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On the taxonomic position of *Panicum scabridum* (Poaceae, Panicoideae, Paspaleae)

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Abstract

Panicum scabridum, an *incertae sedis* species of *Panicum* s.l., is here included in the genus *Coleataenia*, following a phylogenetic analysis based on one new *ndhF* sequence of the species and associated morphological data. *Panicum scabridum* and species of *Coleataenia* are cespitose and perennial plants, with a lower glume (1–)3–5-nerved, 1/3 to 3/4 of the spikelet, upper glume and lower lemma 5–9-nerved, and upper anthecium smooth, shiny, and indurate. Within *Coleataenia*, *P. scabridum* appeared as the sister taxon of the species pair *C. prionitis* and *C. petersonii*; these three species are the only NADP-me taxa of tribe Paspaleae exhibiting two bundle sheaths around the vascular bundles, i.e., with an outer parenchymatous sheath and an inner mestome sheath with specialized chloroplasts. The new combination *Coleataenia scabrida* is proposed and a lectotype is designated.

Key words: *Panicum scabridum*, phylogeny, combined analysis, anatomy

Introduction

Panicum scabridum Döll (1877: 201), originally described from a specimen collected in Brazil, grows in Colombia, Venezuela and the Guianas to northern Brazil and Bolivia, in wet open places at low elevations. *Panicum scabridum* was included by Zuloaga (1987) in *Panicum* Linnaeus (1753: 55) sect. *Laxa* Hitchcock & Chase ex Pilger (1931: 243), which includes species characterized by spikelets arranged in racemose unilateral branches, with the lower glume 3-nerved, 1/2 to 3/4 the length of the spikelet, and upper anthecium indurate to membranous. Later, Zuloaga *et al*. (1992) excluded this species from sect. *Laxa* based on the presence of an indurate upper anthecium, with simple papillae and a black caryopsis. Also, *P. scabridum* has major anatomical differences with species included in sect. *Laxa*: the species has 2–4 mesophyll cells between contiguous vascular bundles and specialized chloroplasts in the mestome sheath (Zuloaga *et al*., 1992), while other taxa of sect. *Laxa* are classified as typically C_3 species, i.e., with several mesophyll cells between contiguous vascular bundles and without specialized chloroplasts (Brown 1977, Zuloaga *et al*. 1992).

Molecular phylogenetic studies have provided valuable information on the relationships within the Panicoideae (Gómez-Martínez & Culham 2000, Duvall *et al*. 2001, Giussani *et al*. 2001, Aliscioni *et al*. 2003, GPWG II 2012, Morrone *et al*. 2012). Aliscioni *et al*. (2003), based on a *ndhF* phylogeny, showed that *Panicum* is polyphyletic and has to be restricted to its type subgenus. Subsequently, several subgenera, sections or species were removed from *Panicum* and transferred to other genera or established as new ones (Morrone *et al*. 2007, 2008, Zuloaga *et al*. 2006, 2007, 2010, 2011, Salariato *et al*. 2012, Scataglini & Zuloaga 2013, Sede *et al*. 2008, 2009). Recently, Morrone *et al*. (2012) published a complete molecular and morphological phylogeny of Panicoideae, including 155 genera, and proposed a new classification for the subfamily. They split Paniceae Brown (1814: 582) into two tribes: Paniceae, with genera with a basic chromosome number of $x = 9$, and Paspaleae J. Presl (1830: 208), including all genera with a basic chromosome number of $x = 10$. Within the Paspaleae, three subtribes are recognized by these authors, Otachyriinae Butzin (1970: 182), Arthropogoninae Butzin (1972: 516), and Paspalinae Grisebach (1846: 468).

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The systematic positions of several *incertae sedis* species of *Panicum* are not fully solved, and in need of further studies. This is the case of *P. scabridum,* which was placed by Aliscioni *et al*. (2003) among the *incertae sedis* taxa of *Panicum* and, until now, not included in any phylogenetic study.

This work has three aims: 1) to resolve the phylogenetic position of *P. scabridum* in the Panicoideae based on molecular and morphological data; 2) to establish and discuss the morphological and anatomical affinities of this species with related taxa, and 3) to classify *P. scabridum* within the subfamily.

Materials and Methods

Morphological studies were based on herbarium specimens from CEN, COL, F, G, IAN, K, LPB, MO, NY, P, RB, SI, UB, US, and VEN (Thiers continuously updated). Fifty seven morphological characters (based on Morrone *et al.* 2012) were scored for *Panicum scabridum* (Appendix 2).

For anatomical studies, based on *Zuloaga 3984, Zuloaga et al. 4384*, and *Davidse 5444*, the second leaf below the inflorescence was selected. Cross-sectional leaf anatomy was determined from hand-sectioned leaf blades of herbarium specimens previously hydrated. The blades were sectioned at approximately one-third the length from the base, after being stained with safranin, and mounted in glycerin jelly. Epidermal preparations for light microscope studies were made following the methodology of Metcalfe (1960). The epidermis was stained in safranin. Anatomical descriptions were prepared using the terminology described in Ellis (1976, 1979). Upper anthecia were viewed on a Zeiss 940 scanning electron microscope at the Darwinion Institute, operating at 10–20 kV.

For DNA sequencing, total genomic DNA from herbarium material of one individual of *P. scabridum* (Appendix 1) was isolated using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's recommendations. The complete plastid *ndhF* gene (ca. 2,100 bp) was amplified by polymerase chain reaction (PCR) using primers specified by Olmstead & Sweere (1994) and Aliscioni *et al*. (2003). Four fragments were amplified (5F–536R, 536F–972R, 972F–1666R and 1666F–3R). PCR reactions were performed in 25 µL final volumes with 50–100 ng of template DNA, 0.2 µM of each primer, 25 µM dNTP, 5 mM $MgCl_2$ 1x buffer and 0.3 units of Taq polymerase (Invitrogen, Brazil). PCR was carried out using the following parameters: 1 cycle of 94°C for 5 min, 39 cycles of 94°C for 30 s, 48°C for 1 min, and 72°C for 1 min 30 s, and a final extension cycle of 72°C for 10 min. PCR products were run out on a 1% TBE agarose gel stained with SYBR Safe DNA gel stain (Invitrogen) and visualized in a blue light transilluminator. Automated sequencing was performed by Macrogen, Inc., Seoul, Korea. The alignment of the new sequence was manually performed, using BioEdit ver. 5.0.9 (Hall 1999).

Phylogenetic Analysis

Morphological characters and the *ndhF* sequence obtained for *P. scabridum* were included in a combined matrix (*ndhF* + 57 morphological characters) containing a representative selection of 109 Panicoideae taxa extracted from Morrone *et al*. (2012). Details of the 110 taxa analyzed and GenBank accession numbers are given in Appendix 1. The molecular matrix was uploaded to Tree BASE (study number 15204), and the morphological matrix is provided in Appendix 2.

Maximum Parsimony (MP) analyses were performed with separated *ndhF* and the combined data, using TNT ver. 1.1 (Goloboff *et al*. 2008). Molecular characters were equally weighted, treated as unordered, and gaps were scored as missing data. In concordance with Morrone *et al*. (2012) morphological characters were treated as unordered except for multistate characters with states considered internested. Prior to heuristic searches, all uninformative characters were excluded. The searches involved 1000 replicates, each of which generated a Wagner tree using a random addition sequence of taxa from the data matrix, swapping the initial tree with TBR (tree bisection and reconnection) and retaining a maximum of 10 trees in each replicate. Subsequently, all optimal trees were swapped using TBR, holding a maximum of 20,000 trees. A strict consensus tree was generated from the most parsimonious trees. Branch support was estimated with Bootstrap (Felsenstein 1985) using a total of 10,000 replicates. Each replicate was analyzed using 10 Wagner trees as the starting point followed by TBR branch swapping, saving only one tree per replicate.

Results

Phylogenetic analysis

The *ndhF* matrix, including the new sequence obtained for *P. scabridum*, consisted of 110 taxa × 2061 characters, of which 401 were informative. The combined matrix (*ndhF* + morphology) included 2118 characters. The MP analysis of the combined matrix resulted in 256 most parsimonious trees of 1672 steps.

In the strict consensus tree from the combined analysis (Fig. 1), *P. scabridum* is placed within the subtribe Arthropogoninae (Morrone *et al*. 2012), and is included in the genus *Coleataenia* Grisebach (1879: 308), as the sister species of the pair *C. prionitis* (Nees 1829: 162) Soreng (2010: 692) and *C. petersonii* (Hitchcock & Ekman 1936: 263) Soreng (2010: 692), the latter with 100% bootstrap support. *Coleataenia* has bootstrap support of 66%, and the monotypic genus *Triscenia* Grisebach (1863: 534) is its sister group. In the analysis of exclusively the *ndhF* data, the phylogenetic position of *Coleataenia* was unresolved, the genus appearing in a polytomy with *Triscenia* with 89% support (Fig. 2A). When *Triscenia* is excluded from the molecular analysis, *Coleataenia* is strongly supported, with 98% support (Fig. 2B). In both of these analyses, *C. scabrida* is moderately supported as the sister species of the pair *C. prionitis*-*C. petersonii* (Fig. 2).

Leaf Anatomy of P. scabridum

Transverse section (Fig. 5A). Leaf outline flat or wide, very open V, 116–160 µm width, with ribs and furrows slightly pronounced; keel developed with adaxial parenchyma or median vascular bundle indistinguishable structurally from lateral first-order vascular bundles; 3–5 secondary vascular bundles between consecutive first-order vascular bundles, with 2–4 mesophyll cells between contiguous vascular bundles, with a distance of 108–150 µm between contiguous vascular bundles. First-order vascular bundles with outer parenchymatous sheath with 9–14 globose, translucent cells, incomplete with sclerenchyma girders towards the abaxial epidermis, inner mestome sheath incomplete, with chloroplasts in the cells. Second-order vascular bundles with outer parenchymatous sheath complete with 6–8 cells, inner mestome sheath complete and with chloroplasts. Adaxial and abaxial girders associated with all first- and second-order vascular bundles. Chlorenchyma indistinctly radiate or irregular, with a few intercellular air-spaces (conspicuous in the specimen *Wurdack et Adderley 42986*, MO). Fusoid cells absent. Groups of 3–4, *Sporobolus* type, bulliform cells present at bases of adaxial furrows, between consecutive vascular bundles.

Abaxial epidermis (Fig. 5B). Silica bodies in costal zones dumbbell-shaped, prickle hairs occasionally present; intercostal long cells rectangular, more than 3 times as long as wide, with longitudinal anticlinal walls undulated and transverse anticlinal walls straight, less frequently angled, separated or not by short cells; stomatal complex with triangular, subsidiary cells, 18.2–23.3 µm long, 13.2–15 µm wide, in 2 to 4 rows on both sides of the costal zones; interstomatal long cells present, rectangular and more than 3 times as long as wide, with longitudinal anticlinal walls undulated and concave transverse anticlinal walls; microhairs 2-celled, 50–61.5 µm long, with basal cell of the same length of the distal cell, distal cell fusiform, obtuse, with the walls thinner than those of the cylindric basal cell; hooks occasionally present; papillae absent; macrohairs not observed.

Discussion

The molecular and combined analysis showed that *Panicum scabridum* should be excluded from *Panicum*, and that this species is related to the genus *Coleataenia. Coleataenia* is an American genus that includes eight species, distributed from the United States and the Caribbean to South America, from Venezuela to Argentina and Uruguay; the genus is distinguished by including cespitose, perennial herbs, with or without strong rhizomes, blades mostly basal, spikelets ellipsoid to obovoid, glabrous, with the lower glume 1/2 to 3/4 the length of the spikelet, (1–)3–5-nerved, upper glume and lower lemma subequal, 5–9-nerved, and upper anthecium indurate, smooth, glabrous, as long as or slightly shorter than the upper glume and lower lemma (Zuloaga *et al*. 2010). Within the genus, *P. scabridum* is grouped with *C. prionitis* and *C. petersonii*. The leaf anatomy of *P. scabridum* shows 2–4 mesophyll cells between contiguous vascular bundles, and the inner mestome sheath with abundant chloroplasts; therefore, we infer that *P. scabridum* is a Kranz species of the NADP-me type. Within this Kranz subtype, *P. scabridum* is anomalous since this species has two bundle sheaths around the vascular bundles, an outer parenchymatous sheath and one inner mestome sheath with specialized chloroplasts; the typical NADP-me subtype is defined by the

presence of a single mestome sheath around the vascular bundles (Brown 1977). This peculiar feature is also present in *Coleataenia prionitis* (Fig. 5C) and *C. petersonii* (Brown 1977, Zuloaga *et al*. 1989, Zuloaga *et al*. 2010); these three species are the only NADP-me taxa of tribe Paspaleae exhibiting this feature. *Coleataenia prionitis* is a common species of inundated habitats from Brazil to Argentina, while *C. petersonii* is an endemic Cuban species; both species are grouped with strong support in the molecular and in the combined analyses. This pair of species, together with *C. scabrida*, constitute the sister group of the remaining species of *Coleataenia* (Fig. 1, Fig 2B).

FIGURE 1. Strict consensus tree obtained in the parsimony analysis of the combined (*ndhF* + morphology) Panicoid matrix, including *C. scabrida* (see arrow). Bootstrap support levels are shown below branches.

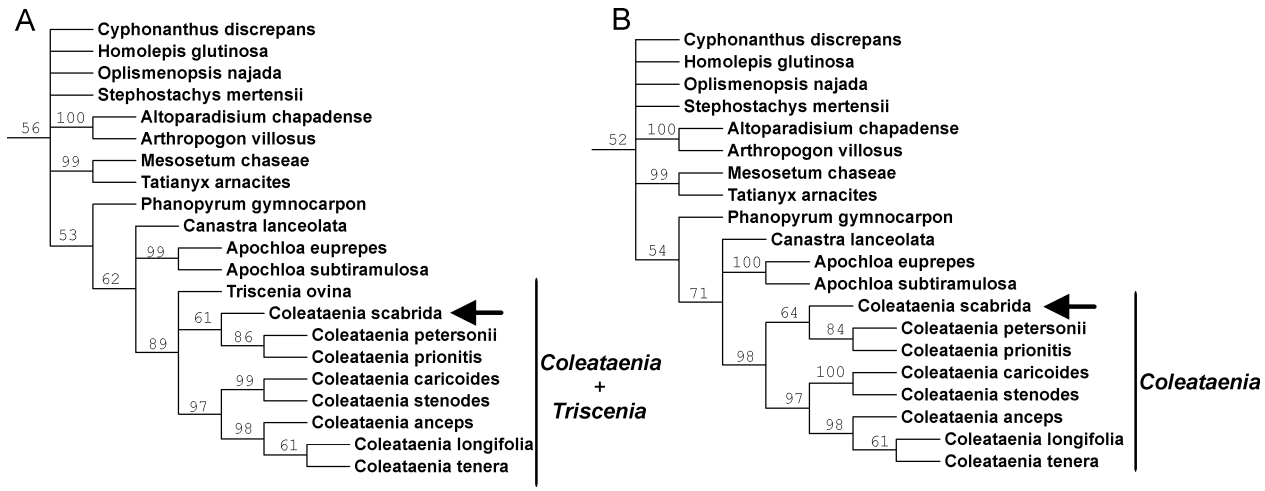

FIGURE 2. Strict consensus trees (only the Arthropogoninae subtribe is shown) obtained in parsimony analysis of the *ndhf* Panicoid matrix, including *C. scabrida* (see arrow). Bootstrap support levels are shown above branches. A. Analysis includes *Triscenia ovina*. B. Analysis excludes *T. ovina.*

Triscenia is a monotypic genus endemic to Cuba, including *Triscenia ovina* Grisebach (1863: 534). Morphological and anatomical characters that distinguish the genus from *Coleataenia* are lanceolate spikelets arranged on spicate main branches, glumes and lower lemma acuminate, upper anthecium membranous, and margins of the lemma flat over the upper palea; additionally, *T. ovina* is a C_3 species. Morrone *et al*. (2012) showed that *Triscenia* was included in *Coleataenia* in their analysis of *ndhF* data; however, the *ndhF* sequence of *Triscenia ovina* used in that study—and also used here—is incomplete, missing 490 bp. In our analysis of the *ndhF* data, *Triscenia* and *Coleataenia* form a polytomy, whereas when *Triscenia* is excluded from the *ndhF* analysis, the monophyly of *Coleataenia* receives 98% bootstrap support. When morphological characters are considered in combination with *ndhF*, *Triscenia* appears as the sister group of *Coleataenia,* the latter with moderate support. Neither of the analyses that include *Triscenia* place *Triscenia* within *Coleataenia*, as in Morrone *et al.* (2012); this may be a function of the inclusion of *P. scabridum* in our analyses. The decreased support of the genus *Coleataenia* in the *ndhF* analysis that includes *Triscenia* may be a function of the incomplete sequence of *Triscenia*, or limited variation in *ndhF* between *Triscenia* and *Coleataenia*. Fresh material of *Triscenia* is needed to better characterize the position of this genus. *Triscenia* was last collected at the beginning of the twentieth century; one of us (FOZ) recently searched for this species at the type locality in Cuba, with no success.

Key to the species of *Coleataenia*

1. Panicles few flowered, with 2–25 spikelets 2
- Panicles multiflowered, with more than 25 spikelets 4
2. Spikelets 1.1–1.6 mm long ..... *C. stenodes* (Grisebach 1864: 547) Soreng (2010: 692)
- Spikelets (1.9–)2–2.8 mm long 3
3. Rachilla conspicuous between the lower and upper glume; spikelets pointed; upper anthecium shorter than the upper glume and lower lemma; pedicels without long hairs; caryopsis pale ..... *C. caricoides* (Nees ex Trinius 1826: 149) Soreng (2010: 691)
- Rachilla inconspicuous between the lower and upper glume; spikelets blunt; upper anthecium as long as the upper glume and lower lemma; pedicels usually with long hairs; caryopsis dark ..... *C. tenera* (Beyrich ex Trinius 1834: 341) Soreng (2010: 692)
4. Upper anthecium with an apical tuft of prickly hairs 5
- Upper anthecium without an apical tuft of prickly hairs 6
5. Plants cespitose, without conspicuous rhizomes; culms and sheaths strongly compressed ..... *C. longifolia* (Torrey 1824: 149) Soreng (2010: 691)
- Plants with conspicuous, scaly rhizomes; culms and sheaths slightly compressed ..... *C. anceps* (Michaux 1803: 48) Soreng (2010: 691)
6. Culms compressed, sheaths and blades keeled; inflorescence terminal; spikelets 2.3–3.2 mm long; lower palea and lower flower present 7
- Culms terete, sheaths and blades not keeled; axillary inflorescences present; spikelets 1.3–1.8 mm long; lower palea and lower flower absent ..... *C. scabrida*
7. Panicle 25–60 cm long; spikelets 2.3–3.2 mm long. South America ..... *C. prionitis*
- Panicle 15–25 cm long; spikelets 2.2–2.3 mm long. Cuba ..... *C. petersonii*

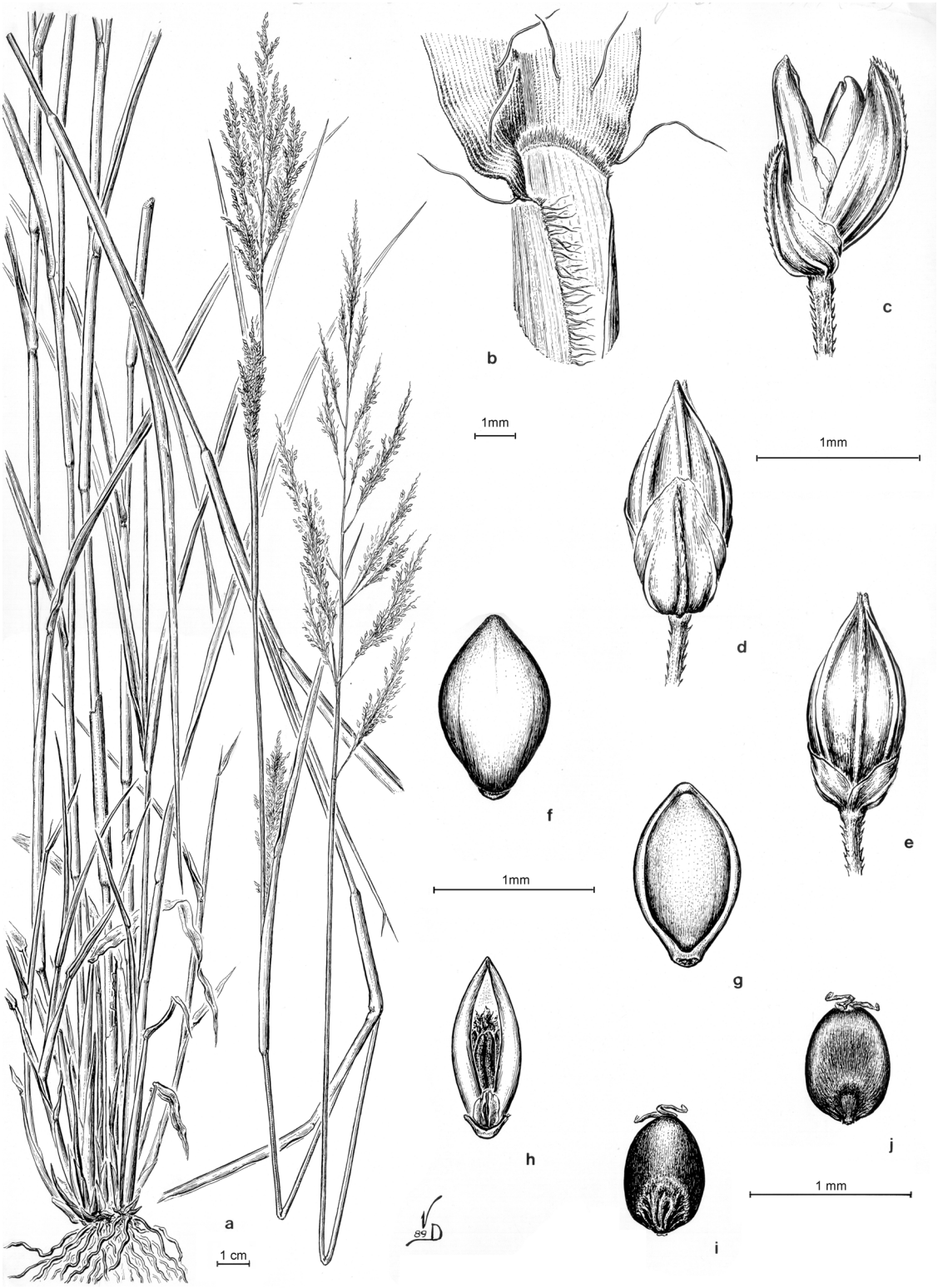

FIGURE 3. *Coleataenia scabrida*. A. Habit. B. Ligular region. C. Spikelet, lateral view. D. Spikelet, ventral view. E. Spikelet, dorsal view. F. Upper anthecium, dorsal view. G. Upper anthecium, ventral view. H. Upper palea, with lodicules and flower. I. Caryopsis, embryo view. J. Caryopsis, hilum view. Based on *Zuloaga et al. 4384*, V. Dudas, illustrator.

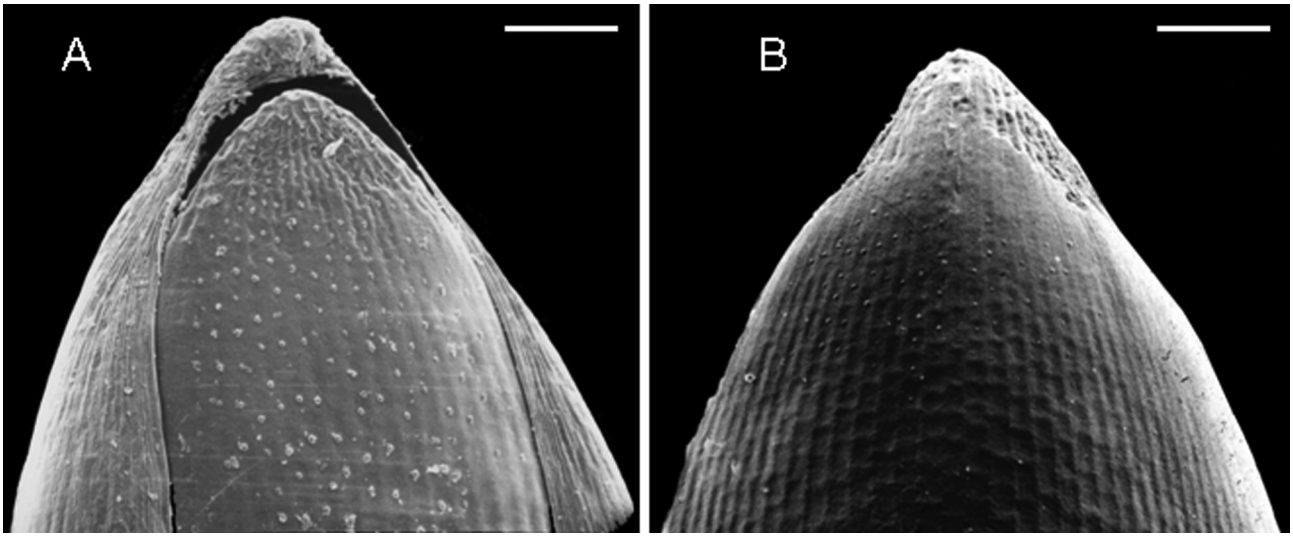

FIGURE 4. Scanning electron micrographs of the upper anthecia of *Coleataenia scabrida.* A. Apex of the upper lemma and palea with simple papillae. B. Apex of the upper lemma with simple papillae. *Zuloaga et al. 4384*. Scale: 100 µm.

Taxonomy

Coleataenia scabrida (Döll) Zuloaga, *comb. nov. Panicum scabridum* Döll (1877: 201). Type:—BRAZIL. Amazonas: Manaus, Campo de Jauari, January 1851, *R. Spruce 1281-3* (lectotype K 003090204!, here designated; isolectotypes P 00740795!, US-00139959! fragment ex K). Fig. 3.

Panicum prieurii Mez (1921: 3). Type:—FRENCH GUIANA. Without locality, *Leprieur s.n.* (holotype B_10_0248950!, isotype US 2830932! fragment ex B).

Panicum manacalensis Swallen (1966: 77). Type:—VENEZUELA. Amazonas: locally abundant in drowned margins of Río Atabapo at Manacal, 125 m, 12 June 1959, *J.J. Wurdack & L.S. Adderley 42986* (holotype US 00132968!, isotypes F 0046921F!, GH 00024154!, K, MO, NY 00414016!, US 00132967!, VEN).

Tufted perennials, culms erect, 50–110 cm tall, freely and densely branching at the upper nodes, internodes cylindric to compressed, 10–15 cm long, solid toward the base, or hollow, nodes compressed, dark, glabrous. Sheaths shorter than the internodes, 6–8 cm long, short-ciliate at the upper margins, otherwise glabrous to completely glabrous. Ligules membranous-ciliate, 0.2–0.6 mm long. Blades linear-lanceolate, 10–21 cm long, 3–10 mm wide, flat or folded, sparingly pilose toward the base on the adaxial surface, glabrous in the rest of its surface, the margins scaberulous. Peduncle 9–23 cm long, glabrous. Inflorescence a densely flowered panicle 7–20 cm long, narrowly ovate; main axis glabrous, occasionally with long hairs, wavy; branches ascending to spreading, scabrous; spikelets singly on capillary, elongate, somewhat flexuous and scabrous pedicels; pedicels occasionally with long, whitish hairs. Spikelets 1.3–1.8 mm long, 0.6–0.8 mm wide, biconvex, ovoid, glabrous, stramineous, strongly nerved, gaping. Lower glume 0.6–1.1 mm long, 1/2 or more the length of the spikelet, ovate-triangular, acute, slightly inflated, 3-nerved, nerves anastomosing at the apex. Upper glume as long as spikelet, ovate, acute, slightly beaked, 5-nerved. Lower lemma nearly as long as spikelet, ovate, acute, 3–5-nerved. Lower palea absent. Upper floret 1.1–1.4 mm long, 0.5–0.6 mm wide, ellipsoid, acute, indurate, smooth, shining, with simple papillae at the apex of lemma and palea (Fig. 4). Caryopsis ellipsoid, 0.9 mm long, 0.5 mm wide, black; hilum punctiform, embryo less than half the length of the caryopsis.

***Distribution and habitat*:—**Colombia, Venezuela and the Guianas to northern Brazil and Bolivia, in wet open places at low elevations.

***Common name*:—**"paja amarga" (in Venezuela).

***Representative specimens*:**—**BOLIVIA**. Beni: Prov. Ballivián, Espíritu, en la zona de influencia del Río Yacuma, *Beck 5390* (LPB), *3221a, 54545, 5007, 3342, 5098* (K). La Paz: Prov. Iturralde, Luisita, bajío del Ayo. Muquí, *Hassch 903* (K). Santa Cruz: Velasco, 20 km W of San Ignacio on road Concepción, 16°00'S, 61°15'W, 350 m, 27 January 1986, *Killeen 1688* (MO). **BRAZIL**. Amapá: Río Vila Nova, *Black & Froes 51-12322* (IAN). Amazonas: Bella Vista, Río Uaupés, *Baldwin 3556* (US); Río Jamundá, chácara da Fazenda Santa Rosa, *Black & Ledoux 50-10813* (IAN); Humaitá, 500 m ao N da BR-230, Km 2, *Janssen 151* (CEN); Cocodinho, *Black &*

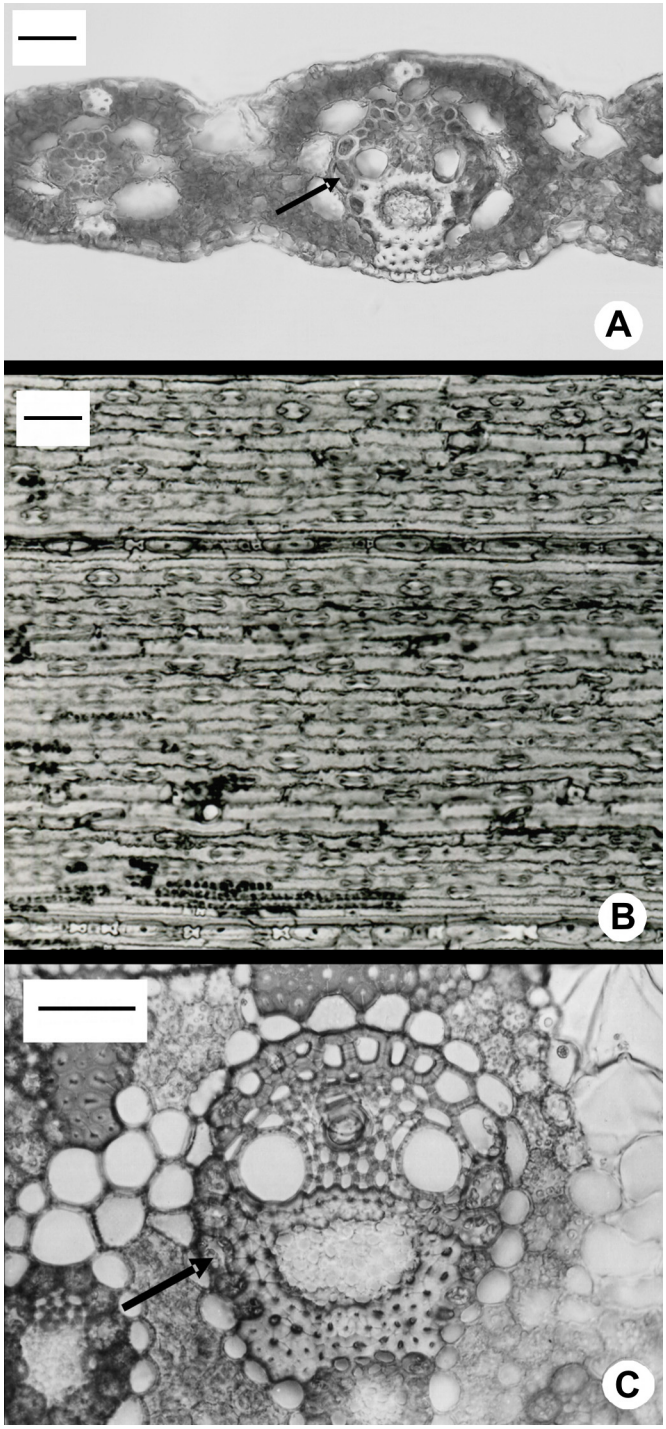

FIGURE 5. Leaf anatomy. A–B, *Coleataenia scabrida*; A, transverse leaf section; B, abaxial epidermis. C, *Coleataenia prionitis*; transverse leaf section. A and C, inner mestome sheath with chloroplasts indicated by arrows. A, Zuloaga *et al*. 4384; B, Davidse 5444; C, reproduced from Zuloaga *et al*. (1989). Scale: A, 25 µm; B, C, 50 µm.

Ledoux 50-10834 (IAN); beira do Río Içana, Camarao, *Black 48-2626* (IAN); Cucuhy, Río Negro, *Baldwin 3249* (CEN, IAN). Maranhão: Mun. Barra do Corda, at village of Copaiba on the old Grajaú-Barra do Corda road, 26 km east of center of village of Alto Alegre, *Eiten & Eiten 10293* (US). Pará: Alto Parú de Cuminá, *Sampaio 5614* (IAN); Conceição do Aruguaia, *Froes 29726* (US). Rondonia: entre Pimenta Bueno e Pres. Hermes, Linha Telg., *Kuhlmann 1784* (SI, US); Porto Velho, estrada da Estação Exp., *Black & Cordeiro 52-14475* (IAN, UB). Roraima: Caracaraí, Río Branco, *Kuhlmann 1086* (IAN, RB, US); ao longo da Estrada Boa Vista- Caracaraí, do outro lado do Río Mucajaí, *Black 51-13508* (CEN, US); Tercado, margem esquerda Uraricuora, *Rondon s.n.* (RB 110814, SI). **COLOMBIA**. Meta: 10 km W of Puerto Gaitán along road to Puerto López, along flood plain of rio Yucao, alt.

150 m, 31 December 1973, *Davidse 5444* (COL, K, MO, US), *Zuloaga 3984* (COL, MO, SI). **GUYANA**. Rupununi District, *Chan Choong 24* (US). **FRENCH GUIANA**. Without locality, *Leprieur 14, 452, s.n.* (P); Cayenne, *Leprieur s.n.* (G). **SURINAME**. Republiek, marais le long du chemin de fer, 23 March 1956, *Hoock 1452* (MO). **VENEZUELA**. Amazonas: Dept. Río Negro, San Carlos de Río Negro, 1°55'N, 67°04'W, 26 June 1984, *Davidse & Miller 26668* (MO, VEN). Anzoátegui: Río Mapire, afluente norte del Río Orinoco medio, 8°30'N, 64°30'W, 11 June 1987, *Rosales & Valles 127* (MO). Apure: northern end of the Galerías de Cinaruco, ca. 62 airline km NNE of Puerto Páez, 6°44'N, 67°20'W, 60–100 m, 28 Feb 1978, *Davidse & González 14617* (MO, NY, VEN). Bolívar: Sabana abierta y bosque húmedo del Río Apa, en el sector "El Caruto", 6° 27'N, 63° 19'W, 13 June 1987, *Stergios 11143* (MO); Distrito Roscio, selva ribereña a lo largo del Río Uairén, 12 km al noreste de Santa Elena de Uairén, Hato Divina Pastora, 900 m, *Steyermark & Liesner 127392* (MO). Delta Amacuro: Isla La Tórtola, *Ramia 2160, 2163* (VEN). Guárico: Sabanas bajas cerca del Caño Caracol, carretera Calabozo-Camaguán, *Badillo 3335* (VEN); Hato Flores Moradas, cerca de Corozopando, *Badillo 3345* (VEN). Monagas: Hato Santa Clara, 20 km W of Tucupita, 11 Agosto 1989, *Zuloaga et al. 4384* (MO, SI, VEN); Dtto. Sotillo, en canal principal Oeste en la Isla Guara, *Trujillo 12958, 12968* (MY); Isla de Guara, *Ramia 3286* (VEN); sabana de la serie Guaratuaro, Isla Guara, *Aristeguieta & Virrueta_7559* (VEN); alrededores de Jusepín, 25 Agosto 1970, hoja muy amarga, *Aristeguieta 7559* (MO).

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Appendix 1.

List of taxa used in the molecular analysis and GenBank accession numbers. The 109 taxa indicated were used previously in the Panicoid analysis of Morrone *et al.* (2012). The voucher information of the new sequence of *Coleataenia scabrida* is boldfaced.

Tribe Arundinelleae. *Arundinella hirta* (Thunb.) Tanaka, AF117393. **Tribe Chasmantheae.** *Chasmanthium laxum* (L.) H. O. Yates subsp. *sessiliflorum* (Poir.) L.G. Clark, U27296. **Tribe Paniceae.** *Acroceras zizanioides* (Kunth) Dandy, AY029618; *Cenchrus ciliaris* L., AY029625; *Chaetium bromoides* (J. Presl) Benth. ex Hemsl., AY029626; *Dichanthelium acuminatum* (Sw.) Gould & Clark, AY188485*; D. clandestinum* (L.) Gould, AY188461; *D. cumbucana* (Renvoize) Zuloaga, AY188464; *D. koolauense* (H.St. John & Hosaka) C.A. Clark & Gould, AY029627*; D. sabulorum* (Lam.) Gould & C.A. Clark, AY029654; *Digitaria setigera* Roth ex Roem. & Schult., AY029629; *Echinochloa colona* (L.) Link, AY029631; *Eriochloa punctata* (L.) Desv., AY029634; *Lasiacis sorghoidea* (Desv.) Hitchc. & Chase, AY029639; *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobsvar, AY029649; *Melinis repens* (Willd.) Zizka, AY029675; *Moorochloa eruciformis* (Sm.) Veldkamp, AY188452; *Oplismenus hirtellus* (L.) P. Beauv. AY029644; *Panicum* Section *Dichotomiflora* (Hitchc.) Honda: *Panicum aquaticum* Poir., AY029658; *P. dichotomiflorum* Michx., AY188466; *P. elephantipes* Nees ex Trin., AY029647; *P. pedersenii* Zuloaga, AY029646; *P. repens* L., AY029651; *Panicum* Section *Panicum*: *P. bergii* Arechav., AY188457; *P. fauriei* Hitchc., AY029650; *P. miliaceum* L., AY188472; *P. nephelophilum* Gaudich., AY029645; *P. stramineum* Hitchc. & Chase, AY188489; *Panicum* Section *Rudgeana* (Hitchc.) Zuloaga: *P. cervicatum* Chase, AY188459; *P. rudgei* Roem. & Schult., AY029661; *Panicum* Section *Urvilleana* (Hitchc.) Pilg.: *P. chloroleucum* Griseb., AY188460; *P. racemosum* (P. Beauv.) Spreng., AY188481; *Panicum* Section *Virgata* Hitchc. & Chase ex Pilg.: *P. tricholaenoides* Steud., AY188493; *P. virgatum* L., U21986; *Panicum incertae sedis*: *P. antidotale* Retz., AY188456; *P. mystasipum* Zuloaga & Morrone, AY188474; *P. olyroides* Kunth, AY188475; *Panicum* Section *Clavelligera* Stapf.: *P. adenophorum* K. Schum., AY188454; *P. claytonii* Renvoize, AY188462. *Panicum* Section *Monticola* Stapf.: *P. millegrana* Poir., AY029660; *P. sellowii* Nees, AY188484. *P. trichanthum* Nees, AY188492. *Panicum* Section *Verrucosa* Hitchc. & Chase ex C.C. Hsu: *P. verrucosum* Muhl., AY188496; *Parodiophyllochloa cordovensis* (E. Fourn.) Zuloaga & Morrone, AY188463; *P. missiona* (Ekman) Zuloaga & Morrone, AY188473; *P. ovulifera* (Trin.) Zuloaga & Morrone, AY029653; *P. penicillata* (Nees ex Trin.) Zuloaga & Morrone, AY18847; *Pseudechinolaena polystachya* (Kunth) Stapf., AY029676; *Sacciolepis indica* (L.) Chase, AY029677; *Setaria lachnea* (Nees) Kunth, AY029683*; S. viridis* (L.) Beauv., U21976; *Stenotaphrum secundatum* (Walter) Kuntze, AY029684; *Zuloagaea bulbosa* (Kunth) Bess, AY029648. **Tribe Paspaleae.** *Altoparadisium chapadense* Filg. et al., AY029619; *Anthaenantia lanata* (Kunth) Benth., AY029640; *Anthaenantiopsis rojasiana* Parodi, AY029620; *Apochloa euprepes* (Renvoize) Zuloaga & Morrone, AY029657; *A. subtiramulosa* (Renvoize & Zuloaga) Zuloaga & Morrone, AY188490; *Arthropogon villosus* Nees, AY029622; *Axonopus anceps* (Mez) Hitchc., AY029623; *Canastra lanceolata* (Filg.) Morrone, Zuloaga, Davidse & Filg., AY029621; *Coleataenia anceps* (Michx.) Soreng, GU253324; *C. caricoides* (Nees ex Trin.) Soreng, GU253329; *C. longifolia* (Torr.) Soreng, AY188482. *C. petersonii* (Hitchc.&Ekman) Soreng, AY188479. *C. prionitis* (Nees) Soreng, AY029652; ***C. scabrida* Bloch 13508 (MO), KF737387**; *C. stenodes* (Griseb.) Soreng, GU253333; *C. tenera* (Beyr. ex Trin.) Soreng, GU253326; *Cyphonanthus discrepans* (Döll) Morrone & Zuloaga, DQ646392*; Echinolaena inflexa* (Poir.) Chase, AY029633; *Homolepis glutinosa* (Sw.) Zuloaga & Soderstr., AY029637; *Hopia obtusa* (Kunth) Zuloaga & Morrone, AY029659; *Hymenachne donacifolia* (Raddi) Chase,

AY029635; *H. grumosa* (Nees) Zuloaga, AY188468; *H. pernambucense* (Spreng.) Zuloaga, AY188478; *Ichnanthus pallens* (Sw.) Munro ex Benth., AY029638; *Mesosetum chaseae* Luces, AY029641; *Ocellochloa chapadensis* (Swallen) Zuloaga & Morrone, AY188486; *O. piauiensis* (Swallen) Zuloaga & Morrone, AY029656; *O. stolonifera* (Poir.) Zuloaga & Morrone, AY18848; *Ophiochloa hydrolithica* Filg. et al., AY029642*; Oplismenopsis najada* (Hack. & Arechav.) Parodi, AY188453; *Otachyrium versicolor* (Döll) Henrard, AY029643; *Panicum incertae sedis*: *Panicum hylaeicum* Mez, AY188470; *P. pilosum* Sw., AY188480; *Panicum* Section *Tuerckheimiana* (Hitchc.) Zuloaga: *P. tuerckheimii* Hack., AY188494; *Panicum* Section *Valida* Zuloaga & Morrone: *P. validum* Mez, AY188495; *Paspalum arundinellum* Mez, AY029663; *P. conjugatum* Bergius, AY029669; *P. glaziovii* (A.G. Burm.) S. Denham, AY029689; *P. remotum* J. Remy, AY029668; *P. vaginatum* Sw., AY029665; *Phanopyrum gymnocarpon* (Elliott) Nash, AY188469; *Plagiantha tenella* Renvoize, AY029674; *R. trinii* (Kunth) Zuloaga & Morrone, EU107781; *Steinchisma decipiens* (Nees ex Trin.) W. V. Br., AY188499; *S. hians* (Elliot) Nash, AY029685*; S. laxa* (Sw.) Zuloaga, AY029655; *S. spathellosa* (Döll) Renvoize, AY188500; *Stephostachys mertensii* (Roth) Zuloaga & Morrone, AY188471; *Streptostachys asperifolia* Desv., AY029687; *Tatianyx arnacites* (Trin.) Zuloaga & Soderstr., AY029688; *Triscenia ovina* (L.) L., JN604712. **Tribe Saccharеae.** *Andropogon gerardii* Vitman, AF117391; *Bothriochloa bladhii* (Retz.) S. T. Blake, AF117395; *Cymbopogon flexuosus* (Nees ex Steud.) Will. Watson, AF117404. **Tribe Thysanolaenae.** *Thysanolaena maxima* (Roxb.) Kuntze, U21984. **Tribe Tristachyideae.** *Danthoniopsis dinteri* (Pilg.) C.E. Hubb., AY029695. **Tribe Zeugiteae.** *Zeugites pittieri* Hack., U21987.

APPENDIX 2.

Codification of the 57 morphological characters and morphological matrix. Data for *Coleataenia scabrida* are boldfaced.

0 Main axis of inflorescences: 0 terminating in a spikelet, 1 terminating in a bristle, 2 terminating in a naked point without a bristle.
1 Rachis: 0 terminating in a spikelet, 1 terminating in a bristle, 2 terminating as a foliaceous axis, 3 terminating in a naked point without a bristle.
2 Foliaceous rachis: 0 absent, 1 present.
3 Bracts of the inflorescences: 0 absent, 1 present.
4 Involucral bristles (cauline): 0 absent, 1 present.
5 Involucral bracts: 0 absent, 1 present.
6 Cleistogenes in leaf axils: 0 absent, 1 present.
7 Apex of the pedicel: 0 truncate, 1 oblique.
8 Disarticulation at the base of the spikelet: 0 absent, 1 present.
9 Disarticulation at the base of the primary branches: 0 absent, 1 present.
10 Disarticulation at the base of the inflorescence: 0 absent, 1 present.
11 Disarticulation between the lower glume and lower lemma: 0 absent, 1 present.
12 Disarticulation at the base of the pedicel: 0 absent, 1 present.
13 Disarticulation at the node of the main axis: 0 absent, 1 present.
14 Disarticulation at the base of the upper anthecium: 0 absent, 1 present.
15 Unilateral spikelet: 0 absent, 1 present.
16 Second order branches in inflorescence: 0 multiflowered, 1 reduced to a single abaxial spikelet, 2 reduced to a single adaxial spikelet.
17 Spikelet shape: 0 not gibbous, 1 gibbous.
18 Presence of incomplete florets distal to fertile florets: 0 absent, 1 present.
19 Breeding system: 0 plants with at least some perfect flowers, 1 no perfect flowers staminate and pistillate flowers on the same plant, 2 no perfect flowers staminate and pistillate flowers on different plants.
20 Hairy callus at the base of the spikelet: 0 absent, 1 present.
21 Stipe at the base of the upper floret: 0 absent, 1 present.
22 Lower glume: 0 present, 1 vestigial, 2 absent.
23 Lower glume: 0 not saccate, 1 saccate.
24 Lower glume: 0 muticous, 1 awned.
25 Upper glume: 0 present, 1 absent.
26 Lower and upper glume: 0 of different size, 1 of the same size.
27 Upper glume: 0 as long as or longer than the lower lemma, 1 1/2 or less the length of the lower lemma.
28 Upper glume: 0 2 or 4-nerved, 1 enerved, 2 1-nerved, 3 1–3-nerved, 4 3–5-nerved, 5 5–11-nerved.
29 Upper glume: 0 muticous, 1 awned.
30 Lower lemma: 0 muticous, 1 awned.
31 Apex of the lower lemma: 0 entire, 1 bifid, 2 trilobite.
32 Lower palea: 0 absent, 1 present not expanded, 2 present and expanded.
33 Upper anthecium: 0 dorsiventrally compressed, 1 laterally compressed, 2 cylindrical.
34 Upper anthecium: 0 crustaceous, 1 cartilaginous, 2 hyaline, 3 membranous to herbaceous.
35 Upper lemma texture: 0 smooth, 1 transversely rugose.
36 Upper lemma with basal scars or appendages: 0 absent, 1 present.
37 Upper lemma: 0 muticous, 1 awned.

38 Upper lemma: 0 not differentiated at the apex, 1 differentiated at the apex.
39 Upper lemma (margins): 0 tucked in onto the palea, 1 lying flat and exposed on the palea.
40 Upper palea: 0 absent, 1 present.
41 Upper palea: 0 tightly clasped by the lemma, 1 gaping.
42 Upper palea: 0 without simple papillae, 1 with simple papillae, 2 with compound papillae.
43 Distribution of papillae in the upper palea: 0 all over surface, 1 at apex only.
44 Upper palea (presence of microhairs): 0 without bicellular microhairs, 1 with bicellular microhairs at the apex and/or base, 2 with bicellular microhairs all over its surface.
45 Upper palea (presence of macrohairs): 0 without macrohairs, 1 with macrohairs at the apex and/or base, 2 with macrohairs all over its surface.
46 Upper palea (apex): 0 straight, 1 recurved.
47 Stamen (number): 0 three, 1 two, 2 one.
48 Lodicules: 0 present, 1 absent.
49 Style base: 0 free, 1 fused.
50 Ovary: 0 glabrous, 1 pilose.
51 Caryopsis (hilum): 0 punctiform, 1 linear.
52 Photosynthetic pathway: 0 C3 XyMS+, 1 C4 XyMS-, 2 C4 XyMS+.
53 Chloroplasts on the parenchymatous sheath: 0 absent, 1 centripetal, 2 centrifugal.
54 Distinctive Kranz cells: 0 absent, 1 present.
55 Fusoid-cells: 0 absent, 1 present.
56 Basic chromosome number: 0 ($x=9$), 1 ($x=10$), 2 ($x=11$), 3 ($x=12$), 4 ($x=13$), 5 ($x=5$), 6 ($x=6$), 7 ($x=7$), 8 ($x=17$).

APPENDIX 2.

Thysanolaena maxima	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?	0	0	0	01	0	0	0	0	0	0	0	01	1	2	0	0	0	0	1	3	0	0	0	0	1	1	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	23
Acroceras zizanioides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	01	0	0	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0
Altoparadisium chapadense	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	-	0	0	1	0	2	0	-	0	-	0	4	1	1	0	0	-	-	-	0	-	-	-	0	-	-	-	-	-	-	0	0	0	0	0	1	-	1	0	?
Andropogon gerardii	0	0	?	01	0	0	01	?	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	?	3	01	0	0	?	?	23	0	-	1	0	1	1	?	?	?	?	?	0	0	0	?	0	0	1	-	0	0	1
Anthaenantia lanata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	-	0	-	0	5	0	0	0	1	0	1	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	1	-	0	0	1
Anthaenantiopsis rojasiana	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	-	-	0	-	0	5	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	-	0	0	1
Apochloa euprepes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1
Apochloa subtiramulosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	?
Arthropogon villosus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	5	1	0	0	1	1	2	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	1	-	0	0	?
Arundinella hirta	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	0	0	1	0	3	0	0	01	0	0	1	0	0	-	?	?	0	0	0	0	0	0	1	-	1	0	?
Axonopus anceps	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	2	0	-	0	-	0	05	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	01	0	0	0	0	0	0	0	1	-	0	0	1
Bothriochloa bladhii	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	03	0	0	0	0	0	2	0	-	1	0	1	01	1	0	-	0	0	0	0	0	0	0	0	1	-	0	0	8
Canastra lanceolata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	1	0	0	1	0	2	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	0	0	0	1	?
Cenchrus ciliaris	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	1	1	1	0	-	0	0	0	0	1	1	0	0	1	-	0	0	0
Chaetium bromoides	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	1	1	0	1	0	1	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	1	2	2	0	0	4
Chasmanthium laxum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	?	0	1	0	?	0	0	0	0	0	1	?	5	0	0	0	0	1	3	0	0	0	0	1	1	1	0	-	0	0	0	2	0	0	0	0	0	0	0	0	3
Coleataenia anceps	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	0
Coleataenia caricoides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	1
Coleataenia longifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	0
Coleataenia petersonii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	?
Coleataenia prionitis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	1
Coleataenia scabrida	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**5**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**-**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**-**	**0**	**0**	**?**
Coleataenia stenodes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	1
Coleataenia tenera	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	1
Cymbopogon flexuosus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	35	0	0	0	0	0	2	0	-	1	0	-	0	-	0	-	-	-	-	0	0	0	0	0	1	-	0	0	8
Cyphonanthus discrepans	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	01	1	0	0	1	0	3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	-	0	0	?
Danthoniopsis dinteri	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	1	1	1	0	0	1	1	0	1	1	0	-	0	0	0	0	0	0	0	1	1	?	?	0	03
Dichanthelium acuminatum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dichanthelium clandestinum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dichanthelium cumbucana	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	?
Dichanthelium koolauense	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dichanthelium sabulorum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Digitaria setigera	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	-	0	-	1	2	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	-	0	0	0
Echinochloa colona	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	1	0	1	1	0	-	1	1	1	0	0	0	0	0	1	-	0	0	0
Echinolaena inflexa	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	01	0	5	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1
Eriochloa punctata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	5	0	0	0	01	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	0	01	0	0	2	2	0	0	0
Homolepis glutinosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	0	0	0	0	1	0	0	0	1	1
Hopia obtusa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	-	0	0	1
Hymenachne donacifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0	0	3	0	0	0	0	1	1	1	1	1	-	0	0	0	0	0	0	0	0	0	0	0	1
Hymenachne grumosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	3	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1
Hymenachne pernambucensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	3	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	01	1
Melinis repens	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	01	0	1	0	0	0	0	0	5	1	1	1	01	1	3	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	2	2	0	0	0
Mesosetum chaseae	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	01	0	0	0	01	0	0	0	35	0	0	0	01	0	1	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	1	1	-	0	0	5
Moorochloa eruciformis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	2	2	0	0	0
Ocellochloa chapadensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	?
Ocellochloa piauiensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1
Ocellochloa stolonifera	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	?
Ophiochloa hydrolithica	2	2	1	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	2	0	-	0	-	0	0	0	0	0	0	0	3	0	0	0	0	1	1	1	0	-	1	0	0	01	1	0	0	0	1	-	0	0	?
Oplismenopsis najada	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	5	1	01	0	1	0	0	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	1	0	0	0	0	1
Oplismenus hirtellus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	5	01	0	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Otachyrium versicolor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	1	1	35	0	0	0	2	0	?	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Panicum adenophorum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	?
Panicum antidotale	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	-	0	0	0

……*continued on next page*

APPENDIX 2. (Countinued)

Panicum aquaticum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	12	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum bergii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum cervicatum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum chloroleucum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	2	0	0	?
Panicum claytonii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	?	?	1	1	0	0	0	0	0	0	0	0	0	0	?
Panicum dichotomiflorum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	12	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum elephantipes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	1	1	0	-	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum fauriei	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum hylaeicum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	1	1
Panicum miliaceum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum millegrana	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Panicum mystasipum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	?
Panicum nephelophilum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum olyroides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	12	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum pedersenii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum pilosum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Panicum racemosum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum repens	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum rudgei	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	1	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum sellowii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Panicum stramineum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	2	2	0	0	0
Panicum trichanthum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Panicum tricholaenoides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Panicum tuerckheimii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	1	0	0	0	0	0	5	0	0	0	01	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	-	0	0	?
Panicum validum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	-	0	0	1
Panicum verrucosum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Panicum virgatum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	0	0	0
Parodiophyllochloa cordovensis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parodiophyllochloa missiona	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parodiophyllochloa ovulifera	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parodiophyllochloa penicillata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paspalum arundinellum	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	0	0	0	0	0	2	0	-	0	-	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	-	0	0	1
Paspalum conjugatum	2	3	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	-	0	0	1
Paspalum glaziovii	2	2	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	-	0	0	1
Paspalum remotum	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	0	0	0	0	0	2	0	-	0	-	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	-	0	0	1
Paspalum vaginatum	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	-	0	-	0	5	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	-	0	0	1
Phanopyrum gymnocarpon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1
Plagiantha tenella	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pseudechinolaena polystachya	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0
Renvoizea trinii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	?
Sacciolepis indica	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	5	0	0	0	01	0	03	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Setaria lachnea	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	-	0	0	0
Setaria viridis	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	-	0	0	0
Steinchisma decipiens	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Steinchisma hians	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	2	0	1	0	0	0	0	0	1	0	2	0	0	0	0	01	0	0	0	0	0	0	0	0	1
Steinchisma laxa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	12	0	-	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Steinchisma spathellosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	2	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Stenotaphrum secundatum	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	01	0	1	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	1	-	0	0	0
Stephostachys mertensii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Streptostachys asperifolia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	5	0	0	0	01	0	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	1	0	0	0	1	1
Tatianyx arnacites	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	1	1	-	0	0	1
Triscenia ovina	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0	1	1	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	?
Zeugites pittieri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	01	0	0	0	1	1	0	0	0	0	0	0	0	0	5	0	0	01	1	1	3	0	0	0	0	1	1	1	0	-	?	0	0	0	0	0	0	0	0	0	0	0	3
Zuloagaea bulbosa	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	-	0	0	0