Cyphonanthus, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae) based on morphological, anatomical and molecular data

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Taxonomic features of *Panicum discrepans,* previously classified in subg. *Agrostoides,* sect. *Discrepantia* of *Panicum,* are reviewed and compared with other taxa in Paniceae. The new genus *Cyphonanthus* is proposed on the basis of morphological and molecular characters to include a species distributed from the Caribbean and Mesoamerica to Brazil and Bolivia. Affinities of the new genus with other genera of Paniceae are also discussed.

KEYWORDS: Gramineae, grasses, *Panicum,* phylogeny, taxonomy

INTRODUCTION

Panicum L., as traditionally circumscribed, is one of the largest genera of Poaceae, with approximately 450 species distributed worldwide (Webster, 1988). Recent phylogenetic studies in this genus, based on morphological and molecular data have clearly shown that *Panicum* is a polyphyletic genus (Gómez-Martínez & Culham, 2000; Zuloaga & al., 2000; Giussani & al., 2001; Duvall & al., 2001, 2003; Aliscioni & al., 2003). As a consequence, subgenera were raised or reinstated at the generic level, such as *Dichanthelium* (Hitchc. & Chase) Gould, *Phanopyrum* Raf., *Steinchisma* Raf., and *Megathyrsus* (Pilg.) B.K. Simon & S.W.L. Jacobs (Zuloaga & al., 1998, 2003; Aliscioni & al., 2003; Freckmann & Lelong, 2003; Simon & Jacobs, 2003; Barkworth, 2006). At the same time, *Panicum* was restricted to its type subgenus (Aliscioni & al., 2003) and all remaining species classified as "incertae sedis" within Paniceae. Among these species, *Panicum discrepans* Döll, previously classified in the monotypic sect. *Discrepantia* (Zuloaga, 1987), is unique by having lower glumes absent or reduced, gibbous spikelet, and upper anthecium open at the apex and with long, curled macrohairs at the apex and base. A detailed discussion of relationships in *Panicum*, segregated genera and "incertae sedis" species can be found in Zuloaga & al. (2006).

The purpose of this study is to evaluate the taxonomic position of *Panicum discrepans.* New molecular evidence from the *ndhF* (NADH dehydrogenase subunit F) gene and from the grass-specific insert in the *rpoC2* (subunit C2 of an RNA polymerase) gene, together with several morphological and anatomical characters support the formation of a new genus.

MATERIALS AND METHODS

Morphological and anatomical analyses. — Morphological studies were based on herbarium specimens from CEN, F, G, IAN, IBGE, K, M, MO, MY, NY, P, R, RB, SI, SP, UB, US, and VEN. Upper anthecia were viewed on a Zeiss 940 A scanning electron microscope, operating at 10–20 kV, at the Darwinion Institute.

For anatomical studies the second leaf below the inflorescence was selected. Specimens compared were *Comastri Filho 75, Oliveira & al. 882, Ortíz & Ramia 4920, Williams 13052,* and *Davidse & al. 16861.* Cross-sectional leaf anatomy was determined from hand-sectioned leaf blades of herbarium specimens previously treated with ethylene glycol for 24–48 hours. The blades were sectioned approximately one-third from the base, after desilification in 30% hydrofluoric acid, stained with safranin and fast green, 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 in Ellis (1976, 1979).

DNA sequencing *ndhF* + *rpoC2*. — A specimen of *Panicum discrepans*, *Mendonça & al. 3611*, was provided by the Missouri Botanical Garden. Total genomic DNA was extracted with the DNeasy Plant Mini Kit (Qiagen) and used as template for the PCR amplification of two chloroplast regions: the *ndhF* gene and the grass specific insert found in the *rpoC2* gene (Cummings & al., 1994; Barker & al., 1999; Duvall & al., 2001, 2003). *ndhF* amplification and sequencing were carried out using four pairs of primers specified by Olmstead & Sweere (1994): 5F/536R, 536F/1318R, 972F/1666R, and 1318F/2110R. For the *rpoC2*

insert, one pair of primers *rpoC2-1/rpoC2-2* (Barker & al., 1999) was used. PCR reactions were performed in 25 µl final volume with 50–100 ng of template DNA, 0.2 µM of each primer, 25 µM of DNTPs, 5 mM $MgCl_2$, 1× buffer and 1.5 units of *Taq* polymerase provided by Invitrogen. The reaction conditions were: a first period of denaturation at 94°C for 5 min., followed by 35 cycles of denaturation at 94°C for 30 sec., annealing at 48°C for 1 min., and extension at 72°C for 1.5 min. Final extension at 72°C for 6 min. terminated the reactions. A negative control with no template was included for each series of amplifications to eliminate the possibility of contamination. PCR products were run out on a 1% TBE agarose gel stained with ethidium bromide. Cleaning of PCR products and automated sequencing were performed by Macrogen, Inc. To edit and assemble sequences the program Chromas Pro version 1.22 (Technelysium Pty, Ltd) was used. The complete sequences have been submitted to the EMBL GenBank under accession numbers #DQ646391 and #DQ646392.

The *ndhF* and the *rpoC2* sequences obtained from *Panicum discrepans* were included in the Panicoid grass 123-taxa matrix from Aliscioni & al. (2003) and in the Panicoid 92-taxa matrix from Duvall & al. (2003), respectively (Appendices 1, 2). Alignments were manually performed using BioEdit version 5.0.9 (Hall, 1999).

The aligned matrices were submitted to TreeBASE (http://www.treebase.org/treebase/). Submission name "Amalia Scataglini", reviewer's P.I.N. code 11026.

In addition, a combined matrix containing 55 taxa shared by both datasets was generated in order to perform a simultaneous analysis (Nixon & Carpenter, 1996).

Phylogenetic analyses. — The matrices were analyzed under the parsimony criterion using Nona (Goloboff, 1999). WinClada version 1.00.08 (Nixon, 2002) was used as the interface to construct trees. Characters were equally weighted and considered unordered. Parsimony uninformative characters were excluded from the analyses and gaps were scored as missing data. Heuristic searches were performed using 1,000 series of random addition sequences followed by TBR branch rearrangements (mult*1000) and retaining 10 trees per series (hold/10). The shortest trees found were additionally TBR swapped with the "max*" command. A strict consensus tree (Nelson, 1979; Rohlf, 1982) was generated from the most parsimonious trees. Branch support was calculated by Jackknifing with 1,000 replicates, using mult*10, hold/1 as search strategy. Support of consensus trees obtained were also compared.

RESULTS

Leaf blade anatomy

The Kranz syndrome is a remarkable feature in which biochemical and physiological characteristics of C_4 photosynthesis are correlated with distinctive anatomical structure (Ellis, 1977; Hattersley, 1987). The presence of a single mestome Kranz sheath around the vascular bundles, and the presence of three chlorenchymatic cells between contiguous vascular bundles, allowed us to conclude that *Panicum discrepans* is a C_4 species of the MS (XyMS–) subtype (Brown, 1977; Hattersley & Watson, 1976) (Fig. 1).

Leaf blade in transverse section. — *Outline:* broadly V-shaped with slightly involute margins; leaf thickness 180–250 µm, arms of the lamina symmetrical. *Ribs and furrows:* adaxial ribs and furrows slightly developed; abaxial ribs and furrows indistinguishable. *Median*

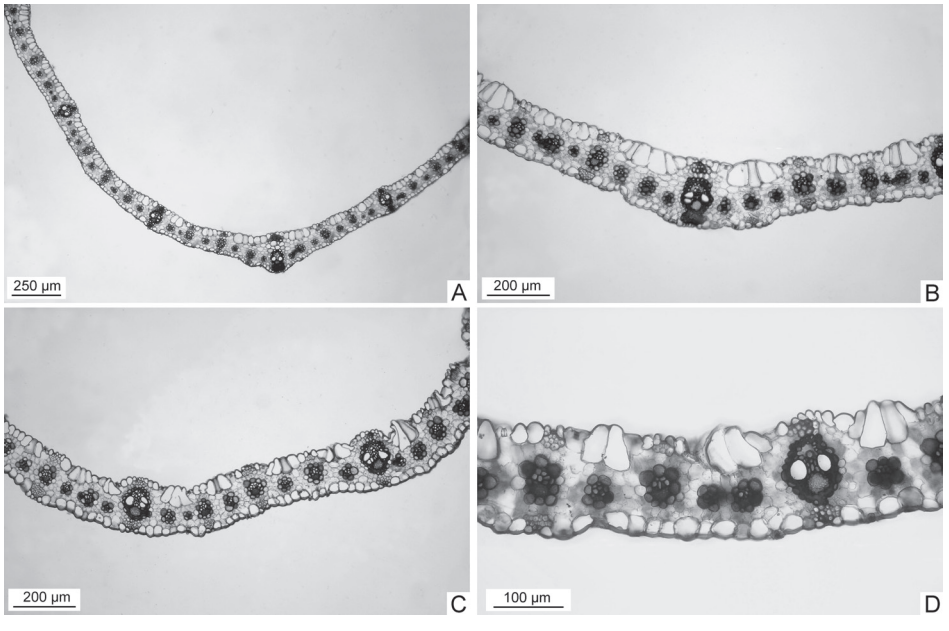

Fig. 1. Leaf blade anatomy of *Cyphonanthus discrepans*. A–D, transverse leaf section; A, general aspect of the keel, with portions of the leaf blade; B, detail of the keel; C, portion of the leaf blade showing first-, second-, and third-order vascular bundles; D, detail of C (based on *Oliveira & al. 882*).

bundle: no structurally distinct, midrib present. *Vascular bundle arrangement:* 8–10, first-order vascular bundles in the entire blade; 1 or 3 second-order vascular bundles between contiguous first-order vascular bundles; all vascular bundles situated in the center of the blade or slightly abaxially displaced. *Vascular bundle structure:* First-order vascular bundles circular in outline; phloem adjoined to the Kranz vascular bundle sheath; angular metaxylem vessels in contact with the Kranz cells. Second-order vascular bundles elliptical in outline, with xylem and phloem tissue distinguishable. Third-order vascular bundles angular in outline, located below the bulliform cells, with xylem and phloem tissue indistinguishable. *Vascular bundle sheath:* mestome Kranz cells sheath of the first-order vascular bundles entire or with adaxial or abaxial interruption of sclerenchyma girders, consisting of 10–15 rounded and inflated cells; mestome Kranz sheath of second-order vascular bundles elliptical in outline, entire, without extensions, formed by 8–10 rounded and inflated cells; mestome Kranz sheath of the third-order vascular bundles circular in outline, complete, without extensions, formed by 5–8 cells similar to the ones of the second-order vascular bundles. *Sclerenchyma:* small, adaxial and abaxial girders associated with the first-order vascular bundles, absent on the second-order and third-order vascular bundles or associated as abaxial strands; fibers lignified; minute sclerenchyma caps present in leaf margins. *Mesophyll:* indistinctly radiate; three chlorenchyma cells between consecutive vascular bundles; colorless cells absent. *Adaxial epidermal cells:* fan-shaped groups of bulliform cells located at base of furrows, not very restricted and up to 8 cells wide. Epidermal cells small, regular in outline, papillae absent. *Abaxial epidermal cells:* bulliform cells absent, cuticle thickened; papillae absent (Fig. 1A–D).

Abaxial epidermis in surface view. — *Zonation:* costal and intercostal zones distinguishable; costal zone with 3–6 rows of long cells; intercostal zone consisting of 4–8 rows of long cells. *Intercostal cells:* elongated, more than 3 times longer than wide, with parallel side walls, vertical end walls, and undulating anticlinal walls. *Stomata complex:* low-dome shaped, 32.5–39.0 µm long, 15–20 µm wide, 2 longitudinal rows of stomata per intercostal zone. *Intercostal short cells:* either solitary or paired; tall and narrow. *Microhairs:* bicellular, finger-like, 45–50 µm long, distal cells with very thin walls and tapered at the apex, basal cell equal or slightly shorter than the distal cells. *Papillae:* absent. *Prickle hairs:* absent or present, small and with base shorter than the stomata; barb longer than the base. *Macrohairs:* absent or present, when present unicellular on intercostal zones. *Costal silica bodies:* dumbell-shaped; intercostal silica bodies tall and narrow, transversely elongated (Fig. 2C–D).

Adaxial epidermis in surface view. — Epidermal cells similar to the abaxial surface, except for the presence of a central band of rectangular cells, 2–4 cells wide, in the intercostal zones (Fig. 2A–B).

Molecular phylogeny

The *ndhF* sequence of *P. discrepans* was included in the 123-taxa matrix used in Aliscioni & al. (2003); 435

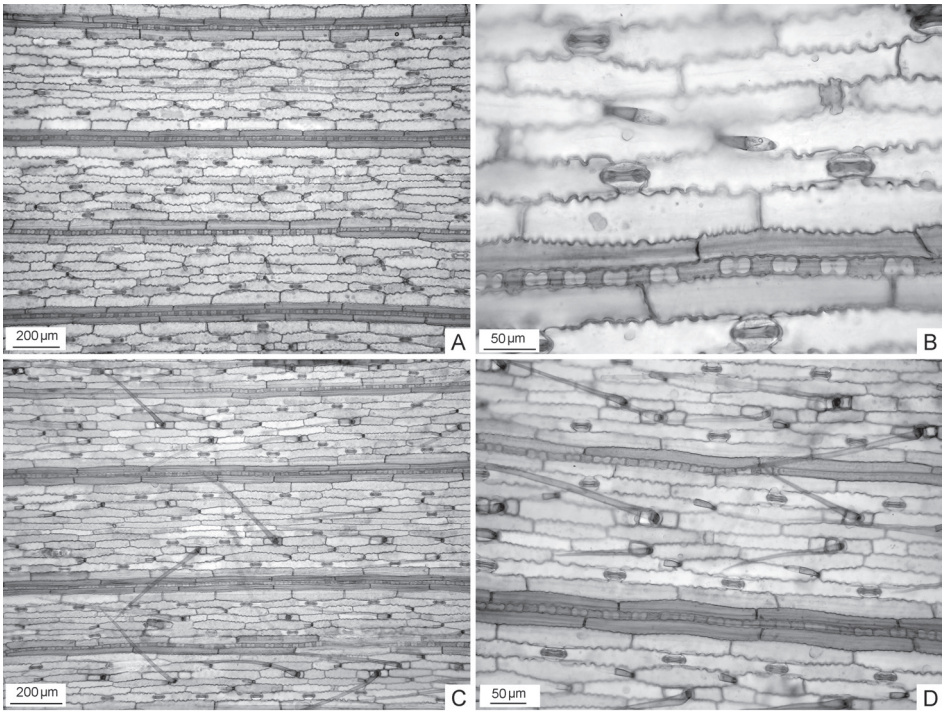

Fig. 2. Leaf blade anatomy of *Cyphonanthus discrepans*. A–B, adaxial epidermis; A, epidermal zonation with narrow intercostal zones; B, detail of stomata, with dome-shaped subsidiary cells, rectangular long cells with moderately undulating anticlinal walls, bicellular microhairs, and short cells; C, abaxial epidermis; D, detail of abaxial epidermis with macrohairs, bicellular microhairs, stomata, and short cells (based on *Comastri Filho 75*).

base-pairs out of a total of 2,061 were parsimony-informative. The cladistic analysis yielded more than 25,000 most parsimonious trees of 1,526 steps, with CI = 0.42 and RI = 0.77. A strict consensus tree with *P. discrepans* forming a 100% supported clade with *Streptostachys ramosa* Zuloaga & Soderstr. was obtained**.**

Regarding the *rpoC2* matrix of Duvall & al. (2003), 197 characters were phylogenetically informative when *P. discrepans* was included, from a total of 903 bp. positions (with gaps). More than 25,000 trees, 510 step-long were obtained (CI = 0.51 and RI = 0.71) under parsimony criterion. In this strict consensus tree, *P. discrepans* appears again forming a clade with *Streptostachys ramosa*. However, there is less than 50% jackknife support for this clade.

When matrices containing shared taxa by both datasets were combined in a new matrix of 55 taxa and 2,964 characters, 428 positions resulted parsimony-informative. The combined analysis yielded 27 trees of 1,207 steps with CI = 0.47 and RI = 0.70. The strict consensus tree showed *P. discrepans* forming a clade with *Streptostachys ramosa* with 100% jackknife support (Fig. 3).

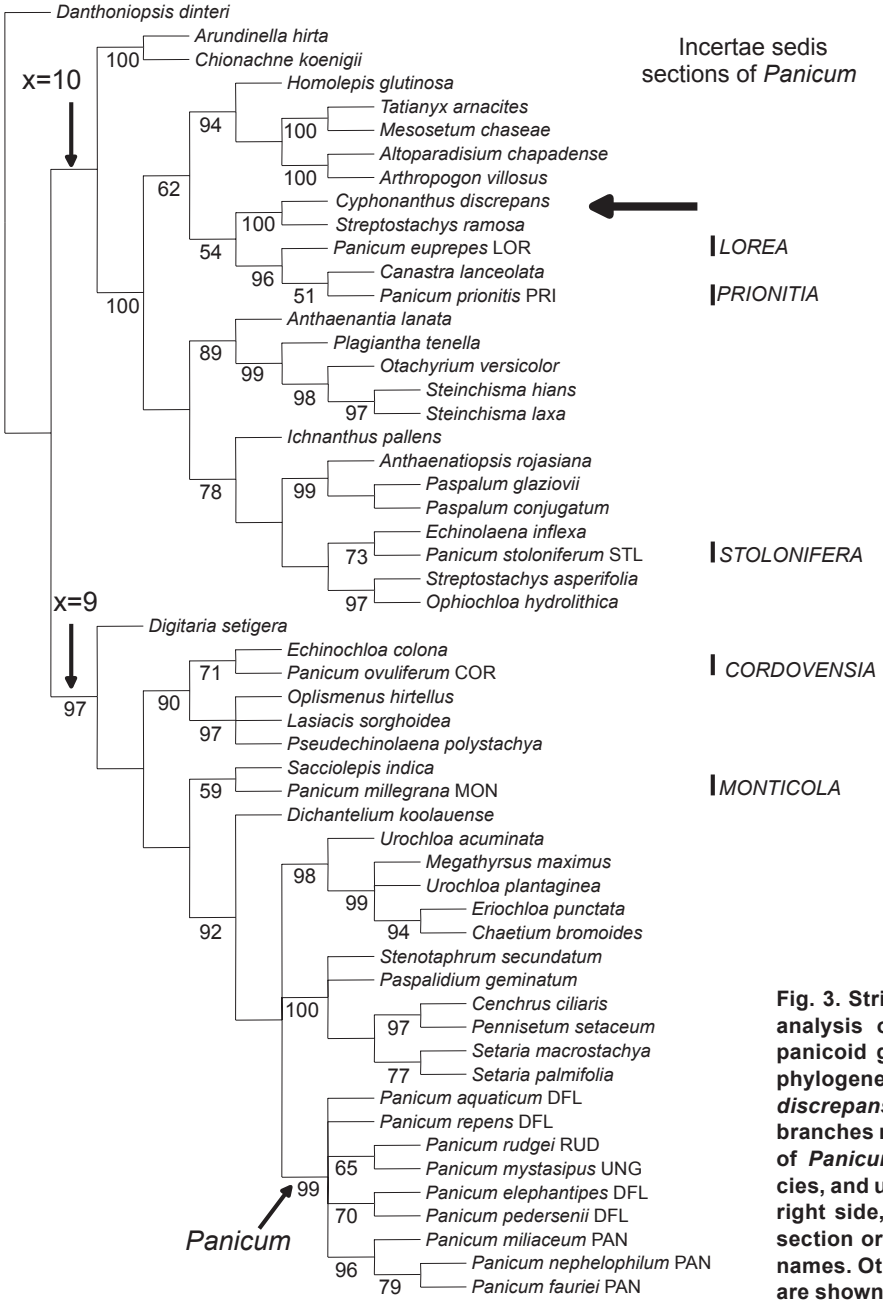

Fig. 3. Strict consensus tree of the combined analysis of *ndhF* and *rpoC2* sequences of panicoid grasses. The cladogram shows the phylogenetic relationships of *Cyphonanthus discrepans* with related taxa. Numbers below branches represent jackknife values. Sections of *Panicum*, including "incertae sedis" species, and ungrouped species are shown on the right side, and the first three letters of each section or ungrouped taxa follow the species names. Other significant monophyletic clades are shown on the left side.

DISCUSSION

As its specific epithet clearly indicates, *Panicum discrepans* has several characteristics that distinguish it from the traditional circumscription of *Panicum*. When we consider the new delimitation of *Panicum* to subg. *Panicum*, *P. discrepans* differs by the following morphological characters: presence of gibbous spikelets (versus not gibbous spikelets in *Panicum*), lower glume usually absent or reduced and nerveless (vs. lower glume ⅙ to ⅘ the length of the spikelet and 1–5 [7–11]-nerved), upper glume and lower lemma 3-nerved (vs. upper glume and lower lemma 7–9[–13]-nerved), upper anthecium gibbous (vs. not gibbous), open at the apex (vs. closed at the apex) and covered by long, curled macrohairs at the tip and base of the lemma and palea (vs. upper anthecium glabrous or just with long and flattened macrohairs at the base of the upper lemma). Also, simple papillae are regularly distributed along the upper lemma and palea in *P. discrepans,* while in *Panicum* subg. *Panicum* simple or compound papillae are present at the tip of the upper palea. Anatomically, *Panicum discrepans* is a Kranz species of the MS (XyMS–), with a single Kranz mestome sheath around the vascular bundles, while all species of *Panicum* subg. *Panicum* are Kranz of the PS (XyMS+) type, with the vascular bundles surrounded by a parenchymatous Kranz sheath and a mestome sheath.

When the *ndhF* and *rpoC2* sequences of *Panicum discrepans* were added to the Panicoid matrices, the molecular analysis show that *Panicum discrepans* is related to members of the Paniceae in the $x = 10$ clade, departing from *Panicum* subg. *Panicum* as presently considered. Furthermore, *P. discrepans* is shown to be related to *Streptostachys ramosa* in both the separate and combined approach, forming a clade with 100% jackknife support in the simultaneous analysis. The genus *Streptostachys* is in need of a careful revision, since *S. asperifolia*, the type species of the genus, appears in previous analyses (Giussani & al., 2001; Aliscioni & al., 2003) in a distant and well supported clade, where it is related to *Ophiochloa* and *Axonopus*. Furthermore, when *S. macrantha* (Trin.) Zuloaga & Soderstr. is included in the analysis (unpublished data), this species appears in a strong clade with *S. ramosa* with 100% jackknife support, with *Panicum discrepans* as the sister group of this clade. *Panicum discrepans* differs from *Streptostachys ramosa* and *S. macrantha* by having the following morphological characteristics: plants stoloniferous and decumbent, rooting at the lower nodes (vs. plants caespitose), spikelets gibbous, ovoid, 1.1–1.3 mm long (vs. biconvex, not gibbous, ellipsoid to long ellipsoid, 5.9–9.3 mm long), rachilla not thickened between the lower glume and upper anthecium (vs. rachilla thickened), lower glume absent or reduced, unnerved (vs. lower glume always present, ⅙ to ½ the length of the spikelet, 1–3-nerved), upper glume and lower lemma 3-nerved, hyaline (vs. 5–7-nerved, and membranous or indurate), lower palea and lower flower absent (vs. lower palea present, almost as long as the lower lemma, and lower flower staminate), upper anthecium with curled macrohairs at the tip and base of lemma and palea (vs. upper anthecium with not curled macrohairs throughout), gaping at the apex of the lemma (vs. the lemma entirely covering the apex of the palea), and caryopsis with a punctiform hilum (vs. caryopsis with a linear hilum). Taking in consideration these morphological characters, *P. discrepans* is clearly unrelated to the clade of *S. ramosa* and *S. macrantha.*

Within this clade, *Panicum discrepans* is also related to "incertae sedis" sections of *Panicum: Agrostoidea* Hitchc. & Chase ex C.C. Hsu*, Lorea* Zuloaga, *Megista* Pilg., *Prionitia* Zuloaga, and *Tenera* Hitchc. & Chase ex Pilg. *Panicum* sect. *Agrostoidea* includes two species present in North America and is characterized by having a caespitose habit, linear blades, non gibbous spikelets with the lower glume 3-nerved and ⅓ to ⅔ the length of the spikelet, and upper anthecium glabrous, not open at the apex and with two prominent hooks at the tip of the upper lemma. *Panicum* sect. *Lorea* includes 27 species found in the highlands of Central Brazil and Venezuela; all taxa are non-Kranz, caespitose, with ligules absent or membranous, pungent leaves, lower glume 3(–5)-nerved and ½ to ⅘ the length of the spikelet, and upper anthecium glabrous, smooth, and not open at the apex. *Panicum* sect. *Megista* is monotypic, with *P. mertensii* Roth widely distributed from the Caribbean and Mesoamerica to Brazil, Paraguay and Argentina. This species can be distinguished by its non-Kranz leaf anatomy, pseudoverticillate inflorescence branches, obovoid spikelets, 3–5-nerved lower glumes, and upper glume and lower lemma 7–9-nerved, upper anthecium not open at the apex, and with stomata and papillae at the apex. *Panicum* sect. *Prionitia* includes two species: *P. petersonii* Hitchc. & Ekman endemic to Cuba and *P. prionitis* Nees in central Brazil, Argentina, Uruguay, and Paraguay. Both species are robust, caespitose with sheaths and blades conspicuously keeled, lower glumes ½ to ¾ the length of the spikelet, 3-nerved, and upper anthecium glabrous and smooth, occasionally with prickle hairs at the apex. Members of *Panicum* sect. *Prionitia* are characterized as having Kranz anatomy of the MS type but with two bundles present, a parenchymatic and a mestome sheath surrounding all first-order vascular bundles. Finally, *Panicum* sect. *Tenera*, with three species found from the Caribbean and Mesoamerica to Bolivia and Brazil, differs by its caespitose habit, filiform leaves, contracted, axillary inflorescences that are few-flowered, upper anthecium not gibbous and glabrous and not open at the apex, and the upper glume and lower lemmas (5–)7–9- nerved.

Based on the previously discussed molecular, morphological, and anatomical data, *Panicum discrepans* is

Table 1. Comparison of *Cyphonanthus discrepans* with related taxa.

Character	*Cyphonanthus*	*Panicum*	*Panicum* sect. *Agrostoidea*	*Panicum* sect. *Megista*	*Panicum* sect. *Lorea*	*Panicum* sect. *Prionitia*	*Panicum* sect. *Tenera*	*Streptostachys*
Habit	Stoloniferous, decumbent	Variable	Caespitose	Rhizomatous, erect	Caespitose	Caespitose	Caespitose	Caespitose
Sheaths and blades	Not keeled	Not keeled	Not Keeled	Not keeled	Not keeled	Keeled	Not keeled	Not keeled
Blade shape	Lanceolate	Ovate lanceolate to filiform	Linear lanceolate	Lanceolate	Linear lanceolate to lanceolate	Linear	Filiform	Lanceolate
Inflorescences	Multiflowered	Multiflowered	Multiflowered	Multiflowered	Multiflowered	Multiflowered	Few flowered	Multiflowered
Inflorescences branches	Not verticillate	Not verticillate	Not verticillate	Verticillate	Not verticillate	Not verticillate	Not verticillate	Not verticillate
Spikelet	Gibbous	Not gibbous	Not gibbous	Not gibbous	Not gibbous	Not gibbous	Not gibbous	Not gibbous
Lower glume lenght	Absent or reduced	⅙ to ⅘	⅓ to ⅔	⅓ to ½	½ to ⅘	½ to ¾	⅓ to ½	⅓ to ½
Lower glume nervation	0	1–5 (7–11)	3	3–5	3(–5)	3	3(7)	3
Upper glume and lower lemma nervation	3	7–9(–13)	5	7–9	5(–7)	5	(5–)7–9	5
Upper anthecium ornamentation	With simple papillae, and unicellular macrohairs at tip and base	With simple or compound papillae at the apex, macrohairs at the base or glabrous	Glabrous, smooth, with hooks at the apex of the lemma	Glabrous, smooth, with stomata at the apex	Glabrous, smooth	Glabrous, smooth, occasionally with prickle hairs	Glabrous, smooth	With simple papillae and bicellular microhairs
Upper anthecium apex	Open	Closed	Closed	Closed	Closed	Closed	Closed	Closed
Hilum	Punctiform	Punctiform	Punctiform	Punctiform	Punctiform	Punctiform	Punctiform	Linear
Anatomical type	C_4MS	C_4PS	C_4MS	C_3	C_3	C_4MS	C_4MS	C_4MS
Distribution	Caribbean and Mesoamerica to Brazil	Widely distributed	North America	Mesoamerica to Argentina	Central Brazil and Guiana Highlands	Disjunct; Cuba and Central Brazil to Uruguay and Argentina	Caribbean and Mesoamerica to Bolivia and Brazil	Central Brazil

here transferred to the new genus *Cyphonanthus*. Morphological and anatomical characteristics that distinguish *Cyphonanthus* from related taxa are given in Table 1.

TAXONOMIC TREATMENT

Cyphonanthus Zuloaga & Morrone, **gen. nov.** – Type: *Panicum discrepans* Döll, in C. Martius, Fl. Bras. 2 (2): 252. 1877. ≡ *Cyphonanthus discrepans* (Döll) Zuloaga & Morrone.

= *Panicum* sect. *Discrepantia* Zuloaga, Grass Syst. Evol.: 294. 1987.

Gramina perennia, rhizomatosa, rhizomatibus brevibus; culmis decumbentibus, simplicibus. Ligulae ciliatae. Laminae lanceolatae. Inflorescentiae laxae, spiculae ovoideae, gibbosae, glabrae. Gluma infera nulla vel usque ⅓ spicula longior, enervia. Gluma supera 3-nervia, lemma

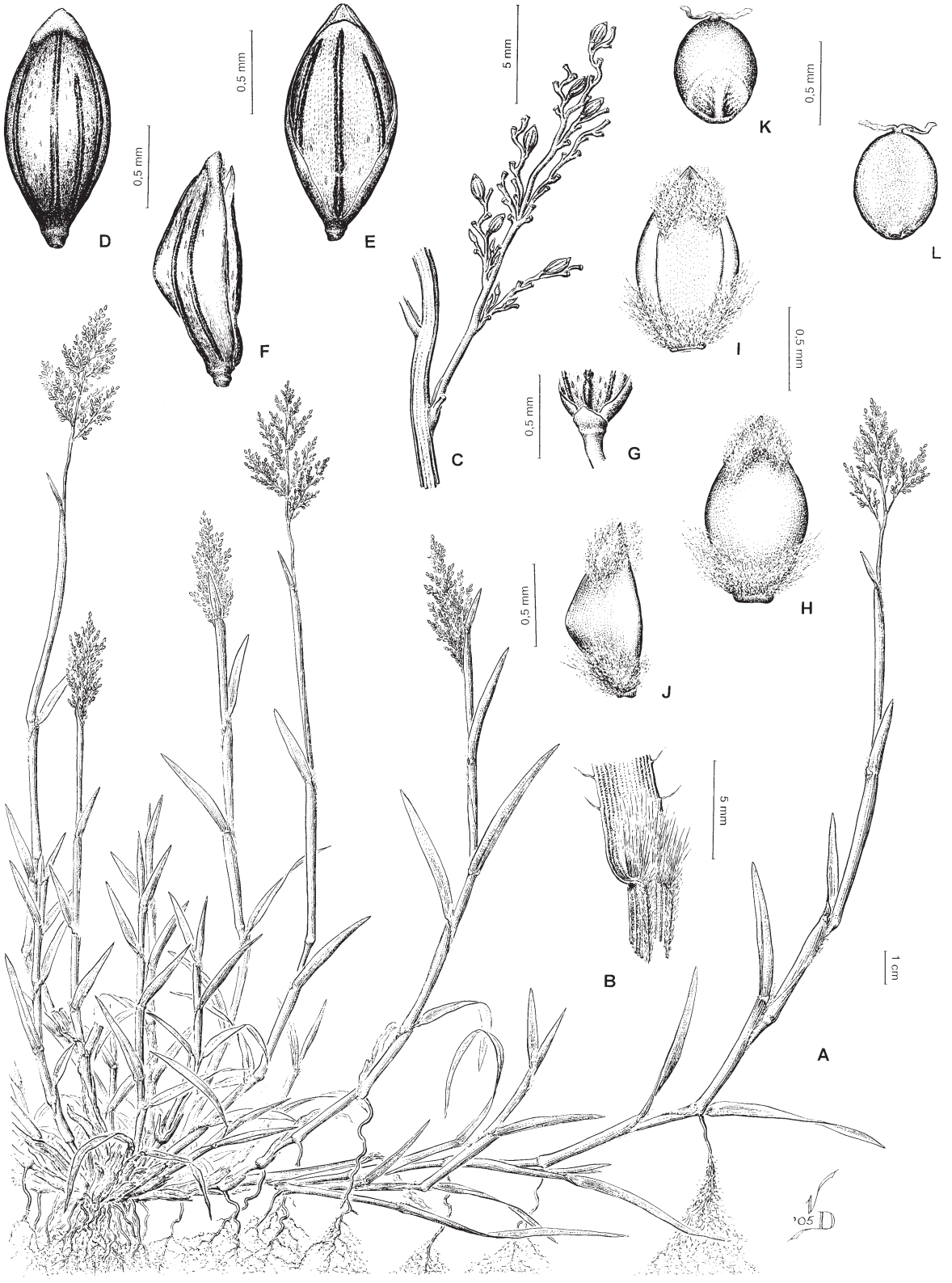

Fig. 4. ***Cyphonanthus discrepans.*** **A, habit; B, detail of ligule; C, detail of branch of the inflorescence with spikelets; D, spikelet, dorsal view; E, spikelet, ventral view; F, spikelet, lateral view; G, lower glume; H, upper anthecium, dorsal view; I, upper anthecium, ventral view; J, upper anthecium, lateral view; K, caryopsis, embryo view; L, caryopsis, hilum view (based on** ***Filgueiras 1925*****).**

inferum 3-nervium. Flos inferus nullus. Anthoecium superum gibbosum, ovoideum, induratum, macro pilis apicem versus et basin ornatum.

Short-rhizomatous perennial with simple culms decumbent, rooting at the lower nodes. Ligules ciliate. Blades lanceolate. Inflorescences lax, spikelets ovoid, gibbous, glabrous. Lower glume absent or reduced, unnerved. Upper glume and lower lemma subequal, 3-nerved. Lower flower and lower palea absent. Upper anthecium ovoid, open at the apex, with macrohairs at the apex and base of lemma and palea.

Cyphonanthus discrepans (Döll) Zuloaga & Morrone, **comb. nov.** ≡ *Panicum discrepans* Döll, in C. Martius, Fl. Bras. 2 (2): 252. 1877. – Lectotype (here designated): Brazil. Pará: Santarem, "Panicum n°7", *R. Spruce 602* (Lectotype: K!; Isolectotypes: F!, M!, MO!; NY!, P!, US-974684!, fragment ex P). Syntypes: Brazil, Goiás, without locality, *G. Gardner 3510* (F!, G!, K!, MO!, P!, US-1066789!, US-823969!). Minas Gerais: São João del Rey, Paracatú, Serra de Christaes et S. Luzia, *J.B.E. Pohl 904* (F-881214!, US-1126917!, fragment ex W). French Guiana: without locality, *Leprieur s.n.* (G!, K!, P!, US-1445787). (Fig. 4).

Description. — Short rhizomatous perennials, stoloniferous and decumbent, rooting at the lower nodes, erect culms 20–40 cm tall, simple, rarely branching (Fig. 4A); internodes glabrous, hollow; nodes dark, compressed, glabrous. *Sheaths* shorter than the internodes, striate, densely pilose at the base of the culms, otherwise glabrous, the margins shortly ciliate. *Ligules* 3–4 mm long, ciliate, a line of whitish hairs (Fig. 4B). *Blades* 2–15 cm long, 0.2–0.6 cm wide, lanceolate, rounded at base, the apex acute, glabrous to densely pilose, mainly at the adaxial surface, the lower margins ciliate. *Inflorescence* terminal, exserted or partially included on the upper sheaths; peduncle up to 5 cm long; panicles 3–6 cm long, 1.5–3.5 cm wide, lax, open, main axis wavy, glabrous, pulvini glabrous; first-order branches divergent, axis of the branches glabrous, smooth; pedicels glabrous, short. *Spikelets* 1.1–1.3 mm long, 0.5–0.6 mm wide, ovoid, gibbous, green or tinged with purple, glabrous, upper glume and lower lemma subequal (Fig. 4D–F). *Lower glume* absent or reduced, a minute scale or up to ⅓ the length of the spikelet, unnerved (Fig. 4G). *Upper glume* gibbous, obtuse or acute, 3-nerved, one central and two marginal, dark nerves (Fig. 4D). *Lower lemma* glumiform, 3-nerved, obtuse or acute (Fig. 4E). *Lower palea* and *lower flower* absent. *Upper anthecium* ovoid, slightly shorter than the upper glume and lower lemma, ovoid, gibbous (Fig. 4H–J), open at the apex, indurated, with simple papillae regularly distributed all over its surface, and long, whitish curled macrohairs at the apex and base of the lemma and palea (Fig. 4H–J, Fig. 5); lemma 3-nerved, stamens 3, anthers 0.3–0.4 mm long; lodicules ca. 0.2 mm long, 2, conduplicate. *Caryopsis* 0.7 mm long, 0.5 mm wide, broadly ovoid; hilum punctiform (Fig. 4K), embryo less than half the length of the caryopsis (Fig. 4L).

Phenology. — Flowering between June and November.

Etymology. — The generic name alludes to the gibbous form of the spikelet and upper anthecium.

Distribution and habitat. — The species grows from Cuba and Belize to central Brazil from sea level to 1,200 m (Fig. 6); it is found in seasonally flooded open fields, edges of swamps, in sandy or rocky soils. In Cuba

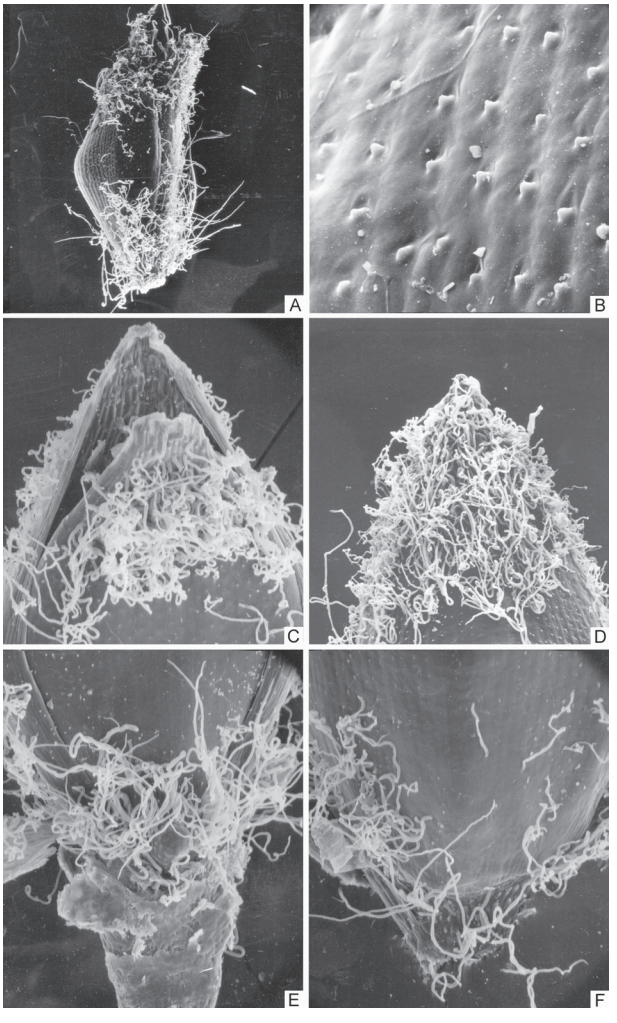

Fig. 5. Scanning electron micrographs of the upper anthecia of *Cyphonanthus discrepans*. A, gibbous spikelet, lateral view macrohairs at tip and base; B, detail of surface of the upper lemma with simple papillae; C, apex of the lemma and palea with macrohairs, lemma not covering the apex of the palea; D, apex of the upper lemma with macrohairs and simple papillae; E, base of the upper anthecium ventral view; F, base of the upper anthecium, dorsal view (based on *Ekman 11439*).

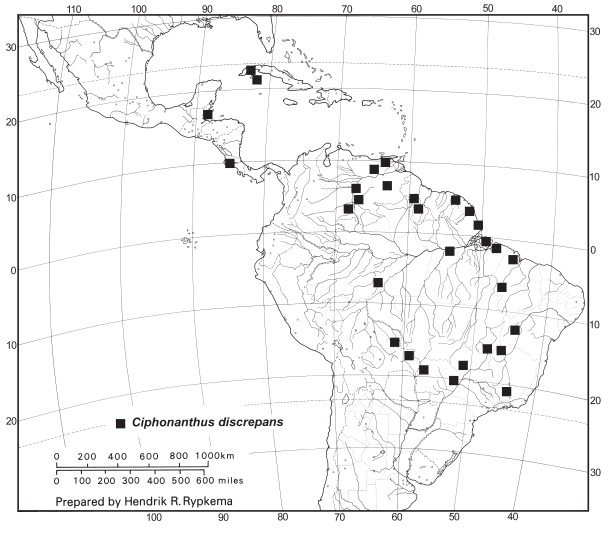

Fig. 6. Distribution of *Cyphonanthus discrepans* in America.

it is found in pinelands and has been reported for the department Guainía, Colombia (Giraldo-Cañas, 2003), and for Costa Rica (Pohl, 1980).

Observation. — Döll (1877) cited the specimens *Spruce 602, Gardner 3510,* and *Pohl 904* from Brazil and *Leprieur s.n.* from French Guiana as syntypes of *P. discrepans* of which *Spruce 602* agrees with the protologue and is here selected as lectotype of the name. The syntype *Gardner 3510* was also cited by Nees (1850) as a syntype of *Paspalum gardnerianum* Nees.

For examined specimens see Appendix 3.

ACKNOWLEDGMENTS

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Appendix 1. List of taxa used in the *ndhF* analysis and GenBank accession numbers.

Tribe Andropogoneae. *Andropogon gerardii* Vitman, AF117391; *Bothriochloa bladhii* (Retz.) S.T. Blake, AF117395; *Chionachne koenigii* (Spreng.) Thwaites, AF117397; *Cymbopogon flexuosus* (Nees ex Steud.) Will. Watson, AF117404; *Phacelurus digitatus* (Sibth. & Sm.) Griseb., AF117418; *Sorghum bicolor* (L.) Moench, U21981; *Zea mays* L., U21985.
Tribe Arundinelleae. *Arundinella hirta* (Thunb.) Tanaka, AF117393.
Tribe Centotheceae. *Chasmanthium laxum* (L.) H.O. Yates subsp. *sessiliflorum* (Poir.) L.G. Clark, U27296; *Zeugites pittieri* Hack., U21987.
Tribe Danthonioideae. *Danthoniopsis dinteri* (Pilg.) C.E. Hubb., AY029695.
Tribe Paniceae (excluding *Panicum*). *Acroceras zizanioides* (Kunth) Dandy, AY029618; *Altoparadisium chapadense* Filg. & al., AY029619; *Anthaenantia lanata* (Kunth) Benth., AY029640; *Anthaenantiopsis rojasiana* Parodi, AY029620; *Arthropogon villosus* Nees, AY029622; *Axonopus anceps* (Mez) Hitchc., AY029623; *Canastra lanceolata* (Filg.) Morrone & al., AY029621; *Cenchrus ciliaris* L., AY029625; *Chaetium bromoides* (J. Presl) Benth. ex Hemsl., AY029626; *Cyphonanthus discrepans* Morrone & Zuloaga, DQ646392; *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; *Echinolaena inflexa* (Poir.) Chase, AY029633; *Eriochloa punctata* (L.) Desv., AY029634; *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; *Lasiacis sorghoidea* (Desv.) Hitchc. & Chase, AY029639; *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs, AY029649; *Melinis repens* (Willd.) Zizka, AY029675; *Mesosetum chaseae* Luces, AY029641; *Moorochloa eruciformis* (Sm.) Veldkamp, AY188452; *Ophiochloa hydrolithica* Filg. & al., AY029642; *Oplismenopsis najada* (Hack. & Arechav.) Parodi, AY188453; *Oplismenus hirtellus* (L.) P. Beauv., AY029644; *Otachyrium versicolor* (Döll) Henrard, AY029643; *Paspalidium geminatum* (Forssk.) Stapf, AY029662; *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; *Pennisetum alopecuroides* (L.) Spreng., AY029672; *P. setaceum* (Forssk.) Chiov. AY029673; *Phanopyrum gymnocarpon* (Elliott) Nash, AY188469; *Plagiantha tenella* Renvoize, AY029674; *Pseudechinolaena polystachya* (Kunth) Stapf, AY029676; *Sacciolepis indica* (L.) Chase, AY029677; *Setaria lachnea* (Nees) Kunth, AY029683; *S. macrostachya* Kunth, AY029678; *S. palmifolia* (J. König) Stapf, AY029680; *S. viridis* (L.) Beauv., U21976; *Steinchisma decipiens* (Nees ex Trin.) W.V. Br., AY188499; *S. hians* (Elliot) Nash, AY029685; *S. laxa* (Sw.) Zuloaga, AY029655; *S. spathellosa* (Döll) Renvoize, AY188500; *Stenotaphrum secundatum* (Walter) Kuntze, AY029684; *Streptostachys asperifolia* Desv., AY029687; *S. ramosa* Zuloaga & Soderstr., AY029686; *Tatianyx arnacites* (Trin.) Zuloaga & Soderstr., AY029688; *Urochloa acuminata* (Renvoize) Morrone & Zuloaga, AY029629; *U. plantaginea* (Link) R.D. Webster, AY029693.
Panicum*. Section *Dichotomiflora (Hitchc.) Honda. *Panicum aquaticum* Poir., AY029658; *P. dichotomiflorum* Michx., AY188466; *P. elephantipes* Nees ex Trin., AY029647; *P. gouinii* E. Fourn., AY188467; *P. pedersenii* Zuloaga, AY029646; *P. repens* L., AY029651. **Section *Panicum***. *P. bergii* Arechav., AY188457; *P. fauriei* Hitchc., AY029650; *P. miliaceum* L., AY188472; *P. neph-*

Appendix 1. Continued.

elophilum Gaudich., AY029645; *P. stramineum* Hitchc. & Chase, AY188489. **Section *Rudgeana*** (Hitchc.) Zuloaga. *P. cervicatum* Chase, AY188459; *P. rudgei* Roem. & Schult., AY029661. **Section *Urvilleana*** (Hitchc.) Pilg. *P. chloroleucum* Griseb., AY188460; *P. racemosum* (P. Beauv.) Spreng., AY188481. **Section *Virgata*** Hitchc. & Chase ex Pilg. *P. tricholaenoides* Steud., AY188493; *P. virgatum* L., U21986. **Ungrouped.** *P. mistasypus* Zuloaga & Morrone, AY188474; *P. olyroides* Kunth, AY188475.
Panicum* "incertae sedis"**. **Section *Agrostoidea Hitchc. & Chase ex C.C. Hsu. *Panicum anceps* Michx., AY188455; *P. rigidulum* Bosc ex Nees, AY188482. **Section *Bulbosa*** Zuloaga. *P. bulbosum* Kunth, AY029648. **Section *Clavelligera*** Stapf. *P. adenophorum* K. Schum., AY188454; *P. claytonii* Renvoize, AY188462. **Section *Cordovensia*** Parodi. *P. cordovense* E. Fourn., AY188463; *P. missionum* Ekman, AY188473; *P. ovuliferum* Trin., AY029653; *P. penicillatum* Nees ex Trin., AY188477. **Section *Lorea*** Zuloaga. *P. euprepes* Renvoize, AY029657; *P. subtiramulosum* Renvoize & Zuloaga, AY188490. **Section *Megista*** Pilg. *P. mertensii* Roth, AY188471. **Section *Monticola*** Stapf. *P. millegrana* Poir., AY029660; *P. sellowii* Nees, AY188484. **Section *Parvifolia*** Hitchc. & Chase ex Pilg. *P. cyanescens* Nees ex Trin., AY188465; *P. parvifolium* Lam., AY188476; *P. schwackeanum* Mez, AY188483; *P. trichanthum* Nees, AY188492; *P. wettsteinii* Hack., AY188497. **Section *Prionitia*** Zuloaga. *P. petersonii* Hitchc. & Ekman, AY188479; *P. prionitis* Nees, AY029652. **Section *Stolonifera*** Hitchc. & Chase ex Pilg. *P. chapadense* Swallen, AY188486; *P. piauiense* Swallen, AY029656; *P. stoloniferum* Poir., AY188488. **Section *Tenera*** Hitchc. & Chase ex Pilg. *P. caricoides* Nees ex Trin., AY188458; *P. stenodes* Griseb., AY188487; *P. tenerum* Beyr. ex Trin., AY188491. **Section *Tuerckheimiana*** (Hitchc.) Zuloaga. *P. tuerckheimii* Hack., AY188494. **Section *Valida*** Zuloaga & Morrone. *P. validum* Mez, AY188495. **Section *Verrucosa*** Hitchc. & Chase ex C.C. Hsu. *P. verrucosum* Muhl., AY188496. **Ungrouped.** *P. antidotale* Retz., AY188456; *P. hylaeicum* Mez, AY188470; *P. pilosum* Sw., AY188480.
Tribe Thysanolaenae. *Thysanolaena maxima* (Roxb.) Kuntze, U21984.

Appendix 2. List of taxa used in the *rpoC2* analysis and GenBank accession numbers.

Tribe Andropogoneae. *Chionachne koenigii* (Spreng.) Thwaites, AY174475; *Coix lacryma jobi* L., AY174476; *Cymbopogon citratus* Stapf, AY174477; *Hyparrehenia hirta* (L.) Stapf, U96320; *Sorghum halepense* (L.) Pers. AY174498; *Saccharum officinarum* L., U96321.
Tribe Arundinelleae. *Arundinella hirta* (Thunb.) Tanaka, AY174474; *Danthoniopsis dinteri* (Pilg.) C.E. Hubb., AF372167; *Tristachya leucothrix* Trin. ex Nees, AY174500.
Tribe Centotheceae. *Chasmanthium latifolium* (Michx.) H.O. Yates, U94334.
Tribe Eriachneae. *Eriachne mucronata* R. Br., AY174478; *Pheidochloa gracilis* Blake, AY174494.
Tribe Isachneae. *Isachne distichophylla* G.C. Munro ex Hillebr., AY174483.
Tribe Paniceae (excluding *Panicum*). *Altoparadisium chapadense* Filg. & al., AF372160; *Anthaenanthia lanata* (Kunth) Benth., AF372178; *Anthaenantiopsis rojasiana* Parodi, AY174472; *Arthropogon villosus* Nees, AY174473; *Axonopus fissifolius* (Raddi) Kuhlm., AY254806; *Brachiaria serrata* (Thunb.) Stapf, AF000019; *Canastra lanceolata* (Filg.) Morrone & al., AF372167; *Cenchrus agrimonoides* Trin., AF372165; *C. ciliaris* L., AF372164; *C. echinatus* L., AF372163; *Chaetium bromoides* (J. Presl) Benth. ex Hemsl., AF372166; *Cyphonanthus discrepans* Morrone & Zuloaga, DQ646391; *Dichantelium koolauense* (H. St. John & Hosaka) C.A. Clark & Gould, AF372169; *Digitaria ciliaris* (Retz.) Koeler, AF372170; *D. insularis* (L.) Fedde, AF372173; *D. radicosa* (J. Presl) Miq., AF372168; *D. setigera* Roth ex Roem. & Schult., AF372171; *D. violascens* Link, AF372172; *Echinochloa colona* (L.) Link, AF372175; *E. crusgalli* (L.) P. Beauv., AF372174; *Echinolaena inflexa* (Poir.) Chase, A372176; *Eriochloa punctata* (L.) Desv., AF372177; *Homolepis glutinosa* (Sw.) Zuloaga & Soderstr., AY174479; *H. isocalycia* (G. Meyer) Chase, AY174480; *Hymenachne donacifolia* (Raddi) Chase, AY174481; *Ichnanthus pallens* (Sw.) Munro ex Benth., AY174482; *Lasiacis sorghoidea* (Desv.) Hitchc. & Chase, AY174484; *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs, AF000021; *Melinis minutiflora* P. Beauv., AF372179; *Melinis repens* (Willd.) Zizka, AF000020; *Mesosetum chaseae* Luces, AF372178; *Ophiochloa hydrolithica* Filg. & al., AF372181; *Oplismenus hirtellus* (L.) P. Beauv., AY174485; *Otachyrium versicolor* (Döll) Henrard, AF372182; *Paspalidium geminatum* (Forssk.) Stapf, AF372190; *Paspalum conjugatum* Bergius, AY174491; *P. conspersum* Schrad. ex Schult., AY174492; *P. fimbriatum* Kunth, AF372187; *P. foliiforme* S. Denham, AF372211; *Paspalum glaziovii* (A.G. Burm.) S. Denham, AF372210; *P. malacophyllum* Trin., AY174493; *P. quadrifarium* Lam., AF372197; *P. scrobiculatum* L., AF372186; *Pennisetum clandestinum* Hochst., AF372201; *P. purpureum* Schumach., AF372200; *P. setaceum* (Forssk.) Chiov., AF372198; *P. sp.*, L25383; *Plagiantha tenella* Renvoize, AF372183; *Pseudechinolaena polystachya* (Kunth) Stapf, AF372202; *Sacciolepis indica* (L.) Chase, AF372207; *Setaria gracilis* Kunth, AF372204; *S. macrostachya* Kunth, AY174495; *S. palmifolia* (J. König) Stapf, AF372208; *S. parviflora* (Poir.) Kerguelen, AY174496; *S. sphacelata* (Schumach.) AY174497; *Steinchisma hians* (Elliot) Nash, AF372205; *S. laxa* (Sw.) Zuloaga, AF372184; *Stenotaphrum secundatum* (Walter) Kuntze, AF372203; *Streptostachys asperifolia* Desv., AY174499; *S. ramosa* Zuloaga & Soderstr., AF372206; *Tatianyx arnacites* (Trin.) Zuloaga & Soderstr., AF372209; *Urochloa acuminata* (Renvoize) Morrone & Zuloaga, AF372212; *U. mutica* (Forssk.) T.Q. Nguyen, AF372162; *U. plantaginea* (Link) R.D. Webster, AY174501; *U. reptans* (L.) Stapf, AF372213.
Panicum*. Section *Dichotomiflora (Hitchc.) Honda. *Panicum aquaticum* Poir., AY174486; *P. elephantipes* Nees ex Trin., AF372193; *P. pedersenii* Zuloaga, AF372194; *P. repens* L., AF372185. **Section *Panicum***. *P. fauriei* Hitchc., AF372188; *P. miliaceum* L., AY174488; *P. nephelophilum* Gaudich., AF372189; *P. tenuifolium* Hook. & Arn., AF372199. **Section *Rudgeana*** (Hitchc.) Zuloaga. *P. rudgei* Roem. & Schult., AY174489. **Ungrouped.** *P. mistasypus* Zuloaga & Morrone, AF372192.
Panicum* "incertae sedis". Section *Cordovensia Parodi. *P. ovuliferum* Trin., AF372195. **Section *Lorea*** Zuloaga. *P. euprepes* Renvoize, AY174487. **Section *Monticola*** Stapf. *P. millegrana* Poir., AF372191. **Section *Prionitia*** Zuloaga. *P. prionitis* Nees, AF372196. **Section *Stolonifera*** Hitchc. & Chase ex Pilg. *P. stoloniferum* Poir., AY174490.

Appendix 3. Additional specimens examined: COUNTRY. STATE: Location, Collector (Herbarium Acronym).

BELIZE. 17 miles NW of Monkey River Town, *Russell 1175* (US). BOLIVIA. SANTA CRUZ: Prov. Velasco, Serranía de Huanchaca, Farallón Suroeste, Estación Los Fierros, Parque Nacional Noell Kempf M., 200–300 m, *Foster & al. 13881* (F); *Mostacedo & al. 1041* (MO); a 150 km de Florida a Bella Vista por el camino que pasa por el aserradero Choré, 210 m, *Guillén & al. 2585* (MO, SI). BRAZIL. AMAPÁ: Rio Oiapoque, entre Clevelendia e Cachoeira do Carrata, *Froes 25763* (IAN); Curiau, proximo de Macapá, *Pires & Silva 4806* (IAN). AMAZONAS: Mun. Humaitá, Rio Madeira, banks of Rio Ipixuna, *Prance & al. 3345* (MO, R, US); Rio Sanariapo, *Williams 13052* (F, US). BAHIA: Mun. São Desidérico, estrada de terra entre Roda Velha e Estiva ca. de 67 km de Roda Velha, *Oliveira & al. 882* (IBGE, SI). ESPÍRITO SANTO: without locality, *St. Hilaire 55* (P, US), *377* (P). GOIÁS: Mun. Jatay, Queixada, *Macedo 1487* (MO); Mun. Alto Paraíso, Parque Nacional de Chapada dos Veadeiros, local entre o Mulungú e Peito de Moça, entrada a 14 km de Alto Paraíso, *Fonseca & al. 1346* (IBGE, SI). MARANHÃO: Carolina to San Antonio de Balsas, wet places, opening in woods, *Swallen 4113* (R, RB, SP, US); Rio Alto Turiacu, entre Araguanã e Nova Esperança, *Jangoux & Bahia 1* (MO, NY, RB). MATO GROSSO: Road 30, 3 km W of Base Camp, *Harley & Souza 10205* (IAN, MO, RB, UB, US); 210 km along new road NNE of village of Xavantina, at Corrego do Gato, *Eiten & Eiten 9102* (MO, SP, US); 2 km W of Base Camp, 12°49′ S, 51°46′ W, *Harley & al. 10743* (IAN, MO, P, RB, UB, US); Sumidouro, Rio Arinas, *Kuhlman 73* (IAN, R), *Falcao 5101* (RB); Correga do Gato, ca. 51 km along road 5 of Base Camp, Base Camp, *Harley & al. 10444* (K, P, RB, UB, US); Mun. de Barra do Garças, 260 km along new road NNE of village of Xavantina, *Eiten & Eiten 8906* (NY, US). MATO GROSSO DO SUL: Mun. Corumbá, Fazenda Santa Ana, *Allem 1166, 1179* (CEN, MO); Corumbá, Fazenda Santo Estevão, *Allem 1206* (CEN, MO); Mun. Corumbá, Fazenda Campo Eunice, *Comastri Filho 75* (SI). MINAS GERAIS: Mun. Formoso, Parque Nacional Grande Sertão Veredas, vereda próximo ao Rio Preto, *Filgueiras 1925* (SI); Parque Nacional Grande Sertão Veredas, *Mendoça & al. 3611* (MO). PARÁ: Lago Cucaru, *Froes 31687* (R); Santarem, edge of swamp, *Swallen 3302* (RB, SP, US); Alto Cuminá, Cachoeira Grande, *Sampaio 5469* (IAN, R, US); Vigia, Campina do Palha, *Black 50-8785* (IAN, SI, US); Rio Capim, *Froes & Pires 24088* (IAN); Lago Preto de Jurutu, *Oliveira 37* (IAN); Lago Cuçarú, Planalto de Santarém, *Froes 31687* (IAN, P, R); Ilha de Colares, sítio Horizonte, *Black 54-16906* (IAN, US). CUBA. ISLA DE PINOS: Santa Barbara, *Ekman 11977* (G). PINAR DEL RÍO: Sábalo, *Ekman 11439* (NY, US); Remates, Laguna Larga de Limones, *Ekman 11217* (G, NY, US); Remates, Laguna Los Indios, *Ekman 11349* (NY, US); La Máquina, *León 17766* (US); Herradura, *Ekman 11582* (G, NY), in pineland, *Ekman 14089* (US). FRENCH GUIANA. Route de Laurent, Savane Chaumiere, *Hoock s.n*. (NY); route de Sinnamary, Passoura, *Hoock 108* (P); Route de Sinnamary, Savane Maroni, *Hoock 312* (US); Passoura, *Hoock 311* (US). GUIANA. Rupununi, *Chan Choong 25* (US), *Black 54-16096*, *50- 8785* (US), Rupununi Savanna, *Melville 104* (US); Rupununi Distr., Lethem, Manari Creek, 6 miles north of Lethem, *Irwin 807* (US); Rupununi Distr., Dadanawa, Tawarawun Mountain, *Jansen-Jacobs & al. 3995* (US). VENEZUELA. AMAZONAS: Dept. Atabapo, 1 km up of Caño Caname, *Davidse & al. 16861* (MO, MY, VEN); Dpto. Atures, alrededores de Pto. Ayacucho, sabana y laja ubicada a 4 km al S, a mano derecha de la carretera hacia Samariapo, en sitio llamado “Los Lirios”, *Huber 803* (VEN); Depto. Atures, 23 km NE of Puerto Ayacucho and 10 km E of the highway area of Rincones de Chacorro, *Davidse & al. 16745* (MO, NY, US); Caño Piojo, *Morillo 7455* (MY, VEN); cerca del rio Sanariapo, *Williams 13052* (US, VEN). APURE: Distr. Pedro Camejo, 4 km directly NE of El Betún along the banks of the río Capanaparo, *Davidse & González 13051* (NY, VEN); Alto Apure, *González s.n.* (VEN 117023). GUÁRICO: without locality, *Ortíz & Ramia 4920* (SI, VEN). MONAGAS: sabanas alrededor de Jusepín, *Blydenstein 441* (VEN); en sabanas de depresión al sur, *Ramia 2466* (VEN); Campo Experimental de la Escuela de Agronomía, U.D.O. Jusepín, *Virrueta s.n*. (VEN).