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Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification

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Abstract

Included in the PACMAD clade of the family Poaceae (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae), the tribe Paniceae s.l. is one of the largest tribes of the subfamily Panicoideae, with more than 2000 species. This tribe comprises a huge morphological, cytological and physiological diversity represented by different inflorescence types, several basic chromosome numbers, and at least four major photosynthetic pathways. The tribe Paniceae has been the subject of molecular studies that have confirmed its paraphyly: two major clades were recognized based on their basic chromosome numbers ($x = 9$, $x = 10$). The $x = 10$ Paniceae clade is sister to the Andropogoneae–Arundinelleae s.s. clade ($x = 10$), while the combined $x = 10$ clade is sister to the $x = 9$ clade that contains the remaining genera of Paniceae. As a result of a recent realignment within the tribe in terms of the phylogenetic position of minor and major Paniceae genera, a reanalysis of the whole sampling is performed and new underrepresented taxa are discussed. A total of 155 genera, currently considered within subfamily Panicoideae, are represented here by almost all genera of Paniceae s.l., representatives of Andropogoneae and Arundinelleae s.s., and the endemic and small tribe Steyermarkochloeae; we also included specimens of subfamily Micrairoideae, tribes Isachneae and Eriachneae. The sampling includes as outgroups 18 genera of the PACMAD clade (excluding Panicoideae) and four genera from the BEP clade (Bambusoideae, Ehrhartoideae, Pooideae), rooting with *Bromus inermis*. A matrix with 265 taxa based on the combined evidence from *ndhF* plastid sequences (2074 bp) and 57 morphological characters was subjected to parsimony analyses. Jackknife resampling was used to calculate group support. Most clades are characterized by morphological, cytological, anatomical, and/or physiological characters. Major tribal changes are based on the basic chromosome number; the pantropical $x = 9$ clade is here recognized as Paniceae s.s., while the American $x = 10$ Paniceae s.l. is restricted to the reinstated tribe Paspaleae. The optimization of the photosynthetic pathway for the Paspaleae–Andropogoneae–Arundinelleae s.s. clade, including the monotypic *Reynaudia*, shows a plesiomorphic C_4 state while the ancestral state for Paniceae s.s. is ambiguous. If *Reynaudia* were not included or placed elsewhere, the ancestral photosynthetic pathway for both the Paspaleae–Andropogoneae–Arundinelleae s.s. clade and the Paniceae s.s. would be unambiguously C_3. In order to explore character evolution further, the morphological characters were mapped onto one of the most parsimonious trees. A relationship between photosynthetic pathways and inflorescence morphology is suggested here for the first time. Based on the optimization of morphological characters and additional data, we propose names for almost all inner clades at the rank of subtribe with a few groups as incertae sedis. With this extensive sampling, we resolved the phylogenetic relationships and the assignation of synapomorphies, and improved the support in subtribe sorting; consequently a robust circumscription of the tribe Paniceae s.l. is proposed.

Paniceae is one of the largest tribes of subfamily Panicoideae (Poaceae), in which more than 2000 species are included. The Paniceae are mainly distributed in tropical and subtropical regions of both hemispheres,

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with only a few representatives in temperate and cold areas.

This tribe includes enormous morphological, cytological and physiological diversity, represented by different developmental patterns of spikelets, inflorescence types, several basic chromosome numbers, leaf anatomy, and at least four major photosynthetic pathways [Clayton and Renvoize, 1986; Watson and Dallwitz, 1992; GPWG (Grass Phylogeny Working Group), 2001].

Cereal and forage grasses [*Panicum miliaceum* L., *Cenchrus americanus* (L.) Morrone, *Setaria italica* (L.) P. Beauv., *Paspalum dilatatum* Poir.] and turf and ornamental species [*Axonopus compressus* (Sw.) P. Beauv., *Cenchrus purpureus* (Schumach.) Morrone, *Stenotaphrum secundatum* (Walter) Kuntze], as well as species used for biofuel (*Panicum virgatum* L.), make the tribe Paniceae important in the economy of the human community. Improvement of crops, developmental studies, genome sequencing, and evolutionary studies have been the subject of major research projects involving panicoid species in recent years (e.g. McLaren, 2005; McLaughlin and Kszos, 2005; Reinheimer et al., 2005; Buell, 2009; Hua et al., 2009).

DNA sequencing has transformed traditional taxonomy and has led to a robust new systematic classification for the family Poaceae (Barker et al., 1995; Clark et al., 1995; Duvall and Morton, 1996; Soreng and Davis, 1998; Hilu et al., 1999; GPWG, 2001). The most recent phylogeny of the entire grass family (GPWG, 2001), based on morphology and seven molecular data sets, divided Poaceae in two major clades: BEP (Bambusoideae, Ehrhartoideae, Pooideae) and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae); the latter acronym as accepted by Duvall et al. (2007) and Sánchez-Ken et al. (2007). These results opened up a new range of evolutionary hypotheses among subfamilies, tribes and genera of grasses, and represent a challenge to reassess the classification within each of the clades. In this regard, molecular phylogenetic studies re-evaluated the traditional classification of major groups: subfamily Bambusoideae by Kelchner and Clark (1997), Zhang and Clark (2000), and Triplett and Clark (2010); subfamily Pooideae by Catalán et al. (1997), Davis and Soreng (2007), Döring et al. (2007), Soreng et al. (2007), and Schneider et al. (2009); subfamily Chloridoideae by Peterson et al. (2010, 2011); subfamily Panicoideae by Giussani et al. (2001), Aliscioni et al. (2003), and Sánchez-Ken et al. (2007).

Subfamily Panicoideae has been consistently highly supported as monophyletic (GPWG, 2001; Vicentini et al., 2008; Sánchez-Ken and Clark, 2010), and several morphological synapomorphies characterize the group: the presence of a two-flowered spikelet, with the lower floret staminate or neuter and the upper one perfect, and with simple starch grains (Kellogg and Campbell, 1987). GPWG (2001) considered 3270 species grouped in 206 genera and six tribes in the subfamily: Andropogoneae, Arundinelleae, Hubbardieae, Isachneae, Paniceae and Steyermarkochloeae (GPWG, 2001). Soreng and Davis (1998) suggested that tribes Centotheceae and Thysanolaeneae should be included in subfamily Panicoideae. Duvall et al. (2007), using two plastid markers (*rbcL* and *ndhF*), proposed that *Isachne* R. Br. and *Eriachne* R. Br. should be excluded from Panicoideae as both genera are closely related to *Micraira* F. Muell. The three genera were placed in subfamily Micrairoideae, which was later emended by Sánchez-Ken et al. (2007) with the addition of other genera of tribes Isachneae and Eriachneae. Recently, Sánchez-Ken and Clark (2010) proposed an expanded classification for the Panicoideae with 12 tribes: Andropogoneae, Arundinelleae, Centotheceae, Chasmanthieae (including *Bromuniola* Stapf and C.E. Hubb. and *Chasmanthium* Link), Gynerieae, Cyperochloeae (proposed to include *Spartochloa* C.E. Hubb. and *Cyperochloa* Lazarides and L. Watson.), Hubbardieae, Paniceae, Steyermarkochloeae, Thysanolaeneae, Tristachyideae (a new tribe with genera previously included in the Arundinelleae) and Zeugiteae.

Tribes Paniceae and Andropogoneae have the greatest number of species and genera within the subfamily Panicoideae. The tribe Paniceae has been the subject of molecular studies in the past decade that have confirmed its paraphyly (Gómez-Martínez and Culham, 2000; Duvall et al., 2001; Giussani et al., 2001; Mathews et al., 2002). The former Paniceae has been divided into two major clades that differ in basic chromosome number ($x = 9$, $x = 10$); the $x = 10$ Paniceae clade is sister to the Andropogoneae–Arundinelleae clade (also $x = 10$) while the combined $x = 10$ clade is sister to the $x = 9$ clade (Gómez-Martínez and Culham, 2000; Giussani et al., 2001; Aliscioni et al., 2003). Increased taxonomic sampling in subsequent phylogenetic studies within Paniceae allowed the recircumscription of minor lineages. *Panicum* L. has proven to be a polyphyletic genus and was consequently restricted to C_4 species with an NAD–malic enzyme (NAD–ME) physiological and anatomical subtype (Aliscioni et al., 2003). As a result, several species of *Panicum* were segregated and new genera were established: *Apochloa* Zuloaga and Morrone, *Canastra* Morrone, Zuloaga, Davidse and Filg., *Coleataenia* Griseb., *Cyphonanthus* Zuloaga and Morrone, *Hopia* Zuloaga and Morrone, *Megathyrsus* (Pilg.) B.K. Simon and S.W.L. Jacobs, *Ocellochloa* Zuloaga and Morrone, *Parodiophyllochloa* Zuloaga and Morrone, *Renvoizea* Zuloaga and Morrone, *Stephostachys* Zuloaga and Morrone, and *Zuloagaea* Bess (Morrone et al., 2001, 2007, 2008; Simon and Jacobs, 2003; Bess et al., 2006; Zuloaga et al., 2007a; Sede et al., 2008, 2009a; Soreng, 2010).

Because of the extensive recent realignment of genera within the Paniceae (Giussani et al., 2001; Aliscioni et al., 2003; Donadío et al., 2009; Ibrahim et al., 2009; Kellogg et al., 2009; Salariato et al., 2009, 2010; Sede et al., 2009b; Chemisquy et al., 2010), a review of the whole tribe is needed, including a comprehensive sample representing its morphological, anatomical and cytogenetic diversity.

The aim of this work is to establish a robust circumscription of the tribe Paniceae and the major clades within it. In order to accomplish this objective, all genera of the tribe were sampled. Relationships among genera are discussed based on the *ndhF* plastid gene, in addition to cytological and morphological evidence. To resolve the monophyly of Paniceae we included, other than the well represented genera of Paniceae, Andropogoneae and Arundinelleae, *ndhF* sequences of the endemic and small tribe Steyermarkochloeae of the subfamily Panicoideae, as well as representatives of subfamily Micrairoideae tribes Isachneae and Eriachneae, among others. Based on a combined morphological and molecular analysis, a new classification for the tribe Paniceae is presented here.

Taxonomic history of the tribe Paniceae

In the middle of the 17th century, Adanson (1763) divided the grass family into nine informal groups, of which the two major ones, the Poae and Panica, currently correspond, in a nomenclatural sense, to the tribes Poeae and Paniceae, respectively. Brown (1810) published a grass classification based on the spikelet structure and the geographical distribution of taxa. Later on, Brown (1814) recognized two tribes within the family: Poeae and Paniceae. Brown's concept included in "Paniceae" the genus *Panicum* among other genera now considered within the tribe Andropogoneae. His concept was later followed by several authors to circumscribe the subfamily Panicoideae (Link, 1827), while the name Paniceae was restricted to the actual tribe (Brown, 1814).

Bentham (1881) recognized the Series Poaceae and Panicaceae [approximately similar to the concept of Brown (1814)], including within Panicaceae genera in which the spikelets disarticulate from the pedicel below the glumes. Bentham (1881) divided Series Panicaceae into six tribes: Paniceae, Maydeae, Oryzeae, Tristegineae, Zoysieae and Andropogoneae. Tribe Paniceae was recognized by the indurate fruiting "glume" with four major groups included: (i) "Paniceae proper" with an arbitrary number of genera and distinctive characters being very uncertain, although still recognizing within it at least 11 genera as follows: *Anthaenantia* P. Beauv., *Amphicarpum* Kunth, *Beckmannia* Host (currently in Poeae s.l.), *Chaetium* Nees, *Eriochloa* Kunth, *Ichnanthus* P. Beauv., *Oplismenus* P. Beauv., *Paspalum* L., *Panicum*, *Reimaria* Humb. and Bonpl. ex Flüggé (= *Paspalum*), and *Setaria*; (ii) "Cenchrus" with spikelets having an involucre of bristles below the spikelets, with four genera: *Cenchrus* L., *Pennisetum* Rich., *Plagiosetum* Benth., and *Paratheria* Griseb.; (iii) "Chamaeraphis" with a fruiting glume less hardened, including seven small genera: *Echinolaena* Desv., *Chamaeraphis* R. Br., *Stenotaphrum* Trin., *Spartina* Schreb. (currently in Chloridoideae), *Phyllorachis* Trimen (now in Ehrhartoideae), *Thuarea* Pers., and *Xerochloa* R. Br.; and (iv) a heterogeneous group of seven genera, of which only *Spinifex* L. is still considered within the tribe. The other six genera placed in Paniceae by Bentham (1881) were: *Anomochloa* Brongn. (now Anomochlooideae), *Leptaspis* R. Br. (Pharoideae), *Lygeum* Loefl. ex L. (Pooideae), *Olyra* L. (Bambusoideae), *Pharus* P. Browne (Pharoideae), and *Streptochaeta* Schrad. ex Nees (Anomochlooideae). The remaining tribes of the Panicaceae proposed by Bentham represent an artificial grouping with some representatives of the panicoid tribes Paniceae and Andropogoneae, but also from other subfamilies such as Chloridoideae and Bambusoideae. Tribe Zoysieae included some panicoid genera such as *Anthephora* Schreb., *Neurachne* R. Br., and *Trachys* Pers., and also several Chloridoideae genera; tribe Maydeae mostly included andropogonoid genera, together with *Pariana* Aubl., a little herbaceous bambusoid grass; tribe Oryzeae included *Achlaena* Griseb., *Beckera* Fresen. (= *Snowdenia* C.E. Hubb.), and a heterogeneous group with *Hydrochloa* P. Beauv. (= *Leersia* Sw.), *Hygroryza* Nees, *Leersia*, *Luziola* Juss., *Oryza* L., *Potamophila* R. Br., *Zizania* L. (Ehrhartoideae), *Alopecurus* L., *Cornucopia* L. (Pooideae), and *Crypsis* Aiton (Chloridoideae); and tribe Tristegineae included several Paniceae genera: *Arthropogon* Nees, *Melinis* P. Beauv., *Reynaudia* Kunth, *Rhynchelytrum* Nees (= *Melinis*), and *Triscenia* Griseb., and also a few representatives of Arundinelleae (such as *Arundinella* Raddi), Andropogoneae (*Cleistachne* Benth.), and Thysanolaeneae (*Thysanolaena* Nees).

Hackel (1887) followed Bentham (1881) with a similar classification, recognizing 12 tribes in the Poaceae, six of which were equivalent to those proposed by Bentham for the Series Panicaceae. Nevertheless, Hackel's descriptions were more detailed and included, as diagnostic characters, novel microcharacters of the fruit such as hilum and starch grain types. During the first half of the 20th century, new anatomical and cytological features were added as valuable characters for the classification of grasses (Avdulov, 1931; Prat, 1932, 1936).

Pilger (1940) recognized four tribes within the subfamily Panicoideae: tribe Paniceae with six subtribes (Anthephorinae, Boivinellinae, Lecomtellinae, Melinidinae, Panicinae and Trachidinae); tribe Andropogoneae with six subtribes (Andropogoninae, Dimeriinae, Ischaeminae, Rottboelliinae, Saccharinae and Sorghinae); tribe Arthropogoneae; and tribe Maydeae. Of these four tribes, Pilger (1954) included tribes Andropogoneae and

Maydeae in subfamily Andropogonoideae, and considered eight tribes in the Panicoideae: of these, Arthropogoneae and Paniceae were already described in his previous work (Pilger, 1940) and accepted as tribes the following taxa: Anthephoreae, with a single genus, *Anthephora*; Boivinelleae, with *Boivinella* A. Camus, *Cyphochlaena* Hack., and *Perulifera* A. Camus; Lecomtelleae, with *Lecomtella* A. Camus; Melinideae, with *Melinis*, *Rhynchelytrum*, and *Tricholaena* Schrad.; and tribe Trachyeae, with *Trachys* Pers. Also, Pilger (1954) recognized tribe Isachneae in the Panicoideae with *Coelachne* R. Br., *Heteranthoecia* Stapf, *Isachne* R. Br., and *Limnopoa* C.E. Hubb.

Brown (1977) divided tribe Paniceae into four subtribes according to a phylogenetic concept based on leaf anatomy and photosynthetic types. Subtribe 1 included mostly species with paniculate inflorescences and leaf cross-sections with Kranz anatomy and a single bundle sheath (Kranz MS); these plants used the NADP–malic enzyme subtype of the C_4 photosynthetic pathway (C_4 NADP–ME). Brown's subtribe 2 included plants that were all non-Kranz and C_3; subtribe 3 included species with racemose inflorescences and leaf cross-sections with Kranz anatomy and a double bundle sheath (Kranz PS), C_4 PEP–carboxykinase subtype (PEP–CK); and subtribe 4 included species with paniculate inflorescences and leaf cross-sections with Kranz PS, C_4 NAD–ME. In this work, Brown proposed evolutionary hypotheses among taxa and related the photosynthetic syndrome to environmental adaptations. He hypothesized that Andropogoneae (all Kranz MS, C_4 NADP–ME) were derived from some ancient Kranz MS Paniceae or Panicoideae, and predicted two or three independent origins for the Kranz syndrome within Paniceae.

Clayton and Renvoize (1986), following in part the classification of Pilger (1954), recognized seven tribes in Panicoideae, based mainly on spikelet morphology, upper floret texture and leaf anatomical type. The two major tribes were Paniceae and Andropogoneae; the former was divided into seven subtribes: Arthropogoninae, Cenchrinae, Digitariinae, Melinidinae, Neurachninae, Setariinae (= Panicinae) and Spinificinae; while Andropogoneae was organized into 11 subtribes. Other minor tribes within Panicoideae include Arundinelleae, Eriachneae, Hubbardieae, Isachneae and Steyermarkochloeae.

Watson and Dallwitz (1992) treated six tribes in the Panicoideae: Andropogoneae, Arundinelleae, Isachneae, Maydeae, Neurachneae and Paniceae. They placed Steyermarkochloeae and Eriachneae within Arundinoideae, and *Hubbardia* in Isachneae.

In one of the most recent treatments of the American Panicoids, Zuloaga et al. (2007b) recognized eight tribes based on morphology and molecular data: Andropogoneae, Arundinelleae, Centotheceae, Gynerieae, Isachneae, Paniceae, Steyermarkochloeae and Thysanolaeneae. Within the Paniceae, a total of seven subtribes were accepted: Arthropogoninae, Cenchrinae, Digitariinae, Melinidinae, Panicinae and Setariinae.

Materials and methods

Taxonomic sampling

We included a total of 155 genera currently considered part of the subfamily Panicoideae, each represented by at least one species (Clayton and Renvoize, 1986; Watson and Dallwitz, 1992; Zuloaga et al., 2000; Sánchez-Ken and Clark, 2010). Among outgroups we included 18 genera of the PACMAD clade (excluding Panicoideae) and four genera from the BEP clade, rooting with *Bromus inermis* Leyss. The final matrix included 265 taxa; 15 genera were only considered with morphology because *ndhF* sequences were not obtained due to lack of voucher material or because vouchers failed to amplify: *Acostia* Swallen, *Acritochaete* Pilg., *Arthragrostis* Lazarides, *Baptorhachis* Clayton and Renvoize, *Eccoptocarpha* Launert, *Holcolemma* Stapf and C.E. Hubb., *Hubbardia*, *Hydrothauma* Hubbard, *Lecomtella*, *Microcalamus* Franch., *Oryzidium* C.E. Hubb. and Schweick., *Streptolophus* Hughes, *Tarigidia* Stent, *Thyridachne* C.E. Hubb., and *Trachys*. *Hubbardia heptaneuron* Bor has been collected only twice, in spray-moistened rocks near the Jog Falls on the Sharavati River (Yadav et al., 2010). We were unable to obtain material of this species, which is critically endangered but is the subject of an effort at restoration (Yadav et al., 2009). A list of the species, voucher material and Genbank accession numbers used in the molecular study is presented in Appendix 1.

Morphological data matrix

The morphological data set was modified from the matrix published by Zuloaga et al. (2000) with particular modifications: two extra characters were added, while other changes included adding states for the expanded outgroup, and changes in the coding scheme concerning the multistate non-additive characters that are here coded as additive whenever the states are considered internested (Lipscomb, 1992). A total of 57 characters were scored (Appendices 2 and S1). In the present analysis, terminals were coded at the species level if DNA sequence data were available. For the terminals where DNA sequence data were not available, we coded the characters at generic level, scoring any polymorphic character as such. The characters were scored on herbarium material deposited at BAA, CAMB, K, MO, NSW, PRE, SI and US (abbreviations according to *Index Herbariorum*; B. Theirs, http://sweetgum.nybg.org/ih); if vouchers were not available, we followed the information found in the DELTA system (Watson and Dallwitz, 1992).

DNA extraction, amplification and sequencing

Total DNA was extracted from leaves of plants collected in the field and dried in silica gel using modified Cetyltrimethylammonium Bromide (CTAB) protocol from Doyle and Doyle (1987). A DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) was used when fresh material was not available, and herbarium specimens were analysed.

A plastid marker, *ndhF*, was amplified; this gene encodes a large subunit of one of the proteins that takes part in photorespiration (the NADPH plastiquinone oxidoreductase). This gene is thought to be conservative within the plant genome although, as an actively evolving gene of the plastome, its nucleotide-substitution rate is twice as high as that of *rbcL* (Seliverstov et al., 2009). These characteristics make *ndhF* valuable for phylogenetic reconstruction and it has proven to be a useful tool in different phylogenetic lineages of plants (Kim and Jansen, 1995; Catalán et al., 1997; Aliscioni et al., 2003; Sánchez-Ken et al., 2007). The complete *ndhF* gene (ca. 2000 bp) was amplified using primers specified by Olmstead and Sweere (1994), Clark et al. (1995), and Aliscioni et al. (2003). For silica-dried samples, three pairs of primers were used (5F–972R, 972F–1666R and 1666F–2110R). For herbarium samples, five smaller fragments were amplified using 5F–536R, 536F–972R, 972F–1318R, 1318F–1666R and 1666F–2110R. For non-overlapping fragments, we filled in missing base pairs with N, although these characters represent a small proportion of the entire sequence.

PCR reactions were performed in 25 μL final volumes with 50–100 ng of template DNA, 0.2 μM of each primer, 25 μM dNTP, 5 mM $MgCl_2$, 1× buffer and 1.5 units of Taq polymerase provided by Invitrogen Life Technologies. 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 s, annealing at 48 °C for 60 s, and extension at 72 °C for 90 s. 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 check for contamination. PCR products were run out on a 1% TBE agarose gel stained with SYBR Safe DNA gel stain (Invitrogen) and visualized in a blue light transilluminator. Cleaning of PCR products was done by Macrogen, Inc. (Seoul, Korea) using the Montage PCR purification kit from Millipore and following the manufacturer's protocol. Sequencing reactions were also performed by Macrogen using the ABI PRISM BigDye Terminator Cycle Sequencing Kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, Korea) following the protocols supplied by the manufacturer. Both forward and reverse strands were sequenced with a minimum overlap of 90% for every taxon. Single-pass sequencing was performed on each template using selected primers to complete a bidirectional contig of the full sequence. Editing and assembling of sequences was conducted using Chromas Pro ver. 1.34 (Technelysium Pty, Ltd, Tewantin, Qld, Australia). Quality of sequences was assessed by visual inspection of the chromatograms. Sequences were manually aligned using BioEdit ver. 5.0.9 (Hall, 1999), adding gaps to the matrix. Each base-pair gap was treated as missing data, but informative indels were considered as presence/absence characters during the analyses.

Phylogenetic analyses

We used TNT ver. 1.1 (Goloboff et al., 2008) for phylogenetic analyses. We analysed both the combined matrix and the *ndhF* sequence matrix on its own. For both matrices we used Driven search, finding the minimum length 100 times with default settings for Sectorial searches and Tree fusing (Goloboff, 1999), all with "Random Seed = 0". The resulting trees were submitted to Ratchet (Nixon, 1999) and Drift (both default settings) until 10 000 trees were found. Since there were no differences among the strict consensus trees calculated from the original 100 optimal trees and the 10 000 optimal trees found during ratchet and drifting, we did not continue the searches. To improve the resolution of the strict consensus tree, we used the "Tree pruning" option to find taxa that caused more than five nodes to collapse. These species were excluded from the final consensus trees. Jackknife values (Farris et al., 1996) were calculated by 10 000 resampling iterations with a removal probability of 36%, using 10 replicates of Ratchet to find the minimum length once in each replication. As for the analyses above, all taxa were retained in the matrix during the resampling, but taxa found to cause conflict under the tree searches were excluded from the consensus when calculating the final jackknife frequencies.

To explore character evolution within the study group, we generated two phylograms, one showing the amount of character changes of the 20 inflorescence characters; the other showing the 31 characters related to the spikelet morphology. Both phylograms were generated on the basis of one of the optimal trees from the combined data set.

Results

ndhF sequence analysis

Sequence alignment was trivial, with five informative indels between 6 and 24 bp long, as already described by Giussani et al. (2001). The aligned sequences included

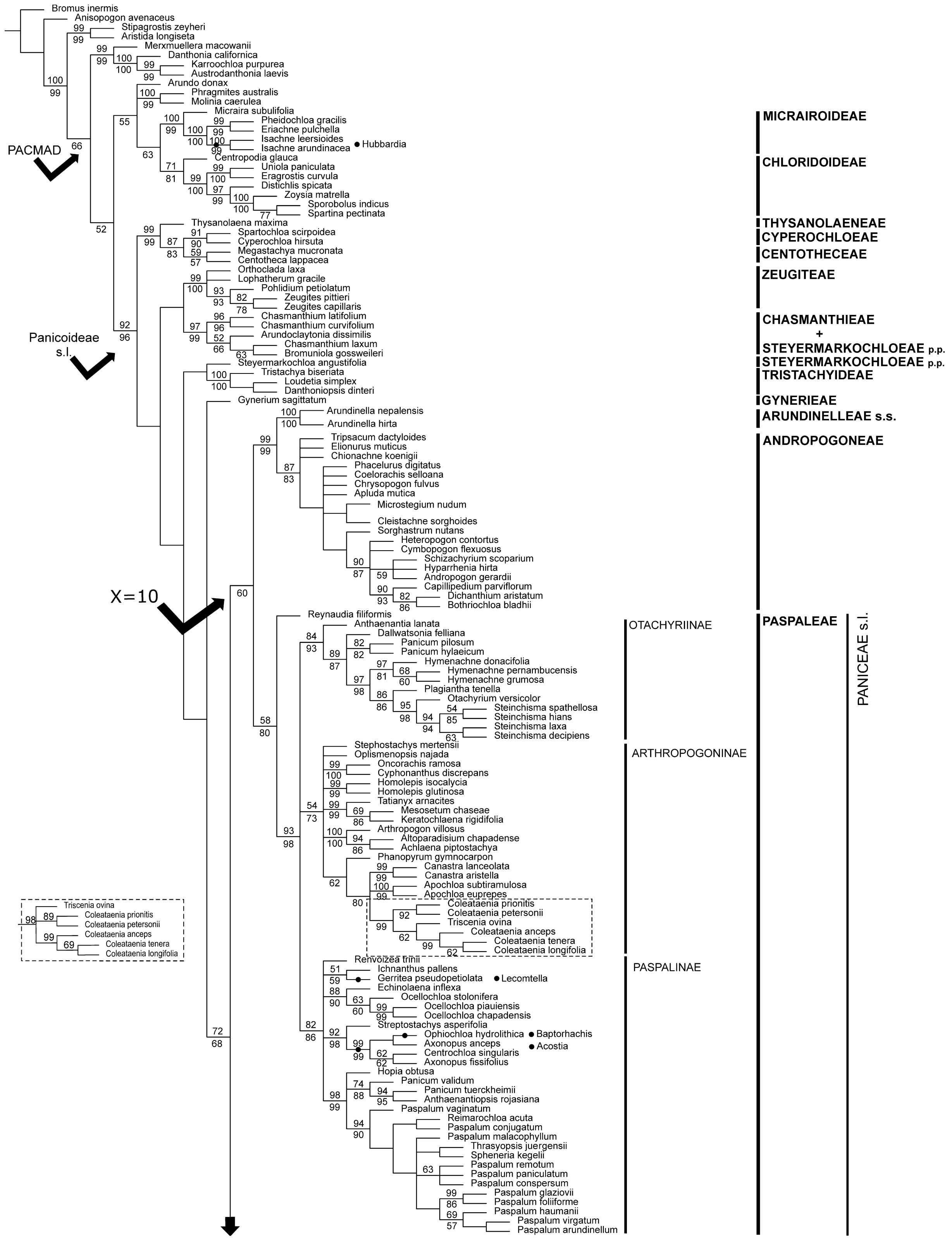

Fig. 1. Strict consensus tree resulting from analysis of the *ndhF* sequences. Numbers below the branches indicate jackknife values from the *ndhF* sequence analysis; numbers above the branches indicate jackknife values from the combined analyses (*ndhF* + morphology). Positions of taxa only included in the combined analysis are marked with black dots. Boxes show an alternative topology resulting from the combined analyses.

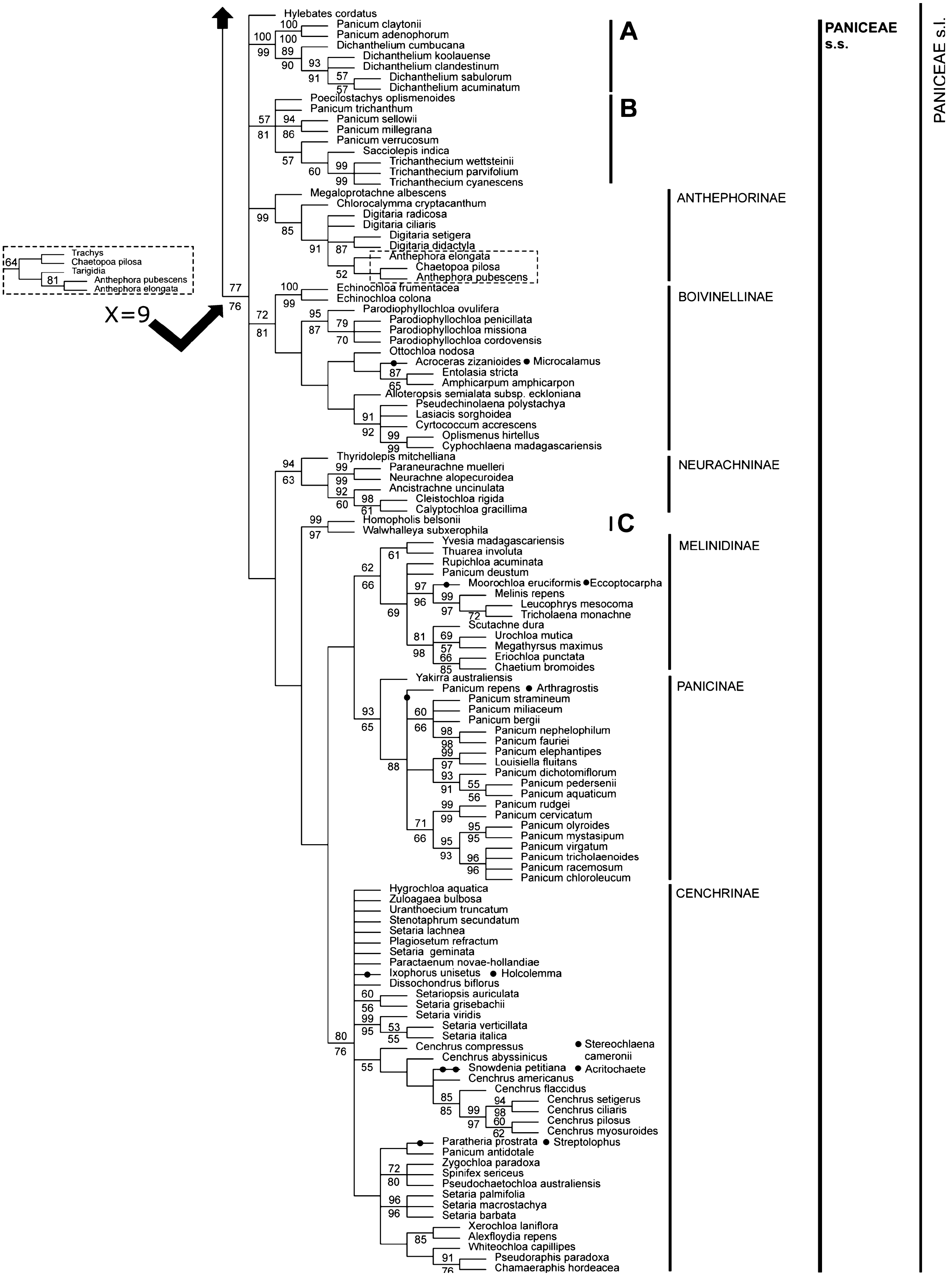

Fig. 1. (*Continued*).

2074 bp, of which 770 were phylogenetically informative. The final tree length was 4000 steps long. To improve resolution, *Stereochlaena cameronii* (Stapf) Pilg. was excluded from the strict consensus tree shown in Fig. 1 and from the consensus when calculating jackknife support.

Combined morphological and molecular analyses

The morphological matrix included 57 characters. A nearly collapsed consensus tree was obtained when analysing the morphological matrix due to a high degree of homoplasy combined with a low character/taxa ratio.

The combined morphological and molecular matrix yields optimal trees 4943 steps long. In general, the consensus tree from the combined matrix was better resolved for most clades, although only few clades showed over 50% jackknife values in the combined data. All supported clades from the combined data matrix were clades also appearing when the *ndhF* matrix was analysed on its own. Consequently, we show the consensus tree and jackknife values found when analysing only the *ndhF* sequences, and compare those with the values that are found when morphology is added to the matrix (Fig. 1). To improve resolution in the jackknife consensus tree from the combined analysis, all taxa lacking DNA sequence data were excluded. Three monotypic genera from tropical Africa—*Hydrothauma*, *Oryzidium* and *Thyridachne*—represented only by morphological data, were excluded in the strict consensus tree. In some trees, *Hydrothauma* is placed as sister to either the Andropogoneae–Arundinelleae s.s.–Paniceae s.l. clade; the Andropogoneae–Arundinelleae s.s.–Paniceae $x = 10$ clade (Paspaleae); or the Paniceae s.s. $x = 9$ clade. *Thyridachne* is placed within Boivinellinae subclade, as sister to subclade Neurachninae, or in one of the three basal nodes within the Paniceae s.s. $x = 9$ clade. *Oryzidium* is placed as sister to *Melinis repens* (Willd.) Zizka within Melinidinae subclade, or as sister to *Reynaudia filiformis* (Spreng. ex Schult.) Kunth.

Discussion

Our phylogeny revealed good resolution within the PACMAD clade, and several major groups were recovered by *ndhF* in agreement with previous works (Gómez-Martínez and Culham, 2000; Duvall et al., 2001, 2007; Giussani et al., 2001; GPWG, 2001; Sánchez-Ken and Clark, 2007, 2010; Sánchez-Ken et al., 2007; Bouchenak-Khelladi et al., 2008).

Subfamily Micrairoideae

Recent phylogenetic studies (Duvall et al., 2007; Sánchez-Ken and Clark, 2007), based on DNA sequences, showed that the subfamily Panicoideae would be polyphyletic if tribe Isachneae was included. Sánchez-Ken et al. (2007) consequently reinstated the subfamily Micrairoideae including tribes Micraireae, Isachneae and Eriachneae. We sequenced two additional species of tribes Isachneae and Eriachneae, *Isachne leersioides* Griseb. and *Pheidochloa gracilis* S.T. Blake, respectively. Both taxa grouped within the Micrairoideae clade supported by a strong jackknife value of 99, in agreement with previous results (Duvall et al., 2007; Sánchez-Ken and Clark, 2007; Sánchez-Ken et al., 2007).

Hubbardia is a monotypic endemic genus from east India, which is recognized by having spikelets dorsally compressed with two flowers, disarticulation above the glumes, both glumes persistent, and the palea of both florets absent. Clayton and Renvoize (1986) and Sánchez-Ken and Clark (2010) treated this genus in tribe Hubbardieae, subfamily Panicoideae. Although DNA sequences were not obtained for *Hubbardia* in the present study, the combined analysis clearly indicates that the genus belongs to the Micrairoideae clade and is sister to *Isachne* (Fig. 1). All genera of subtribe Micrairioideae are characterized by having the upper anthecium cartilaginous. The placement of *Hubbardia* outside the Panicoideae is consistent with current molecular phylogenetic studies (Sánchez-Ken, unpublished data).

Subfamily Panicoideae s.l.

Subfamily Panicoideae s.l. (including Panicoideae + Centhothecoideae) is well supported with a strong jackknife value of 96 and 92 in the *ndhF* and combined analyses, respectively. Both analyses supported 11 out of 12 tribes proposed by Sánchez-Ken and Clark (2010) within the Panicoideae, because Hubbardieae was included into Micrairioideae (Fig. 1). Gynerieae and Thysanolaeneae are both monotypic tribes, while the other six tribes are monophyletic: Andropogoneae, Arundinelleae s.s., Centotheceae, Cyperochloeae, Tristachyideae and Zeugiteae. Our analyses do not support the monophyly of tribes Chasmanthieae, Paniceae s.l. and Steyermarkochloeae.

Tribe Steyermarkochloeae

Tribe Steyermarkochloeae includes two monotypic genera: *Steyermarkochloa* Davidse and R.P. Ellis and *Arundoclaytonia* Davidse and R.P. Ellis, endemic to Amazonian South America. Taxonomic classification of this tribe has been contradictory; Davidse and Ellis (1984, 1987), on the basis of anatomical and morphological characters, included this tribe under Arundinoideae, while Watson and Dallwitz (1992) suggested its close relation to Bambusoideae. GPWG (2001) and Zuloaga et al. (2003, 2007b) considered tribe Steyermarkochloeae in the Panicoideae, in agreement with Clayton and Renvoize (1986), who mentioned its resemblance to *Hymenachne* P. Beauv.

Steyermarkochloa angustifolia (Spreng.) Judz. is here included for the first time in a phylogenetic analysis. Whether using *ndhF* sequences alone or in combination with morphology, *Steyermarkochloa angustifolia* is sister to the Tristachyideae clade within the Panicoideae. However, the branch in the *ndhF* tree, together with that of *Reynaudia filiformis* [35 steps long, see below], is one of the longest in the data matrix, with a total of 45 changes. Since the sister clade of *Steyermarkochloa angustifolia* is a relatively long branch (38 changes), we excluded the Tristachyideae clade to explore if the position of *Steyermarkochloa angustifolia* was affected by long-branch attraction (Pol and Siddall, 2001). When the Tristachyideae clade was left out of the analyses, *Steyermarkochloa angustifolia* drifted to several positions and appeared related to the *Thysanolaena* clade or the *Orthoclada–Chasmanthium* clade, but was never sister to *Arundoclaytonia dissimilis*. Davidse and R.P. Ellis

Unfortunately, we failed to obtain a complete *ndhF* sequence of *Arundoclaytonia dissimilis*, hence we used the partial one obtained by Sánchez-Ken and Clark (2007). In our combined analysis (*ndhF* + morphology), *Arundoclaytonia* is nested within the Chasmanthieae clade, closely related to *Chasmanthium* and *Bromuniola*, in agreement with previous results reported by Sánchez-Ken and Clark (2010). While the monophyly of tribe Steyermarkochloeae should be tested further, its inclusion in subfamily Panicoideae is corroborated here.

Tribe Paniceae s.l.

We obtained *ndhF* sequences for almost all the diversity of the tribe Paniceae s.l.; 90% of the currently recognized genera of the tribe are represented here. Our molecular sampling is unique in the addition of many underrepresented genera and Old World entities, principally from Africa and Australia, such as taxa from subtribes Cenchrinae, Neurachninae, Setarinae and Spinificinae. We incorporated in the morphological matrix all genera recognized within the Paniceae. A previous phylogenetic study based only on morphology (Zuloaga et al., 2000) also included a large sample with more than 100 genera of Paniceae. However, the monophyly of the tribe was not tested (Zuloaga et al., 2000), as the tree was rooted with *Isachne* and no species of Andropogoneae or other panicoid tribes were considered.

In agreement with previous molecular studies (Gómez-Martínez and Culham, 2000; Giussani et al., 2001), our results showed that tribe Paniceae is paraphyletic and splits in two major clades, one including taxa with a basic chromosome number of $x = 10$. Most of the $x = 10$ Paniceae are plants of the Americas, with the exception of *Dallwatsoni*a B.K. Simon from Australia, and *Lecomtella* and *Baptorhachis* from Africa. This clade is clearly related to the Andropogoneae–Arundinelleae s.s. $x = 10$ clade, indicating that the basic chromosome number may be a synapomorphy. The second clade includes genera with a basic chromosome number of $x = 9$ and a pantropical distribution.

The American $x = 10$ Paniceae s.l. (= tribe Paspaleae)

Based on the *ndhF* phylogeny, the American $x = 10$ clade is moderately supported with jackknife values of 80 (58 in the combined analysis) if *Reynaudia* is considered part of it. If *Reynaudia* is excluded, the clade is strongly supported, with jackknife support values of 98 (93 in the combined analysis). *Reynaudia filiformis*, an endemic species from Cuba, is sister to the remaining $x = 10$ clade and shares with it a 6 bp insertion. However, the *ndhF* sequence of *R. filiformis* differs in several positions from the remainder sequences in the $x = 10$ clade, and is one of the longest branches, with 35 changes; the chromosome number is unknown for this species. *Reynaudia* differs from other members of the American $x = 10$ Paniceae s.l. in several characters of the spikelet, such as awned and bilobed glumes, and the fertile floret with two stamens. Although it is possible that *Reynaudia* is part of the American $x = 10$ clade, the taxon remains incertae sedis because of the moderate jackknife value and the divergent spikelet morphology. The genus was previously included in subtribe Arthropogoninae (Clayton and Renvoize, 1986; Zuloaga et al., 2007b), but it is distinct from *Achlaena*, *Altoparadisium* Filg., Davidse, Zuloaga and Morrone, and *Arthropogon* according to its phylogenetic position (see below).

Excluding *Reynaudia*, all other American $x = 10$ genera form a highly supported (98/93) monophyletic group with C_3, C_4 NADP–ME and intermediate C_3–C_4 genera, and 10 nucleotide synapomorphies; this group is assigned to tribe Paspaleae. The tribe is divided into three major subclades corresponding to the subtribes Arthropogoninae, Otachyriinae and Paspalinae.

Subtribe Otachyriinae

This subclade, which is concordant with previous groupings (Duvall et al., 2001; Giussani et al., 2001; Aliscioni et al., 2003), includes species of *Anthaenantia*, *Dallwatsonia*, *Hymenachne*, "*Panicum*" sect. Laxa, *Plagiantha* Renvoize, *Otachyrium* Nees, and *Steinchisma* Raf. The subclade is strongly supported both when analysing the *ndhF* data set independently or combined with morphology (jackknife values 93 versus 84). *Dallwatsonia*, a monotypic genus endemic to Australia

(Simmon, 1992), is morphologically similar to the American incertae sedis "*Panicum*" sect. Laxa. This genus shares with sect. Laxa the presence of a lax inflorescence with crowded spikelets disposed unilaterally on the branches, and an ellipsoid spikelet, with the lower glume shorter than the spikelet, while the upper anthecium is membraneous. It is noteworthy that *Dallwatsonia* and species of sect. Laxa share fusoid cells as seen in leaf cross-sections, although these are irregularly distributed in *Dallwatsonia*. This genus may have been introduced recently into Australia, as reported for *Cliffordiochloa parvispiculata* B.K. Simon [= *Steinchisma laxa* (Sw.) Zuloaga] (Simon, 2003) and for *Fasciculochloa sparshottiorum* B.K. Simon and C.M. Weiller [= *Steinchisma hians* (Elliot) Nash] (Simon, 1999).

Subtribe Paspalinae

Subclade Paspalinae includes *Anthaenantiopsis*, *Axonopus* P. Beauv., *Centrochloa* Swallen, *Echinolaena* Desv., *Gerritea* Zuloaga, Morrone and Killeen, *Hopia*, *Ichnanthus*, *Ocellochloa*, *Ophiochloa* Filg., Davidse and Zuloaga, *Paspalum*, *Reimarochloa* Hitchc., *Renvoizea*, *Spheneria* Kuhlm., *Streptostachys* Desv., *Thrasyopsis* Parodi, *Panicum validum* Mez, and *P. tuerckheimii* Hack. (both "*Panicum*" species as incertae sedis), most of them having unilateral inflorescences, with C_3 or C_4 NADP–ME photosynthetic pathways. Some genera have a stipe and disarticulate at the base of the upper anthecium, while other genera are characterized by the presence of simple papillae and bicellular microhairs at the apex or base of the upper palea. The clade is moderately supported (jackknife values for *ndhF* 86; combined 82; Fig. 1) and characterized by three molecular synapomorphies. In the combined analysis, the genera *Lecomtella* and *Baptorhachis* are represented by morphological data and fall within subclade *Paspalinae*, although the position has little jackknife support. *Lecomtella* is a monotypic genus endemic to Madagascar with an unusual arrangement of spikelets on the branches, having bisexual spikelets at the tips of the branches and staminate ones below (Clayton and Renvoize, 1986), and a peculiar winged stipe at the base of the upper floret. *Baptorhachis* is endemic to Mozambique, and has an inflorescence with a solitary raceme with broad foliaceous rachis and spikelets with the lower glume absent.

The largest genera within subclade Paspalinae, *Axonopus* and *Paspalum* are both paraphyletic (Giussani et al., 2001; Aliscioni, 2002). *Centrochloa* and *Ophiochloa* are nested within *Axonopus* in a clade supported by 17 molecular synapomorphies, four of which are non-homoplastic, in agreement with López and Morrone (2010). *Reimarochloa*, *Spheneria* and *Thrasyopsis* are included within the *Paspalum* clade by three homoplastic molecular synapomorphies, in agreement with previous results (Scataglini et al., 2007; Rua et al., 2010). During the past decade, the circumscription of *Paspalum* has changed to include *Thrasya* in *Paspalum* subgenus Harpostachys (Denham, 2005; Denham and Zuloaga, 2007). In order to keep *Axonopus* and *Paspalum* both monophyletic, it would be necessary to include *Centrochloa* and *Ophiochloa* in *Axonopus*; and *Spheneria*, *Thrasyopsis* and *Reimarochloa* in *Paspalum*.

When describing *Acostia*, a monotypic genus from Ecuador, Swallen (1968) pointed out its resemblance to *Digitaria* Haller and *Panicum*, distinguishing the genus by the absence of the lower glume. Webster et al. (1989) related this genus to *Panicum* and included *Acostia* in its synonymy. In our results, based on the combined analysis, *Acostia* is not related to *Panicum* s.s. or to *Digitaria*, but is sister to the *Axonopus–Centrochloa–Ophiochloa* clade, with which it shares a reduced or absent lower glume, and a cartilaginous upper anthecium.

Subtribe Arthropogoninae

The relationship of the genera of Arthropogoninae to other Panicoideae has been controversial. Some of them were placed in the tribe Andropogoneae (Kunth, 1833; Steudel, 1853–1855); Tristegineae (Bentham, 1881; Hackel, 1887); or Melinidinae (Bews, 1929; Hitchcock, 1936; Roshevitz, 1937), or were grouped in an independent tribe, Arthropogoneae (Pilger, 1954). Our results place the Arthropogoneae within the tribe Paspaleae, so their name becomes subtribe Arthropogoninae; the other tribes are distantly related, with tribe Andropogoneae in the $x = 10$ Andropogoneae clade, and tribes Melinidinae and Tristegineae (= Melinidinae) as part of the $x = 9$ Paniceae s.s. clade.

Subclade Arthropogoninae, also called the "Ambiguous clade" by Giussani et al. (2001), included several heterogeneous genera with noteworthy variation in morphological, anatomical and physiological characters. This subclade is weakly supported when analysing the *ndhF* sequences on their own (jackknife value of 73) but with very low support when jackknifing the combined data set (jackknife value of 54); a total of three molecular synapomorphies define the group. Subclade Arthropogoninae includes seven genera with C_3 photosynthetic pathway (*Apochloa*, *Canastra*, *Homolepis* Chase, *Oplismenopsis* Parodi, *Phanopyrum* (Raf.) Nash, *Stephostachys* and *Triscenia*) while the remaining nine genera are C_4 NADP–ME (*Achlaena*, *Altoparadisium*, *Arthropogon*, *Coleataenia*, *Cyphonanthus*, *Keratochlaena*, *Mesosetum* Steud., *Oncorachis*, and *Tatianyx* Zuloaga and Soderstr.). *Apochloa*, *Canastra*, *Coleataenia* and *Cyphonanthus* have been segregated recently from *Panicum* s.l. (Zuloaga et al., 2006, 2010; Morrone et al., 2007; Sede et al., 2008), whereas *Kera-*

tochlaena and *Oncorachis* (Sede et al., 2009b) were segregated from *Streptostachys*. In the *ndhF* phylogeny, three minor subclades within the subclade Arthropogoninae are highly supported and include anatomically uniform C_4 NADP–ME genera (with the exception of *Triscenia*, a monotypic non-Kranz genus). The *Achlaena*, *Altoparadisium* and *Arthropogon* subclade (jackknife value of 100 in both analyses) is supported by 18 nucleotide substitutions; these genera share a hairy callus at the base of the spikelet and the upper anthecium is laterally compressed; *Achlaena* and *Altoparadisium* show distinctive Kranz cells. In the second subclade, *Coleataenia* and *Triscenia* share five base-pair changes. *Triscenia* is a monotypic genus endemic to Cuba, and similar to *Coleataenia* in its racemose inflorescence and spikelet morphology; *Triscenia* differs from *Coleataenia* by having the upper anthecium cartilaginous with flat margins and non-Kranz anatomy. A third group is a subclade comprised of three genera, *Keratochlaena*, *Mesosetum* and *Tatianyx*, that have a caryopsis with a linear hilum; this subclade is supported by 10 substitutions (jackknife value of 99 in both analyses). The linear hilum is, however, a homoplasious character state, being also present in *Homolepis*, *Oncorachis* and *Oplismenopsis* (Arthropogoninae), in *Streptostachys* (Paspalinae), and in *Acroceras* Stapf and *Louisiella* C.E. Hubb. and J. Léonard ($x = 9$ Paniceae s.s.).

The Pantropical $x = 9$ Paniceae (= tribe Paniceae s.s.)

The Paniceae s.s. clade, most members of which have a basic chromosome number of $x = 9$, has a jackknife value of 76 for *ndhF* data alone and 77 when combining both data sets; the group is distributed in tropical and subtropical regions of the world. Although the basal generic relationships are not resolved, there are well established groups within the $x = 9$ clade.

Subtribe Anthephorinae

Traditionally, all genera with highly modified inflorescences were grouped in subtribe Cenchrinae sensu Clayton and Renvoize (1986). Our study showed that Cenchrinae is not monophyletic, and that modified inflorescences have evolved independently by non-homologous characters in two different lineages: within genera of the "Bristle clade" (see below), bristles are homologous to an inflorescence branch (Koch, 1843; Sohns, 1955; Butzin, 1977); in the Anthephorinae subclade, the involucral bracts are possibly derived from the lower glume or from sterile spikelets (Reeder, 1960; Clayton and Renvoize, 1986). In the present analysis, the Anthephorinae subclade is supported by 16 base changes and an 18 bp long deletion, with a strong jackknife value of 99 and 88 in the *ndhF* or the combined analysis, respectively. Anthephorinae includes seven genera, of which *Anthephora*, *Chaetopoa* C.E. Hubb., *Chlorocalymma* Clayton, *Tarigidia* and *Trachys* have involucral structures (the other two genera are represented only by morphological data). These five genera are related to *Megaloprotachne* C.E. Hubb. and *Digitaria*, which lack involucral bracts. *Tarigidia* represents an intermediate form between *Anthephora* and *Digitaria* (Loxton, 1974; Vega et al., 2010); its resemblance to *Anthephora* is represented by spicifom and terete inflorescences, spikelets grouped in clusters and surrounded by several glumes, occasionally fused, which are almost as long as the lower lemmas. Similarities between *Digitaria* and *Tarigidia* are mostly due to the characteristic flattened upper lemma with broad, thin margins. In *Trachys*, the spikelets are associated with bractiform involucres, which are formed by reduced spikelets surrounding the clusters.

Subtribe Cenchrinae

The "Bristle clade" or subtribe Cenchrinae within Paniceae s.s. is moderately well supported, with jackknife values of 76/80 in the *ndhF* versus combined analysis. The genera in this subtribe are characterized by setae in the inflorescence, although the setae can be modified in various ways. The position and abundance of setae is variable; they can be solitary and present only at the tips of the branches, or numerous and associated with every spikelet, or solitary and associated with only a few spikelets of the inflorescence. Doust and Kellogg (2002), in their study of the development of the inflorescence in species of the "Bristle clade", showed that all taxa are quite similar at early stages of development; later on, changes in the extent of branching, the differentiation pattern of primordia, and the elongation of the inflorescence axis together caused the marked differences seen among the mature inflorescences. Among genera here included in the subtribe Cenchrinae, several were previously placed in the "Bristle clade": *Cenchrus*, *Ixophorus* Schltdl., *Odontelytrum* Hack. (= *Cenchrus*), *Paspalidium* Stapf (= *Setaria* L.), *Pennisetum* (= *Cenchrus*), *Pseudoraphis* Griff., *Setaria*, *Spinifex* L., *Stenotaphrum* Trin., *Uranthoecium* Stapf, and *Zygochloa* S.T. Blake. In addition, we have confirmed the placement here of two taxa without bristles: *Panicum antidotale* Retz. and *Zuloagaea bulbosa* (Kunth) Bess (Gómez-Martínez and Culham, 2000; Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001; Doust and Kellogg, 2002; Aliscioni et al., 2003; Doust et al., 2007; Donadío et al., 2009; Kellogg et al., 2009; Chemisquy et al., 2010). The *ndhF* sequence data also confirm the placement in this clade of *Chamaeraphis*, *Dissochondrus* (Hillebr.) Kuntze, *Hygrochloa* Lazarides, *Paractaenum* P. Beauv., *Paratheria*, *Pseudochaetochloa* Hitchc., *Setariopsis* Scribn. and *Xerochloa*, a result consistent with the presence of setae in their inflorescences. Morphological data in the combined analysis also place *Holcolemma* and *Streptolophus* in the Cenchrinae. *Holcolemma* is a genus of four species that grow in Eastern Africa, Southern Asia and Australia; this genus is characterized by a contracted inflorescence, with the terminal spikelet of each branch associated with an inconspicuous seta. *Holcolemma* is similar to species of *Setaria*, but is distinguished by its winged lower palea; the latter character is also a feature of the monotypic Mexican genus *Ixophorus*. In the combined analysis, *Holcolemma* and *Ixophorus* appear as sister species. *Streptolophus*, a monotypic genus from Angola with spikelets surrounded by a spiny involucre, is sister to *Paratheria prostrata* Griseb., which has solitary spikelets subtended by large, solid setae.

In addition to *Zuloagaea bulbosa* and *Panicum antidotale*, our analyses identified four genera of the clade that also lack setae: *Acritochaete* (morphology only), *Alexfloydia* B.K. Simon, *Snowdenia*, and *Whiteochloa* C.E. Hubb. Bess et al. (2005) reported that the inflorescence development of *Zuloagaea bulbosa* is similar to that of *Panicum miliaceum* L. (type species of *Panicum* s.s.), and that the former species is anomalous in having lost the synapomorphy of the "Bristle clade". As in *Zuloagaea bulbosa*, *Panicum antidotale*, *Whiteochloa capillipes* (Benth.) Lazarides, and *Alexfloydia repens* B.K. Simon have spikelets and inflorescences that are morphologically similar to those of *Panicum* s.s.; developmental patterns in these species should be studied to determine the basis for the absence of bristles. *Acritochaete*, a monotypic genus of Eastern Africa, without setae, was thought by Clayton and Renvoize (1986) to be related to *Digitaria*; this genus has a small lower glume and a chartaceous–cartilaginous upper anthecium similar to that in *Cenchrus* and related genera; its inclusion in this clade needs to be confirmed by DNA data. In addition, *Snowdenia*, nested within *Cenchrus*, has spikelets similar to those present in *Cenchrus unisetus* (Clayton and Renvoize, 1986), and could represent a distinct case of suppression of setae during inflorescence development. The absence of setae in at least six taxa in the group represents independent losses during evolution.

Subtribe Melinidinae

Our analysis confirms previous results in this subtribe (Gómez-Martínez and Culham, 2000; Giussani et al., 2001; Aliscioni et al., 2003; Christin et al., 2007, 2008; Vicentini et al., 2008; Salariato et al., 2010). The Melinidinae includes 12 genera plus *Panicum deustum* Thunb., and is weakly supported by jackknife values of 66 in the *ndhF* analysis and 62 in the combined analysis. The subtribe is characterized by mainly C_4 photosynthesis, with leaf anatomy characteristic of the PEP–CK subtype. The subtribe includes genera that are remarkably variable in vegetative and reproductive characters. Some genera have lax branched inflorescences (e.g. *Melinis*, *Tricholaena*) whereas others have unilateral racemes (e.g. *Moorochloa* Veldkamp, *Urochloa* P. Beauv.). The genus *Thuarea* has highly specialized inflorescences, with one to two persistent bisexual spikelets in the basal portion of a leafy rachis and several deciduous staminate spikelets in the distal portion; also, in this genus the rachis, after fertilization, bends to enclose the fruit in a structure similar to a capsule. Within the Melinidinae, the lower glume varies greatly in length, from absent (in *Yvesia* A. Camus and *Thuarea*), to rudimentary or nearly as long as the spikelet; both glumes, the lower lemma and the upper anthecium are muticous or aristate, the upper anthecium is smooth or with conspicuous transverse rugosities with simple or compound papillae present. *Eccoptocarpha*, a monotypic genus from Africa, Tanzania and Zambia, is sister to *Moorochloa* in the analyses of the combined matrix. This genus has PEP–CK anatomy, and is distinguished morphologically from *Moorochloa* by having the upper anthecium borne on a slender, sinuous rachilla internode, and by having a reticulate network of veins on the upper glume and lower lemma; the latter character was also observed in some species of *Urochloa* (e.g. *U. humidicola*, *U. dictyoneura*). In spite of the morphological variability found in this clade, two subclades were recovered. The first subclade, which includes *Leucophrys* Rendle, *Melinis*, *Moorochloa* and *Tricholaena*, is strongly supported: the genera share five base changes and morphological characters, such as disarticulation at the base of the upper anthecium, and the upper anthecium smooth and shiny. The other subclade, which includes *Chaetium*, *Eriochloa*, *Megathyrsus*, *Scutachne* Hitchc. and Chase, and *Urochloa*, is also strongly supported: all these genera share seven base changes, although we found no morphological characters as synapomorphies.

Subtribe Panicinae

Based on our molecular and combined analyses, *Arthragrostis*, *Louisiella*, *Panicum* s.s., and *Yakirra* Lazarides and R.D. Webster form a well supported clade, the subtribe Panicinae (jackknife values of 65 and 93 in the *ndhF* and combined analysis, respectively). All these genera are C_4 NAD–ME. *Arthragrostis*, a monotypic genus from Australia, is in a large polytomy together with *Panicum* and *Louisiella*. *Arthragrostis* is distinguished by having primary inflorescence branches deciduous and upper anthecium stipitate; this stipe is formed by a filiform internode of the rachilla without lateral appendages (see discussion of this character below). *Yakirra*, a genus with five species that grow in Myanmar and Australia, is also characterized by the presence of a homogeneous stipe at the base of the upper anthecium; this stipe includes two small auricles in its distal portion. In the molecular analysis, *Yakirra* is placed as sister to the remaining species of the Panicinae, while in the combined analysis it is nested in a clade with some species of *Panicum* s.s. and *Arthragrostis*. Both *Arthragrostis* and *Yakirra* are morphologically similar to species of *Panicum* sect. Rudgeana in having an open and lax panicle, spikelets dorsiventrally compressed, similar nervation of glumes and lower lemma, and upper anthecium indurate, glabrous, and with simple or compound papillae toward the apex of lemma and palea (Zuloaga, 1987); moreover, all species of *Panicum* sect. Rudgeana have a stipitate upper anthecium. However, this stipe is heterogeneous in sect. Rudgeana and homogeneous in both *Arthragrostis* and *Yakirra*. A stipitate upper anthecium has originated several times independently within the Paniceae s.l. It has been observed in *Echinolaena*, *Ichnanthus* and *Paspalum*, and in some species of *Dichanthelium* (Hitchc. and Chase) Gould, *Renvoizea* and *Ocellochloa*. The elongation of the rachilla between the lower and the upper lemma could be part of a strategy for dispersal of the caryopsis; Davidse (1987) pointed out that the stipe at the base of the anthecium in species of *Echinolaena*, *Ichnanthus* and *Panicum* is an elaiosome, connected with dispersal by ants. Based on our results and the similar features observed in *Arthragrostis*, *Panicum* s.s. and *Yakirra*, these three taxa could eventually be considered in a single genus. *Louisiella*, the remaining genus in subtribe Panicinae, is monotypic and grows in western Africa; this genus is in a strongly supported clade, both in the molecular and combined analysis, with *Panicum elephantipes* Nees ex Trin., an American member of sect. Dichotomiflora of *Panicum* s.s. *Louisiella* shares with *P. elephantipes* several characters and ecological preferences, such as plants floating or decumbent on mud, culm internodes spongy, ligules membraneous–ciliate, spikelets with the lower glume reduced, upper glume and lower lemma acuminate, longer than the upper anthecium. *Louisiella* differs from *P. elephantipes* and members of sect. Dichotomiflora in having a caryopsis with a linear hilum. A more detailed study of *Panicum* s.s. is necessary to circumscribe this genus and to establish its relationships with *Arthragrostis*, *Louisiella* and *Yakirra*.

Subtribe Neurachninae

Blake (1972) grouped *Neurachne*, *Paraneurachne* S.T. Blake, and *Thyridolepis* S.T. Blake in tribe Neurachneae. Later, Clayton and Renvoize (1986) included these genera in the subtribe Neurachninae within the tribe Paniceae s.l. Our study showed a close relationship of these three genera with others previously included in subtribe Setariinae (Clayton and Renvoize, 1986): *Ancistrachne* S.T. Blake, *Calyptochloa* C.E. Hubb., and *Cleistochloa* C.E. Hubb. As a result, the Neurachninae clade includes in our analysis six genera, four of them endemic to Australia: *Calyptochloa*, *Neurachne*, *Paraneurachne* and *Thyridolepis*; while *Ancistrachne* also extends to south-eastern Asia, the Philippines and New Caledonia; and *Cleistochloa* grows in Australia and New Guinea. The Neurachninae clade is only weakly supported in the molecular analysis, with a jackknife value of 63, but is strongly supported in the combined analysis (jackknife value of 94). The subtribe is characterized by having inflorescences with reduced secondary branches, and spikelets abaxially disposed. From an anatomical and physiological point of view, the Neurachninae includes four non-Kranz genera: *Ancistrachne*, *Calyptochloa*, *Cleistochloa* and *Thyridolepis*) and one Kranz genus of the NADP–ME subtype, (*Paraneurachne*); while *Neurachne* is atypical in including non-Kranz species, Kranz species of the subtype NADP–ME but with anatomical deviations, and C_3/C_4 intermediates such as *N. minor* S.T. Blake. The NADP–ME photosynthetic subtype represents here a derived feature from C_3, and has evolved independently from the rest of the Paniceae; the C_3/C_4 intermediate species appear to be transitional stages. *Calyptochloa* and *Cleistochloa* are closely related genera with several synapomorphies, such as the presence of cleistogenes in leaf axils, secondary inflorescence branches reduced to a single adaxial spikelet, the lack of a lower palea, and macrohairs on the upper palea.

Subtribe Boivinellinae

Giussani et al. (2001) recognized as the "Forest shade clade" a group of genera of forest shade habitats: *Acroceras*, *Echinochloa* P. Beauv., *Lasiacis* (Griseb.) Hitchc., *Oplismenus* P. Beauv., *Parodiophyllochloa*, and *Pseudechinolaena* Stapf. In this study, the clade is expanded to include *Alloteropsis* J. Presl, *Amphicarpum* Kunth, *Cyrtococcum* Stapf, *Cyphochlaena*, *Entolasia* Stapf, *Ottochloa* Dandy and *Microcalamus*; all 10 genera are therefore taxonomically circumscribed in subtribe Boivinellinae. *Microcalamus* is represented only by morphological data; nevertheless, preliminary *ndhF* data for *Microcalamus* confirms its position in the subtribe (C. Grennan and M. Duvall, pers. comm.); when including morphological data in the combined analysis, *Microcalamus* is sister to *Acroceras*. The Boivinellinae was moderately supported by jackknife values of 81/72 when using *ndhF* sequences or combined data sets, respectively; the subtribe is supported by three molecular changes. Furthermore, several genera, such as *Acroceras*, *Amphicarpum*, *Cyphochlaena*, *Cyrtococcum*, *Entolasia*, *Lasiacis*, *Microcalamus*, *Oplismenus*, *Ottochloa*, *Parodiophyllochloa* and *Pseudechinolaena*, are C_3, prefer the interior or edge of forests, and all have broad leaves. *Echinochloa* is a C_4 NADP–ME genus; its position, when analysing sequences of *phyB*, a coding gene from the nucleus, is unrelated to the Boivinellinae clade (Vicentini et al., 2008), a fact that might be attributed to hybridization or reticulation events. Finally, *Alloteropsis* is a heterogeneous genus, including C_4 PEP–CK, C_4 NADP–ME, C_4 NAD–ME, or non-Kranz species (Ellis, 1977; Hattersley and Watson, 1992; Ibrahim et al., 2009).

Subclade A (Dichanthelium—"Panicum" sect. Clavelligerae)

This subclade, previously described by Giussani et al. (2001) and Aliscioni et al. (2003), includes American species of the genus *Dichanthelium* and African species of "*Panicum*" sect. Clavelligerae. Although the *Dichanthelium*–Clavelligerae subclade is well supported in our analyses, with 15 bp substitutions and jackknife values of 99/100, its final position and relationships with other Paniceae are uncertain. Species of *Dichanthelium* (ca. 55) are characterized by having inflorescences with cleistogamous and chasmogamous flowers, and many species with foliar dimorphism. Species of "*Panicum*" sect. Clavelligerae (ca. 10) share the presence of spikelets with conspicuous glandular hairs. To confirm relationships within this subclade, it will be necessary to study more representatives of *Dichanthelium* and Clavelligerae.

Subclade B (Poecilostachys–Sacciolepis–Trichanthecium–Panicum incertae sedis)

Subclade B comprises the genera *Sacciolepis* Nash and *Trichanthecium* (Zuloaga et al., 2011), together with species of *Panicum* incertae sedis of sections Monticola and Verrucosa (Aliscioni et al., 2003), and ungrouped species of "*Panicum*". Most of the taxa included here are non-Kranz, have a disarticulation zone at the base of the upper anthecium, and have bicellular microhairs at the apex or all over the anthecium surface. Morphological synapomorphies need to be explored for better characterization of all species of the clade. Also, relationships among species of this clade and those of subtribe Boivinellinae should be scrutinized with the addition of other American and African species. The genus *Poecilostachys* Hack. is embedded in this clade only when using molecular data, with a jackknife value of 81. In the combined analysis, *Poecilostachys* and *Hylebates* Chippin. are sister taxa, although this subclade is unsupported. Both genera occur in forest shade areas and are characterized by their broad leaves and open panicles. As a result, the relationship of both genera with other Paniceae s.s. is still not resolved.

Subclade C (Walwhalleya–Homopholis)

Homopholis C.E. Hubb. is a small genus with two species endemic to Australia (Webster, 1987). Recently, Willis et al. (2000) and Bruhl et al. (2006) restricted the genus to only one species, *Homopholis belsonii* C.E. Hubb., and transferred *H. proluta* (F. Muell.) R.D. Webster and *Panicum subxerophilum* Domin to the new Australian genus *Walwhalleya* Wills and J.J. Bruhl, with an additional new species, *W. pungens* (Wills and J.J. Bruhl) Wills and J.J. Bruhl. Our study grouped both genera in a well supported clade with jackknife values of 97/99. This result contradicts that of Willis et al. (2000), who related *Walwhalleya* to *Digitaria*, *Entolasia*, and species of *Panicum* s.l. *Homopholis* and *Walwhalleya* are both physiologically C_3 genera and sister to the subclade that includes the three photosynthetic C_4 pathways (NADP–ME, PEP–CK and NAD–ME) in subtribes Cenchrinae, Melinidinae and Panicinae. This sister relationship is present in the strict consensus tree of both *ndhF* and the combined analyses, and could represent a link to a non-Kranz ancestor for the three C_4 subtribes.

Character evolution

Photosynthetic pathway. In all optimal trees, from both the combined data set and the *ndhF* sequence analyses, C_4 photosynthesis is plesiomorphic for the Paspaleae–Andropogoneae–Arundinelleae s.s. clade, and is followed by four reversals to C_3. This unambiguous optimization is obtained because the C_4 species *Reynaudia* is the sister group to the Paspaleae in all optimal trees. When analysing the combined data set, all three main clades within the Paspaleae (Arthropogoninae, Otachyriinae and Paspalinae) are ambiguous concerning the plesiomorphic state of the photosynthetic pathway. For these three clades, the ambiguous optimization is resolved in favour of a plesiomorphic C_4 pathway due to the position of *Reynaudia* and the Andropogoneae–Arundinelleae s.s. clade (see optimization in Fig. 2). The position of *Reynaudia* is weakly to moderately supported, and remains as incertae sedis (see above). If *Reynaudia* was placed elsewhere in the tree, or was not included, the ancestral photosynthetic pathway for the Paspaleae–Andropogoneae–Arundinelleae s.s. clade as well as the Paniceae s.s. would be unambiguously C_3, and there would be multiple origins of C_4. The latter result is consistent with the previous work of Christin et al. (2008) and Vicentini et al. (2008).

When analysing the combined data set, Anthephorinae is basal in the Paniceae s.s. This topology causes an ambiguous optimization of the photosynthetic pathway at the root of Paniceae s.s., as well as an ambiguous optimization of the entire Paniceae s.l. (Paniceae s.s. + Paspaleae) + Andropogoneae–Arundinelleae s.s. clade. Note that these two ambiguous optimizations are resolved in favour of a plesiomorphic C_3 photosynthesis both in Paniceae s.s. and at the base of the Paniceae s.l.–Andropogoneae–Arundinelleae s.s. clade in some trees

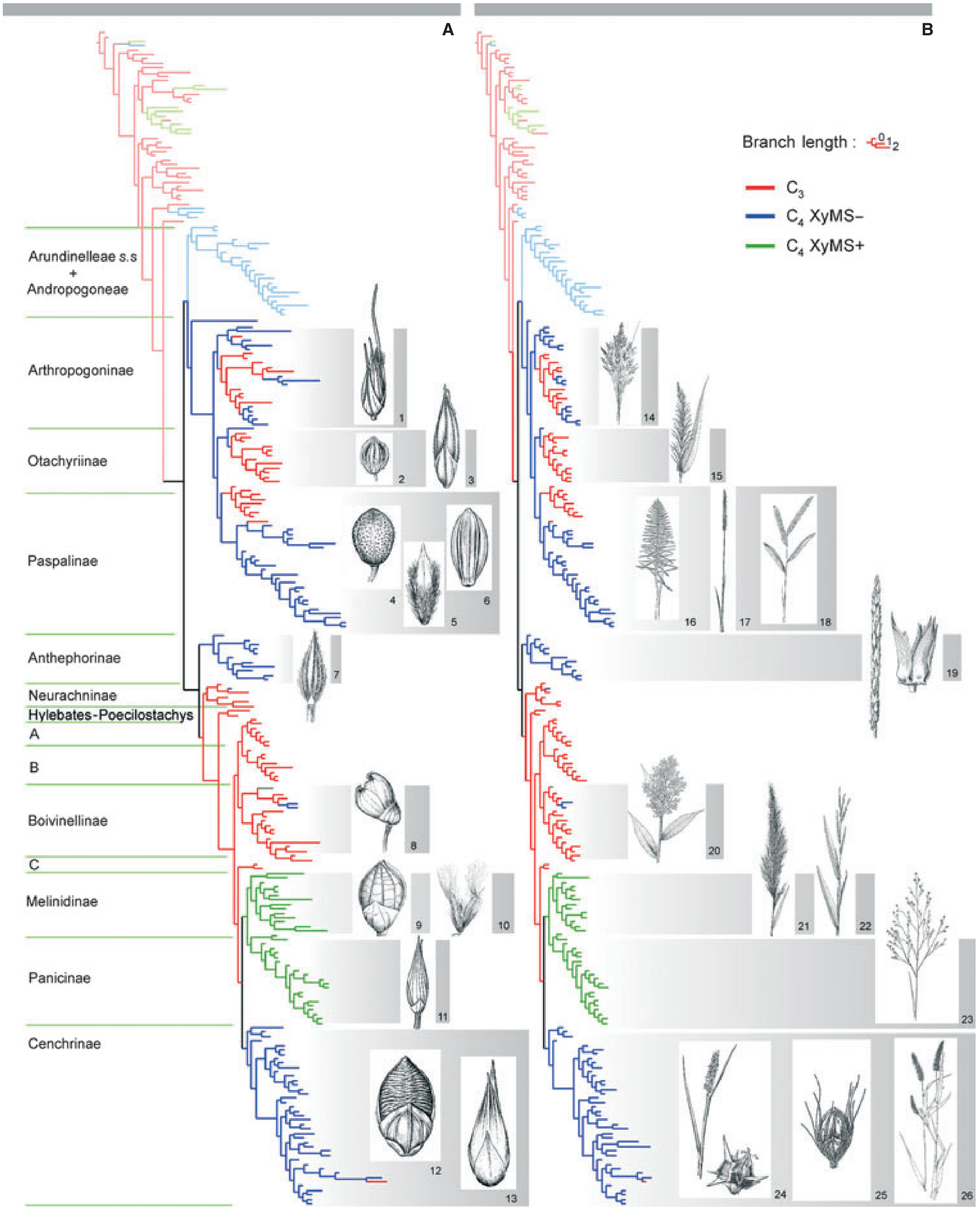

Fig. 2. Character evolution within the subfamily Panicoideae s.l. shown as phylograms for 35 spikelet characters (A) and 17 inflorescence characters (B) when optimized on one of the optimal trees for the combined data set. Changes in the photosynthetic pathway have been optimized on both phylograms. Line drawings represent morphological variations in the spikelets (1–13) and quantitatively modified inflorescences in subtribes Paspalinae, Anthephorinae and Cenchrinae. References: 1, *Oplismenopsis najada*; 2, *Otachyrium versicolor*; 3, 15, *Hymenachne amplexicaulis*; 4, *Paspalum arenarium*; 5, *Paspalum lilloi*; 6, *Paspalum simplex*; 7, *Digitaria ciliaris*; 8, 20, *Lasiacis sorghoidea*; 9, *Urochloa fusca*; 10, *Melinis repens*; 11, *Panicum elephantipes*; 12, 25, *Setaria parviflora*; 13, *Cenchrus myosuroides*; 14, *Coleataenia prionitis*; 16, *Paspalum densum*; 17, *Paspalum lachneum*; 18, *Paspalum ceresia*; 19, *Anthephora hermaphrodita*; 21, *Melinis minutiflora*; 22, *Urochloa plantaginea*; 23, *Panicum peladoense*; 24, *Cenchrus spinifex*; 26, *Setaria verticilliformis*.

when the C_3 species *Hydrothauma manicatum* is included in the matrix. In the three possible placements of *H. manicatum* (see Results), an ambiguous optimization of the photosynthetic pathway is retained only when *H. manicatum* is placed as sister to the entire Paniceae s.l.–Andropogoneae–Arundinelleae s.s. clade. Obtaining a DNA sample for *Hydrothauma* could therefore potentially add information concerning the plesiomorphic photosynthetic pathway within the Paniceae s.s.

Morphological characters. Paniceae s.l. includes an enormous morphological diversity, mainly recognized as different patterns of spikelet and inflorescence type. Changes in the spikelets, such as size and nervation of the glumes, as well as texture and ornamentation of lemma and palea, were among the most common morphological modifications and constituted nearly two-thirds of the coded morphological characters. Illustrations of the morphological variability of the spikelets within the tribes Paspaleae and Paniceae s.s. are shown in Fig. 2A. Branch lengths in Fig. 2A show that changes in spikelet characters have occurred in all subtribes. Major groups are defined by some changes, such as papillae at the apex of the upper palea in the Panicinae; absence of lower glume in most species of the Paspalinae (Fig. 2A, 4–6); and reduction in number of nerves in the glume in all species of Anthephorinae (Fig. 2A, 7). However, most spikelet characters characterize minor clades within subtribes, such as awned glumes in *Oplismenopsis*, *Canastra*, *Arthropogon*, *Altoparadisium* and *Achlaena* (Arthropogoninae, Fig. 2A, 1); expanded lower palea in *Otachyrium*, *Plagiantha* and *Steinchisma* (Otachyriinae, Fig. 2A, 2); and herbaceous lemma and palea in *Hymenachne* (Otachyriinae, Fig. 2A, 3).

The inflorescences show fewer qualitative changes than the spikelets do within the tribes Paspaleae and Paniceae s.s. In general, most of the variation among the inflorescences is found in quantitative changes of the lateral branching as well as internode length within the panicles, yielding large, lax, multiflorous to smaller, more compressed, and few flowered inflorescences.

Qualitative modifications of the inflorescences within Paniceae s.l. include abortion of the fertile apex of the main axes and rachises in Paspalinae, Anthephorinae and Cenchrinae; lack of branching beyond first order; and modification of the disarticulation zone of the diaspores. The plesiomorphic diaspore involves disarticulation at the base of the spikelet, such that the caryopsis falls together with the glumes. This disarticulation has been modified towards more inclusive diaspores that articulate at the base of the primary branches or main axes. For more thorough description of these characters and their morphological implications in each clade, see the discussion of the subtribes above.

Notably, qualitative inflorescence character changes are nearly absent in several of the major C_3 clades, not contributing to the branch lengths in these clades or in subtribes Melinidinae and Panicinae (Fig. 2B). Qualitative modifications of the inflorescences seem to have occurred nearly exclusively within the major C_4 XyMS clades Paspalinae, Anthephorinae and Cenchrinae (Fig. 2B, 16–19, 24–26), the one exception being the highly modified inflorescences in *Thuarea* (Melinidinae).

A relationship between C_4 XyMS photosynthesis and modified inflorescences is reported here for the first time. The basis for such a co-evolution is uncertain, but the presence of unmodified inflorescences at the base of the major C_4 XyMS clades suggests that the modification of the inflorescences in terminal clades would be a delayed response to the change in photosynthetic pathway (see Giannini and Goloboff, 2010 for a discussion on delayed responses of phylogenetic correlated characters).

Taxonomic considerations

Based on our results, we propose changes to the classification of Panicoideae to realign the genera of the subfamily with particular emphasis on the tribe Paniceae s.l. *Hubbardia*, treated under the monotypic tribe Hubbardieae in Panicoideae, is now included in the subfamily Micrairoideae. Tribe Paniceae s.l. must be split into two tribes: Paspaleae, to include the American $x = 10$ Paniceae genera; and Paniceae s.s., to include the Pantropical $x = 9$ Paniceae genera. Within this classification we propose a new realignment of subtribes based on molecular and morphological synapomorphies.

Tribe **Paspaleae** J. Presl, Reliq. Haenk. 1(4–5): 208. 1830. TYPE: *Paspalum* L., Syst. Nat. (ed. 10) 2: 846, 855, 1359. 1759.

= Lecomtelleae Pilg. ex Potztal, Willdenowia 1: 771. 1957. TYPE: *Lecomtella* A. Camus, Compt. Rend. Hebd. Séances Acad. Sci. 181: 567. 1925.

We propose to reinstate the tribe Paspaleae for the species in the Paniceae $x = 10$ clade. The genera of this clade are mostly native to the Americas, with a basic chromosome number of $x = 10$. Ecologically and morphologically, the group is remarkably variable and includes species that are non-Kranz, species that are Kranz with the C_4 NADP–ME subtype, and species that are physiologically intermediate between C_3 and C_4.

Subtribe **Arthropogoninae** Butzin, Willdenowia 6(3): 516. 1972. TYPE: *Arthropogon* Nees, Fl. Bras. Enum. Pl. 2(1): 319. 1829.

Photosynthetic pathway. C_3, C_4 NADP–ME.

The subtribe includes 16 genera and approximately 68 American species:

Achlaena (1), *Altoparadisium* (2), *Apochloa* (15), *Arthropogon* (3), *Canastra* (2), *Coleataenia* (7), *Cyphonanthus* (1), *Homolepis* (5), *Keratochlaena* (1), *Mesosetum*

(25), *Oncorachis* (2), *Oplismenopsis* (1), *Phanopyrum* (1), *Stephostachys* (1), *Tatianyx* (1), *Triscenia* (1).

Subtribe **Otachyriinae** Butzin, Willdenowia 6: 182. 1970. TYPE: *Otachyrium* Nees, Fl. Bras. Enum. Pl. 2(1): 271 (misprinted as p. 273). 1829.

Photosynthetic pathway. C_3, C_4 NADP–ME and C_3–C_4 intermediates.

The subtribe includes six genera and incertae sedis species of "*Panicum*" sect. Laxa; five genera are American, and one endemic to Australia. The subtribe has a total of seven genera and approximately 38 species:

Anthaenantia (4), *Dallwatsonia* (1), *Hymenachne* (7), *Otachyrium* (7), *Panicum* group *Laxa* (12), *Plagiantha* (1), *Steinchisma* (6).

Subtribe **Paspalinae** Griseb., Spic. Fl. Rumel. 2: 468. 1846. TYPE: *Paspalum* L., Syst. Nat. (ed. 10) 2: 846, 855, 1359. 1759.

= Reimarochloinae Caro, Dominguezia 4: 41. 1982. TYPE: *Reimarochloa* Hitchc., Contr. U.S. Natl. Herb. 12(6): 198. 1909.

Photosynthetic pathway. C_3 and C_4 NADP–ME.

The subtribe includes 19 genera, mainly from America, with two Old World genera: *Lecomtella* and *Baptorhachis*, and approximately 475 species:

Acostia (1), *Anthaenantiopsis* (4), *Axonopus* (85), *Baptorhachis* (1), *Centrochloa* (1), *Echinolaena* (8), *Gerritea* (1), *Hopia* (1), *Ichnanthus* (30), *Lecomtella* (1), *Ocellochloa* (12), *Ophiochloa* (2), *Panicum* s.l. (2), *Paspalum* (310), *Reimarochloa* (3), *Renvoizea* (10), *Spheneria* (1), *Streptostachys* (2), *Thrasyopsis* (2).

Tribe **Paniceae** R. Br., Voy. Terra Austral. 2: 582. 1814. TYPE: *Panicum* L., Sp. Pl.: 55. 1753.

Subtribe **Anthephorinae** Benth., J. Linn. Soc., Bot. 19: 30. 1881. TYPE: *Anthephora* Schreb., Beschr. Gras. 2: 105. 1810.

= Unranked Digitariastrae Stapf, Fl. Trop. Afr. 9: 12. 1917. Subtribe Digitariinae (Stapf) Butzin, Willdenowia 6: 509. 1972. TYPE: *Digitaria* Haller, Hist. Stirp. Helv. 2: 244. 1768, nom. cons.

Photosynthetic pathway. C_4 NADP–ME.

The subtribe includes seven genera and approximately 238 species:

Anthephora (12), *Chaetopoa* (2), *Chlorocalymma* (1), *Digitaria* (220), *Megaloprotachne* (1), *Tarigidia* (1), *Trachys* (1).

Subtribe **Cenchrinae** (Dumort.) Dumort., Anal. Fam. Pl. 64. 1829. Unranked Cenchrinae Dumort., Observ. Gramin. Belg.: 139.1824. TYPE: *Cenchrus* L., Sp. Pl. 2: 1049. 1753.

= Subtribe Setariinae (Dumort.) Dumort., Anal. Fam. Pl. 64. 1829. Unranked Setariinae Dumort., Observ. Gramin. Belg.: 137. 1824. TYPE: *Setaria* P. Beauv., Ess. Agrostogr. 51, 178, pl. 13, f. 3. 1812, nom. cons. and typ. cons.

= Subtribe Paspalidinae Keng and Keng f. ex S.L. Chen and Y.*X*. Jin, Acta Phytotax. Sin. 22(6): 475. 1984. TYPE: *Paspalidium* Stapf, Fl. Trop. Afr. 9: 582. 1920.

= Subtribe Spinificinae Ohwi, Acta Phytotax. Geobot. 11(1): 56. 1942. TYPE: *Spinifex* L., Mant. Pl.: 163, 300. 1771.

= Subtribe Uranthoeciinae Butzin, Willdenowia 6: 182. 1970. TYPE: *Uranthoecium* Stapf, Hooker's Icon. Pl. 31: t. 3073. 1916.

= Subtribe Xerochloinae Butzin, Willdenowia 6: 184. 1970. TYPE: *Xerochloa* R. Br., Prodr. 196. 1810.

= Subtribe Snowdeniinae Butzin, Willdenowia 6(3): 516. 1972. TYPE: *Snowdenia* C.E. Hubb., Bull. Misc. Inform. Kew 1929(1): 30. 1929.

= Subtribe Pseudoraphidinae Keng and Keng f., Bull. Nanjing Bot. Gard. 1988-1989: 7. 1990. TYPE: *Pseudoraphis* Griff., Not. Pl. Asiat. 3: 29. 1851.

Photosynthetic pathway. C_4 NADP–ME.

The subtribe includes 26 genera and approximately 328 species;

Acritochaete (1), *Alexfloydia* (1), *Cenchrus* (110), *Chamaeraphis* (1), *Dissochondrus* (1), *Holcolemma* (4), *Hygrochloa* (2), *Ixophorus* (1), *Panicum antidotale*, *Paractaenum* (1), *Paratheria* (2), *Plagiosetum* (1), *Pseudochaetochloa* (1), *Pseudoraphis* (6), *Setaria* (160), *Setariopsis* (2), *Snowdenia* (4), *Spinifex* (4), *Stenotaphrum* (7), *Stereochlaena* (5), *Streptolophus* (1), *Uranthoecium* (1), *Whiteochloa* (5), *Xerochloa* (4), *Zuloagaea* (1), *Zygochloa* (1).

Subtribe **Melinidinae** (Hitchc.) Pilg., Nat. Pflanzenfam. (ed. 2) 14e: 95. 1940. Tribe Melinideae Hitchc., U.S.D.A. Bull. (1915-23) 772: 18. 1920. TYPE: *Melinis* P. Beauv., Ess. Agrostogr.: 54. 1812.

= Subtribe Tristegininae Harv., Gen. S. Afr. Pl. (ed. 2): 428. 1869, nom. illeg. TYPE: *Tristegis* Nees, Horae Phys. Berol: 47, 54. 1820, nom. illeg. superfl.

= Subtribe Brachiariinae Butzin, Willdenowia 6: 189. 1970. TYPE: *Brachiaria* (Trin.) Griseb., Fl. Ross. (14): 469. 1853.

Photosynthetic pathway. C_4, PEP–CK.

The subtribe includes 14 genera and approximately 210 species:

Chaetium (3), *Eccoptocarpha* (1), *Eriochloa* (30), *Leucophrys* (1), *Megathyrsus* (3), *Melinis* (27), *Moorochloa* (3), *Panicum deustum*, *Rupichloa* (2), *Scutachne* (2), *Thuarea* (2), *Tricholaena* (4), *Urochloa* (130), *Yvesia* (1).

Subtribe **Boivinellinae** (A. Camus) Pilg., Nat. Pfl.-Syst. (ed. 2) 14e: 101. 1940. Tribe Boivinelleae A. Camus, Bull. Mus. Hist. Nat. 31: 393. 1925. TYPE: *Boivinella* A. Camus, Bull. Soc. Bot. France 72: 175. 1925.

= Subtribe Microcalaminae Butzin, Willdenowia 6: 189. 1970. TYPE: *Microcalamus* Franch., J. Bot. (Morot) 3(17): 282, f. b. 1889.

Photosynthetic pathway. C_3, C_4 NADP–ME and C_3–C_4 intermediates.

The subtribe includes 13 genera and approximately 129 species:

Acroceras (19), *Alloteropsis* (6), *Amphicarpum* (2), *Cyphochlaena* (2), *Cyrtococcum* (12), *Echinochloa* (40), *Entolasia* (5), *Lasiacis* (21), *Microcalamus* (1), *Oplismenus* (5), *Ottochloa* (4), *Parodiophyllochloa* (6), *Pseudechinolaena* (6).

Subtribe **Neurachninae** (S.T. Blake) Clayton and Renvoize, Kew Bull., Addit. Ser, 13: 377. 1986. Tribe Neurachneae S.T. Blake, Contr. Queensland Herb. 13: 4. 1972. TYPE: *Neurachne* R.Br.

Photosynthetic pathway. C_3, C_4 NADP–ME and C_3–C_4 intermediates.

The subtribe includes six genera and approximately 18 species:

Ancistrachne (4), *Calyptochloa* (1), *Cleistochloa* (3), *Neurachne* (6), *Paraneurachne* (1), *Thyridolepis* (3).

Subtribe **Panicinae** Fr., Fl. Scan. 195. 1835. TYPE: *Panicum* L., Sp. Pl. 1: 55. 1753.

Photosynthetic pathway. C_4, NAD–ME.

The subtribe includes four genera and approximately 107 species:

Arthragrostis (1), *Louisiella* (1), *Panicum* (100), *Yakirra* (5).

Incertae sedis genera and species:
Dichanthelium (23)
Homopholis (1)
Hydrothauma (1)
Hylebates (2)
Oryzidium (1)
"*Panicum*" sect. Clavelligerae (15)
"*Panicum*" sect. Monticola (5)
"*Panicum*" sect. Verrucosa (2)
"*Panicum*" spp. incertae sedis (4)
Poecilostachys (20)
Reynaudia (1)
Sacciolepis (26)
Trichanthecium (38)
Thyridachne (1)
Walwahalleya (3)

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Morphological matrix used in the analyses. Numbers in the first row represent the characters described in the Appendix 2, together with their coding. Numbers within brackets show a polymorphism for the particular character of the species involved. Dashes indicate character inapplicable for a taxon.

Appendix 1

Species of Poaceae used for the molecular phylogenetic analyses, voucher specimens from which DNA was extracted for sequencing, and GenBank accession numbers. Specimens sequenced for this paper are underlined. *, Partial sequence.

Achlaena piptostachya Griseb., *Greuter* et al. *25810* (HAJB), JN604671*. ***Acroceras zizanioides*** (Kunth) Dandy, AY029618. ***Alexfloydia repens*** B.K. Simon, *Floyd 2165* (MO), JN604672. ***Alloteropsis semialata*** (R. Br.) Hitchc. subsp. ***eckloniana*** (Nees) Pilg., EU159708. ***Altoparadisium chapadense*** Filg. et al., AY029619. ***Amphicarpum amphicarpon*** (Pursh) Nash, *Hill 13262* (MO), JN604673. ***Ancistrachne uncinulata*** (R. Br.) S.T. Blake, *Thompson* and *Sharpe BUC898* (MO), JN604674. ***Andropogon gerardii*** Vitman, AF117391. ***Anisopogon avenaceus*** R. Br., AF251447. ***Anthaenantia lanata*** (Kunth) Benth, AY029640. ***Anthaenantiopsis rojasiana*** Parodi, AY029620. ***Anthephora elongata*** De Wild., *Malcomber 3081* (MO), JN604675. ***Anthephora pubescens*** Nees, *Rua 525* (SI), JN604676. ***Apluda mutica*** L., AF117392. ***Apochloa euprepes*** (Renvoize) Zuloaga and Morrone, AY029657. ***Apochloa subtiramulosa*** (Renvoize and Zuloaga) Zuloaga and 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 and 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 and C.E. Hubb., AY847124. ***Bromus inermis*** Leyss., BIU71037. ***Calyptochloa gracillima*** C.E. Hubb., *Pollock 298* (BRI), JN604677. ***Canastra aristella*** (Döll) Zuloaga and Morrone, DQ355988. ***Canastra lanceolata*** (Filg.) Morrone et 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 setigerus*** Vahl, AF499153. ***Centotheca lappacea*** (L.) Desv., AY847122. ***Centrochloa singularis*** Swallen, *Rua 790* (BAA), JN604678. ***Centropodia glauca*** (Nees) Cope, AF251462. ***Chaetium bromoides*** (J. Presl) Benth. ex Hemsl., AY029626. ***Chaetopoa pilosa*** Clayton, *Bidgood* et al. *G-59* (K), JN604679. ***Chamaeraphis hordeacea*** R. Br., *Craven 4098* (CAMB), JN604680. ***Chasmanthium curvifolium*** (Valdés-Reyna, Morden and S.L. Hatch) Wipff and 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, *Greenway* and *Kanuri 14210* (MO), JN604681. **Chrysopogon fulvus** (Spreng.) Chiov., AF117398. **Cleistachne sorghoides** Benth., AF117400. **Cleistochloa rigida** (S.T. Blake) R.D. Webster, *Thompson BIL-160* (BRI), JN604682. **Coleataenia anceps** (Michx.) Soreng, AY188455. **Coleataenia longifolia** (Torr.) Soreng, AY188482. **Coleataenia petersonii** (Hitchc. and 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 and L. Watson, AY847139. **Cyphochlaena madagascariensis** Hack., *Pignal 1146* (MO), JN604683. **Cyphonanthus discrepans** (Döll) Zuloaga and Morrone, DQ646392. **Cyrtococcum accrescens** (Trin.) Stapf, *Hu* and *But 23191* (MO), JN604684. **Dallwatsonia felliana** B.K. Simon, *Clarkson* and *Neldner 9872* (BRI), JN604685. **Danthonia californica** Bol., AF251459. **Danthoniopsis dinteri** (Pilg.) C.E. Hubb., AY847116. **Dichanthelium acuminatum** (Sw.) Gould and C.A. Clark, AY188485. **Dichanthelium clandestinum** (L.) Gould, AY188461. **Dichanthelium cumbucana** (Renvoize) Zuloaga, AY188464. **Dichanthelium koolauense** (H. St. John and Hosaka) C.A. Clark and Gould, AY029627. **Dichanthelium sabulorum** (Lam.) Gould and 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., *Wood* and *Perlaan 1998* (MO), 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, *Snow* and *Simon 7297* (MO), JN604687. **Eragrostis curvula** (Schrad.) Nees, U21989. **Eriachne pulchella** Domin, AY618659. **Eriochloa punctata** (L.) Desv. ex Ham., AY029634. **Gerritea pseudopetiolata** Zuloaga, Morrone and Killeen, *Morrone* et al. *4219* (SI), JN604688. **Gynerium sagittatum** (Aubl.) P. Beauv., AY847120. **Heteropogon contortus** (L.) P. Beauv. ex Roem. and Schult., AF117411. **Homolepis glutinosa** (Sw.) Zuloaga and Soderstr., AY029637. **Homolepis isocalycia** (G. Mey.) Chase, AY029636. **Homopholis belsonii** C.E. Hubb., *Blake 13252* (BRI), JN604689*. **Hopia obtusa** (Kunth) Zuloaga and Morrone, AY029659. **Hygrochloa aquatica** Lazarides, *Craven 2379* (CANB), JN604690*. **Hylebates cordatus** Chippindall, *Davidse 73-2633* (MO), 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., *Zuloaga* and *Morrone 9572* (SI), JN604692. **Ixophorus unisetus** (J. Presl) Schltdl., AY623749. **Karroochloa purpurea** (L. f.) Conert and Türpe, AF251458. **Keratochlaena rigidifolia** (Filg., Morrone and Zuloaga) Morrone and Zuloaga, EU805492. **Lasiacis sorghoidea** (Desv. ex Ham.) Hitchc. and Chase, AY029639. **Leucophrys mesocoma** (Nees) Rendle, GU594628. **Lophatherum gracile** Brongn., AY847129. **Loudetia simplex** (Nees) C.E. Hubb., AY847117. **Louisiella fluitans** C.E. Hubb. and J. Léonard, *Fay 6160* (MO), JN604693*. **Megaloprotachne albescens** C.E. Hubb., *Hansen 3382* (MO), JN604694. **Megastachya mucronata** (Poir.) P. Beauv., AY847123. **Megathyrsus maximus** (Jacq.) B.K. Simon and 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 and Sosef, AF117401. **Molinia caerulea** (L.) Moench, U21995. **Moorochloa eruciformis** (Sm.) Veldkamp, AY188452. **Neurachne alopecuroidea** R. Br., *Kellogg 1029* (MO) JN604695. **Ocellochloa chapadensis** (Swallen) Zuloaga and Morrone, AY188486. **Ocellochloa piauiensis** (Swallen) Zuloaga and Morrone, AY029656. **Ocellochloa stolonifera** (Poir.) Zuloaga and Morrone, AY188488. **Oncorachis ramosa** (Zuloaga and Soderstr.) Morrone and Zuloaga, AY029686. **Ophiochloa hydrolithica** Filg., Davidse and Zuloaga, AY029642. **Oplismenopsis najada** (Hack. and Arechav.) Parodi, AY188453. **Oplismenus hirtellus** (L.) P. Beauv., AY029644. **Orthoclada laxa** (Rich.) P. Beauv., AY847128. **Otachyrium versicolor** (Döll) Henrard, AY029643. **Ottochloa nodosa** (Kunth) Dandy, *Maxwell 89-561* (MO), 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 and 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. and Schult., AY029661. **Panicum sellowii** Nees, AY188484. **Panicum stramineum** Hitchc. and Chase, AY188489. **Panicum trichanthum** Nees, AY188492. **Panicum tricholaenoides** Steud., AY188493.

Panicum tuerckheimii Hack., AY188494. ***Panicum validum*** Mez, AY188495. ***Panicum verrucosum*** Muhl., AY188496. ***Panicum virgatum*** L., U21986. ***Paractaenum novae-hollandiae*** P. Beauv., *Speek 1264* (CANB), JN604697. ***Paraneurachne muelleri*** (Hack.) S.T. Blake, Newbey 10800 (MO), JN604698. ***Paratheria prostrata*** Griseb., *Laergaard* et al. *16915* (C), JN604699*. ***Parodiophyllochloa cordovensis*** (E. Fourn.) Zuloaga and Morrone, AY188463. ***Parodiophyllochloa missiona*** (Ekman) Zuloaga and Morrone, AY188473. ***Parodiophyllochloa ovulifera*** (Trin.) Zuloaga and Morrone, AY029653. ***Parodiophyllochloa penicillata*** (Nees ex Trin.) Zuloaga and 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. and Sm.) Griseb., AF117418. ***Phanopyrum gymnocarpon*** (Elliott) Nash, AY188469. ***Pheidochloa gracilis*** S.T. Blake, *Lazarides 8871* (MO), JN604700. ***Phragmites australis*** (Cav.) Trin. ex Steud., U21997. ***Plagiantha tenella*** Renvoize, AY029674. ***Plagiosetum refractum*** Benth., EU819409. ***Poecilostachys oplismenoides*** (Hack.) Clayton, *Carvalho 4202* (C), JN604701*. ***Pohlidium petiolatum*** Davidse, Soderstr. and R.P. Ellis, AY847130. ***Pseudechinolaena polystachya*** (Kunth) Stapf, AY029676. ***Pseudochaetochloa australiensis*** Hitchc., *Simon 3826* (CAMB), JN604702. ***Pseudoraphis paradoxa*** Pilg., EF189892. ***Reimarochloa acuta*** (Flüggé) Hitchc., *Zuloaga* and *Morrone 9537* (SI), JN604703. ***Renvoizea trinii*** (Kunth) Zuloaga and Morrone, EU107783. ***Reynaudia filiformis*** (Spreng. ex Schult.) Kunth, *Zuloaga* and *Morrone 9538* (SI), JN604704. ***Rupichloa acuminata*** (Renvoize) D. Salariato and Morrone, AY029692. ***Sacciolepis indica*** (L.) Chase, AY029677. ***Schizachyrium scoparium*** (Michx.) Nash, AF117420. ***Scutachne dura*** (Griseb.) Hitchc. and 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., *Cóbar* and *García 1082* (MO), JN604705. ***Snowdenia petitiana*** (A. Rich.) C.E. Hubb., *Barney 113* (K), JN604706*. ***Sorghastrum nutans*** (L.) Nash, AF117421. ***Spartina pectinata*** Link, AF251465. ***Spartochloa scirpoidea*** (Steud.) C.E. Hubb., AY847140. ***Spheneria kegelii*** (Müll. Hal.) Pilg., *Hill* and *Horn 27203* (MO), 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 laxa*** (Sw.) Zuloaga, AY029655. ***Steinchisma spathellosa*** (Döll) Renvoize, AY188500. ***Stenotaphrum secundatum*** (Walter) Kuntze, AY029684. ***Stephostachys mertensii*** (Roth) Zuloaga and Morrone, AY188471. ***Stereochlaena cameronii*** (Stapf) Pilg., *Davidse* and *Handlos 7214* (MO), JN604708*. ***Steyermarkochloa angustifolia*** (Spreng.) Judz., *Berry* et al. *6016* (MO), JN604709. ***Stipagrostis zeyheri*** (Nees) De Winter, AF251455. ***Streptostachys asperifolia*** Desv., AY029687. ***Tatianyx arnacites*** (Trin.) Zuloaga and Soderstr., AY029688. ***Thrasyopsis juerguensii*** (Hack.) Soderstr. and A.G. Burm., *Rua 728* (BAA), 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*** (Lam.) Zuloaga and Morrone, AY188465. ***Trichanthecium parvifolium*** (Lam.) Zuloaga and Morrone, AY188476. ***Trichanthecium wettsteinii*** (Hack.) Zuloaga and Morrone, Y188497. ***Tricholaena monachne*** (Trin.) Stapf and C.E. Hubb., FJ486535. ***Tripsacum dactyloide***, AF117433. ***Triscenia ovina*** (L.) L., *Ekman 989* (MO), JN604712*. ***Tristachya biseriata*** Stapf, AY847118. ***Uniola paniculata*** Stapf, AF251463. ***Uranthoecium truncatum*** (Maiden and Betche) Stapf, SJ9599. ***Urochloa mutica*** (Forssk.) T.Q. Nguyen, AY029691. ***Walwhalleya subxerophila*** (Domin) Wills and J.J. Bruhl, *Snow* and *Simon 7316* (MO), JN604713. ***Whiteochloa capillipes*** (Benth.) Lazarides, *Risler 1804* (MO), JN604714. ***Xerochloa laniflora*** Benth., *Latz 11688* (MO), JN604715. ***Yakirra australiensis*** (Domin) Lazarides and R.D. Webster, *Latz 12164* (MO), 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

Characters and coding; a description of the characters and character states presented as considered in the analyses. Characters 22, 28, 32, 42, 44 and 45 were coded additive. *, Characters and character states that differ from Zuloaga et al. (2000).

Inflorescence

*Char. 0. **Main axis of inflorescences:** terminating in a spikelet (0), terminating in a bristle (1), terminating in a naked point, without a bristle (2).

*Char. 1. **Rachis:** terminating in a spikelet (0), terminating in a bristle (1), terminating as a foliaceous axis (2), terminating in a naked point, without a bristle (3).

Char. 2. **Foliaceous rachis:** absent (0), present (1).

Char. 3. **Bracts of the inflorescences:** absent (0), present (1).

Char. 4. **Involucral bristles** (**cauline**): absent (0), present (1).

Char. 5. **Involucral bracts:** absent (0), present (1).

Char. 6. **Cleistogenes in leaf axils:** absent (0), present (1).

Char. 7. **Apex of the pedicel:** truncate (0), oblique (1).

Char. 8. **Disarticulation at the base of the spikelet:** absent (0), present (1).

Char. 9. **Disarticulation at the base of the primary branches:** absent (0), present (1).

Char. 10. **Disarticulation at the base of the inflorescence:** absent (0), present (1).

Char. 11. **Disarticulation between the lower glume and lower lemma:** absent (0), present (1).

Char. 12. **Disarticulation at the base of the pedicel:** absent (0), present (1).

Char. 13. **Disarticulation at the node of the main axis:** absent (0), present (1).

Char. 14. **Disarticulation at the base of the upper anthecium:** absent (0), present (1).

*Char. 15. **Unilateral spikelet:** absent (0), present (1).

*Char. 16. **Second order branches in inflorescence:** multiflowered (0), reduced to a single abaxial spikelet (1), reduced to a single adaxial spikelet (2).

Spikelet

*Char. 17. **Spikelet shape:** not gibbous (0), gibbous (1).

*Char. 18. **Presence of incomplete florets distal to fertile florets:** absent (0), present (1).

Char. 19. **Breeding system:** plants with at least with some perfect flowers (0), no perfect flowers, staminate and pistillate flowers on the same plant (1), no perfect flowers, staminate and pistillate flowers on different plants (2).

Char. 20. **Hairy callus at the base of the spikelet:** absent (0), present (1).

*Char. 21. **Stipe at the base of the upper floret:** absent (0), present (1).

Glumes

Char. 22. **Lower glume:** present (0), vestigial (1), absent (2).

Char. 23. **Lower glume:** not saccate (0), saccate (1).

Char. 24. **Lower glume:** muticous (0), awned (1).

Char. 25. **Upper glume:** present (0), absent (1).

Char. 26. **Lower and upper glume:** of different size (0), the same size (1).

*Char. 27. **Upper glume:** as long as or longer than the lower lemma (0), 1/2 or less the length of the lower lemma (1).

*Char. 28. **Upper glume:** 2 or 4-nerved (0), enerved (1), 1-nerved (2), 1–3 nerved (3), 3–5-nerved (4), 5–11 nerved (5).

Char. 29. **Upper glume:** muticous (0), awned (1).

Floret

Char. 30. **Lower lemma:** muticous (0), awned (1).

Char. 31. **Apex of the lower lemma:** entire (0), bifid (1), trilobate (2).

Char. 32. **Lower palea:** absent (0), present, not expanded (1), present and expanded (2).

*Char. 33. **Upper anthecium:** dorsiventrally compressed (0), laterally compressed (1), cylindrical (2).

*Char. 34. **Upper anthecium:** crustaceous (0), cartilaginous (1), hyaline (2), membraneous to herbaceous (3).

Char. 35. **Upper lemma texture:** smooth (0), transversely rugose (1).

Char. 36. **Upper lemma with basal scars or appendages:** absent (0), present (1).

Char. 37. **Upper lemma:** muticous (0), awned (1).

Char. 38. **Upper lemma:** not differentiated at the apex (0), differentiated at the apex (1).

Char. 39. **Upper lemma** (**margins**): tucked in onto the palea (0), lying flat and exposed on the palea (1).

Char. 40. **Upper palea:** absent (0), present (1).

Char. 41. **Upper palea:** tightly clasped by the lemma (0), gaping (1).

*Char. 42. **Upper palea:** without simple **papillae** (0), with simple papillae (1), with compound papillae (2).

*Char. 43. **Distribution of papillae in the upper palea:** all over surface (0), at the apex only (1).

*Char. 44 **Upper palea** (**presence of microhairs**): without bicellular microhairs (0), with bicellular microhairs at the apex and/or base (1), with bicellular microhairs all over its surface (2).

*Char. 45. **Upper palea** (**presence of macrohairs**): without macrohairs (0), with macrohairs at the apex and/or base (1), with macrohairs all over its surface (2).

Char. 46. **Upper palea** (**apex**): straight (0), recurved (1).

Char. 47. **Stamen** (**number**): three (0), two (1), one (2).

Char. 48. **Lodicules :** present (0), absent (1).

Char. 49. **Style base**: free (0), fused (1).

Char. 50. **Ovary:** glabrous (0), pilose (1).

Fruit

*Char. 51. **Caryopsis** (**hilum**): punctiform (0), linear (1).

Leaf anatomy

*Char. 52. **Photosynthetic pathway:** C_3 XyMS+ (0), C_4 XyMS– (1), C_4 XyMS+ (2).

*Char. 53. **Chloroplasts on the parenchymatous sheath:** absent (0), centripetal (1), centrifugal (2).

Char. 54. **Distinctive Kranz cells:** absent (0), present (1).

Char. 55. **Fusoid cells:** absent (0), present (1).

*Char. 56. **Basic chromosome number** (***x***): 9 (0), 10 (1), 11 (2), 12 (3) 13 (4), 5 (5), 6 (6), 7 (7), 17 (8).