Taxonomic re-evaluation of *Panicum* sections *Tuerckheimiana* and *Valida* (Poaceae: Panicoideae) using morphological and molecular data

Mabel A. Lizarazu, Marcela V. Nicola & Diego L. Salariato

Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, B1642HYD, San Isidro, Buenos Aires, Argentina
Author for correspondence: *Mabel A. Lizarazu, mlizarazu@darwin.edu.ar*

DOI http://dx.doi.org/10.12705/632.34

Abstract The taxonomic status of *Panicum* sect. *Tuerckheimiana* and sect. *Valida* has remained as "incertae sedis" within *Panicum*. To resolve the systematic position of both sections within Paniceae s.l., morphological studies and phylogenetic analyses based on chloroplast sequence data (*ndhF*) were conducted. Our study shows that both sections are included in the subtribe Paspalinae of tribe Paspaleae, where they are related with the genus *Anthaenantiopsis*. These results support the recent transfer of these species to the recently described genera *Aakia* and *Osvaldoa*; they are restricted to forests of Mesoamerica and lowlands of southern South America respectively. These genera are described and compared with other allied genera of subtribe Paspalinae.

Keywords *Aakia*; *Anthaenantiopsis*; *ndhF* phylogeny; *Osvaldoa*; Paniceae; *Panicum*; Paspaleae; Paspalinae; *Tuerckheimiana*; *Valida*

Supplementary Material The alignment is available at TreeBASE, http://www.treebase.org/, study accession no. S14182.

INTRODUCTION

Panicum L. has traditionally been considered as one of the largest genera of Poaceae with nearly 450 species worldwide distributed mainly in tropical and subtropical regions (Webster, 1988). The taxonomy of the genus has always been controversial, mainly due to the great amount of variability of morphological, anatomical, and physiological characters (Ellis, 1988; Crins, 1991). During the 19th century, the traditional broad concept of *Panicum* and related genera was challenged by Chase (1906, 1908a, b, 1911) for the New World species, and Stapf (1920) for Old World species (especially Africa); they pointed out the need of excluding outlying species from the genus. Hitchcock & Chase (1910) recognized two subgenera and 13 informal groups for *Panicum* species of North America. Pilger (1931, 1940), Hsu (1965), and Brown (1977), using morphological, anatomical, and physiological characters, divided *Panicum* in different groups, sections, and subgenera. Later, Zuloaga (1987) proposed a classification for the New World species of *Panicum*, based on exomorphological, anatomical, and karyological characters, in which he recognized 6 subgenera and 25 sections.

Several phylogenetic studies of Panicoideae based on chloroplast (*ndhF*, *trnL-F*, *rpoC$_2$*) and ribosomal nuclear (ETS) sequence data, as well as morphology corroborated the polyphyly of *Panicum* (Gómez-Martínez & Culham, 2000; Zuloaga & al., 2000; Duvall & al., 2001, 2003; Giussani & al., 2001; Aliscioni & al., 2003). Aliscioni & al. (2003), in a phylogenetic analysis based on *ndhF* gene sequences, restricted *Panicum* to those taxa usually placed in *Panicum* subg. *Panicum*, and characterized it by including caespitose plants, with ciliate or membranaceous-ciliate ligules, spikelets arranged in open and lax inflorescences, with the upper glume and lower lemma (5–)7–13-nerved, the upper anthecium indurated, and the palea with simple or compound papillae toward the apex. Species of *Panicum* s.str. are C_4, of the NAD-me subtype, and have a basic chromosome number of $x = 9$. Consequently, Aliscioni & al. (2003) transfered species to other panicoid genera (such as *Dichanthelium* (Hitchc. & Chase) Gould, *Hymenachne* P.Beauv., and *Steinchisma* Raf.), and recognised *Phanopyrum* (Raf.) Nash as an independent genus. Aliscioni & al. (2003) also suggested that all "incertae sedis" species of *Panicum* should be segregated from the genus and transfered to new taxa or to extant genera. As a result, many species were transferred recently to other panicoid genera, i.e., *Apochloa* Zuloaga & Morrone (Sede & al., 2008), *Canastra* Morrone & al. (Zuloaga & al., 2006), *Cyphonanthus* Zuloaga & Morrone (Morrone & al., 2007), *Hopia* Zuloaga & Morrone (Zuloaga & al., 2007), *Ocellochloa* Zuloaga & Morrone (Sede & al., 2009), *Parodiophyllochloa* Zuloaga & Morrone (Morrone & al., 2008), *Renvoizea* Zuloaga & Morrone (Sede & al., 2008), and *Stephostachys* Zuloaga & Morrone (Zuloaga & al., 2010).

Among the "incertae sedis" taxa that were still remaining in *Panicum,* there are two monospecific Kranz sections: sect. *Tuerckheimiana* (Hitchc.) Zuloaga, with *P. tuerckheimii* Hack., a species restricted to humid forests of southern Mexico, Belize, Guatemala, and Nicaragua; and sect. *Valida* Zuloaga & Morrone with *P. validum* Mez, a species growing in borders of rivers and streams in southern Brazil, Uruguay, and

Received: 2 May 2013 | returned for revision: 12 Nov 2013 | revision received: 7 Jan 2014 | accepted: 23 Jan 2014 | published online ahead of inclusion in print and online issues: 3 Apr 2014 ||

Argentina. Recently, Grande Allende (2014) proposed the establishment of the new genera *Aakia* J.R.Grande and *Osvaldoa* J.R.Grande for *P. tuerckheimii* and *P. validum*, respectively. The paper by Grande Allende is solely based on previously published literature and does not contain any new analyses. In consequence, the aim of this study is to evaluate the taxonomic position of sect. *Tuerckheimiana* and sect. *Valida* using a morphological analysis of the taxa and a chloroplast (*ndhF*) DNA phylogeny of Paniceae s.l.

MATERIALS AND METHODS

Morphological data. — Morphological characters were recorded from herbarium specimens from ANSM, BAA, BAB, CHAPA, CTES, F, G, LIL, MEXU, MO, NY, R, SI, SP, and US. Upper anthecia were examined with a JEOL.J.S.M. 25SII Scanning Electron Microscope (SEM) at the Facultad de Odontología of the Universidad de Buenos Aires, Argentina.

Molecular data and phylogenetic analyses. — The *ndhF* gene was amplified and sequenced for two specimens of *Panicum validum*, one specimem of *Panicum tuerckheimii*, and one specimen of *Anthaenantiopsis fiebrigii* Mez (for voucher information and GenBank accession numbers, see Appendix 1).

For this purpose total DNA was isolated from herbarium material using a DNeasy plant mini kit (Qiagen, Hilden, Germany). The *ndhF* gene was amplified in four fragments using primer pairs 5F/536R, 536F/972R, 972F/1666R, and 1666F/3R (Olmstead & Sweere, 1994). Polymerase chain reactions (PCRs) were performed in 25 or 50 µL containing 20–40 ng/µL of DNA template, and a final concentration of 1× PCR buffer without Mg, 5 mM $MgCl_2$, 0.025 mM of each dNTP, 0.2 mM of each primer, and 1.25–3 U *Taq* polymerase (Invitrogen, Buenos Aires, Argentina). The PCR amplifications were set at 1 cycle of 96°C for 4 min; 39 cycles of 94°C for 1 min 30 s, 55°C for 1 min, and 72°C for 1 min 30 s; and a final extension cycle of 73°C for 7 min. Macrogen (Seoul, Korea) performed cleaning of PCR products using Montage PCR purification kits from Millipore (Billerica, Massachusetts, U.S.A.) following manufacturer's protocol. Sequencing reactions were also performed by Macrogen using a MJ Research (Watertown, Massachusetts, U.S.A.) PTC-225 Peltier thermal cycler and ABI PRISM BigDyeTM terminator cycle sequencing kits with AmpliTaq DNA polymerase (Applied Biosystems, Foster City, California, U.S.A.), following protocols supplied by the manufacturer. Sequences were assembled and edited using the program Chromas Pro v.1.41 (Technelysium Pty, Brisbane, Queensland, Australia).

The *ndhF* sequences for *P. tuerckheimii* and *P. validum* obtained by Aliscioni & al. (2003; AY188494 and AY188495, respectively) were also included in the phylogenetic analyses. The *nhdF* dataset was deposited in TreeBase (http://www.treebase.org/; study accession number, S14182).

Phylogenetic analyses were conducted using a *ndhF* matrix of 247 taxa extracted from Morrone & al. (2012). This matrix was especially suitable since it presents an extensive sampling of Paniceae s.l. (Paspaleae J.Presl + Paniceae s.str.; GenBank numbers are given in Appendix 1). Sequence alignments were generated with Muscle v.3.6 (Edgar, 2004) using the default settings. Alignment was improved by visual refinement using the program BioEdit v.7.0.9.0 (Hall, 1999) preserving the reading frame.

The *ndhF* dataset was analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) approaches. In the analyses, gaps were treated as missing data. For MP analyses, tree searches were generated with the program TNT v.1.1 (Goloboff & al., 2008) using heuristic searches with 1000 random addition sequences, tree bisection-reconnection branch swapping (TBR), and holding 10 trees per replicate; generated trees were then submitted to a new round of TBR branch swapping to completion. Support values for nodes were estimated using Jackknife (JK) analysis (Farris & al., 1996) with 2000 replicates of 10 random-addition sequences, holding four trees per replicate and using the default removal probability (0.36). Maximum likelihood analyses were conducted using RAxML v.7.2.6 (Stamatakis, 2006). The model of nucleotide substitution TVM+I+G was selected with the Akaike information criterion (AIC) implemented in Modeltest v.3.7 (Posada & Crandall, 1998). The algorithm implemented in RAxML was used for carrying out nonparametric bootstrap (BS) analyses (Felsenstein, 1985) and searches for the best-scoring ML tree in one single run (Stamatakis & al., 2008). We executed 1000 rapid bootstrap inferences and thereafter a thorough ML search under the GTRGAMMAI model. Bayesian analyses were conducted in BEAST v.1.7.2 (Drummond & al., 2012), with settings as follows: GTR+I+G substitution model, empirical base frequencies, four gamma categories, uncorrelated rate variation with lognormal distribution, random starting tree, a Yule process as tree prior, auto-optimization option for operator, and default values for all other settings. Two runs of 8×10^6 generations, sampling every 1000th generation, and discarding the first 25% of the samples as burn-in (2000 samples) were used. Additionally, the hypothesis of inclusion of *P. tuerckheimii* and *P. validum* in subtribe Panicinae with the remaining species of *Panicum* s.str. was tested using the Bayes factor (BF; Brown & Lemmon, 2007). The BF approach was based on smoothed estimates of marginal likelihood estimated with Tracer v.1.5 (Rambaut & Drummond, 2007). A difference of lnBF (unconstrained/constrained) >20, taking into account the standard error, was used to indicate support on the unconstrained topology over the constrained topology (*P. tuerckheimii* and *P. validum* included into Panicinae).

RESULTS

Morphological data. — *Panicum tuerckheimii* is a caespitose perennial herb with culms erect to ascendant; ligules membranaceous, brown; with collar purplish, shortly pilose to glabrous; blades lanceolate, flat, herbaceous, narrowed and incurved at the base; inflorescences composed of a lax and diffuse panicle with branches divergent from the main axis; spikelets lanceolate, sparsely pilose on the upper glume and lower lemma with appressed hairs; lower glume reduced, nerveless;

upper glume 5-nerved; lower lemma glumiform, 5-nerved; lower palea and lower flower absent; upper anthecium oblongoid, pale, shiny, with simple papillae distributed all over the lemma and palea, and with long unicellular macrohairs toward the apex (Fig. 1A).

Plants of *Panicum validum* are caespitose, shortly rhizomatous perennials herbs with culms erect, hard, solid or with a small lumen, many-noded, and elliptic in transverse section; ligules membranaceous; blades linear-lanceolate, the lower leaf blades keeled, hard, with a manifest midnerve, the upper leaf blades flat and herbaceous; inflorescence composed of an oblong and contracted panicle; spikelets long-ellipsoid, glabrous, and with the nerves conspicuous and anastomosing toward the apex; lower glume ovate-lanceolate (1–)3-nerved; upper glume and lower lemma 5(–7)-nerved; lower palea present, elliptic, membranaceous; pistillode occasionally present; upper anthecium ellipsoid, pale, shiny, more or less indurated, papillose all over its surface, with simple papillae regularly distributed, and apex of the lemma and palea with multicellular, fusiform microhairs (Fig. 1B).

Molecular data. — The *ndhF* alignment had a length of 2074 bp, of which 708 were phylogenetically informative (ca. 34%). Sequence alignment was trivial, with five informative indels from 6 to 24 bp long, as already obtained and described by Giussani & al. (2001) and Morrone & al. (2012). The MP analyses recovered more than 10,000 most parsimonious trees, and the ML and BI analyses recovered similar topologies showing the same strongly supported clades. All the phylogenetic analyses recovered *P. tuerckheimii* and *P. validum* in subtribe Paspalinae Griseb., included in a well-supported clade with the genera *Anthaenantiopsis* Mez ex Pilg., *Hopia* Zuloaga & Morrone, and *Paspalum* L. (JK = 99%, BS = 100%, PP = 100%; Fig. 2A–B). These two species of *Panicum* were recovered in a clade with *Anthaenantiopsis* (JK = 87%, BS = 83%, PP = 99%; Fig. 2B) in which *Panicum tuerckheimii* appeared sister to the latter genus (JK = 94%, BS = 99%, PP = 100%). However, species of *Panicum* s.str. appeared in a strongly supported clade with other members of subtribe Panicinae Fr. (JK = 88%, BS = 93%, PP = 100%; Fig. 2C). The Bayes Factor test strongly rejected the inclusion of *P. tuerckheimii* and *P. validum* in subtribe Panicinae (lnBF [inclusion unconstrained/inclusion constrained] = 227 ± 0.8).

■ DISCUSSION

The phylogenetic analyses conducted here strongly support the inclusion of *Panicum tuerckheimii* and *P. validum* in tribe Paspaleae. *Panicum validum* and *P. tuerckheimii* are the only remnant, non segregated species of *Panicum* subg. *Agrostoides* (sensu Zuloaga, 1987). Both species are C_4 of the MS anatomical subtype, i.e., they have a single Kranz mestome sheath around each vascular bundle (Zuloaga, 1987; Zuloaga & al., 1989). In grasses, this anatomical feature is correlated with the physiological NADP-me subtype or malate formers (Hattersley, 1987). This anatomical/physiological subtype is characteristic of most members of tribe Paspaleae, whereas in *Panicum* s.str. the characteristic anatomical/physiological subtype is the PS/NAD-me, with a mestome sheath and a Kranz parenchymatous sheath around each vascular bundle (Brown, 1977; Hattersley, 1987; Zuloaga 1987). Additionally, the basic chromosome number for *P. validum* was reported as $x = 10$ (Zuloaga & al., 1989), in agreement with the typical basic chromosome number of tribe Paspaleae. On the contrary, the typical basic chromosome number is $x = 9$ in the Paniceae s.str. (Morrone & al., 2012).

Within subtribe Paspalinae, *Paspalum* species differ from *P. tuerckheimii* and *P. validum* by having the former branches of the inflorescences unilateral (vs. branches of the inflorescences radiate in *P. tuerckheimii* and *P. validum*), rachis narrowly to broadly foliaceus or membranaceous (vs. rachis triquetrous), and lower glume usually absent (vs. lower glume present). *Hopia obtusa* is distinguished from *P. tuerckheimii* and *P. validum* mainly by being stoloniferous (vs. caespitose), by having biconvex spikelets (vs. spikelets plano-convex), lower glume 4/5–1 the length of the spikelet (vs. 1/5–1/3 in *P. tuerckheimii* and 3/4 in *P. validum*), upper glume 7–11-nerved (vs. 5(–7)-nerved), and with spikelets arranged in contracted inflorescences (vs. spikelets disposed in lax and open panicles); also, *H. obtusa* further differs from *P. tuerckheimii* by the presence of a lower palea and lower flower (vs. lower palea and lower flower absent in *P. tuerckheimii*), and from *P. validum* by its hollow internodes, rounded in transverse section and sheaths not keeled (vs. internodes solid or with a small lumen, elliptic in transverse section, and sheaths keeled in *P. validum*). Additionally, *Hopia* is restricted to southwestern U.S.A. and northern and central Mexico while *P. tuerckheimii* is present in southern

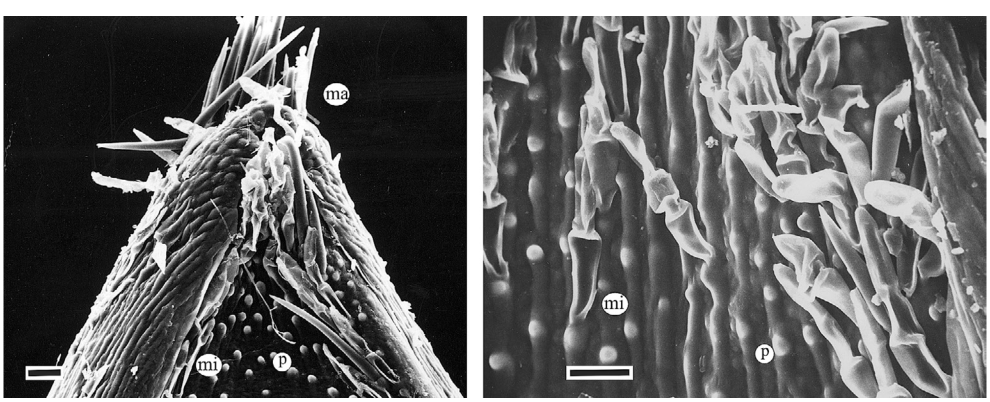

Fig. 1. SEM photographs of the upper anthecium. **A,** *Aaika tuerckheimii* (*Smart 41,* SI), apex of upper palea with papillae and macrohairs; **B,** *Osvaldoa valida* (*Smith & Klein 15722,* SI), apex of upper palea with papillae and microhairs. — ma, macrohairs; mi, microhairs; p, papillae. Scale bars, 10 µm.

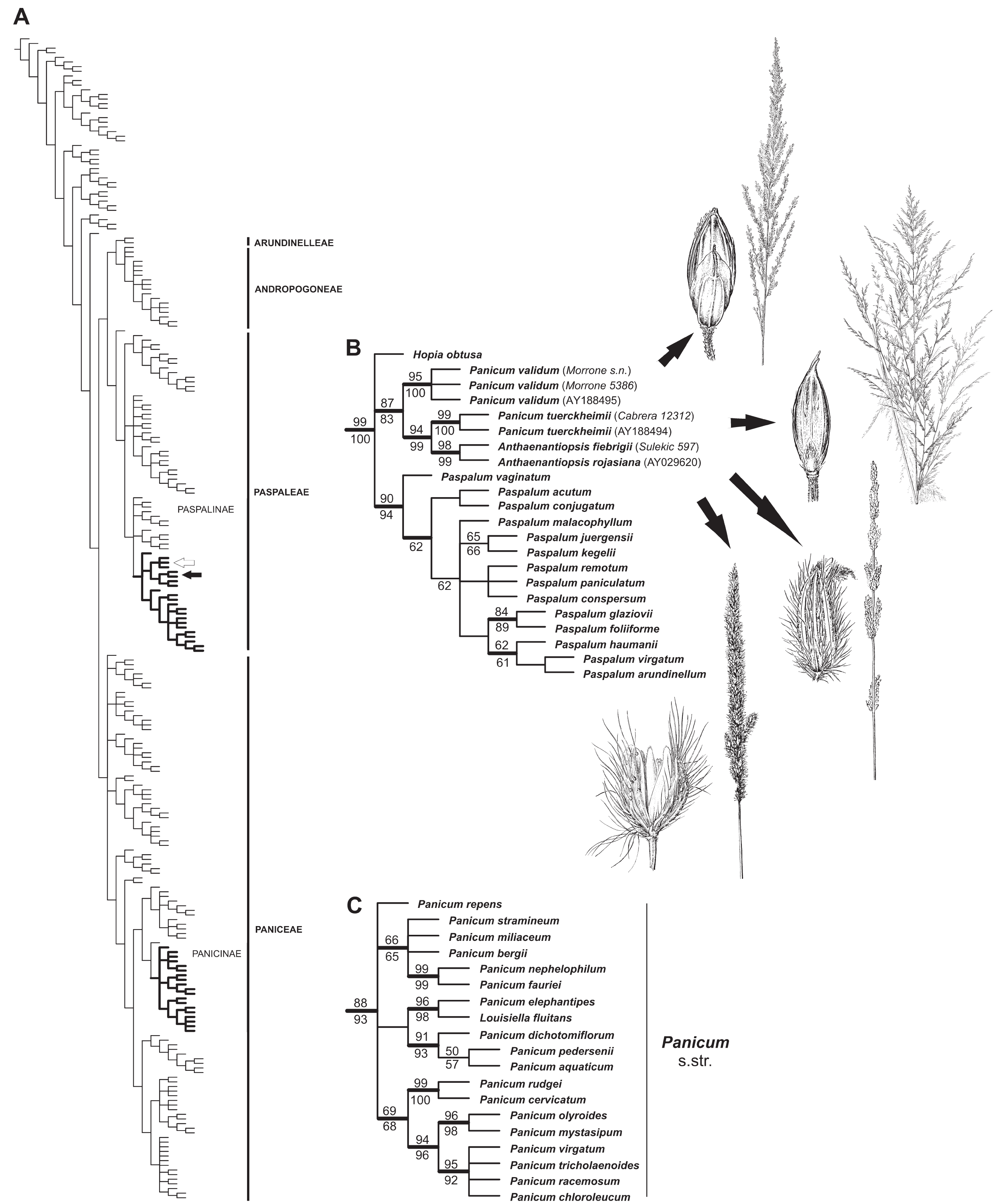

Fig. 2. Strict consensus tree of 10,000 most parsimonious trees obtained using the *ndhF* chloroplast gene. **A,** complete strict consensus tree, black and white arrows, respectively, indicate positions of *Panicum validum* and *P. tuerckheimii* within subtribe Paspalinae; branches in bold are shown in B and C; **B,** clade of subtribe Paspalinae including *Hopia*, *Paspalum*, *Anthaenantiopsis*, *P. validum* and *P. tuerckheimii*; inflorescence and spikelet are shown for the last three taxa; values above/below branches represent parsimony jackknife/maximum likelihood bootstrap values; thick branches indicate >0.95 Bayesian posterior probability; **C,** "*Panicum* s.str. clade", values above/below branches represent parsimony jackknife/maximum likelihood bootstrap values; thick branches indicate >0.95 Bayesian posterior probability.

Mexico, Guatemala, Belize, and Nicaragua; *P. validum* is distributed from southern Brazil to Argentina and Uruguay.

Anthaenantiopsis has four South American species which inhabit tropical and subtropical open areas. The genus is characterized by including caespitose, shortly rhizomatous perennials with erect culms, blades linear-lanceolate to filiform, inflorescences contracted, spiciform, spikelets ellipsoid, densely papillose-pilose, with the lower glume scale-like, 1–3-nerved or nerveless, upper glume and lower lemma subequal, 5–7(–9)-nerved, lower palea and lower flower present, and upper anthecium indurated, with bicellular microhairs and prickle hairs toward the apex of lemma and palea, the lemma with flat margins, not inclosing the apex of the palea (Morrone & al., 1993). *Panicum tuerckheimii* shares with *Anthaenantiopsis* species a reduced lower glume, and upper anthecium with simple papillae and long macrohairs toward the apex of lemma and palea. However, *P. tuerckheimii* differs from the latter genus by having lanceolate blades up to 70 × 3.3 cm, inflorescence lax and diffuse, spikelets lanceolate and sparsely pilose, upper glume and lower lemma 5-nerved, and lower palea and lower flower absent. Also, *P. tuerckheimii* is restricted to tropical forests of Mesoamerica while all species of *Anthaenantiopsis* grow in open savannas in South America. On the other hand, *P. validum* can be distinguished from *Anthaenantiopsis* species by its hard and solid (or with a small lumen) culms, sheaths and lower blades keeled, spikelets glabrous with the lower glume 3/4 the length of the spikelet, and upper anthecium with multicellular, fusiform microhairs.

While morphological and molecular evidence strongly support the exclusion of *P. validum* and *P. tuerckheimii* from *Panicum*, their inclusion in subtribe Paspalinae could be done principally in two ways: either within *Anthaenantiopsis* or in the new monospecific genera described by Grande Allende (2014; *Osvaldoa* and *Aakia*, respectively). The inclusion of these two species in *Anthaenantiopsis* would lead to expanding the diagnostic features of this genus. For example, *P. validum* has lower glume 3/4 as long as the spikelet (vs. lower glume scale-like in *Anthaenantiopsis*), and *P. tuerckheimii* has a lax and diffuse inflorescence (vs. the contracted inflorescence in *Anthaenantiopsis*). *Anthaenantiopsis* is strongly distinguished from other genera of Paniceae by several morphological characters (see above), and the inclusion of *P. validum* and *P. tuerckheimii* would blur the morphological circumscription of this genus. Therefore, based on the molecular phylogenies obtained and on anatomical/morphological characters, the expansion of the circumscription of *Anthaenantiopsis* to include these two species would result in a rather polythetic *Anthaenantiopsis*, with some of the previous diagnostic characters no longer being diagnostic. In conclusion we prefer to include them in the monospecific genera *Osvaldoa* and *Aakia*.

■ TAXONOMIC TREATMENT

Key to distinguish *Aakia* and *Osvaldoa* from related genera

1. Spikelets arranged in unilateral branches, lower glume absent, ocassionally present .... ***Paspalum***
1. Spikelets not arranged in unilateral branches, lower glume present 2
2. Lower glume reduced, scale-like; spikelets sparsely to densely pilose 3
2. Lower glume 3/4 to 4/5 as long as spikelet; spikelets glabrous 4
3. Inflorescence an open and lax panicle; spikelets without lower palea and flower; blades lanceolate, up to 3.3 cm wide. Mexico, Belize, Guatemala, and Nicaragua . ***Aakia***
3. Inflorescence a contracted panicle; spikelets with lower palea and flower (lower flower sometimes absent in *Osvaldoa*); blades filiform or linear-lanceolate, up to 1 cm wide. Argentina, Bolivia, Brazil, and Paraguay .... ***Anthaenantiopsis***
4. Inflorescence contracted; spikelets with upper glume and lower lemma 7–11-nerved; sheaths and blades not keeled; rhizomatous perennials, with short and strong rhizomes producing widely creeping stolons .... ***Hopia***
4. Inflorescence open; spikelets with upper glume and lower lemma 5(–7)-nerved; sheaths and blades keeled; cespitose, shortly rhizomatous perennials .... ***Osvaldoa***

Aakia J.R.Grande in Phytoneuron 22: 1. 2014 ≡ *Panicum* [unranked] *Tuerckheimiana* Hitchc. in Britton, N. Amer. Fl. 17(3): 201, 210. 1915 ≡ *Panicum* sect. *Tuerckheimiana* (Hitchc.) Zuloaga in Soderstrom & al. (ed.), Grass Syst. Evol.: 296. 1988 – Type: *Aakia tuerckheimii* (Hack.) J.R.Grande.

Caespitose perennial; culms erect to ascendent, geniculate; internodes compressed, hollow, glabrous; nodes dark, pilose. *Sheaths* shorter than internodes, herbaceous, keeled, pilose toward the ligular region, otherwise glabrous; *ligules* membranaceous, brown; collar purplish, shortly pilose to glabrous; *blades* lanceolate, flat, herbaceous, narrowed and incurved at base, apex acuminate, adaxial surface shortly pilose, more so toward the base, lower margins ciliate, midnerve manifest. *Inflorescence* a lax and diffuse panicle, with branches divergent from the main axis, spikelets paired and shortly pedicellate; main axis triquetrous, scabrous; pulvini densely pilose; branches triquetrous, scabrous. *Spikelets* lanceolate, greenish to brownish, dorsiventrally compressed, sparsely pilose with appressed hairs on upper glume and lower lemma, upper glume and lower lemma subequal, acuminate; *lower glume* reduced, ovate, pale brown, nerveless; *upper glume* 5-nerved, hyaline; *lower lemma* glumiform, 5-nerved; *lower palea* and *lower flower* absent; *upper anthecium* oblongoid, pale, shiny, with simple papillae distributed all over the lemma and palea, with long macrohairs toward the apex; lemma 5-nerved, palea 2-nerved. *Caryopsis* ovoid; hilum punctiform, embryo less than half as long as caryopsis.

Distribution and habitat. – Tropical rain forests of Mexico, Guatemala, Belize, and Nicaragua.

Aakia tuerckheimii (Hack.) J.R.Grande in Phytoneuron 22: 2. 2014 ≡ *Panicum tuerckheimii* Hack. in Allg. Bot. Z. Syst. 12: 60. 1906 – Holotype: GUATEMALA. Alta Verapaz, Cubilqüitz, 350 m, 1930, *H. von Tuerckheim II 820* (W!;

isotypes: GH!, NY!, US Nos. 973890!, 973891! & 81303!).

See Fig. 3 for an illustration of *A. tuerckheimii.*

Distribution and habitat. – Tropical rain forests of Mexico, Guatemala, Belize, and Nicaragua, where it is found between 200 and 800 m elevation (Fig. 5).

Phenology. – In flower and fruit between July and December.

Osvaldoa J.R.Grande in Phytoneuron 22: 5. 2014 ≡ *Panicum* sect. *Valida* Zuloaga & Morrone in Syst. Bot. 14: 228. 1989 – Type: *Osvaldoa valida* (Mez) J.R.Grande.

Caespitose, shortly rhizomatous perennials; culms erect, many-noded; internodes hard, solid or with a small lumen, elliptic in transverse section; nodes purplish, thickened, glabrous. *Sheaths* distichous, open, keeled, pale and glabrous, margins membranaceous; *ligules* membranaceous, arcuate; collar inconspicuous, glabrous; *blades* linear-lanceolate, shortly pilose toward the base on adaxial surface, otherwise glabrous, margins scabrous, base rounded, apex attenuate; lower leaf blades keeled, hard, with a manifest midnerve, upper leaf blades flat and herbaceous. *Inflorescence* an oblong and open panicle; main axis wavy, scabrous; pulvini short-pilose; branches alternate to subopposite, more or less appressed to main axis; axis of branches triquetrous, scabrous and pilose toward the base; spikelets densely disposed in pairs or solitary on both sides of the branches; pedicels short, scabrous to scarcely pilose, triquetrous. *Spikelets* long-ellipsoid, glabrous, brownish, with upper glume and lower lemma subequal, nerves conspicuous and anastomosing toward the apex;

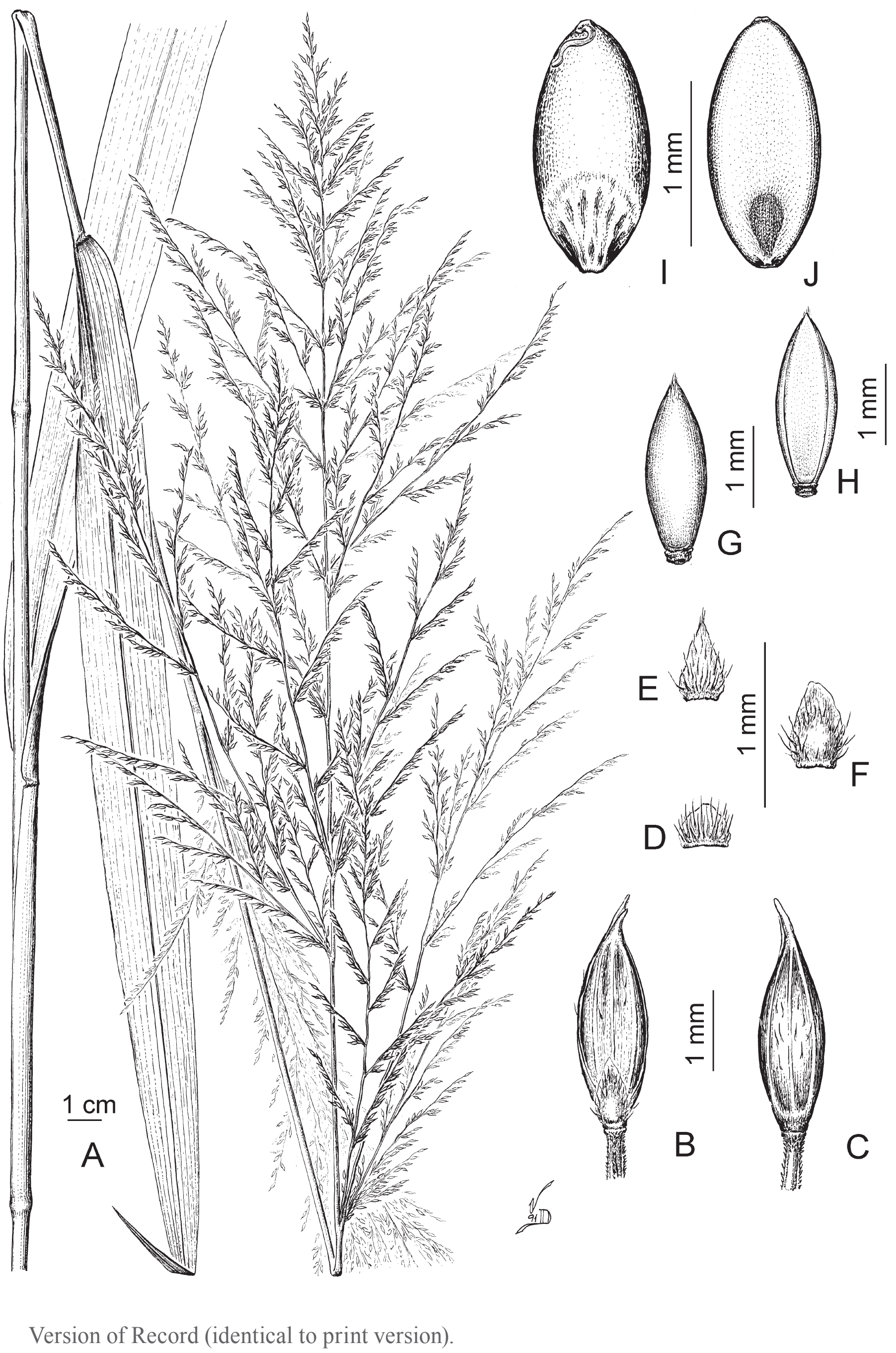

Fig. 3. *Aaika tuerckheimii* (Hack.) J.R.Grande (*H. von Tuerckheim II 1457*, SI). **A,** habit; **B,** spikelet, ventral view; **C,** spikelet, dorsal view; **D–F,** lower glume, dorsal view; **G,** upper anthecium, dorsal view; **H,** upper anthecium, ventral view; **I,** caryopsis, scutellar view; **J,** caryopsis, hilar view. — Drawn by Vladimiro Dudas.

lower glume ovate-lanceolate, (1–)3-nerved, acute, midnerve scabrous; *upper glume* 5(–7)-nerved; *lower lemma* glumiform, 5(–7)-nerved; *lower palea* elliptic, membranaceous, glabrous, brownish, pistillode occasionally present; *upper anthecium* ellipsoid, pale, shiny, more or less indurated, papillose all over its surface, with simple papillae regularly distributed, apex of lemma and palea with multicellular, fusiform microhairs; lemma 5-nerved; lodicules 2, conduplicate. *Caryopsis* obovoid; hilum oblong; embryo less than half as long as caryopsis.

Distribution and habitat. – Southern Brazil, western Uruguay, and eastern Argentina; borders of rivers and streams.

Osvaldoa valida (Mez) J.R.Grande in Phytoneuron 22: 5. 2014 ≡ *Panicum validum* Mez in Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921 – Lectotype (designated by Grande Allende in Phytoneuron 2014-22: 5. 2014): ARGENTINA. Entre Ríos; Concepción del Uruguay, Arroyo La China, Sep 1876, *P.G. Lorentz 840* (CORD!; isolectotypes: B! BAA-1988!, fragment ex B, BAF!, GOET006793!, US!; probable isolectotypes: G!, P!).

See Fig. 4 for illustration of *O. valida*.

Note. – It may seem strange that Grande Allende (2014) designated as lectotype the specimen *P.G. Lorentz 840* (CORD) as specimen used by Mez to describe *Panicum validum* would probably be the one housed at B. However, Mez did not cite any herbaria for the three gatherings that he cited in the protologue and all representatives of these gatherings are therefore syntypes (Art. 9.5 of the ICN, final sentence). The specimens

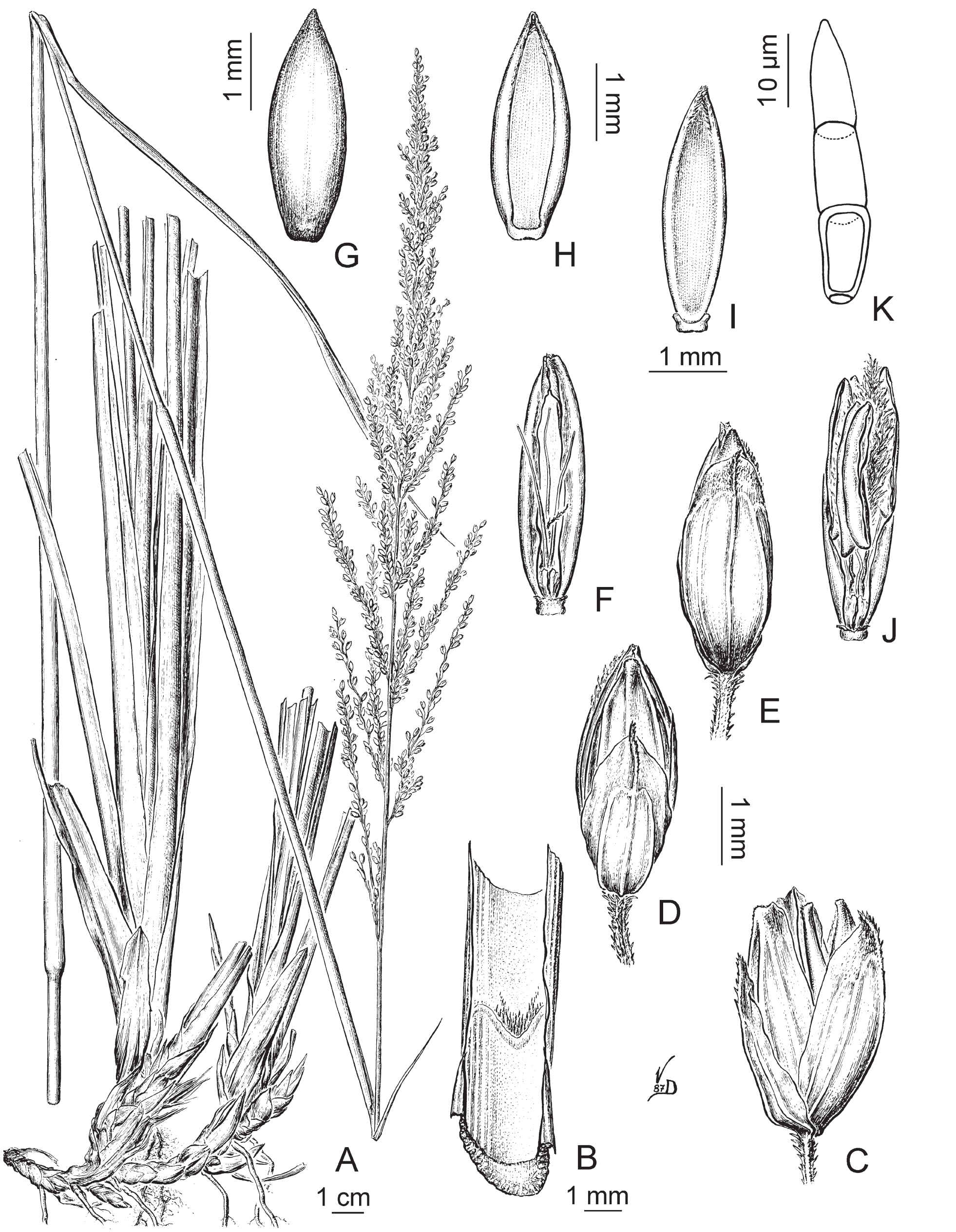

Fig. 4. *Osvaldoa valida* (Mez) J.R. Grande (*Zuloaga & Deginani 2493*, SI). **A,** habit; **B,** ligule, ventral view; **C,** spikelet, lateral view; **D,** spikelet, ventral view; **E,** spikelet, dorsal view; **F,** lower palea with lodicules; **G,** upper anthecium, dorsal view; **H,** upper anthecium, ventral view; **I,** upper palea; **J,** upper palea with lodicules, stamens, and stigmas; **K,** multicellular microhair. — Drawn by Vladimiro Dudas.

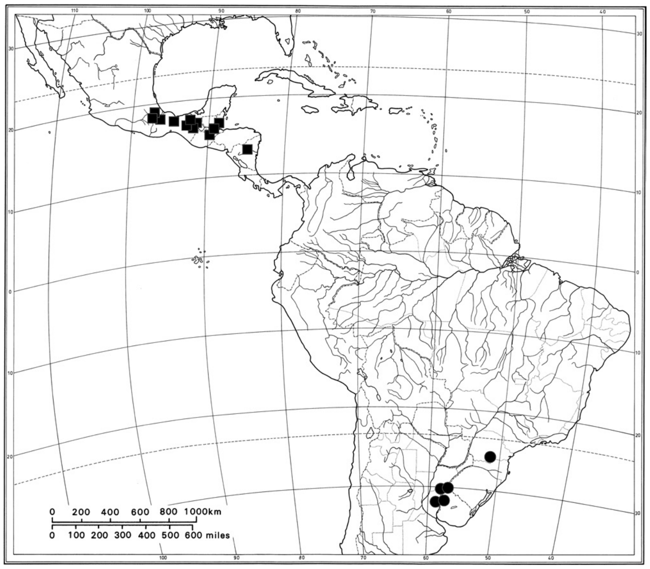

Fig. 5. Distribution of *Aaika tuerckheimii* (Hack.) J.R.Grande (squares) and *Osvaldoa valida* (Mez) J.R.Grande (circles).

in the herbaria other than CORD, included the one kept at B, are isolectotypes.

Distribution and habitat. – Restricted to borders of rivers and streams in southern Brazil, where it is found occasionally, western Uruguay, and eastern Argentina, near sea level (Fig. 5).

Phenology. – In flower and fruit between October and February.

Chromosome number. – 2*n* = 20 (Zuloaga & al., 1989).

For additional specimens examined of *Aaika tuerckheimii* and *Osvaldoa valida* see Appendix 2.

■ ACKNOWLEDGEMENTS

Funding of this research was provided by CONICET, grant 11220100100207. We like to express our deep gratitude to F.O. Zuloaga for his help, guidance, and valuable suggestions in this work. We also thank to A.A. Sulekic for the specimens of *Anthaenantiopsis*.

■ LITERATURE CITED

Aliscioni, S.S., Giussani, L.M., Zuloaga, F.O. & Kellogg, E.A. 2003. A molecular phylogeny of *Panicum* (Poaceae: Paniceae): Tests of monophyly and phylogenetic placement within the Panicoideae. *Amer. J. Bot.* 90: 796–821. http://dx.doi.org/10.3732/ajb.90.5.796

Brown, J.M. & Lemmon, A. 2007. The importance of data partitions and the utility of Bayes factors in Bayesian phylogenetics. *Syst. Biol.* 56: 643–655. http://dx.doi.org/10.1080/10635150701546249

Brown, W.V. 1977. The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Bot. Club* 23: 1–97.

Chase, A. 1906. Notes on genera of the Paniceae I. *Proc. Biol. Soc. Washington* 19: 183–192.

Chase, A. 1908a. Notes on genera of the Paniceae II. *Proc. Biol. Soc. Washington* 21: 1–10.

Chase, A. 1908b. Notes on genera of the Paniceae III. *Proc. Biol. Soc. Washington* 21: 175–188.

Chase, A. 1911. Notes on genera of the Paniceae IV. *Proc. Biol. Soc. Washington* 24: 103–160.

Crins, W. 1991. The genera of Paniceae (Gramineae: Panicoideae) in the southeastern United States. *J. Arnold Arbor., Suppl. Ser.* 1: 171–312.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molec. Biol. Evol.* 29: 1969–1973. http://dx.doi.org/10.1093/molbev/mss075

Duvall, M.R., Noll, J.D. & Minn, A.H. 2001. Phylogenetics of Paniceae (Poaceae). *Amer. J. Bot.* 88: 1988–1992. http://dx.doi.org/10.2307/3558426

Duvall, M.R., Saar, D.E., Grayburn, W.S. & Holbrook, G.P. 2003. Complex transitions between C_3 and C_4 photosynthesis during the evolution of Paniceae: A phylogenetic case study emphasizing the position of *Steinchisma hians* (Poaceae), a C_3–C_4 intermediate. *Int. J. Pl. Sci.* 164: 949–958. http://dx.doi.org/10.1086/378657

Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucl. Acids Res.* 32: 1792–1797. http://dx.doi.org/10.1093/nar/gkh340

Ellis, R.P. 1988. Leaf anatomy and systematics of *Panicum* (Poaceae: Panicoideae) in southern Africa. Pp. 129–156 in: Goldblatt, P. & Lowry, P.P. (eds.), *Modern systematic studies in African botany*. Monographs in Systematic Botany from the Missouri Botanical Garden 25. St. Louis: Missouri Botanical Garden.

Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 10: 315–319. http://dx.doi.org/10.1111/j.1096-0031.1994.tb00181.x

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791. http://dx.doi.org/10.2307/2408678

Giussani, L.M., Cota-Sánchez, J.H., Zuloaga, F.O. & Kellogg, E.A. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C_4 photosynthesis. *Amer. J. Bot.* 88: 1993–2012. http://dx.doi.org/10.2307/3558427

Goloboff, P., Farris, J. & Nixon, K. 2008. TNT: Tree analysis using new technology. Program and documentation, available at http://www.zmuc.dk/public/phylogeny/tnt

Gómez-Martínez, R. & Culham, A. 2000. Phylogeny of the subfamily Panicoideae with emphasis on the tribe Paniceae: Evidence from the *trnL-F* cpDNA region. Pp. 136–140 in: Jacobs, S.W.L. & Everett, J.E. (eds.), *Grasses: Systematics and evolution*. Collingwood: CSIRO.

Grande Allende, J.R. 2014. Novitates Agrostologicae, IV. Additional segregates from *Panicum* incertae sedis. *Phytoneuron* 22: 1–6.

Hall, T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids Symp. Ser.* 41: 95–98.

Hattersley, P.W. 1987. Variation in photosynthetic pathway. Pp. 49–64 in: Soderstrom, T.R., Hilu, K.W., Campbell, C.S. & Barkworth, M.E. (eds.), *Grass systematics and evolution*. Washington, D.C.: Smithsonian Institution Press.

Hitchcock, A.S. & Chase, A. 1910. The North American species of *Panicum*. *Contr. U.S. Natl. Herb.* 15: 1–136.

Hsu, C.C. 1965. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 9: 43–150.

Morrone, O., Filgueiras, T.S., Zuloaga, F.O. & Dubcovsky, J. 1993. A revision of *Anthaenantiopsis* (Poaceae: Panicoideae: Paniceae). *Syst. Bot.* 18: 434–453. http://dx.doi.org/10.2307/2419418

Morrone, O., Scataglini, M.A. & Zuloaga, F.O. 2007. *Cyphonanthus*, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae) based on morphological, anatomical and molecular data. *Taxon* 56: 521–532.

Morrone, O., Denham, S.S., Aliscioni, S.S. & Zuloaga, F.O. 2008. *Parodiophyllochloa*, a new genus segregated from *Panicum* (Paniceae, Poaceae) based on morphological and molecular data. *Syst. Bot.* 33: 66–76. http://dx.doi.org/10.1600/036364408783887393

Morrone, O., Aagesen, L., Scataglini, M.A., Salariato, D.L.,

Denham, S.S., Chemisquy, M.A., Sede, S.M., Giussani, L.M., Kellogg, E.A. & Zuloaga, F.O. 2012. Phylogeny of the Paniceae (Poaceae: Panicoideae): Integrating plastid DNA sequences and morphology into a new classification. *Cladistics* 28: 333–356. http://dx.doi.org/10.1111/j.1096-0031.2011.00384.x

Olmstead, R.G. & Sweere, J.A. 1994. Combining data in phylogenetic systematics: An empirical approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467–481. http://dx.doi.org/10.1093/sysbio/43.4.467

Pilger, R. 1931. Bemerkungen zu *Panicum* und verwandten Gattungen. *Notizbl. Bot. Gart. Berlin-Dahlem* 11: 240–245.

Pilger, R. 1940. Gramineae III: Unterfamilie Panicoideae. Pp. 208 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, ed. 2, vol. 14e. Leipzig: Engelmann.

Posada, D. & Crandall, K.A. 1998. Modeltest: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818. http://dx.doi.org/10.1093/bioinformatics/14.9.817

Rambaut, A. & Drummond, A.J. 2007. Tracer, version 1.4. http://beast.bio.ed.ac.uk/Tracer

Sede, S.M., Morrone, O., Giussani, L.M. & Zuloaga, F.O. 2008. Phylogenetic studies in the Paniceae (Poaceae): A realignment of section *Lorea* of *Panicum*. *Syst. Bot.* 33: 284–300. http://dx.doi.org/10.1600/036364408784571626

Sede, S.M., Zuloaga, F.O. & Morrone, O. 2009. Phylogenetic studies in the Paniceae (Poaceae-Panicoideae): *Ocellochloa*, a new genus from the New World. *Syst. Bot.* 34: 684–692. http://dx.doi.org/10.1600/036364409790139655

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. http://dx.doi.org/10.1093/bioinformatics/btl446

Stamatakis, A., Hoover, P. & Rougemont, J. 2008. A rapid bootstrap algorithm for the RAxML webservers. *Syst. Biol.* 57: 758–771. http://dx.doi.org/10.1080/10635150802429642

Stapf, O. 1920. *Panicum*. Pp. 638–738 in: Prain, D. (ed.), *Flora of tropical Africa*, vol. 9. London: Reeve & Co.

Webster, R.D. 1988. Genera of the North American Paniceae (Poaceae: Panicoideae). *Syst. Bot.* 13: 576–609. http://dx.doi.org/10.2307/2419204

Zuloaga, F.O. 1987. Systematics of New World species of *Panicum* (Poaceae: Paniceae). Pp. 287–306 in: Soderstrom, T.R., Hilu, K.W., Campbell, C.S. & Barkworth, M.E. (eds.), *Grass systematics and evolution*. Washington, D.C.: Smithsonian Institution Press.

Zuloaga, F.O., Morrone O. & Dubcovsky, J. 1989. Exomorphological, anatomical, and cytological studies in *Panicum validum* (Poaceae: Panicoideae: Paniceae): Its systematic position within the genus. *Syst. Bot.* 14: 220–230. http://dx.doi.org/10.2307/2418908

Zuloaga, F.O., Morrone, O. & Giussani, L.M. 2000. A cladistic analysis of the Paniceae: A preliminary approach. Pp. 123–135 in: Jacobs, S.W.L. & Everett, J.E. (eds.), *Grasses: Systematics and evolution*. Collingwood: CSIRO.

Zuloaga, F.O., Giussani, L.M. & Morrone, O. 2006. On the taxonomic position of *Panicum aristellum* (Poaceae: Panicoideae: Paniceae). *Syst. Bot.* 31: 497–505. http://dx.doi.org/10.1600/036364406778388548

Zuloaga, F.O., Giussani, L.M. & Morrone, O. 2007. *Hopia*, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae). *Taxon* 56: 145–156.

Zuloaga, F.O., Scataglini, M.A. & Morrone, O. 2010. A phylogenetic evaluation of *Panicum* sects. *Agrostoidea*, *Megista*, *Prionitia* and *Tenera* (Panicoideae, Poaceae): Two new genera, *Stephostachys* and *Sorengia*. *Taxon* 59: 1535–1546.

Appendix 1. Species of Poaceae used for the molecular phylogenetic analyses, voucher specimens from which DNA was extracted for sequencing, and GenBank accession numbers. GenBank numbers of sequences generated for this study are in bold.

Acroceras zizanioides (Kunth) Dandy, AY029618. ***Alexfloydia repens*** B.K.Simon, JN604672. ***Alloteropsis semialata*** (R.Br.) Hitchc. subsp. ***eckloniana*** (Nees) Gibbs Russ., EU159708. ***Altoparadisium chapadense*** Filg. & al., AY029619. ***Amphicarpum amphicarpon*** (Pursh) Nash, JN604673. ***Ancistrachne uncinulata*** (R.Br.) S.T.Blake, JN604674. ***Andropogon gerardii*** Vitman, AF117391. ***Anisopogon avenaceus*** R.Br., AF251447. ***Anthaenantia lanata*** (Kunth) Benth, AY029640. ***Anthaenantiopsis fiebrigii*** Parodi, Argentina: Salta, La Caldera, El Gallinato, *Sulekic 597* (SI), **KF982002.** ***Anthaenantiopsis rojasiana*** Parodi, AY029620. ***Anthephora elongata*** De Wild.,, JN604675. ***Anthephora pubescens*** Nees,, JN604676. ***Apluda mutica*** L., AF117392. ***Apochloa euprepes*** (Renvoize) Zuloaga & Morrone, AY029657. ***Apochloa subtiramulosa*** (Renvoize & Zuloaga) Zuloaga & Morrone, AY188490. ***Aristida longiseta*** Steud., U21966. ***Arthropogon villosus*** Nees, AY029622. ***Arundinella hirta*** (Thunb.) Tanaka, AF117393. ***Arundinella nepalensis*** Trin., AF117394. ***Arundo donax*** L., U21998. ***Arundoclaytonia dissimilis*** Davidse & R.P.Ellis, AY847121. ***Austrodanthonia laevis*** (Vickery) H.P.Linder, AF251460. ***Axonopus anceps*** (Mez) Hitchc., AY029623. ***Axonopus fissifolius*** (Raddi) Kuhlm., AY029624. ***Bothriochloa bladhii*** (Retz.) S.T.Blake, AF117395. ***Bromuniola gossweileri*** Stapf & C.E.Hubb., AY847124. ***Bromus inermis*** Leyss., BIU71037. ***Calyptochloa gracillima*** C.E.Hubb., JN604677. ***Canastra aristella*** (Döll) Zuloaga & Morrone, DQ355988. ***Canastra lanceolata*** (Filg.) Morrone & al., AY029621. ***Capillipedium parviflorum*** (R.Br.) Stapf, AF117396. ***Cenchrus abyssinicus*** (Hack.) Morrone, GU561512. ***Cenchrus americanus*** (L.) Morrone, F499149. ***Cenchrus ciliaris*** L., AY029625. ***Cenchrus compressus*** (R.Br.) Morrone, AY029672. ***Cenchrus flaccidus*** (Griseb.) Morrone, AF499150. ***Cenchrus myosuroides*** Kunth, AF499152. ***Cenchrus pilosus*** Kunth, AY623746. ***Cenchrus setiger*** Vahl, AF499153. ***Centotheca lappacea*** (L.) Desv., AY847122. ***Centrochloa singularis*** Swallen, JN604678. ***Centropodia glauca*** (Nees) Cope, AF251462. ***Chaetium bromoides*** (J.Presl) Benth. ex Hemsl., AY029626. ***Chaetopoa pilosa*** Clayton, JN604679. ***Chamaeraphis hordeacea*** R.Br., JN604680. ***Chasmanthium curvifolium*** (Valdés-Reyna, Morden & S.L.Hatch) Wipff & S.D.Jones, AY847125. ***Chasmanthium latifolium*** (Michx.) H.O.Yates, AY029694. ***Chasmanthium laxum*** (L.) H.O.Yates, AY847126. ***Chionachne koenigii*** (Spreng.) Thwaites, AF117397. ***Chlorocalymma cryptacanthum*** Clayton, JN604681. ***Chrysopogon fulvus*** (Spreng.) Chiov., AF117398. ***Cleistachne sorghoides*** Benth., AF117400. ***Cleistochloa rigida*** (S.T.Blake) R.D.Webster, JN604682. ***Coleataenia anceps*** (Michx.) Soreng, AY188455. ***Coleataenia longifolia*** (Torr.) Soreng, AY188482. ***Coleataenia petersonii*** (Hitchc. & Ekman) Soreng, AY188479. ***Coleataenia prionitis*** (Nees) Soreng, AY029652. ***Coleataenia tenera*** (Beyr. ex Trin.) Soreng, AY188491. ***Cymbopogon flexuosus*** (Nees ex Steud.) Will. Watson, AF117404. ***Cyperochloa hirsuta*** Lazarides & L.Watson, AY847139. ***Cyphochlaena madagascariensis*** Hack., JN604683. ***Cyphonanthus discrepans*** (Döll) Zuloaga & Morrone, DQ646392. ***Cyrtococcum accrescens*** (Trin.) Stapf, JN604684. ***Dallwatsonia felliana*** B.K.Simon, JN604685. ***Danthonia californica*** Bol., AF251459. ***Danthoniopsis dinteri*** (Pilg.) C.E.Hubb., AY847116. ***Dichanthelium acuminatum*** (Sw.) Gould & C.A.Clark, AY188485. ***Dichanthelium clandestinum*** (L.) Gould, AY188461. ***Dichanthelium cumbucanum*** (Renvoize) Zuloaga, AY188464. ***Dichanthelium koolauense*** (H.St. John & Hosaka) C.A.Clark & Gould, AY029627. ***Dichanthelium sabulorum*** (Lam.) Gould & C.A.Clark, AY029654. ***Dichanthium aristatum*** (Poir.) C.E.Hubb., AF117409. ***Digitaria ciliaris*** (Retz.) Koeler, AY029630. ***Digitaria didactyla*** Willd., AM849203. ***Digitaria radicosa*** (J.Presl) Miq., AY029628. ***Digitaria setigera*** Roth, AY029629. ***Dissochondrus biflorus*** Kuntze ex Hack., JN604686. ***Distichlis spicata*** (L.) Greene, AF251464. ***Echinochloa colona*** (L.) Link, AY029631. ***Echinochloa frumentacea*** Link, AY029632. ***Echinolaena inflexa*** (Poir.) Chase, AY029633. ***Elionurus muticus*** (Spreng.) Kuntze, AF117410. ***Entolasia stricta*** (R.Br.) Hughes, JN604687. ***Eragrostis curvula*** (Schrad.) Nees, U21989. ***Eriachne pulchella*** Domin, AY618659. ***Eriochloa punctata*** (L.) Desv. ex Ham., AY029634. ***Gerritea pseudopetiolata*** Zuloaga, Morrone & Killeen, JN604688. ***Gynerium sagittatum*** (Aubl.) P.Beauv., AY847120. ***Heteropogon contortus*** (L.) P.Beauv. ex Roem. & Schult., AF117411. ***Homolepis glutinosa*** (Sw.) Zuloaga & Soderstr., AY029637. ***Homolepis isocalycia*** (G.Mey.) Chase, AY029636. ***Homopholis belsonii*** C.E.Hubb., JN604689. ***Hopia obtusa*** (Kunth) Zuloaga & Morrone, AY029659. ***Hylebates cordatus*** Chippindall, JN604691. ***Hymenachne donacifolia*** (Raddi) Chase, AY029635. ***Hymenachne grumosa*** (Nees) Zuloaga, AY188468. ***Hymenachne pernambucensis*** (Spreng.) Zuloaga, AY188478. ***Hyparrhenia hirta*** (L.) Stapf, AF117412. ***Ichnanthus pallens*** (Sw.) Munro ex Benth., AY029638. ***Isachne arundinacea*** (Sw.) Griseb., AY847119. ***Isachne leersioides*** Griseb., JN604692. ***Ixophorus unisetus*** (J.Presl) Schltdl., AY623749. ***Karroochloa purpurea*** (L.f.) Conert & Türpe, AF251458. ***Keratochlaena rigidifolia*** (Filg., Morrone & Zuloaga)

Appendix 1. Continued.

Morrone & Zuloaga, EU805492. ***Lasiacis sorghoidea*** (Desv. ex Ham.) Hitchc. & Chase, AY029639. ***Leucophrys mesocoma*** (Nees) Rendle, GU594628. ***Lophatherum gracile*** Brongn., AY847129. ***Loudetia simplex*** (Nees) C.E.Hubb., AY847117. ***Louisiella fluitans*** C.E.Hubb. & J.Léonard, JN604693. ***Megaloprotachne albescens*** C.E.Hubb., JN604694. ***Megastachya mucronata*** (Poir.) P.Beauv., AY847123. ***Megathyrsus maximus*** (Jacq.) B.K.Simon & S.W.L.Jacobs, AY029649. ***Melinis repens*** (Willd.) Zizka, AY029675. ***Merxmuellera macowanii*** (Stapf) Conert, AF251457. ***Mesosetum chaseae*** Luces, AY029641. ***Micraira subulifolia*** F.Muell., AY622316. ***Microstegium nudum*** (Trin.) A.Camus, AF443813. ***Mnesithea selloana*** **(**Hack.) de Koning & Sosef, AF117401. ***Molinia caerulea*** (L.) Moench, U21995. ***Moorochloa eruciformis*** (Sm.) Veldkamp, AY188452. ***Neurachne alopecuroidea*** R.Br., JN604695. ***Ocellochloa chapadensis*** (Swallen) Zuloaga & Morrone, AY188486. ***Ocellochloa piauiensis*** (Swallen) Zuloaga & Morrone, AY029656. ***Ocellochloa stolonifera*** (Poir.) Zuloaga & Morrone, AY188488. ***Oncorachis ramosa*** (Zuloaga & Soderstr.) Morrone & Zuloaga, AY029686. ***Ophiochloa hydrolithica*** Filg., Davidse & Zuloaga, AY029642. ***Oplismenopsis najada*** (Hack. & Arechav.) Parodi, AY188453. ***Oplismenus hirtellus*** (L.) P.Beauv., AY029644. ***Orthoclada laxa*** (Rich.) P.Beauv., AY847128. ***Otachyrium versicolor*** (Döll) Henrard, AY029643. ***Ottochloa nodosa*** (Kunth) Dandy, JN604696. ***Panicum adenophorum*** K.Schum., AY188454. ***Panicum antidotale*** Retz., AY188456. ***Panicum aquaticum*** Poir., AY029658. ***Panicum bergii*** Arechav., AY188457. ***Panicum cervicatum*** Chase, AY188459. ***Panicum chloroleucum*** Griseb., AY188460. ***Panicum claytonii*** Renvoize, AY188462. ***Panicum deustum*** Thunb., GU594631. ***Panicum dichotomiflorum*** Michx., AY188466. ***Panicum elephantipes*** Nees ex Trin., AY029647. ***Panicum fauriei*** Hitchc., AY029650. ***Panicum hylaeicum*** Mez, AY188470. ***Panicum miliaceum*** L., AY188472. ***Panicum millegrana*** Poir., AY029660. ***Panicum mystasipum*** Zuloaga & Morrone, AY188474. ***Panicum nephelophilum*** Gaudich., AY029645. ***Panicum olyroides*** Kunth, AY188475. ***Panicum pedersenii*** Zuloaga, AY029646. ***Panicum pilosum*** Sw., AY188480. ***Panicum racemosum*** (P.Beauv.) Spreng., AY188481. ***Panicum repens*** L., AY188467. ***Panicum rudgei*** Roem. & Schult., AY029661. ***Panicum sellowii*** Nees, AY188484. ***Panicum stramineum*** Hitchc. & Chase, AY188489. ***Panicum trichanthum*** Nees, AY188492. ***Panicum tricholaenoides*** Steud., AY188493. ***Panicum tuerckheimii*** Hack., AY188494; Mexico: Chiapas, 6 km al S de Palenque, sobre la carretera Catazaje-Ococingo, *Cabrera 12312 (SI)*, **KF982003. *Panicum validum*** Mez, AY188495; Argentina: Entre Ríos: Colon, *Morrone s.n.* (SI), **KF982004;** Argentina, Entre Ríos, A 5 km de la ciudad de Colón hacia el sur sobre el río Uruguay, *Morrone 5386* (SI), **KF982005. *Panicum verrucosum*** Muhl., AY188496. ***Panicum virgatum*** L., U21986. ***Paractaenum novae-hollandiae*** P.Beauv., JN604697. ***Paraneurachne muelleri*** (Hack.) S.T.Blake, Newbey 10800 (MO), JN604698. ***Paratheria prostrata*** Griseb., JN604699. ***Parodiophyllochloa cordovensis*** (E.Fourn.) Zuloaga & Morrone, AY188463. ***Parodiophyllochloa missiona*** (Ekman) Zuloaga & Morrone, AY188473. ***Parodiophyllochloa ovulifera*** (Trin.) Zuloaga & Morrone, AY029653. ***Parodiophyllochloa penicillata*** (Nees ex Trin.) Zuloaga & Morrone, AY188477. ***Paspalum arundinellum*** Mez, AY029663. ***Paspalum conjugatum*** P.J.Bergius, AY029669. ***Paspalum conspersum*** Schrad., AY029666. ***Paspalum foliiforme*** S.Denham, AY029690. ***Paspalum glaziovii*** (A.G.Burm.) S.Denham, AY029689. ***Paspalum haumanii*** Parodi, AY029664. ***Paspalum malacophyllum*** Trin., AY029671. ***Paspalum paniculatum*** L., AY029667. ***Paspalum remotum*** J.Rémy, AY029668. ***Paspalum vaginatum*** Sw., AY029665. ***Paspalum virgatum*** L., AY029670. ***Phacelurus digitatus*** (Sibth. & Sm.) Griseb., AF117418. ***Phanopyrum gymnocarpon*** (Elliott) Nash, AY188469. ***Pheidochloa gracilis*** S.T.Blake, JN604700. ***Phragmites australis*** (Cav.) Trin. ex Steud., U21997. ***Plagiantha tenella*** Renvoize, AY029674. ***Plagiosetum refractum*** Benth., EU819409. ***Poecilostachys oplismenoides*** (Hack.) Clayton, JN604701. ***Pohlidium petiolatum*** Davidse, Soderstr. & R.P.Ellis, AY847130. ***Pseudechinolaena polystachya*** (Kunth) Stapf, AY029676. ***Pseudochaetochloa australiensis*** Hitchc., JN604702. ***Pseudoraphis paradoxa*** (R.Br.) Pilg., EF189892. ***Reimarochloa acuta*** (Flüggé) Hitchc., *Zuloaga & Morrone 9537* (SI), JN604703. ***Renvoizea trinii*** (Kunth) Zuloaga & Morrone, EU107783. ***Reynaudia filiformis*** (Spreng. ex Schult.) Kunth,, JN604704. ***Rupichloa acuminata*** (Renvoize) D.Salariato & Morrone, AY029692. ***Sacciolepis indica*** (L.) Chase, AY029677. ***Schizachyrium scoparium*** (Michx.) Nash, AF117420. ***Scutachne dura*** (Griseb.) Hitchc. & Chase, GU594616. ***Setaria barbata*** (Lam.) Kunth, AF499145. ***Setaria geminata*** (Forssk.) Veldkamp, AY029662. ***Setaria grisebachii*** E.Fourn., AF499141. ***Setaria italica*** (L.) P.Beauv., AF499140. ***Setaria lachnea*** (Nees) Kunth, AY029683. ***Setaria macrostachya*** Kunth, AY029678. ***Setaria palmifolia*** (J.König) Stapf, AY029680. ***Setaria verticillata*** (L.) P.Beauv., AF499139. ***Setaria viridis*** (L.) P.Beauv., U21976. ***Setariopsis auriculata*** (E.Fourn.) Scribn., JN604705. ***Snowdenia petitiana*** (A.Rich.) C.E.Hubb., JN604706. ***Sorghastrum nutans*** (L.) Nash, AF117421. ***Spartina pectinata*** Link, AF251465. ***Spartochloa scirpoidea*** (Steud.) C.E.Hubb., AY847140. ***Spheneria kegelii*** (Müll. Hal.) Pilg., JN604707. ***Spinifex sericeus*** R.Br., EF189895. ***Sporobolus indicus*** (L.) R.Br., U21983. ***Steinchisma decipiens*** (Nees ex Trin.) W.V.Br., AY188499. ***Steinchisma hians*** (Elliott) Nash, AY029685. ***Steinchisma laxum*** (Sw.) Zuloaga, AY029655. ***Steinchisma spathellosum*** (Döll) Renvoize, AY188500. ***Stenotaphrum secundatum*** (Walter) Kuntze, AY029684. ***Stephostachys mertensii*** (Roth) Zuloaga & Morrone, AY188471.. ***Steyermarkochloa angustifolia*** (Spreng.) Judz., JN604709. ***Stipagrostis zeyheri*** (Nees) De Winter, AF251455. ***Streptostachys asperifolia*** Desv., AY029687. ***Tatianyx arnacites*** (Trin.) Zuloaga & Soderstr., AY029688. ***Thrasyopsis juerguensii*** (Hack.) Soderstr. & A.G.Burm., JN604711. ***Thuarea involuta*** (G.Forst.) R.Br. ex Sm., GU594624. ***Thyridolepis mitchelliana*** (Nees) S.T.Blake, *Latz 13500* (MO), JN604710. ***Thysanolaena maxima*** (Roxb.) Kuntze, U21984. ***Trichanthecium cyanescens*** (Nees ex Trin.) Zuloaga & Morrone, AY188465. ***Trichanthecium parvifolium*** (Lam.) Zuloaga & Morrone, AY188476. ***Trichanthecium wettsteinii*** (Hack.) Zuloaga & Morrone, Y188497. ***Tricholaena monachne*** (Trin.) Stapf & C.E.Hubb., FJ486535. ***Tripsacum dactyloides*** (L.) L**.**, AF117433. ***Triscenia ovina*** Griseb. JN604712. ***Tristachya biseriata*** Stapf, AY847118. ***Uniola paniculata*** L., AF251463. ***Uranthoecium truncatum*** (Maiden & Betche) Stapf, SJ9599. ***Urochloa mutica*** (Forssk.) T.Q.Nguyen, AY029691. ***Walwhalleya subxerophila*** (Domin) Wills & J.J.Bruhl, JN604713. ***Whiteochloa capillipes*** (Benth.) Lazarides, JN604714. ***Xerochloa laniflora*** Benth., JN604715. ***Yakirra australiensis*** (Domin) Lazarides & R.D.Webster, JN604716. ***Yvesia madagascariensis*** A.Camus, GU594636. ***Zeugites capillaris*** (Hitchc.) Swallen, AY847133. ***Zeugites pittieri*** Hack., AY632374. ***Zoysia matrella*** (L.) Merr., U21975. ***Zuloagaea bulbosa*** (Kunth) Bess, AY029648. ***Zygochloa paradoxa*** (R.Br.) S.T.Blake, EF189896.

Appendix 2. Representative specimens examined: species, country, state, locality, collector, collector number, and herbarium acronym (in parentheses).

Aaika tuerckheimii (Hack.) J.R.Grande — BELIZE: Toledo, on rock, in high ridge, riverbank beyond Resemideres, *Gentle 6917* (F). — GUATEMALA: Alta Verapaz, Cubilquitz, *Von Tuerckheim II-1457* (F, G, MO, SI). Petén, San Luis, en orillando el camino para la cumbre, a km 120, *Ortíz 1449* (F, MO); La Cumbre, km 135, bordering Chacte Rivere, in low forest, *Contreras 6288* (F, MEXU, MO). — MEXICO: Chiapas, 6 km al S de Palenque, sobre la carretera Catazaje-Ococingo, *Cabrera 12312* (SI); 19.2 km from turnoff to ruins on road from Palenque toward Ococingo, then take turnoff to Cascada Misolha, *Huft & Cabrera 2431* (MO); a 5 km al S de Campamento COFOLASA el cual está a 24 km al de Crucero Corozal, camino Palenque-Boca Lacantum, *Martínez 7853* (MO); El Ocote, orilla perturbada de la selva alta sub-perennifolia, *Hernández X. s.n.* (MEXU 96395); Mun. Tila, Kokijaz, *Ton 4687* (MO); Mun. Ocosingo, a 16 km al NW de Boca Lacantum camino a Palenque, *Martínez 14783* (MO); 16 km NW of Tumbo, roadside, 17°09′ N, 91°45′ W, *Stevens & Martínez 25890* (MO); Mun. Palenque, tropical rain forest adjacent to small cascading river at Agua Azul, *Breedlove & Davidse 55244* (MO); Mun. Palenque, slopes and small streams with tropical rain forest along the ridges 6–12 km south of Palenque on the road to Ocosingo, *Breedlove 28825* (MEXU, MO); Mun. Palenque, steep slope with lower montane rain forest near Agua Azul, *Breedlove & Davidse 55426* (MO); Mun. Ocosingo, tropical rain forest near Cascada Mizola, 25 km south of Palenque on road to Ocosingo, *Breedlove & Davidse 55380* (MO). Oaxaca, Chiltepec, *Martínez Calderón 750* (MEXU). Puebla, El Rancho de Cocojapa, on the lower slopes of El Cerro de Cuhuatepetl, Tehuacán, *Vera Santos 3706a* (CHAPA, NY). Veracruz, Matalarga a orillas del Río Metlac, a 2 km de Fortín, *Lot 551* (F), *552* (MEXU); Hidalgotitlán, brecha Cedillo-A. Melgar, *Vázquez 1328* (ANSM, MEXU, MO). — NICARAGUA: Región Autónoma del Atlántico Norte, Municipio de Siuna, Reserva Bosawas, en las cercanías de la desembocadura del caño el Macho, *Rueda & al. 3831* (MO). ***Osvaldoa valida*** (Mez) J.R.Grande — ARGENTINA: Corrientes, Dpto. Monte Caseros, Ruta 127 y Arroyo Curuzú Cuatiá, *Schinini & al. 17411* (CTES). Entre Ríos, Dpto. Colón, Colón, *Morrone s.n.* (SI); A 5 km de la ciudad de Colón hacia el sur sobre el Río Uruguay, *Morrone 5386* (SI); Dpto. Uruguay, Isla del Puerto, *Meyer 10455* (LIL); Isla Uruguay, *Báez 17* (BAB); Concepción del Uruguay, Arroyo La China, *Burkart 18013, Irigoyen 344, Nicora 3001* (SI), *Zuloaga & Deginani 2493* (BAA, MO, NY, SI, SP, US), *Zuloaga & al. 3090* (MO, SI), *Bacigalupo & al. 583* (MO). — BRAZIL: Rio Grande do Sul, Barra do Quaraí, *Valls & al. 1705* (US). Santa Catarina, Porto União, *Smith & Klein 15722* (R, US). — URUGUAY: Paysandú, Isla Queguay, en el río Uruguay, *Rosengurtt 3798* (BAA, LIL, SP).