrower. Panicles 22–38 cm long, oblong-pyramidal, branches 3–11 in the first whorl, divergent when mature, branches 2.8–7.5 cm long, without spikelets in the lower 1/3–1/2 or more; pedicels usually with short hairs and prickles. Spikelets 4.2–5.0 mm

Fig. 7. *Sporobolus multinodis*. **A,** Habit; **B,** fruit; **C,** spikelet; **D,** detail of ligule. From *Swallen 9142* (US).

long, light brownish; lower glumes 1/2–3/4 as long as the spikelet, apex long-acute, 1-nerved, with prickles or short hairs on the nerve and surface; upper glumes almost 1/3 longer than the lemma, apex long acuminate, 1–3-nerved, with prickles and short hairs on the nerve and surface; lemma as long as the palea, usually with short hairs. Stamens 3, anthers 2.3–2.4 mm long, light brownish. Fruit 2.0–2.1 mm long, elliptic, embryo ½ the length of the fruit.

Notes. – *Sporobolus multinodis* is distinguished from other species in the complex by the blades markedly narrower than sheaths and by its long oblong-pyramidal inflorescences, and short hairs and prickles on the glumes. Prickles on pedicels and glumes have also been observed in *S. aeneus* and *S. recurvatus* and some short hairs on pedicels of *S. aeneus* (not on glumes). Blade pilosity varies between floriferous culm blades and new innovation blades, the latter ones usually densely pilose. This species also has V-shaped laminas (open almost 180º) with the central keel developed and adaxial colourless parenchyma, also noted by Parodi (1928) (Fig. 4F).

Distribution and habitat. – In Rio Grande Do Sul (Brazil) and Rivera (Uruguay), on high, rocky or sandy campos; 0–200 m. This region corresponds to the Uruguayense district of the Pampeana province (Cabrera & Willink, 1973).

Specimens examined. – BRAZIL. Rio Grande Do Sul: Inconfidencia, 15 Mar 1939, *Araujo 409* (BAA); Bagé, 25 Apr 1926, *Esteves 125b* (BAA); without locality, *Orth 1951* (US); Pelotas, 10 Mar 1954, *Sacco 97* (US); Pelotas Instituto Agronómico do Sul, 20 Apr 1946, *Swallen 9142* (US). URUGUAY. Rivera: Cuchilla Cuñapirú, 28 Jan 1978, *Rosengurtt 7033* (BAA, MVM, MVFA); Picada de Castro, escuela agraria, 30 Jan 1958, *Rosengurtt 7074* (US).

4. *Sporobolus recurvatus* Boechat & Longhi-Wagner in Bradea 6(20): 177. 1993 – Type: Brasil, Mato Grosso, Bonito-Rondópolis, 8-IV-1930, *Chase 11887* (holotype SP [photo seen]; isotypes US [photo seen], SI!).

Iconography: Boechat & Longhi-Wagner, 1993: 176.

Plants perennial, cespitose; culms 80–140 cm long, 2.5–3.5 mm diam., fistulous to hollow, erect, simple; nodes 6–7, glabrous; sheaths 4–5 cm long, rounded, basal ones densely arranged, shorter, lanate at margins, with woolly, caducous hairs which persist between sheaths, culm sheaths 7–11 cm long, longer than the internodes, lanate or glabrous if lost hairs; ligule with a short line of hairs, ligule lobules glabrous or with hairs 2 mm long; blades 12–20(–30) cm long, 2.5–6.0 mm wide, convolute, glabrous, with tuberculate hairs on margins, basal ones recurved, distal blades shorter. Panicles 25–30 cm long, pyramidal, branches 6–12 in the first whorl, divergent when mature, branches 3.5–6.5 cm long, without spikelets in the lower 1/3–1/2 or more; pedicels glabrous. Spikelets 4.5–6.0 mm long, brownish or purplish tinged; lower glumes (1/2–)3/4 as long as the spikelet, apex acute, 1-nerved, with prickles on the nerve and surface; upper glumes slightly longer than the lemma, apex acute or acuminate, 1–3-nerved, with prickles on the nerve and surface; lemma as long as the palea. Stamens 3, anthers 2.4 mm long, dark brownish. Fruit 2.4–2.6 mm long, obovoid to elliptic, embryo 1/2 the length of the fruit.

Notes. – This species is distinguished by its woolly hairs at sheath margins, basal blades that are typically recurved, and long, pyramidal panicles.

Distribution and habitat. – Endemic to Brazil, in the states of Mato Grosso and Goias, in the Cerrado biogeographical province; on rocky hillsides or sandy campos, locally common; from 500–1200 m.

Specimens examined. – BRAZIL. Goias: ca 50 km da cidade, em dieccion a Jataí, Mineiros, 28 Apr 1992, *Filgueiras 2320* (SI); serra do Caiapó, 27 Jun 1966, *Irwin 17840* (CTES); serra do Caiapó, 50 km S of Caiaponia on road to Jataí, 26 Oct 1964, *Irwin 7389* (SI); Serra do Caiapó, ca. 30 km (straigth line) S of Caiaponia, 29 Apr 1973, *Anderson 9416* (CTES).

5. *Sporobolus aeneus* (Trin.) Kunth, Enum. Pl. 1: 213. 1833 ≡ *Vilfa aenea* Trin., Sp. Gram. 1: t. 23. 1824 – Type: Brazil: Minas Gerais, Tejuco, "specimen Brasiliense.", 1813–1820, *G.H. von Langsdorff s.n.* (holotype, LE-TRIN-1647.01; isotype, G-00168405 [photo seen], US-fragm. ex hb. Munich).

Plants perennial, cespitose; culms (30–)50–120 cm long, 2–4 mm diam., hollow, less frequently fistulous, erect, simple; nodes 3–8, glabrous; basal sheaths 2–7 cm long, rounded, glabrous to pubescent at margins, culm sheaths 7–15(–30) cm long, longer than the internodes; ligule with a short line of hairs, ligule lobules glabrous or with hairs 2 mm long; blades 12–20(–30) cm long, 1.5–12.0 mm wide, convolute, involute or planar, mostly basal or arranged along the culms, glabrous to densely pilose, tuberculate hairs on margins present or absent. Panicles 5–42 cm long, pyramidal or oblong-pyramidal, branches 3–18 in the first whorl, ascendant to divergent, branches 1.5–12.0 cm long, spikelets all along the branches or without spikelets in the lower 1/3–1/2; pedicels generally glabrous, sometimes with short hairs or prickles. Spikelets 2.5–5.3 mm long, light-brownish, purplish, greenish or plumbeous; lower glumes 1/3–1/2(–3/4) as long as the spikelet, apex acute, 0–1-nerved, smooth or with prickles on the nerve; upper glumes almost as long as the lemma, apex acute or acuminate, 1–3-nerved, smooth or with prickles; lemma as long as the palea. Stamens 3, anthers (1.5–)2.0–2.5 mm long, light-brownish. Fruit 1.6–2.5 mm long, elliptic, embryo 1/3–1/2 the length of the fruit.

a. *Sporobolus aeneus* (Trin.) Kunth var. ***aeneus*.** Figure 8.

= *Vilfa acuminata* Trin., Sp. Gram. 3(29): 348, t. 348. late 1835–early 1836, **syn. nov.** ≡ *Sporobolus acuminatus* (Trin.) Hack., Repert. Spec. Nov. Regni Veg. 7: 373. 1909 – Type: Illustration "*Vilfa acuminata*" in Trinius, Sp. Gram. 3: t. 348. 1835 (lectotype designate here; holotype unknown, not at LE).

= *Sporobolus aeneus* var. *barbicollis* Hack. in Bull. Herb. Boissier, ser. 2, 4(3): 278. 1904 – Type: Paraguay: Cordillera, "in campis pr. Tobaty", Sep, *Hassler 6278* (holotype, W; isotypes, G [photo seen], US-92020 ex W [photo seen]).

= *Sporobolus acuminatus* var. *longispiculus* Boechat & Longhi-Wagner in Acta Bot. Brasil. 9: 29. 1995, **syn. nov. –** Type: Brasil, Mato Grosso do Sul: Pedro Gomez, 28-X-1985, *Valls & al. 9452* (holotype, ICN [photo seen]; isotype, CEN).

= *Sporobolus eximius* var. *latifolius* Boechat & Longhi-Wagner, Acta Bot. Brasil. 9(1): 50. 1995, **syn. nov.** – Type: Brasil, Paraná, Jaguariaíva, 26-XI-1987, *Valls & al. 11269* (holotype, CEN; isotype, ICN [photo seen]).

Culms 70–120 cm tall, with 5–8 nodes. Blades 12–25 cm long aprox., 3.9–12.0 mm wide, numerous at base, planar or conduplicate, glabrous, rarely abaxially pubescent, uppermost reduced. Panicles 17–42 cm long, branches of the first whorl 2.6–11.0 cm long, with spikelets all along the branches or mostly less than 1/3 the length naked (the lower 0.4–3.6 cm of the branch is naked). Spikelets 2.5–4.1 mm, pale; anthers light brown.

Notes. – In the protologue of *Vilfa acuminata*, Trinius indicated "Figura ad specimen Brasilianum", but the holotype is unknown and no other type material was found in B, LE, MW, and US. The high quality illustration accompanying the original description of *Vilfa acuminata* is therefore designated as the lectotype. This figure and Trinius description show all characters assigned here to *S. aeneus* var. *aeneus*; we therefore consider them as conspecific.

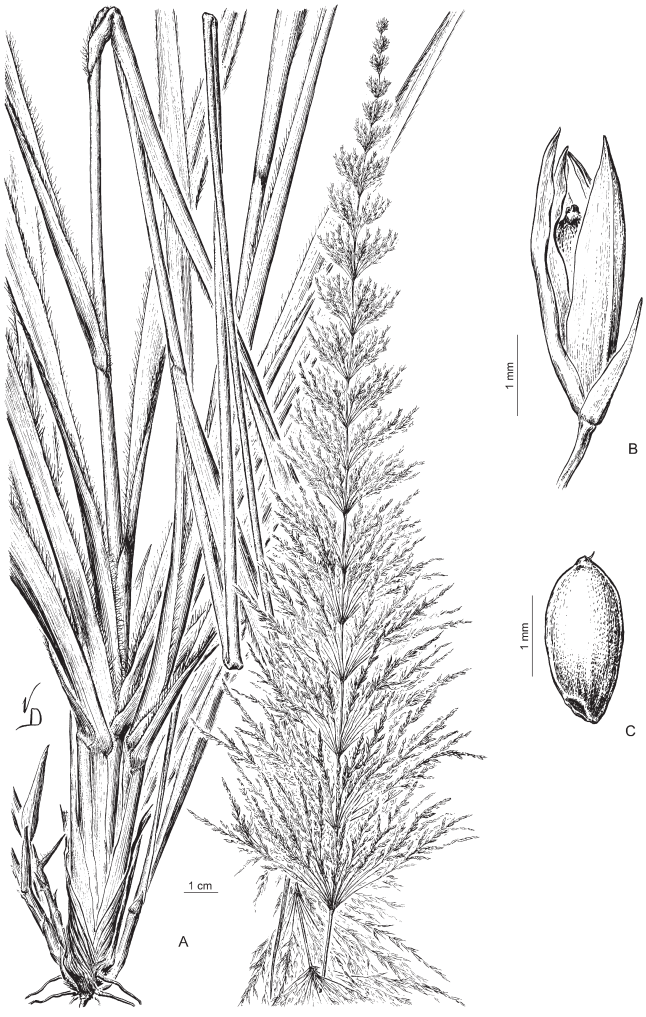

Fig. 8. *Sporobolus aeneus* var. *aeneus*. **A,** Habit; **B,** spikelet; **C,** fruit. A and B, from *Rojas 3697* (BAA), C, from *Quarín 3484* (SI).

Type material and the original descriptions of *Sporobolus aeneus* var. *barbicollis* and *S. acuminatus* var. *longispiculus* agree with our concept of *S. aeneus* var. *aeneus*, and these names are therefore replaced in synonymy.

Boechat & Longhi-Wagner (1995) noted the incongruence between the descriptions by Döll (1878), Hitchcock (1927), Parodi (1928), and Renvoize (1984) of *S. eximius*, and created *S. eximius* var. *latifolius* to accommodate for the morphological variation observed. They mentioned that the holotype of *Vilfa eximia* (erroneously cited as *Riedel s.n.*) has only the dorsal blade surface pubescent and that the variety *latifolius* corresponds to plants with both surfaces pilose. Considering quantitative characters of the original description and examination of the isotype, this variety corresponds to *S. aeneus var. aeneus*, and is placed in synonymy. Some material (*Rúgolo 1739*, *Hatschbach 33060, 3211*) considered as *S. eximius* var. *latifolius* by Boechat & Longhi-Wagner (1995) corresponds to *Sporobolus aeneus var. angustifolia*. As shown in the Discussion, blade pilosity is not a good character for recognizing taxa in the *S. aeneus* complex.

Distribution and habitat. – This variety grows mostly in the Cerrado biogeographical province, in Brazil (in southern Mato Grosso, Goias and Minas Gerais), eastern Paraguay (Amambay, rarely in Concepción, Cordillera and San Pedro), eastern Bolivia (Santa Cruz and Chuquisaca), and Argentina at San Ignacio (Misiones). The Argentinean province of Misiones is included in the Paranense biogeographical province, but the locality of San Ignacio corresponds to a discontinuity of the Sierra de Amambay from Paraguay (Soria, 1996). Chébez (1996) considers these "campos" as remnants or poor cerrado.

Specimens examined. – ARGENTINA. Misiones: Depto. San Ignacio, Camino a Teyucuaré, 25 Sep 1972, *Schinini 5467* (SI); camino hacia el Paraje "El Payal", 15 Dec 2008, *Denham 222* (SI); de San Ignacio al Teyú Cuaré, 18 Dec 2007, *Zuloaga 9956* (SI); entrada al Parque Provincial Teyucuaré, 21 Apr 1996, *Zuloaga 5757* (SI); Parque Provincial Teyucuaré, 21 Apr 1996, *Zuloaga 5705* (SI); Dpto. antes del Parque Teyú Cuaré, 16 Dec 2008, *Denham 247* (SI); entrada al Parque Teyú Cuaré, 15 Dec 2008, *Denham 212* (SI); Teyú Cuaré, 10 Dec 1987, *Vanni 1047* (CTES); Teyucuaré, 19 sep 2000, *Múlgura 2080* (SI); Paraje Payal, 20 Feb 1996, *Morrone 1003* (SI); San Ignacio, 12 Nov 1976, *Quarín 3484* (SI); San Ignacio, 6 May 1998, *Biganzoli 11* (SI); San Ignacio, 18 Dec 2001, *Forzza 2026* (SI). BOLIVIA. Chuquisaca: El Salvador, CIMBOC, 20 Mar 1992, *Toledo 10847* (SI). Santa Cruz: Chiquitos, Serranía De Santiago, Oct 1987, *Killen 2791* (US). BRAZIL. Distrito Federal: Area do Cristo Redentor, 29 Nov 1990, *da Silva 1069* (SI); BR 153, 1 km before crossing Goiás, 28 Jan 1978, *Pedersen 12116* (CTES). Goias: Ao longo da rodovia Brasilia Cristalina, 26 Nov 1992, *Filgueiras 2139* (SI); ca. 15 km S of Niquelândia, 21 Jan 1972, *Irwin 34680* (US); Contraforte Central, 24 Jan 1970, *Irwin 25327* (US); Rodovia 40, Cristalina a Paracatu, 26 Feb 1992, *Filgueiras 2171* (SI). Mato Grosso: Mun. Sidrolandia, 10 Nov 1973, *Hatschbach 33010* (CTES, LP). Minas Gerais: Municipio de Formoso, 4 Dec 1997, *Alvarenga 1125* (IBGE); 60 km de Pirapora para Canoeiras, 31 Jan 1965, *Belém 461* (US); Diamantina, Serra de San Antonio, 30 Dec 1929, *Chase 10343* (SI); Municipio de

Formoso, Parque Nacional Grande Sertao Veredas, 1 Dec 1997, *Alvarenga 1114* (IBGE); Rodovia de Cardeal Mota a Conceiçao do Mato Dentro, 7 Feb 1993, *Zuloaga 4576* (SI); Serra da Anta, 6 Feb 1970, *Irwin 26139* (US); Serra do Cipó, Municipio Mato Dentro, 15 Jan 1951, *Macedo 2987* (US); Serra do Lenheiro, São João Del Rey, Jan 1960, *Duarte 5161* (US). PARAGUAY. Amambay: 1 km sur de ruta 5, camino a Colonia Aceite, 18 Dec 1999, *Ferrucci 1705* (CTES); camino a Bella Vista, 25 Oct 1994, *Krapovickas 46018* (CTES); Camino a Colonia Estrella, 10 Dec 1997, *Schinini 33659* (CTES); Cerro Corá, Sierra de Amambay, Mar 1934, *Rojas 6786* (BAA); oeste de Cap. Bado, 11 Dec 1992, *Nicora 9858* (SI). Concepción: entre R. Apa y Aquidabán, San Luis, Feb 1909, *Fiebrig 4494* (BAA). San Pedro: Rio Verde, May 1921, *Rojas 3697* (BAA).

b. *Sporobolus aeneus* (Trin.) Kunth var. ***angustifolia*** (Döll) S. Denham & Aliscioni, **comb. nov.** ≡ *Vilfa adusta* Trin. in Mem. Acad. Imp. Sci. Saint-Petersbourg, Ser. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1–2): 80. 1840 ≡ *Vilfa aenea* var. *angustifolia* Döll in Martius, Fl. Bras. 2(3): 34. 1878 ≡ *Sporobolus adustus* (Trin.) Roseng., B.R. Arril. & Izag., Gram. Urug.: 270. 1970 – Type: Brasil, "in campis desertorum prope Rio de S. Francisco", *J.B.E. Pohl 326* (holotype, LE-TRIN-1673.01; isotypes, US-1126778 [photo seen], W [photo seen]). Figure 9.

= *Sporobolus subbulbosus* Arechav. in Anales Mus. Nac. Montevideo 1: 343, t. 35. 1896 ≡ *Sporobolus aeneus* var. *subbulbosus* (Arechav.) Parodi in Revista Fac. Agron. Veterin. (Buenos Aires) 6(2): 161, f. 16. 1928. Type: Uruguay, "en terrenos elevados, pedregosos, colinas de las sierras de las Minas, campos de Mercedes, estancia del Sr.. D.M.B. Berro" (holotype, MVM!; probable isotype, G [photo seen]).

= *Sporobolus aeneus* f. *parviflora* Parodi, Revista Fac. Agron. Veterin. 6(2): 161. 1928 – Type: Argentina, Corrientes, Mercedes, 11-II-1925, *A.R. Millan 422* (holotype BAA!).

= *Sporobolus camporum* Swallen in Sellowia 7: 10. 1956 – Type: Brazil, Santa Catarina, Sao Joaquin, 1200 m, I-1950, *P.R. Reitz 3431* (holotype US-2042484 [photo seen]).

= *Sporobolus reflexus* Boechat & Longhi-Wagner in Iheringia, Bot. 44: 38. 1994, **syn. nov. –** Type: Brazil, Distrito Federal, Brasilia, 10-X-1990, *A.L. Brochado & T. Filgueiras 68* (holotype, IBGE; isotype, ICN).

= *Sporobolus minarum* Boechat & Longhi-Wagner, Iheringia, Bot. 44: 34. 1994, **syn. nov. –** Type: Brasil, Minas Gerais, Lavras, 11-III-1981, *H.F. Leitão Filho & al. 1191* (holotype, ESAL).

= *Sporobolus paucifolius* Boechat & Longhi-Wagner in Iheringia, Bot. 44: 37. 1994, **syn. nov. –** Type: Brasil, Goiás, Alto Paraíso-Teresina, 10-X-1979, *E.P. Heringer & al. 2382* (holotype, IBGE [photo seen]).

Culms (30–)65–80 cm tall, with 3–4 nodes observable. Blades 12–20 cm long aprox., 1.5–6.0 mm wide, numerous at base, from involute to planar, glabrous or pilose on both or either adaxial or abaxial surfaces. Panicles 5–27 cm long, branches of the first whorl 1.6–4.6 cm long, mostly more than 1/3 naked. Spikelets 2.9–5.3 mm long, brown, pale greenish, purplish or plumbeous; anthers pale to brown.

Notes. – *Sporobolus subbulbosus* was created to include plants with semibulbous rhizomes, but the remaining characters described are coincident with this variety. Studying numerous specimens we conclude that semibulbous rhizomes can not be separated from non bulbous ones. The main character used by Boechat & Longhi-Wagner (1994) to distinguish *Sporobolus reflexus* is the presence of reflexed branches of the inflorescence. We tried to score this attribute but since it was impractical to do it unequivocally for many of the specimens, we consider this character inadequate to separate species. In addition, some specimens determined by Boechat & Longhi-Wagner as *S. reflexus* present both reflexed and divergent branches. These authors also commented that quantitative characters of *S. reflexus* agree with those of *S. adustus*. *Sporobolus minarum* is only known from the type collection housed at ESAL and one other specimen at UEC, both from Minas Gerais, Brazil. The protologue, including the original illustration indicate this

Fig. 9. *Sporobolus aeneus* var. *angustifolia*. **A,** Habit; **B,** spikelet; **C,** fruit. A and C, from *Balansa 261* (G), C, from *Dusén 16063* (BAA).

taxon is synonymous with *S aeneus* var. *angustifolia*. The type specimen of *S. camporum* fitted near the limit between *S. aeneus* var. *aeneus* and var. *angustifolia*, but considering blade width (the most discriminant character among varieties from discriminant analysis), and geographical distribution (Santa Catarina, Brasil), this species should be synonym of *S. aenea* var. *angustifolia*.

Distribution and habitat. – This variety is the most widespread, growing in NE Argentina, in Paraguay, Uruguay and southern Brazil (Distrito Federal, Goias, Mato Grosso, Minas Gerais, Paraná, Santa Catarina and Rio Grande do Sul). This distribution includes Cerrado, Chaqueña, Espinal, Paranaense and Pampeana biogeographic provinces, from sea level to 1500 m. One specimen was recorded in Bolivia, growing at 2200 m alt.

Specimens examined. – ARGENTINA. Corrientes: Dep. Mercedes, Mercedes, 22 Mar 1967, *Royo 478* (CTES); Mercedes, 11 Feb 1925, *Parodi 6358* (BAA, US); Mercedes, E.E.A. Inta de Mercedes, 22 Mar 1967, *Fernandez 478* (CTES); Paso de Los Libres, 6 Apr 1972, *Carnevalli 3144* (LIL). Entre Rios: Concordia, San Carlos, 28 Sep 1944, *Morcó s.n.* (BAA). BOLIVIA. Tarija, Tojo, Dec 1903, *Fiebrig 2384* (BAA). BRAZIL. Distrito Federal: na confluencia dos córregos Cana do Reino/Vicente Pires, 23 Jul 1981, *Heringer 7225* (US); Area do Cristo Redentor, 21 Aug 1990, *Cámara 29* (SI); Chapada dos Veadeiros, 25 Nov 1994, *Filgueiras 3201* (SI); Reserva Ecológica do IBGE, 13 Sep 1999, *Fonseca 2065* (IBGE). Mato Grosso: Capão Redodndo, Mun. Camapuã, 11 Nov 1973, *Hatschbach 33060* (CTES); Mun. Rondonopolis, Ponte de Pedra, 14 Nov 1973, *Hatschbach 33211* (CTES). Minas Gerais: Hargreaves, 22 Dec 1929, *Chase 10267* (US); Ituiutaba, Serra de S. Vicente, 12 Nov 1948, *Macedo 1366* (BAA); Poços de Caldas, 18 Jan 1930, *Chase 10672* (BAA, US). Paraná: Campos de Irai, 5 Apr 1945, *Swallen 9031* (US); Castro, Nov 1948, *Araujo 30* (BAA); Jaguariahyva, 20 Nov 1914, *Dusén 16063* (SI, BAA); Jaguariaiva, 21 Oct 1910, *Dusén 13232* (LIL); Jaguariaiva, 23 Oct 1911, *Dusén 13252* (SI); Jaguariaiva, Parque Estadual do Cerrado, 13 Dec 1992, *Rúgolo 1739* (SI); Laranjeiras do Sul, Rinção Grande, 13 Oct 1974, *Hatschbach 35230* (CTES); Mun. Lapa, Volta Grande, 13 Nov 1999, *Cordeiro 1582* (CTES); Serrinha, 22 Nov 1909, *Dusén 8940* (US). Rio Grande Do Sul: Furna do Tigre, 19 Nov 1949, *Rambo 44462* (BAA, CTES, LIL); Morro do Osso, 21 Oct 1949, *Rambo 44022* (LIL); Porto Alegre, Jardim Botânico de Porto Alegre, 22 Nov 1982, *Martins 389* (CTES). Santa Catarina: Lajes, 4 Jan 1946, *Swallen 8137* (US); Lajes, Morro do Pinheiro Sêco, 1 Nov 1963, *Klein 4497* (US); Lajes, Morro do Pinheiro Sêco, 19 Dec 1971, *Smith 15927* (US); Morro de Iquererim, Campo Alegre, 18 Oct 1957, *Reitz 5311* (US); Mun. Bom Jardim do Serra, 14 Dec 1971, *Smith 15789* (SI); Mun. Xanxeré, 19 Feb 1957, *Smith 11478* (US); São Joaquin, Mantiqueira, 1 Feb 1958, *Luattos 5073* (US); São Joaquin, Mantiqueira, 1 Feb 1958, *Luattos 5404* (US). PARAGUAY. Boquerón: Parque Nacional "Defensores del Chaco", Nov 1984, *Duré 448* (CTES). Paraguarí: Chololó, 14 Nov 1969, *Pedersen 9293* (CTES, MVFA). URUGUAY. Flores: Rincon de San Antonio, Próximo al rio Ji, 15 Nov 1921, *Montoro Guarch 125a* (BAA, MVFA). Florida: Potrero Los Olivos, Estancia "San Pedro", Nov 1924, *Montoro Guarch 3125* (BAA). Lavalleja: Minas, Cerro de Verdúm, 18 Dec 1911, *Montoro Guarch 6178* (BAA, MVFA); Minas, Salus, 30 Oct 1949, *Rosengurtt 5669* (BAA, MVFA). Rivera: Cerro de las Animas, Dec 1937, *Chebataroff 6091* (BAA). Soriano: Vera, Dec 1895, *Montoro Guarch 929* (BAA).

c. *Sporobolus aeneus* (Trin.) Kunth var. ***eximius*** (Nees ex Trin.) S. Denham & Aliscioni, **comb. & stat. nov.** ≡ *Vilfa eximia* Nees ex Trin. in Mem. Acad. Imp. Sci. Saint-Petersbourg, Ser. 6, Sci. Math., Seconde Pt. Sci. Nat. 4(1–2): 77. 1840 ≡ *Sporobolus eximius* (Nees ex Trin.) Ekman in Ark. Bot. 13(10): 41, tab II, 3. 1913 – Type: Brasil, "in hb. Brasil Berol., 315" (lectotype, LE-TRIN-1700.02, designated here [see comments below]; isotypes, B destroyed, BAA-3469 (fragm.) not located, LE-TRIN-1700.01 "Sto. Paolo, 266", US-fragm. ex LE-TRIN-1700.01). Fig. 10.

= *Sporobolus nudiramus* Boechat & Longhi-Wagner in Iheringia, Bot. 44: 36, f. 3–6. 1994, **syn. nov.** – Type: Brasil, Paraná, Ponta Grossa, 15 Mar 1976, *Davidse, Ramamoorthy & Vital 11354* (holotype, SP; isotype, MO [photo seen]).

Fig. 10. *Sporobolus aeneus* var. *eximius*. **A,** Habit and inflorescence; **B,** detail of ligule; **C,** spikelet; **D,** fruit. From *Hatschbach 18853* (US).

Culms 70–115 cm tall, with 3–5 observable nodes. Blades 10–30 cm long, aprox. 2.0–6.2 mm wide, mostly convolute, glabrous or abaxially pilose. Panicles 26–35 cm long, branches of the first whorl 5.1–7.6 cm long, more than 1/2 naked. Spikelets 2.7–4.5 mm long, greenish-plumbeous or pale greenish; anthers pale.

Distribution and habitat. – This variety occurs in southern Brazil (Paraná, Rio Grande do Sul) and is also recorded from Paraguay. It grows in the Paranense biogeographical province, in remnants of cerrado vegetation, at 600–1200 m, on wet ground or rocky outcrops.

Notes. – The original material of *Vilfa eximia* consists of two sheets from LE-TRIN (1700.01 and 1700.02); a third one at B was destroyed. Peterson & al. (2001: 236) cited 1700.01 as the holotype, a specimen with smooth spikelets. We select here 1700.02 as lectotype because it agrees with original description in having scabrous keeled bracts. It is not evident who was the collector of 315, but duplicates of the paralectotype 266 (see LE-TRIN- catalogue microfiche 438 A2 & A3) indicate that the latter was not a Sellow collection. The present lectotypification was possible due to Dr. Robert Soreng's observations of type material at LE using the IDC microfiche of the Trinius Herbarium (Soreng & al., 1995), and of fragmentary type material at US.

Sporobolus nudiramus is only known from the type collection; the studied isotype from MO presents the same characters as our variety (large panicles (41 cm) with long branches (up to 10 cm long) naked at the basal 1/2–2/3, blades 8.5–25.0 cm long, 4–7 mm wide, and obscure spikelets). We consider this specimen at the extreme of the quantitative variation of *S. aeneus* var. *eximius*.

Specimens examined. – BRAZIL. Paraná: Arapoti, 21 Mar 1968, *Hatschbach 18853* (US); Jaguariaiva, 25 Feb 1946, *Swallen 8669* (US); Jaguaruaiva, Parque Estadual do Cerrado, 20 Apr 2005, *Longhi Wagner 9463* (SI); Jaguaruaiva, Parque Estadual do Cerrado, 8 Mar 2005, *Longhi Wagner 9481* (SI). Rio Grande Do Sul: 12 km de Sao Francisco hacia Cambará do Sul, 6 Dec 1992, *Rúgolo 1428* (SI); San Jose dos Ausentes, 28 Nov 1988, *Longhi Wagner 1857* (SI). PARAGUAY. Amambay: alrededores de Juan Pedro Caballero, 23 Oct 1994, *Krapovickas 45884* (SI).

Related species

American species of *Sporobolus* morphologically related with species of the *S. aeneus* complex are *S. lasiophyllus* Pilg., *S. pyramidatus* (Lam.) Hitchc., *S. apiculatus* Boechat & Longhi-Wagner, and *S. bogotensis* Swallen & García-Barr.

Sporobolus lasiophyllus has pyramidal inflorescences with verticillate branches, and villous sheaths, similar to *S. recurvatus*. It can be easily distinguished by its erect rhizomes, shorter sheaths and blades, inflorescences 4–14 cm long, and lower and upper glumes as long as as the spikelet. It is endemic to Peru, Colombia, and Venezuela, occuring in Andean regions from 2300–3800 m (Giraldo-Cañas & Peterson, 2009).

Sporobolus pyramidatus is a small herb up to 60 cm long, it presents short inflorescences with verticillate branches, inflorescences are open but contracted when immature; lateral inflorescence are common and branches of the inflorescences are capillary; blades are typically basal and planar. It can be easily distinguished from "*Sporobolus aeneus* complex" by shorter spikelets 1.2–1.8 mm long. It is a widely distributed

Table 4. Taxonomic classification of taxa in the *Sporobolus aeneus* complex.

Acepted taxon in this work	Synonymy
Sporobolus cubensis	
Sporobolus linearifolius	
Sporobolus multinodis	*Sporobolus multinodis* var. *exasperatus*
Sporobolus recurvatus	
Sporobolus aeneus var. *aeneus*	*Vilfa acuminata* ≡ *Sporobolus acuminatus* (syn. nov.) *Sporobolus acuminatus* var. *longispiculus* (syn. nov.) *Sporobolus aeneus* var. *barbicollis* *Sporobolus eximius* var. *latifolius* (syn. nov.)
Sporobolus aeneus var. *angustifolia*	*Vilfa adusta* ≡ *Vilfa aenea* var. *angustifolia* ≡ *Sporobolus adustus* *Sporobolus aeneus* fo. *parviflora* *Sporobolus camporum* (syn. nov.) *Sporobolus minarum* (syn. nov.) *Sporobolus paucifolius* (syn. nov.) *Sporobolus reflexus* (syn. nov.) *Sporobolus subbulbosus* ≡ *Sporobolus aeneus* var. *subbulbosus*
Sporobolus aeneus var. *eximius*	*Vilfa eximia* ≡ *Sporobolus eximius* *Sporobolus nudiramus* (syn. nov.)
Doubtful name: *Sporobolus sprengelii*	

species, from the U.S.A. to Argentina, growing in disturbed soils, roadsides, railways, from 0 to 1500 m.

Sporobolus apiculatus occurs in Brazil (Distrito Federal, Goiás, Rio Branco) and may be confused with *S. cubensis* due to short inflorescences and densely pilose sheath margins. It can be differentiated from species of the complex by having narrow and non-pyramidal, short exerted (exceeded by the blades) panicles with basal branches arranged in a whorl and the upper branches alternate.

Sporobolus bogotensis is somewhat similar to species of the complex due to its open pyramidal inflorescences, but branches are verticillate to sub-verticillate, ascending or reflexed; sheaths are glabrous and finely ciliate on margins, and blades are involute and glabrous or glabrescent. It is endemic to the high Andes of Colombia, Ecuador, and Peru (Giraldo-Cañas & Peterson, 2009), between 2000–3300 m.

Doubtful name

Agrostis sporobolus Spreng., Novi Provent.: 46. 1818 ≡ *Vilfa sporobolus* (Spreng.) Trin., Gram. Unifl. Sesquifl.: 160. 1824 ≡ *Vilfa elatior* Nees, Fl. Bras. Enum. Pl. 2(1): 396. 1829, nom. superfl. ≡ *Sporobolus sprengelii* Kunth, Revis. Gramin. 1: 68. 1829 [≡ "*Sporobolus sporobolus*" (Spreng.) Kuntze, Revis. Gen. Pl. 3(3): 369. 1898, non rite publ. (Art. 23.4)] – Type: "Brasil, Otto" (holotype B destroyed).

Sporobolus sprengelii is considered a doubtful name because of the destruction of the type material (duplicates were successfully separated for at BAA, W, K, G, UT and M) and because its succinct description eliminates a trustworthy placement to any of the species accepted in this work.

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