



A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees

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ABSTRACT

We conducted a molecular phylogenetic study of the subfamily Chloridoideae using six plastid DNA sequences (*ndhA* intron, *ndhF*, *rps16-trnK*, *rps16* intron, *rps3*, and *rpl32-trnL*) and a single nuclear ITS DNA sequence. Our large original data set includes 246 species (17.3%) representing 95 genera (66%) of the grasses currently placed in the Chloridoideae. The maximum likelihood and Bayesian analysis of DNA sequences provides strong support for the monophyly of the Chloridoideae; followed by, in order of divergence: a Triraphideae clade with *Neyraudia* sister to *Triraphis*; an Eragrostideae clade with the Cotteinae (includes *Cottea* and *Enneapogon*) sister to the Unioliinae (includes *Entolpocamia*, *Tetrachne*, and *Uniola*), and a terminal Eragrostidinae clade of *Ectrosia*, *Harpachne*, and *Psammagrostis* embedded in a polyphyletic *Eragrostis*; a Zoysieae clade with *Urochondra* sister to a Zoysiinae (*Zoysia*) clade, and a terminal Sporobolinae clade that includes *Spartina*, *Calamovilfa*, *Pogoneura*, and *Crypsis* embedded in a polyphyletic *Sporobolus*; and a very large terminal Cynodonteae clade that includes 13 monophyletic subtribes. The Cynodonteae includes, in alphabetical order: Aeluropodinae (*Aeluropus*); Boutelouinae (*Bouteloua*); Eleusininae (includes *Apochiton*, *Astrebla* with *Schoenefeldia* embedded, *Austrochloris*, *Brachyachne*, *Chloris*, *Cynodon* with *Brachyachne* embedded in part, *Eleusine*, *Enteropogon* with *Eustachys* embedded in part, *Eustachys*, *Chrysochloa*, *Coelachyrum*, *Leptochloa* with *Dinebra* embedded, *Lepturus*, *Lintonia*, *Microchloa*, *Saugetia*, *Schoenefeldia*, *Sclerodactylon*, *Tetrapogon*, and *Trichloris*); Hilariinae (*Hilaria*); Monanthochloinae (includes *Distichlis*, *Monanthochloa*, and *Reederochloa*); Muhlenbergiinae (*Muhlenbergia* with *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, and *Schedonardus* all embedded); Orcuttiinae (includes *Orcuttia* and *Tuctoria*); Pappophorinae (includes *Neesiochloa* and *Pappophorum*); Scleropogoninae (includes *Blepharidachne*, *Dasyochloa*, *Erioneuron*, *Munroa*, *Scleropogon*, and *Swallenia*); Traginae (*Tragus* with *Monelytrum*, *Polevansia*, and *Willkommia* all embedded); Tridentinae (includes *Gouinia*, *Tridens*, *Triplasis*, and *Vaseyochloa*); Triodiinae (*Triodia*); and the Tripogoninae (*Melanocenchris* and *Tripogon* with *Eragrostiella* embedded). In our study the Cynodonteae still include 19 genera and the Zoysieae include a single genus that are not yet placed in a subtribe. The tribe **Triraphideae** and the subtribe **Aeluropodinae** are newly treated at that rank. We propose a new tribal and subtribal classification for all known genera in the Chloridoideae. The subfamily might have originated in Africa and/or Asia since the basal lineage, the Triraphideae, includes species with African and Asian distribution.

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1. Introduction

The grass (Poaceae) subfamily Chloridoideae was first validly published by *Beilschmied* (1833), a German botanist and pharmacist, who used an earlier description of sect. Chlorideae by *Kunth*

(1815). That same year, *Kunth* (1833) published his *Agrostographia Synoptica* in which he recognized the following genera in the group (Chlorideae): *Chloris*, *Ctenium*, *Cynodon*, *Dactyloctenium*, *Eleusine*, *Eustachys*, *Gymnopogon*, *Harpochloa* *Kunth*, *Leptochloa*, *Microchloa*, *Pleuraphis* *Torr.*, *Schoenefeldia*, *Spartina*, *Triplasis*, and 8 genera now treated as synonyms of *Bouteloua*. Clearly our modern understanding of Chloridoideae is much greater, and there now appear to be more than 1420 species in approximately 140 genera in the subfamily worldwide (*Clayton et al.*, 2008; *Watson and Dallwitz*, 1992b).

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The core species in the subfamily share two structural synapomorphies: all exhibit Kranz or C_4 leaf anatomy (except *Eragrostis walteri* Pilg. from South Africa; Ellis, 1984) and most have chloridoid bicellular microhairs (broad, short terminal cell the same thickness as the basal cell) present on leaf surfaces. Two main subtypes of C_4 photosynthesis, NAD-ME (nicotinamide adenine dinucleotide co-factor malic enzyme) and PCK (phosphoenolpyruvate carboxykinase), have been found and verified by biochemical assay to occur in Chloridoideae (Gutierrez et al., 1974; Brown, 1977; Hattersley and Watson, 1992). Ecologically, there appears to be some separation in habitat preference according to C_4 subtype (Ellis et al., 1980; Hattersley, 1992). The PCK subtype is thought to represent an apomorphy in grasses because this C_4 cycle appears to be a modification of the NAD-ME subtype (Hattersley and Watson, 1992). In addition, the PCK subtype is known only to occur in grasses, whereas the NAD-ME subtype is also found in other monocot and dicot families (Hattersley and Watson, 1992; Peterson and Herrera Arrieta, 2001).

Other character trends in Chloridoideae include a base chromosome number of $x = 10$, fruits (caryopses) with nonlinear hila that are usually punctiform or small, embryos with elongated mesocotyl internodes, and two non-membranous (fleshy) lodicules (Soreng and Davis, 1998; GPWG, 2001). However, most of these character trends are seen in the closely related subfamilies Aristidoideae, Arundinoideae, Centothecoideae, Danthonioideae, and Panicoideae of the PACCAD clade. A recent morphological and ecological description of the subfamily is given in GPWG (2001). Some salient features include: plants herbaceous, rarely woody, occurring in dry climates, sheaths usually non-auriculate, inflorescence paniculate, racemose, or spicate, spikelets bisexual or unisexual (plants monoecious or dioecious) with one to many fertile florets, usually laterally compressed, usually disarticulating above the glumes, palea well developed, lodicules usually two, fleshy, ovary glabrous, styles and stigmas two, caryopsis with pericarp often free or loose, hilum short, endosperm hard without lipid, embryo with an epiblast (usually), scutellar cleft, and elongated mesocotyl internode.

The Chloridoideae have appeared monophyletic in all previous molecular analyses, however the classification within the subfamily, until recently, has been controversial (Van den Borre and Watson, 1997; Soreng and Davis, 1998; Hilu et al., 1999; Hsiao et al., 1999; Hilu and Alice, 2001; Roodt-Wilding and Spies, 2006; Columbus et al., 2007; Peterson et al., 2007; Soreng et al., 2009). Earlier studies based entirely on morphological characters, while not entirely misleading in depicting closely related genera, were often erroneous in elucidating evolutionary alignment of the tribes (Hilu and Wright, 1982; Van den Borre and Watson, 1997). Clayton and Renvoize (1986) recognized a large Eragrostideae tribe that included 77 genera whereas Columbus et al. (2007) and Peterson et al. (2007), based on parsimony analyses of DNA sequences, have circumscribed a much smaller Eragrostideae (± 8 genera) and a very large Cynodonteae (± 60 genera) that included the following 10 subtribes: Boutelouinae, Chloridinae, Eleusininae, Gouiniinae, Hilariinae, Monanthochloinae, Munroinae, Muhlenbergiinae, Orcuttiinae, and Traginae. Roodt-Wilding and Spies (2006) investigated phylogenetic relationships among 38 southern African chloridoid species using *trnL-F* and ITS sequences. The largest molecular phylogenetic survey of chloridoid grasses included 80 species in 66 genera (Columbus et al., 2007). A recent plastid multi-gene (three) phylogeny of the grasses incorporating 78 chloridoids provides a good estimate of the tribal relationships among this subfamily (Bouchenak-Khelladi et al., 2008). A major problem with this work is that it contains a large amount of missing data, since 61 of the 78 chloridoid species are based on single gene sequence, 10 species are based on two genes, and only seven species are based on three genes. Consequently, misleading results are re-

ported such as *Schedonorus*, sister to *Lolium* in the Poeae, and *Anisopogon* in the Phaenospermateae are included in their Chloridoideae assemblage (Davis and Soreng, 2007). Placement of these two genera in the Chloridoideae was based on each containing a single *rbcl* sequence. Obviously, *Schedonorus* and *Anisopogon* should have been omitted from their study.

In our study, we provide the latest estimates of the phylogeny within the Chloridoideae by analyzing six sequences from the plastid genome – *rps3* (coding), *rps16* intron, *rps16-trnK* (spacer), *ndhF* (coding), *ndhA* intron, and *rpl32-trnL* (spacer); and one from the nuclear genome – ITS. To do this we assembled a large data set including 254 species in 99 genera. We compare phylogenetic trees based on ITS and plastid datasets, combine the data set in a total evidence tree, discuss previous molecular and morphological studies where appropriate, interpret biogeographical relationships, and present a new classification for the subfamily. Based on our phylogenetic evidence we propose a change in rank for two taxa, the subtribe Triraphidinae and the tribe Aeluropodeae.

2. Materials and methods

2.1. Taxon sampling

The following 8 taxa were chosen as outgroups from the PACCAD clade: one species of *Danthonia* (Danthonioideae), two species of *Rytidosperma* (Danthonioideae), two species of *Aristida* (Aristidoideae), and three species of *Chasmanthium* (Centothecoideae or Centothecoaceae) (GPWG, 2001; Davis and Soreng, 2007). The Chloridoideae subset of data is partitioned as following: six species of tribe Triraphideae, 34 species (two multiple accessions) of tribe Eragrostideae, 18 species of Zoysieae (one multiple accession) and 188 species (11 multiple accessions) of Cynodonteae. The dataset of Cynodonteae includes three species of subtribe Aeluropodiinae, 10 species of Triodiinae, five species of Orcuttiinae, four species of Tridentinae, six species of Tripogoninae, 51 species of (five multiple accessions) of Eleusininae, 11 species of Traginae, one species (one multiple accession) of Hilariinae, three species (one multiple accession) of Monanthochloinae, 13 species of Boutelouinae, 10 species of Scleropogoninae, and 33 species (one multiple accession) of Muhlenbergiinae. In addition, the Cynodonteae includes 31 species (three multiple accessions) with uncertain taxonomic or phylogenetic position.

Voucher information and GenBank numbers for 268 original accessions representing 254 species are given in Appendix A. All vouchers are deposited in the Smithsonian Institution, United States National Herbarium (US). The majority of samples used in this study were collected by PMP during the period from 1984 to 2008. In addition, we sampled older herbarium specimens to maximize the number of genera in the Chloridoideae. Collections from areas we have not visited, i.e., India and Africa, were included.

2.2. DNA extraction, primers design, amplification, and sequencing

All procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA was isolated using the BioSprint 96 DNA Plant Kit (Qiagen, Valencia, California, USA) following the protocol of the manufacturer. PCR amplifications were performed in a MJ Research or PE 9700 thermal cycler. Genomic DNA was combined with $1 \times$ reaction buffer (200 mM Tris-HCl, 500 mM NH_4) (Bioline Biolase Taunton, Madison, USA) without Mg^{++} , 2 mM $MgCl_2$, 200 mM dNTP's, 1.5 μ l of Taq polymerase (Bioline Biolase Taunton, Madison, USA), 40 pmol/ μ l each of forward and reverse primers. We targeted seven regions for sequencing: three from chloroplast genome large single-copy re-

gions (LSC) – *rps3* (coding region), *rps16* intron and 3'*rps16*–5'*trnK* (spacer); three from small single-copy regions (SSC) – *ndhF* (coding region), *ndhA* intron, and *rpl32-trnL* (spacer); and nrDNA ITS region. Intergenic spacers *rpl32-trnL* (SSC) and *rps16-trnK* (LSC) are two of the top ranked, most variable non-coding regions for phylogenetic studies in the Angiosperms (Shaw et al., 2007). To our knowledge, *rpl32-trnL* intergenic spacer and *ndhA* intron (SSC) have not been previously used for phylogenetic inference within the Poaceae. We have chosen the widely used *ndhF* gene (SSC) to recover phylogenetic relationships since it proved useful in other groups of grasses (Giussani et al., 2001; Soreng et al., 2007). Another commonly used gene in phylogenetic studies of Poaceae, *matK* (LSC) was initially considered as a comparative region to *ndhF* in our dataset (Hilu et al., 1999; Hilu and Alice, 1999;2001; Soreng et al., 2007; Schneider et al., 2009). However, difficulties with amplification of *matK* over the entire range of species and especially for old samples encouraged us to explore other coding regions of the chloroplast genome that could fit the conditions of easy amplification, of reasonable size with a sufficient amount of parsimony informative characters (PIC's). The *rps3* (LSC) gene was chosen as a substitute for *matK* in our analysis. To our knowledge, the *rps3* region has not been used for phylogenetic inference before. The combined datasets include 1574 sequences of the nuclear and chloroplast genome regions of chloridoid grasses and 49 sequences of the species from the adjacent phylogenetic groups of the PACCAD clade.

Based on sequences of the complete chloroplast genome of *Oryza*, *Zea*, *Hordeum*, *Lolium*, *Triticum*, and *Agrostis* available from GenBank we designed primers for *rps3* and *ndhA* intron regions and modified or designed Poaceae specific primers for 3'*rps16*–5'*trnK* and *rps16* intron regions. The programme FastPCR 4.0.27 was employed to adjust the temperature and the quality of the newly designed or modified primers in order to increase the PCR efficiency. The sequences, melting temperature, quality, and references for the primers used are given in Table 1. The *rps3* is a ribosomal protein S3 coding gene anchored at the 79300 position, according to the *Oryza* complete genome sequence, and flanked by the *rpl22* (L22 – core protein of the large ribosomal subunit encoding region) from 5' end and intergenic spacer with *rpl16* (L16 essential protein of the large subunit encoding region) from the 3' end. Unlike its mitochondrial analogue that was previously used in phylogenetic studies (Jian et al., 2008), the plastid *rps3* gene lacks an intron and has reasonable size (~720 bp in *Oryza* and 678–684 bp in Chloridoideae) and is suitable for routine amplification and sequencing with one pair of primers. The fraction value of PIC's to the total sequence length for this region is comparable to the value of such fast-evolving plastid protein-coding genes as *ndhF* (Table 2). Two newly designed primers, *rps3C28F* and

rps3C697R are anchored in conservative zones close to the 5' and 3' ends of the gene. The labelling numbers indicate positions of the primers from the first nucleotide of the start codon according to the *Oryza* sequence. Using this set of primers the portion of the *rps3* gene of approximately 580 bp (excluding primers area) was easily amplified and sequenced for the majority of the samples.

Of roughly 2230 bp of entire *ndhF* gene, ~740 bp fragment of the most variable 3' end of the region was amplified and sequenced using one set of forward and reverse primers, *ndhF1311F* and *ndhF2091R* (Romaschenko et al., in press). We redesigned primers for amplification and sequencing of the *ndhA* intron making them less degenerate and more suitable for Poaceae than those designed by Small et al. (1998) or Shaw et al. (2005). In addition, the amplification with newly designed primers, *ndhA* × 4 and *ndhA* × 3 was steadier when working with older herbarium material. Both primers are anchored in flanking exons of the *ndhA* gene.

The amplification parameters for all plastid regions were: 95 °C for 3 min; followed by 35 cycles of 94 °C for 40 s, 51–56 °C for 40 s and 72 °C for 1 min 40 s; the temperature of the final extension was set for 72 °C for 10 min. Most of the plastid regions chosen for this study have a sequence length between 579 and 745 bp, which is suitable for routine amplification using standard PCR parameters and one set of primers for each region. The nuclear ribosomal ITS region was amplified using primers ITS4 and ITS5A using the following thermocycler settings: initial denaturation step of 4 min at 95 °C, followed 35 cycles at 94 °C for 30 s, 52 °C for 30 s, 72 °C for 1 min 30 s, and a final extension of 10 min at 72 °C (Table 1).

All PCR products were cleaned with ExoSAP-IT (USB, Cleveland, Ohio, USA). DNA sequencing was performed with BigDye Terminator Cycle Sequencing v.3.1 (PE Applied Biosystems, Foster City, CA, USA) according to the following parameters: 80 °C, 5 min; 25 or 30 cycles of 95 °C for 10 s, 50 °C for 5 s and 60 °C for 4 min. Sequenced products were analyzed on an ABI PRISM 3730 DNA Analyzer 7900HT (ABI). The regions *rpl32-trnL*, *rps3*, *rps16* intron, 3'*rps16*–5'*trnK*, *ndhF* (coding region) and ITS were sequenced in one direction. Relatively short regions (500–750 bp) covered by our primers were easily interpreted allowing us to accumulate sequences from different parts of the genome for phylogenetic inference (Shaw et al., 2005;2007). Only *ndhA* intron (~933 bp) was sequenced in both directions and the program Sequencer 4.8 (Gene Code Corporation, 1991–2007) was employed to produce the contig sequence for the entire region.

2.3. Phylogenetic analyses

Sequence alignment was done manually using BioEdit v.7.0.5.3 (Hall, 1999). The indels and ambiguously aligned regions were

Table 1
Regions studied, sequences, melting temperature (°C), and quality of primers used for PCR and sequencing.

Region	Primers	Sequence (5'–3')	Tm	Quality	Reference
<i>ndhF</i>	<i>ndhF2091R</i>	GACCCACTCCATTGCGTAATTC	57.8	70	Romaschenko et al. (in press)
	<i>ndhF1311F</i>	ACTGCAGGATTAACCTGCGTT	56.8	113	Romaschenko et al. (in press)
<i>rpl32-trnL</i>	<i>trnL^(UAG)</i>	CTGCTTCCTAAGAGCAGCGT	60.0	120	As Shaw et al. (2007)
	<i>rpl32-F</i>	CAGTTCCAAAAAACGTACTTC	53.7	103	As Shaw et al. (2007)
<i>rps16-trnK</i>	<i>rpS16–900F</i>	TATCGAATCGTTGCAATTGATG	53.9	108	Modified <i>rpS16R</i> of Shaw et al. (2005)
	<i>3914PR</i>	CATTGAGTTAGCAACCCAGATA	55.3	105	Modified <i>trnK3914F</i> of Johnson and Soltis (1995)
<i>rps3</i>	<i>rps3C697R</i>	TCTTCGTCTACGAATATCCA	57.8	105	This study
	<i>rps3C29F</i>	TCAGACTTGGTACAACCCAA	53.4	64	This study
<i>rps16</i> intron	<i>rpS16F</i>	AAACGATGTGGTAGAAAGCAAC	56.3	80	Modified as Shaw et al. (2005)
	<i>rpS16R</i>	ACATCAATTGCAACGATTCGATA	55.0	100	Modified as Shaw et al. (2005)
<i>ndhA</i>	<i>ndhA</i> × 4	CTAGCAATATCTCTACGTGYGATTCCG	53.9	55	This study
	<i>ndhA</i> × 3	GACTGTGCTTCAACTATATCAACTG	53.7	69	This study
ITS	ITS5a	CCTTATCATTTAGAGGAAGGAG	53.7	82	Stanford et al. (2000)
	ITS4	TCCTCCGCTATTGATATGC	55.0	38	White et al., 1990

Table 2

Summary of six plastid regions and nrDNA ITS used in this study.

	<i>ndhF</i>	<i>rpl32-trnL</i>	<i>rps16-trnK</i>	<i>rps3</i>	<i>rps16</i> intron	<i>ndhA</i> intron	Plastid	ITS	Combined plastid + ITS
Aligned sequence length (aSL)	796	1389	1222	590	1368	1424	6789	814	7603
Average sequence length (SL)	734	695	723	579	745	933	4409	669	5078
No. of taxa	211	246	244	250	225	219	268	234	268
No. of excluded characters	2	364	213	0	0	0	579	89	668
Proportion of excluded characters (%)	0.3	26.2	17.4	0.0	0.0	0.0	8.5	10.9	8.8
No. of parsimony informative characters (PIC)	286	385	411	152	283	431	1948	428	2377
PIC/SL	0.39	0.554	0.568	0.263	0.380	0.462	0.442	0.640	0.468
PIC/TL	0.237	0.259	0.309	0.263	0.319	0.293	0.259	0.093	0.19.3
Tree length (TL)	1205	1487	1328	577	886	1470	7534	4627	12332
Consistency index (CI)	0.3627	0.4385	0.4819	0.3588	0.5011	0.4687	0.4153	0.209	0.3323
Homoplasy index (HI)	0.6373	0.5615	0.5181	0.6412	0.4989	0.5313	0.5847	0.791	0.6677
Retention index (RI)	0.7899	0.7997	0.8304	0.7876	0.8235	0.8243	0.7932	0.7346	0.7658
Rescaled consistency index (RC)	0.2865	0.3506	0.4002	0.2826	0.4127	0.3864	0.3294	0.1535	0.2545
AIC	GTR + G	GTR + G	HKY + G	TVM + G	TIM + G	GTR + G	GTR + G	GTR + G	GTR + G

excluded from analyses. The length of sequences and amount of excluded data for each region is presented in Table 2. No data was excluded from *rps3*, *rps16* intron, and *ndhA* intron. All gaps were treated as missing data. We used maximum likelihood and Bayesian analysis to infer phylogeny. The maximum likelihood analysis was conducted with the programme GARLI 0.951 (Zwickl, 2006). All separate and combined maximum likelihood analyses were run under single model GTR + I + G. The maximum likelihood bootstrap analyses were performed with the default parameters with “bootstrapreps” option set for 1000 replicates. The majority-rule consensus tree of resulting best trees found for each bootstrap reweighted dataset was constructed in PAUP* 4.0b10 (Swofford, 2000). The output file containing best trees found for each bootstrap reweighted dataset was then read into PAUP* 4.0b10 (Swofford, 2000) where the majority-rule consensus tree was constructed and bootstrap support values were calculated. Bootstrap (BS) values of 90–100 were interpreted as strong support; 70–89 as moderate, and 50–69 as weak.

Bayesian posterior probabilities were estimated using MrBayes 3.01 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2005) and the appropriate evolutionary models were selected using MrModeltest 1.1b (Nylander, 2002). MrModeltest selected models with gamma-distributed rate variation across sites with number of substitution types $N_{st} = 6$ for almost all datasets with exception of the 3′*rps16*–5′*trnK* region where the HKY + G ($N_{st} = 2$) was selected as best-fitted model by Akaike information criterion (AIC) (Table 2). The plastid dataset and combined plastid + ITS dataset for Bayesian analysis were then partitioned into two subsets that were processed implementing different parameters suggested by MrModeltest concerning the model for among site rate variation, number of substitution types, substitution rates and gamma shape parameter. All other parameters were left at default settings. Each Bayesian analysis was initiated with random starting trees and was initially run for two million generations with sampling frequency of the chains set at the 100th iteration. The analysis was continued until the value of standard deviation of split sequences dropped below 0.01 as convergence diagnostic value (Huelsenbeck and Ronquist, 2001). The fraction of the sampled values discarded as burn in was set at 0.25. Posterior probabilities (PP) of 0.95–1.00 were considered statistically significant.

3. Results

3.1. Analysis of ITS sequences

The number of taxa included in the ITS analysis was 234 (including five outgroup); average sequence length was 669; num-

ber of PIC's was 428; and the tree length was 4627 with a consistency index (CI) of 0.209, homoplasy index (HI) of 0.791, retention index (RI) of 0.7346, and a rescaled consistency index (RC) of 0.1535 (Table 2). The best maximum likelihood tree with bootstrap (BS) values shown above the branches and posterior probabilities (PP) shown below the branches is illustrated in Fig. 1. The major tribes within a monophyletic Chloridoideae (BS = 95, PP = 1.00) are well resolved. The tribes Cynodonteae (BS = 69, PP = 1.00) and Zoysieae (BS = 63, PP = 0.92) are sister, sister to this clade (BS = 96, PP = 1.00) is the Eragrostideae (BS = 74, PP = 0.98), and sister to this clade (BS = 100, PP = 1.00) is the Triraphideae (BS = 97, PP = 1.00).

The Cynodonteae is composed of the following 13 well resolved subtribes: Aeluropodinae (BS = 100, PP = 1.00), Boutelouinae (BS = 94, PP = 1.00), Eleusininae (BS = 78, PP = 0.50), Tridentinae (BS = 88, PP = 0.99), Hilariinae (BS = 100, PP = 1.00), Monanthochloinae (BS = 81, PP = 1.00), Muhlenbergiinae (BS = 75, PP = 0.52), Scleropogoninae (BS = 53, PP = 0.87), Orcuttiinae (BS = 100, PP = 1.00), Pappophorinae (BS = 78, PP = 0.96), Traginae (BS = 100, PP = 1.00), Triodiinae (BS = 91, PP = 1.00), and the Tripogoninae (BS = 53). There is very little backbone support in the tree and relationships among subtribes are not well resolved. The Aeluropodinae, Boutelouinae, Orcuttiinae, Triodiinae, and Tripogoninae each contain multiple species in a single genus, *Aeluropus* (3 spp.), *Bouteloua* (12 spp.), *Tuctoria* (2 spp.), *Triodia* (10 spp.), and *Tripogon* (2 spp.), respectively. The Tridentinae includes four genera, *Gouinia*, *Tridens*, *Triplasis*, and *Vaseyochloa*, each represented by a single species. The Hilariinae includes two accessions of *Hilaria cenchroides*. The Traginae includes four genera: a polyphyletic *Tragus* that includes *Monelytrum luederitzianum*-*Willkommia sarmentosa*-*Willkommia texana* (BS = 69, PP = 1.00) that are sister to four species of *Tragus* (BS = 100, PP = 1.00), sister to all these species is *Polevansia rigida* (BS = 100, PP = 1.00). The Tripogoninae includes *Eragrostiella leioptera*, *Tripogon yunnanensis*, and *Tripogon spicatus* as a clade (BS = 100, PP = 1.00) and sister to this is *Melanocenchris royleana* (BS = 53). The Monanthochloinae includes three genera: a polyphyletic *Distichlis*, imbedded is a clade with *Monanthochloe littoralis* and *Reederchloa eludens* (BS = 66, PP = 1.00). The Scleropogoninae includes six genera: two species of *Munroa* are sister (BS = 100, PP = 1.00), sister to this is *Dasyochloa pulchella* (BS = 100, PP = 1.00), sister to this clade (BS = 100, PP = 1.00) are two species of *Erioneuron* (BS = 100, PP = 1.00); two species of *Blepharidachne* are sister (BS = 77, PP = 0.99), sister to this is an unsupported clade of *Scleropogon brevifolius*, *Blepharidachne*, *Dasyochloa*, *Erioneuron*, *Munroa*, and *Scleropogon* form a clade (BS = 78, PP = 1.00) and sister to this is *Swallenia alexandrae* (BS = 53, PP = 0.87). The Muhlenbergiinae includes nine genera (10 genera included in the plastid and combined tree): a poly-

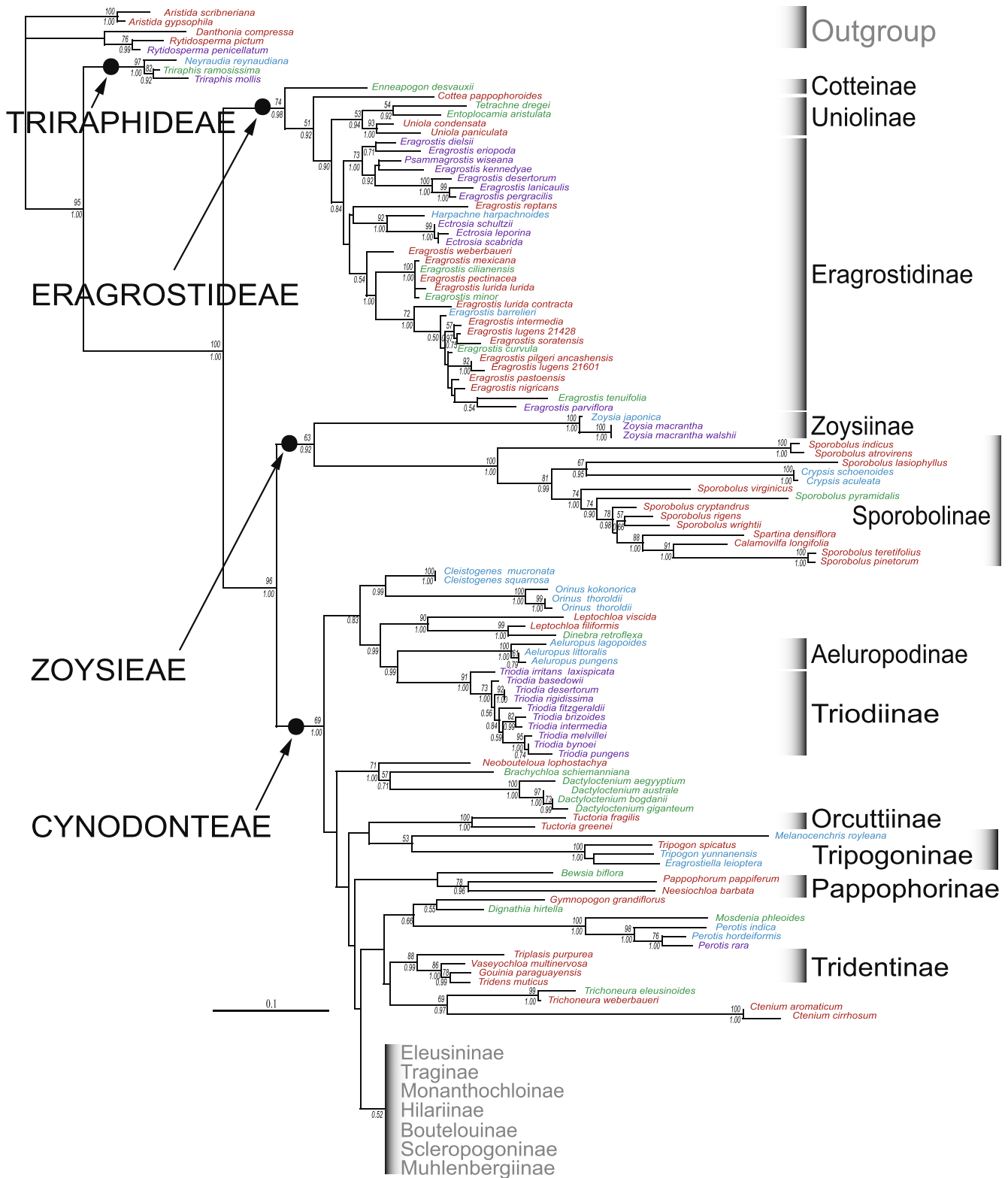


Fig. 1. Phylogram of best maximum likelihood tree from analysis of nuclear ITS data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values; taxon colour indicates native distribution as follows: green = African, blue = Asian, purple = Australian, red = American (includes North and South America). (For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)

phyletic *Muhlenbergia*, embedded are clades of *Bealia mexicana*, *Blepharoneuron shepherdii*, and *B. tricholepis* (BS = 86, PP = 0.99); three species of *Pereilema* (BS = 54, PP = 0.63); two species of *Aegopogon* (BS = 100, PP = 1.00); *Redfieldia flexuosa*, *Schedonnardus paniculatus*; two accessions of *Lycurus setosus* (BS = 100, PP = 1.00); and

three species of *Chaboissaea* (BS = 99, PP = 1.00). The Eleusininae includes 20 genera: a polyphyletic *Cynodon* clade (BS = 100, PP = 1.00) that includes *Brachyachne convergens* and *B. tenella*, sister to this is *Chrysochloa hindsii* (BS = 52, PP = 0.65), sister to these is a clade (BS = 84, PP = 0.97) of three species of *Brachyachne* (BS = 100,

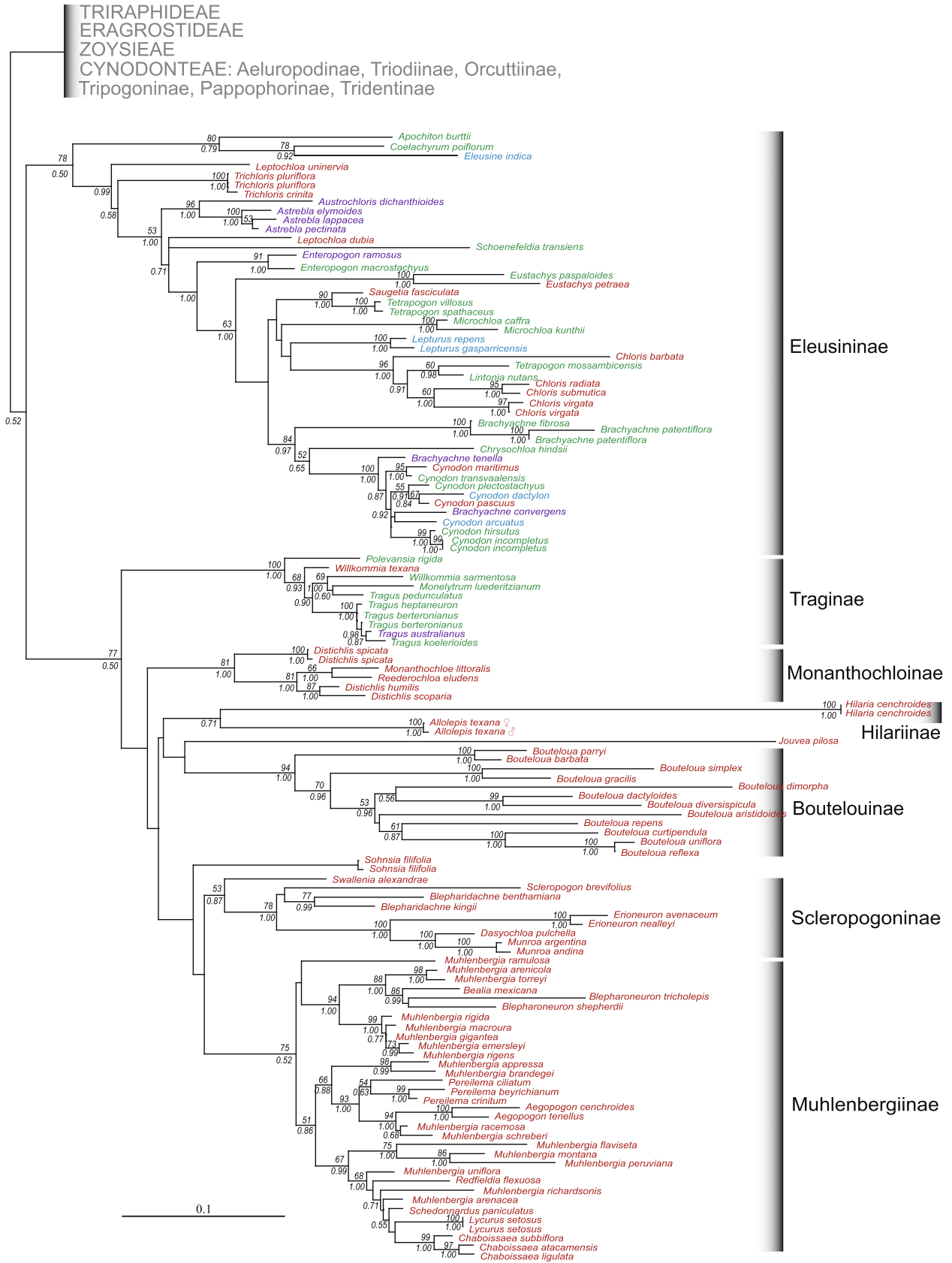


Fig. 1 (continued)

PP = 1.00); a polyphyletic *Chloris* clade (BS = 96, PP = 1.00) that includes a clade of *Tetrapogon mossambicensis* and *Lintonia nutans* (BS = 60, PP = 0.98); two species of *Lepturus* (BS = 100, PP = 1.00);

two species of *Microchloa* (BS = 100, PP = 1.00); *Tetrapogon spathaceus* and *T. villosus* are sister (BS = 100, PP = 1.00), sister to this is *Saugetia fasciculata* (BS = 90, PP = 1.00); two species of *Eustachys*

(BS = 100, PP = 1.00); two species of *Enteropogon* (BS = 91, PP = 1.00); three species of *Astrebula* (BS = 100, PP = 1.00) that is sister to *Austrochloris dichanthioides* (BS = 96, PP = 1.00); two species of *Trichloris* that includes two accessions of *T. pluriflora* (BS = 100, PP = 1.00); *Ceolachyrum poiflorum* and *Eleusine indica* are sister (BS = 78, PP = 0.92), sister to this is *Apochiton burtii* (BS = 80, PP = 0.79); and unsupported clades of *Leptochloa dubia*, *L. uninervia*, and *Schoenefeldia transiens*. The following genera do not align within these 13 subtribes: two species of *Cleistogenes* (BS = 100, PP = 1.00) form a clade (PP = 0.99) with three species of *Orinus* (BS = 100, PP = 1.00); *Leptochloa filiformis* and *Dinebra retroflexa* (BS = 99, PP = 1.00) are sister, sister to this is *Leptochloa viscida* (BS = 90, PP = 1.00); four species of *Dactyloctenium* form a clade (BS = 100, PP = 1.00), sister to this is *Brachychloa schiemanniana* (BS = 57, PP = 0.71), and sister to these is *Neobouteloua lophostachya* (BS = 71, PP = 1.00); *Bewisia biflora* is an unsupported sister to the Pappophorinae; *Dignathia hirtella* and *Gymnopogon grandiflorus* are sister (PP = 0.55); three species of *Perotis* form a clade (BS = 98, PP = 1.00), sister to this is *Mosdenia phleoides* (BS = 100, PP = 1.00); two species of *Ctenium* (BS = 100, PP = 1.00) form a clade, sister to this is a clade (BS = 69, PP = 0.97) with two species of *Trichoneura* (BS = 99, PP = 1.00); male and female accessions of *Allolepis texana* form a clade (BS = 100, PP = 1.00) that is sister (PP = 0.71) with the Hilariinae; *Jouvea pilosa* is an unsupported sister to the Boutelouinae; and two accessions of *Sohnsia filifolia* (BS = 100, PP = 1.00) are sister to an unsupported clade containing the Muhlenbergiinae and the Scleropogoninae.

Sister to the Cynodonteae is the Zoysieae that consists of two well resolved subtribes, the Sporobolinae (BS = 100, PP = 1.00) and the Zoysiinae (BS = 100, PP = 1.00). The Sporobolinae includes a polyphyletic *Sporobolus* with *Calamovilfa longifolia*, *Spartina densiflora*, and a clade of two species of *Crypsis* (BS = 100, PP = 1.00) embedded within. The Zoysiinae is represented by a single genus, *Zoysia* with three taxa in two species. Sister to the Cynodonteae and Zoysieae clade (BS = 96, PP = 1.00) is the Eragrostideae. The Eragrostideae is composed of three subtribes, the Eragrostidinae (PP = 0.90) is sister to the Unioliinae (BS = 53, PP = 0.94), this clade is sister to *Cottea pappophoroides* (PP = 0.90), and sister to all is *Enneapogon desvauxii* (BS = 51, PP = 0.92) (*Cottea* and *Enneapogon* form a well resolved Cotteinae in the plastid and combined tree, see Figs. 2 and 3). The Unioliinae contains a clade of two species of *Uniola* (BS = 93, PP = 1.00) that is sister to a clade with *Entoplocamia aristulata* and *Tetrachne dregei* (BS = 54, PP = 0.92). Within the Eragrostidinae, *Eragrostis* is polyphyletic and embedded within is a clade of three species of *Ectrosia* (BS = 99, PP = 1.00) that is sister to *Harpachne harpachnoides* (BS = 92, PP = 1.00); *Psammagrostis wiseana* is an unsupported member of an Australian clade (BS = 73, PP = 1.00) of *Eragrostis* that includes *E. desertorum*, *E. dielsii*, *E. eriopoda*, *E. kennedyae*, *E. lanicaulis*, and *E. pergracilis*. The Triraphideae is sister to the all remaining members of the Chloridoideae and this tribe consists of two genera: two species of *Triraphis* (BS = 82, PP = 0.92) form a clade that is sister to *Neyraudia reynaudiana* (BS = 97, PP = 1.00).

3.2. Analysis of plastid sequences

The number of species included in the plastid analysis was 254 (268 total taxa, 14 species with two samples; 8 outgroup); average sequence length was 4409; number of PIC's was 1948; and the tree length was 7534 with a consistency index (CI) of 0.4153, homoplasy index (HI) of 0.5847, retention index (RI) of 0.7932, and a re-scaled consistency index (RC) of 0.3294 (Table 2). The overall topology of the plastid-derived phylogram is very similar to the ITS tree, although BS and PP values are usually higher for most clades (Fig. 2). The Eragrostideae (BS = 96, PP = 1.00) and Zoysieae (BS = 97, PP = 1.00) are now strongly supported and the Cynodonteae (BS = 85, PP = 1.00) is moderately supported. The Triraphideae

(BS = 91, PP = 1.00) includes a monophyletic *Triraphis* clade (BS = 52, PP = 0.80) of five species that is sister to *Neyraudia reynaudiana*. Within the Eragrostideae, *Cottea pappophoroides* and *Enneapogon desvauxii* form a strongly supported Cotteinae clade (BS = 100, PP = 1.00) that is sister to remaining members (BS = 91, PP = 1.00). The Unioliinae (BS = 80, PP = 1.00) consists of *Entoplocamia aristulata* and *Tetrachne dregei* clade (BS = 74, PP = 1.00) sister to a monophyletic *Uniola* with *U. condensata* and *U. paniculata* (BS = 96, PP = 1.00). The Eragrostidinae still contains a polyphyletic *Eragrostis* (BS = 91, PP = 1.00) with most nodes supported by high BS and PP values. A major clade of *Eragrostis* species primarily from the Americas and Africa (BS = 65, PP = 0.84) is sister to a strongly supported clade of *Harpachne harpachnoides* plus three species of *Ectrosia* (BS = 100, PP = 1.00), together these are sister to a strongly supported Australian clade (BS = 100, PP = 1.00) of *Psammagrostis wiseana* plus five species of *Eragrostis*. In the Zoysieae, *Pogoneura biflora* is embedded within a polyphyletic *Sporobolus* and is aligned in a clade with two species of *Crypsis* (BS = 100, PP = 1.00). The bootstrap and posterior probability values (BS = 64, PP = 1.00) for the Sporobolinae are lower than in the ITS tree. *Urochondra setulosa* is sister to all remaining members of the Zoysieae (BS = 81, PP = 1.00).

In the Cynodonteae, the 13 subtribes are well resolved although the Eleusininae has no bootstrap value (PP = 1.00), Tridantinae (BS = 61, PP = 1.00), Hilariinae (BS = 95, PP = 1.00), Orcuttiinae (BS = 91, PP = 1.00), and Traginae (BS = 92, PP = 1.00) have somewhat lower support values and the Boutelouinae (BS = 100, PP = 1.00), Monanthochloinae (BS = 97, PP = 1.00), Muhlenbergiinae (BS = 95, PP = 1.00), Scleropogoninae (BS = 99, PP = 1.00), and Pappophorinae (BS = 89, PP = 1.00) have higher support values. *Lepturidium insulare*, not in the ITS data set, is the closest sister to the Muhlenbergiinae, followed by *Sohnsia* with weak support (BS = 53, PP = 0.81). Alignment of the taxa within the Muhlenbergiinae is very similar to the ITS tree, although some support values are higher in the plastid phylogeny. *Schaffnerella gracilis* (not in ITS data) is sister (BS = 88, PP = 0.99) to *Lycurus* and together these are sister (BS = 78, PP = 0.99) to the *Chaboissaea* clade (BS = 100, PP = 1.00). The Scleropogoninae is not the immediate sister to the Muhlenbergiinae as in the ITS tree but is sister to the *Sohnsia*–*Lepturidium*–Muhlenbergiinae clade. Within the Scleropogoninae, *Scleropogon* is the basal member and *Swallenia* is sister to *Blepharidachne*. Monanthochloinae is sister to the Boutelouinae (BS = 77, PP = 1.00). In between the Pappophorinae and the Eleusininae is the Tripogoninae (PP = 1.00) that includes *Melanocenchris* sister to *Tripogon* plus *Eragrostiella* embedded within. This same relationship was recovered in the ITS phylogeny but the Tripogoninae was placed as sister to the Orcuttiinae. The Pappophorinae falls between the Tripogoninae and the Traginae. Within the Eleusininae, *Leptochloa uninervia* is basal followed by *Austrochloris dichanthioides* as sister to four species of *Astrebula* (BS = 63, PP = 0.91) with *Schoenefeldia gracilis* embedded within. *Lintonia nutans* is embedded in a clade with four other species of *Chloris* (BS = 90, PP = 1.00). Five species of *Lepturus* form a monophyletic lineage (BS = 70, PP = 1.00) as does *Microchloa* (BS = 100, PP = 1.00). *Brachyachne chrysolepis*, *B. fibrosa*, and *B. pateniflora* again form a strongly supported clade (BS = 100, PP = 1.00), and nine species of *Cynodon* form a strongly supported clade (BS = 90, PP = 1.00) with *Brachyachne convergens* and *B. tenella* embedded within (also found in the ITS tree). *Saugetia* forms a strongly supported clade (BS = 99, PP = 1.00) with two species of *Tetrapogon*. In the incertae sedis genera, the *Orinus* clade (BS = 100, PP = 1.00) forms a clade (BS = 70, PP = 1.00) with the Triodiinae (BS = 90, PP = 1.00) and this clade is sister to the Aeluropodinae. *Bewisia biflora* and *Gymnopogon grandiflorus* are sister (BS = 78, PP = 1.00) and they form a clade (BS = 61, PP = 1.00) with two species of *Dignathia* (BS = 98, PP = 1.00).

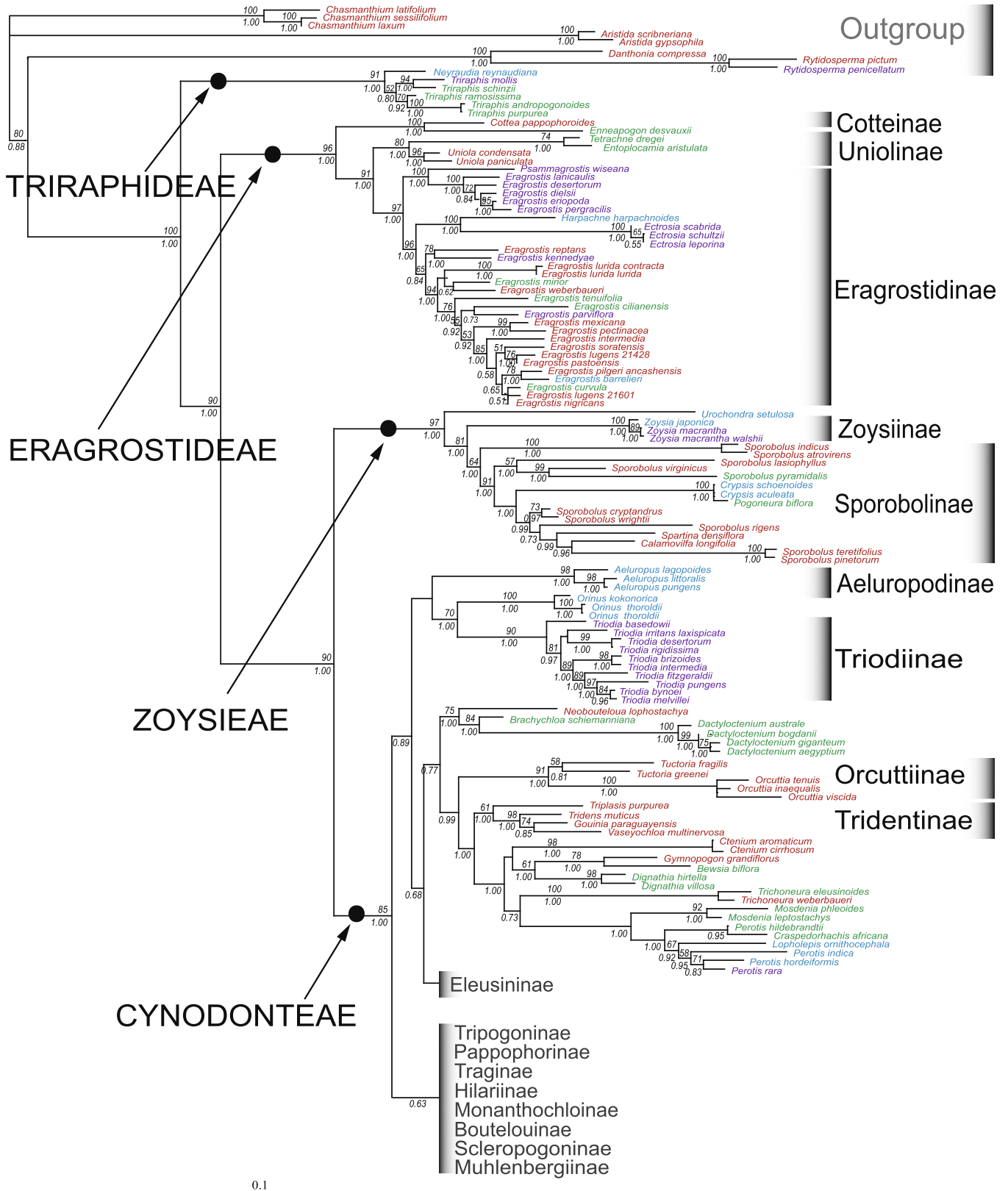


Fig. 2. Phylogram of best maximum likelihood tree from analysis of plastid data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values; taxon colour indicates native distribution as follows: green = African, blue = Asian, purple = Australian, red = American (includes North and South America). (For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)

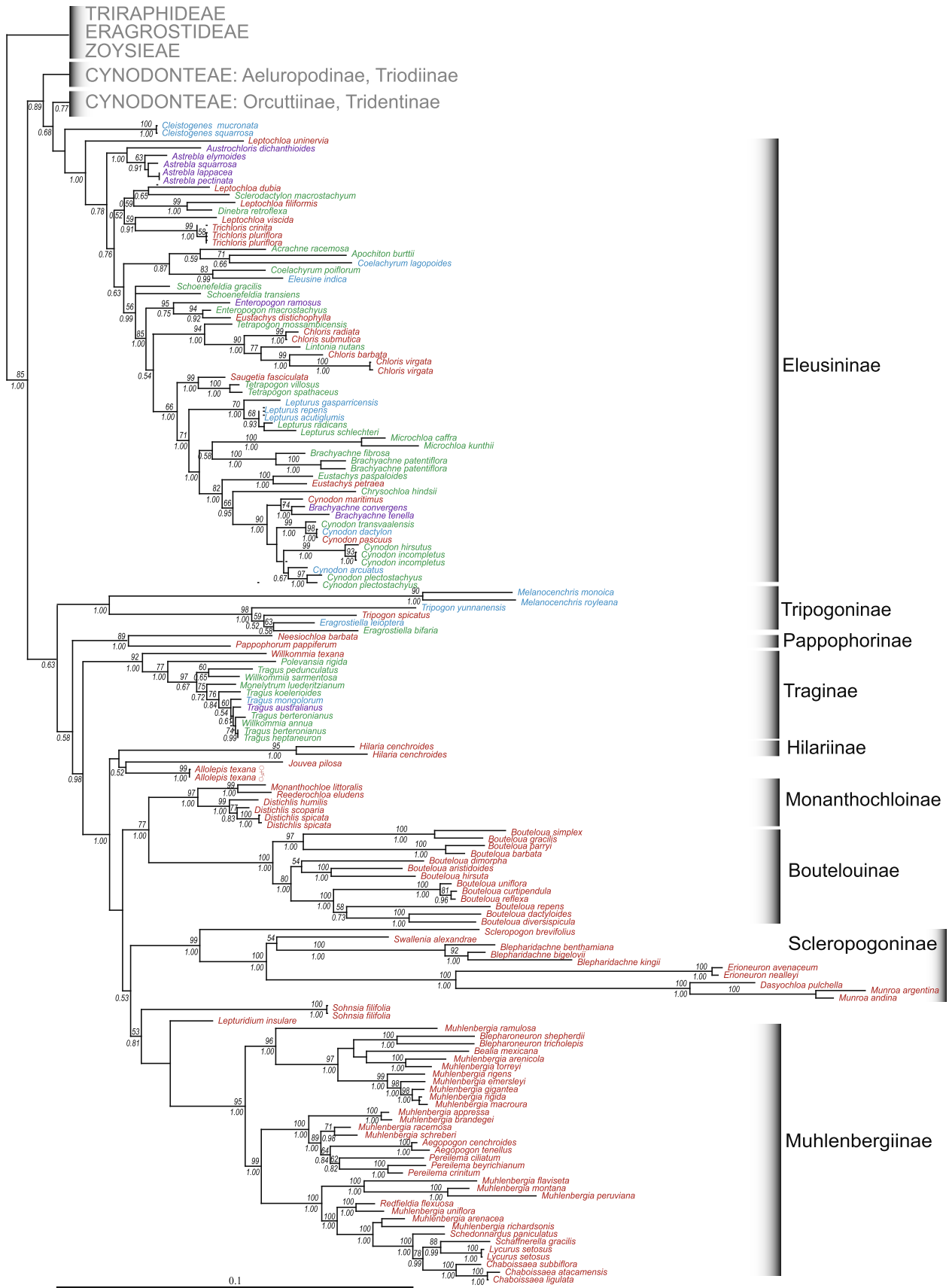


Fig. 2 (continued)

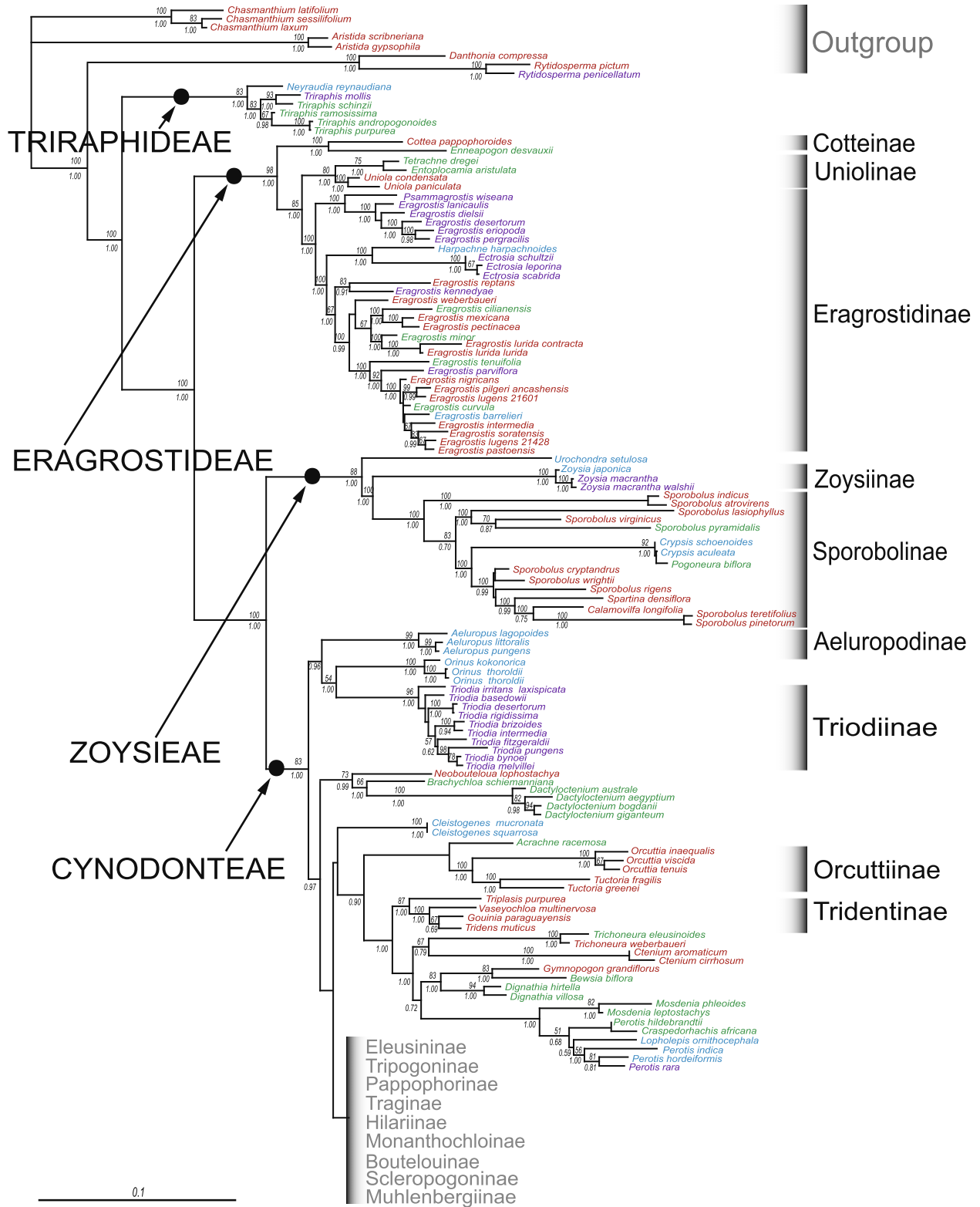


Fig. 3. Phylogram of best maximum likelihood tree from analysis of combined plastid and nuclear ITS data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values; taxon colour indicates native distribution as follows: green = African, blue = Asian, purple = Australian, red = American (includes North and South America). (For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)

3.3. Combined plastid and ITS sequences

The number of taxa included in the combined plastid and ITS analysis was 268 (8 outgroup); average sequence length was

5078; number of PIC's was 2377; and the tree length was 12332 with a consistency index (CI) of 0.3323, homoplasy index (HI) of 0.6677, retention index (RI) of 0.7658, and a rescaled consistency index (RC) of 0.2545 (Table 2). The overall topology of the com-

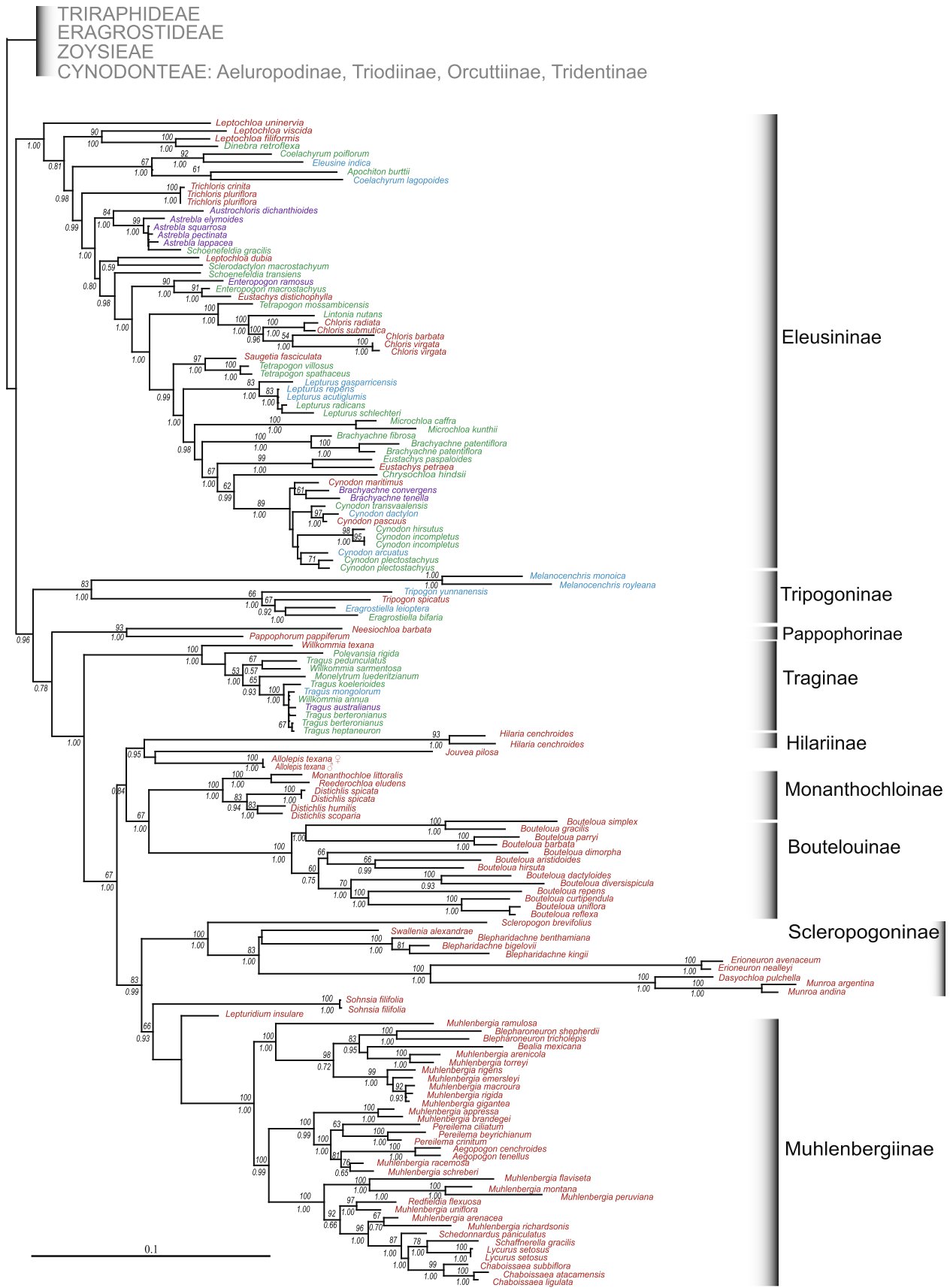


Fig. 3 (continued)

bined plastid and ITS-derived phylogram is similar to the plastid tree. The major tribes within a monophyletic Chloridoideae (BS = 100, PP = 1.00) are well resolved. The Cynodonteae (BS = 83, PP = 1.00) and Zoysieae (BS = 88, PP = 1.00) form a clade (BS = 100, PP = 1.00) and they are sister to the Eragrostideae (BS = 98, PP = 1.00), and sister to all of these tribes is the Triraphideae (BS = 83, PP = 1.00).

Within the Cynodonteae, the Aeluropodinae, Boutelouinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, Orcuttiinae, Pappophorinae, Traginae, and the Triodiinae are strongly supported clades (BS = 93–100, PP = 1.00). The Eleusininae has only posterior probability support (PP = 1.00) and the Tridentinae (BS = 87, PP = 1.00) and Tripogoninae (BS = 83, PP = 1.00) are moderately supported. There is support for relationships among these subtribes since there is some structure within the deep nodes of this phylogram. The Muhlenbergiinae is the most derived subtribe, there is weak support for the *Sohnsia–Lepturidium–Muhlenbergiinae* clade (BS = 66, P = 0.93), and the Scleropogoninae is moderately supported as the sister to *Sohnsia–Lepturidium–Muhlenbergiinae* clade (BS = 83, PP = 0.99). The Boutelouinae and the Monanthochloinae are weakly supported (BS = 67, PP = 1.00) as sister and the Hilariinae–Boutelouinae–Monanthochloinae–Scleropogoninae–*Sohnsia–Lepturidium–Muhlenbergiinae* is weakly supported (BS = 67, PP = 1.00). The Traginae has posterior probability support (PP = 1.00) as sister to the Hilariinae–Boutelouinae–Monanthochloinae–Scleropogoninae–*Sohnsia–Lepturidium–Muhlenbergiinae* clade. Alignment within the Eleusininae is very similar to that found in the plastid tree, again with strong support (BS = 99–100, PP = 1.00) for the following: three species of *Brachyachne*, three species of *Trichloris*, a polyphyletic *Astrebula* with *Schoenefeldia gracilis* embedded, four species of *Chloris*, and two species of *Microchloa*. A polyphyletic *Cynodon* that includes *Brachyachne convergens* and *B. tenella* and five species of *Lepturus* are moderately supported (BS = 89, PP = 1.00).

3.4. Nomenclature novelties

Based on our results we propose a new classification for the Chloridoideae (Table 3) and the following names are necessary to realign the genera now recognized in the subfamily. *Merxmuellera papposa* (Nees) Conert, *M. rangei* (Pilg.) Conert, and the four species now currently placed in *Centropodia* Rchb. are not included in the proposed new classification since their placement as sister to the Chloridoideae is equivocal in all molecular trees to date (Barker et al., 1999, 2000; GPWG, 2001; Roodt-Wilding and Spies, 2006; Bouchenak-Khelladi et al., 2008). One or both genera may possibly align within the Chloridoideae but this has not been thoroughly investigated.

Tribe Cynodonteae, subtribe **Aeluropodinae** P. M. Peterson, stat. nov. – TYPE: *Aeluropus* Trin., Fund. Agrost. 143, pl. 12. 1820. Basionym: Aeluropodeae trib. Nevski ex Bor, Oesterr. Bot. Z. 112: 184. 1965. Included genera: *Aeluropus*.

Tribe **Triraphideae** P. M. Peterson, stat. nov. – TYPE: *Triraphis* R. Br., Prodr. 185. 1810. Basionym: Triraphidinae subtrib. Stapf, Fl. Trop. Afr. 9: 22. 1917. Included genera: *Neyraudia*, *Triraphis*.

4. Discussion

4.1. Phylogenetic relationships

4.1.1. Tribes and subtribes

In our overall tribal relationships, Cynodonteae and Zoysieae are sisters, and sister to this are Eragrostideae, and sister to all are Triraphideae. This corroborates results by Hilu et al. (1999) using only a few taxa, by Columbus et al. (2007) in their ITS and

trnL-F study, and by Bouchenak-Khelladi et al. (2008) in their three plastid gene (*rbcl*, *matK*, and *trnL-F*) survey of the grasses. Only the latter study included members of the Triraphideae, and they found it to be sister to the Eragrostideae, and these in turn sister to a clade containing the Zoysieae and the Cynodonteae. Bell and Columbus (2008a) reported in an oral paper and abstract that their combined data set of ITS, *trnL-F*, and *ndhF* sequences yielded a tree with the following order of divergence: “*Triraphis*, an *Eragrostis* clade, and a *Sporobolus* clade that is sister to a large clade with two sub lineages, one comprised of primarily Old World and cosmopolitan taxa and the other primarily New World.” Based on *matK* sequences and a full sampling of genera and species, Hilu and Alice (2001) found support for the recognition of the Zoysieae, Eragrostideae, Cynodonteae, and *Triraphis* but their order of derivation was equivocal. Our hypothesized phylogeny is the first to verify with medium to strong support values the stepwise derivation of the Triraphideae, Eragrostideae, Zoysieae, to the Cynodonteae.

In the Triraphideae, Bouchenak-Khelladi et al. (2008) were first to show strong support for *Neyraudia* and *Triraphis* as being sister. We offer moderate support for the monophyly of *Triraphis* having sampled five of the seven known species. Clayton and Renvoize (1986) pointed out that *Triraphis* was perhaps an ally of *Neyraudia* since both genera possess slender panicoid-like microhairs and the two have keeled lemmas that are villous on the lateral nerves (Watson and Dallwitz, 1992a). Hilu and Alice (2001) and Bouchenak-Khelladi et al. (2008) who both used the same *matK* sequence place this taxon in the Unioliinae. We have ITS and *rps16*-spacer sequences support (although only weakly) for *Tetrachne* as sister to *Uniola*. We have moderate to strong support (BS = 85, PP = 1.00) for order of divergence of the Cotteinae, Unioliinae, and the Eragrostidinae. Within the Eragrostidinae, our data indicate that *Eragrostis* is polyphyletic since three genera (*Ectrosia*, *Harpachne harpachnoides*, and *Psammagrostis wiseana*) are embedded within. We advocate subsuming the previous three genera within *Eragrostis* since it would be much easier to expand the circumscription than to begin splitting out small clades within this large genus (400+ spp., Simon et al., 2009). *Ectrosia* along with *Pogonarthria squarrosa* (Roem. & Schult.) Pilg. were found embedded within a polyphyletic *Eragrostis* (Columbus et al., 2007). Based on a survey of *rps16* and nuclear waxy gene sequences from a broad range of *Eragrostis* species, Ingram and Doyle (2003, 2004, 2007) have advocated that other small segregate genera such as *Acamptocladus* Nash, *Diandrochloa* De Winter, and *Neeragrostis* Bush be included with *Eragrostis*. Roodt-Wilding and Spies (2006) in their ITS and *trnL-F* strict consensus tree found *Catalepis*, *Cladoraphis*, and *Pogonarthria* all embedded in a polyphyletic *Eragrostis* clade. There is a geographic signal within our expanded *Eragrostis* since the clade containing *Psammagrostis wiseana*, *E. desertorum*, *E. dielsii*, *E. eriopoda*, *E. lanicaulis*, and *E. pergracilis*, all endemic to Australia, are sister to the remaining species in the genus. The thickened to coriaceous spikelets of *Psammagrostis* are very similar to those found in *E. dielsii* and *E. lanicaulis* (Clayton and Renvoize, 1986; Lazarides, 1997). *Harpachne* has a raceme inflorescence with reflexed spikelets that are very similar to other species of *Eragrostis* whereas species of *Ectrosia* have 1-nerved glumes and awned lemmas that are 1–3-nerved (Watson and Dallwitz, 1992a; Nightingale and Weiller, 2005a). Mucronate lemmas have been reported for a few species of *Eragrostis* but by addition of the 12 Australian–Malaysian species of *Ectrosia* the circumscription will need emendation.

Sister to the Eragrostidinae is the Unioliinae where we provide the first molecular evidence for *Entoplocamia* and *Tetrachne* (BS = 75, PP = 1.00 in Fig. 3) each monotypic genera from Africa, as being sister to two species of *Uniola*. Clayton (1982) included *Fingerhuthia* Stapf and *Tetrachne* in this subtribe, and this has been corroborated with molecular studies (Hilu and Alice, 2001; Colum-

Table 3
A proposed tribal and subtribal classification of genera in subfamily Chloridoideae (Poaceae). The proposed assignments are based on plastid and nuclear DNA analyses (*= not examined in this study) and/or morphology. See footnotes legend below for placement of taxon by Clayton and Renvoize (1986).

Subfamily Chloridoideae
Incertae sedis: * <i>Afrotrichloris</i> Chiov., * <i>Daknopholis</i> Clayton, * <i>Decaryella</i> A. Camus, * <i>Desmostachya</i> (Hook.f) Stapf, * <i>Drake-Brockmania</i> Stapf, * <i>Farrago</i> Clayton, * <i>Habrochloa</i> C.E. Hubb., * <i>Halopyrum</i> Stapf, * <i>Hubbardochloa</i> Auquier, * <i>Indopoa</i> Bor., * <i>Kamprochloa</i> Clayton, * <i>Kaokochloa</i> De Winter, * <i>Leptocarydion</i> Stapf, * <i>Leptothrium</i> Kunth, * <i>Lepturopetium</i> Morat, * <i>Lophachme</i> Stapf, * <i>Myriostachya</i> (Benth.) Hook.f., * <i>Neostapfiella</i> A. Camus, * <i>Ochthochloa</i> Edgew., * <i>Odyssea</i> Stapf, * <i>Oropetium</i> Trin., * <i>Pogonochloa</i> C.E. Hubb., * <i>Pommereulla</i> L.f., * <i>Pseudozoysia</i> Chiov., * <i>Psilolemma</i> S.M. Phillips, * <i>Silentvalleya</i> V.J. Nair, * <i>Tetrachaete</i> Chiov., * <i>Viguierella</i> A. Camus
Tribe Triraphideae P.M. Peterson: <i>Neyraudia</i> Hook. f. ^a , <i>Triraphis</i> R. Br. ^a
Tribe Eragrostideae Stapf
Incertae sedis: * <i>Cladoraphis</i> Franch.
Subtribe Cotteinae Reeder ^b : <i>Cottea</i> Kunth ^b , <i>Enneapogon</i> P. Beauv. ^b , * <i>Schmidtia</i> Steud. ex J.A. Schmidt
Subtribe Eragrostidinae J. Presl ^a : * <i>Catalepis</i> Stapf, <i>Ectrosia</i> R. Br. ^a [includes * <i>Ectrosiopsis</i> (Ohwi) Ohwi ex Jansen, see Nightingale and Weiller, 2005], <i>Eragrostis</i> Wolf ^a (includes * <i>Acampoclados</i> Nash, * <i>Diandrochloa</i> De Winter, and <i>Neeragrostis</i> Bush), <i>Harpachne</i> A. Rich. ^a , * <i>Heterachne</i> Benth., * <i>Pogonarthria</i> Stapf, <i>Psammagrostis</i> C.A. Gardner & C.E. Hubb. ^a , * <i>Richardsiella</i> Elffers & Kenn.-O'Byrne, * <i>Steirachne</i> Ekman
Subtribe Unioliinae Clayton: <i>Entoplocamia</i> Stapf, * <i>Fingerhuthia</i> Nees ex Lehmann, * <i>Stiburus</i> Stapf, <i>Tetrachne</i> Nees, <i>Uniola</i> L.
Tribe Zoysiaceae Benth. ^c
Incertae sedis: <i>Urochondra</i> C.E. Hubb. ^d
Subtribe Zoysiinae Benth. ^c : <i>Zoysia</i> Willd.
Subtribe Sporobolinae Benth. ^c : <i>Calamovilfa</i> (A. Gray) Scribn. ^d , <i>Crypsis</i> Aiton ^d , <i>Pogoneura</i> Napper ^a , <i>Spartina</i> Schreb. ^f , <i>Sporobolus</i> R. Br. ^d , * <i>Thellungia</i> Stapf
Tribe Cynodonteae Dumort.
Incertae sedis: <i>Acrachne</i> Wight & Arn. ex Chiov. ^a , <i>Allolepis</i> Soderstr. & H.F. Decker ^g , <i>Bewsia</i> Goossens ^a , <i>Brachyachne</i> S.M. Phillips ^a , <i>Cleistogenes</i> Keng ^a , <i>Craspedorhachis</i> Benth. ^f , <i>Ctenium</i> Panz. ^f , <i>Dactyloctenium</i> Willd. ^a , <i>Dignathia</i> Stapf ^m , <i>Gymnopogon</i> P. Beauv. ^f , <i>Jouvea</i> E. Fourn. ^g , <i>Lepturidium</i> Hitchc. & Ekman ^f , <i>Lopholepis</i> Decne. ^m , <i>Mosdenia</i> Stent ^l , <i>Neobouteloua</i> Gould ^l , <i>Orinus</i> Hitchc. ^a , <i>Perotis</i> Aiton ^l , <i>Sohnsia</i> Airy Shaw ^a , <i>Trichoneura</i> Andersson ^a
Subtribe Aeluropodinae P.M. Peterson: <i>Aeluropus</i> Trin. ^e
Subtribe Triodiinae Benth. ^g : * <i>Monodia</i> S.W.L. Jacobs, * <i>Symplectrodia</i> Lazarides, <i>Triodia</i> R. Br. (includes * <i>Plectrachne</i> Henrard see Lazarides et al., 2005)
Subtribe Orcuttiinae P.M. Peterson & Columbus ^h : * <i>Neostapfia</i> Burt Davy, <i>Orcuttia</i> Vasey, <i>Tuctoria</i> Reeder
Subtribe Tridentinae Keng & Keng f. ^a : <i>Gouinia</i> E. Fourn. ex Benth. & Hook ^a (includes <i>Schenckochloa</i> J.J. Ortiz), <i>Tridens</i> Roem. & Schult. ^a , <i>Triplasis</i> P. Beauv. ^a , <i>Vaseyochloa</i> Hitchc. ^a
Subtribe Eleusiniinae Dumort. ^e : <i>Apochiton</i> C.E. Hubb. ^a , <i>Astrebla</i> F. Muell. ⁱ , <i>Austrochloris</i> Lazarides ^f , <i>Brachyachne</i> (Benth.) Stapf ^f , <i>Chloris</i> Sw. ^f , <i>Chrysochloa</i> Swallen ^f , <i>Coelachyrum</i> Hochst. & Nees ^a (includes <i>Coelachyropsis</i> Bor., <i>Cypholepis</i> Chiov.), <i>Cynodon</i> Rich. ^f , <i>Dinebra</i> Jacq. ^a , <i>Eleusine</i> Gaertn. ^a , <i>Enteropogon</i> Nees ^f , <i>Eustachys</i> Desv. ^f , * <i>Harpochloa</i> Kunth, <i>Leptochloa</i> P. Beauv. ^a , <i>Lepturus</i> R. Br. ^j , <i>Lintonia</i> Stapf ^f , <i>Microchloa</i> R. Br. ^f , * <i>Oxychloris</i> Lazarides, * <i>Rendlia</i> Chiov., * <i>Rheochloa</i> Filg., P.M. Peterson & Y. Herrera, <i>Tetrapogon</i> Desf. ^f , <i>Trichloris</i> Benth. ^f , <i>Saugetia</i> Hitchc. & Chase ^k , <i>Schoenefeldia</i> Kunth ^f , <i>Sclerodactylon</i> Stapf ^o
Subtribe Tripogoninae Stapf ^a : <i>Eragrostiella</i> Bor ^a , <i>Melanocenchris</i> Nees ^l , <i>Tripogon</i> Roem. & Schult. ^a
Subtribe Pappophorinae Dumort. ^b : <i>Neesiochloa</i> Pilg. ^a , <i>Pappophorum</i> Schreb. ^b
Subtribe Traginae P.M. Peterson & Columbus: <i>Monelytrum</i> Hack. ^m , <i>Polevansia</i> De Winter ^f , <i>Tragus</i> Haller ^m , <i>Willkommia</i> Hack. ^f
Subtribe Hilariinae P.M. Peterson & Columbus: <i>Hilaria</i> Kunth ^l , * <i>Pleuraphis</i> Torr. ⁿ
Subtribe Monanthochloinae Pilg. ex Potzta ^o : <i>Distichlis</i> Raf. (includes <i>Monanthochloa</i> Engelm., <i>Reederochloa</i> Soderstr. & H.F. Decker)
Subtribe Boutelouinae Stapf: <i>Bouteloua</i> Lag. (includes <i>Buchloe</i> Engelm., * <i>Buchlomimus</i> Reeder, C. Reeder & Rzed., <i>Cathesticum</i> J. Presl, <i>Chondrosium</i> Desv., <i>Cyclostachya</i> Reeder & C. Reeder, * <i>Griffithsochloa</i> G.J. Pierce, <i>Opizia</i> J. Presl, * <i>Pentarraphis</i> Kunth, * <i>Pringleochloa</i> Scribn., and * <i>Soderstromia</i> C.V. Morton, see Columbus, 1999)
Subtribe Scleropogoninae Pilg. ^a : <i>Blepharidachne</i> Hack. ^a , <i>Dasyochloa</i> Rydb. ^o , <i>Erioneuron</i> Nash ^a , <i>Munroa</i> Torr. ^a , <i>Scleropogon</i> Phil. ^a , <i>Swallenia</i> Soderstr. & H.F. Decker ^g
Subtribe Muhlenbergiinae Pilg. ^d : <i>Aegopogon</i> Humb. & Bonpl. ex Willd. ^l , <i>Bealia</i> Scribn. ^p , <i>Blepharoneuron</i> Nash ^a , <i>Chaboissaea</i> E. Fourn. ^p , <i>Lycurus</i> Kunth ^d , <i>Muhlenbergia</i> Schreb. ^d , <i>Pereilema</i> J. Presl ^d , <i>Redfieldia</i> Vasey ^a , <i>Schaffnerella</i> Nash ^l , <i>Schedonnardus</i> Steud. ^l

^a Placed in tribe Eragrostideae, subtribe Eleusiniinae.

^b Placed in tribe Pappophoreae Kunth.

^c Placed in tribe Cynodonteae.

^d Placed in tribe Eragrostideae, subtribe Sporobolinae.

^e Placed in tribe Eragrostideae.

^f Placed in tribe Cynodonteae, subtribe Chloridinae J. Presl.

^g Placed in tribe Eragrostideae, subtribe Monanthochloinae.

^h Placed in tribe Orcuttiinae Reeder.

ⁱ Placed in tribe Cynodonteae, subtribe Pommereullinae Pilg. ex Potzta.

^j Placed in tribe Leptureae Holmberg.

^k Placed in *Enteropogon*.

^l Placed in subtribe Boutelouinae.

^m Placed in subtribe Zoysiinae.

ⁿ Placed in *Hilaria*.

^o Placed in *Erioneuron*.

^p Placed in *Muhlenbergia*.

bus et al., 2007; Bouchenak-Khelladi et al., 2008). Roodt-Wilding and Spies (2006) in their strict consensus tree of ITS sequence data found strong support for a clade containing *Entoplocamia* and *Fingerhuthia*. All three genera have a raceme inflorescence, a line of hairs for the ligule, and 5–11-nerved lemmas (Watson and Dall-

witz, 1992a). The basal member of the Eragrostideae is the Cotteinae and this has been recovered along with the inclusion of *Schmidtia* Steud. ex J.A. Schmidt in other molecular studies (Hilu and Alice, 2001; Columbus et al., 2007; Bouchenak-Khelladi et al., 2008).

The Sporobolinae in our study includes a polyphyletic *Sporobolus* with *Calamovilfa*, *Crypsis*, *Pogoneura*, and *Spartina* embedded within. These genera have been verified as being embedded with *Sporobolus* in other molecular studies with the exception of *Pogoneura* (reported here) (Ortiz-Diaz and Culham, 2000; Hilu and Alice, 2001; Columbus et al., 2007; Bouchenak-Khelladi et al., 2008). Even though *Sporobolus* includes 200 species worldwide (Simon et al., 2009) and sampling within the genus for molecular studies have been rather small (42 species in Ortiz-Diaz and Culham, 2000), we recommend expansion of *Sporobolus* to include these genera. The monotypic genus, *Pogoneura biflora* from east Africa, is morphologically quite distinct from others members of *Sporobolus* since it has 2 or 3-flowered spikelets with short awned lemmas (Clayton and Renvoize, 1986). Sister to the Sporobolinae and Zoysiinae in our plastid and combined trees (we lack ITS sequence) is *Urochondra setulosa*, a monotypic species from northeast Africa. Like *Zoysia*, *Urochondra* has 1-flowered spikelets with 1-nerved and awnless glumes, 1-nerved lemmas, and lacks lodicules (Watson and Dallwitz, 1992a).

The most derived tribe within the Chloridoideae, the Cynodonteae exhibits a wide range of morphological variation and we currently recognize 13 well supported subtribes. Relationships among these subtribes are fairly well elucidated since there are support indexes at many of the deep nodes in our combined plastid-ITS phylogram. Our clade uniting, in order of divergence, the Hilariinae with *Allolepis* and *Jouvea*, Monanthochloinae, Boutelouinae, Scleropogoninae, *Sohnsia*, *Lepturidium*, and Muhlenbergiinae is almost entirely New World (western hemisphere) in origin and current distribution.

The Muhlenbergiinae are here represented by 33 species and it is clear that *Muhlenbergia* is polyphyletic and that *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, and *Schedonnardus* are nested within (Duvall et al., 1994; Columbus et al., 2007; in press; Peterson et al., in review). The subgeneric classification within the Muhlenbergiinae has recently been studied and there is strong support for a subgeneric classification to recognize five clades (Peterson, 2000; Peterson and Herrera Arrieta, 2001; Peterson et al., in review). In the combined plastid and ITS tree in Peterson et al. (in review) there is moderate support for *M. sect. Bealia* that includes *Bealia*, two species of *Blepharoneuron*, *M. arenicola*, and *M. torreyi* (BS = 83, PP = 0.95); strong support of *M. subg. Trichochloa* that includes *M. emersleyi*, *M. gigantea*, *M. macroura*, *M. rigens*, and *M. rigida* (BS = 99, PP = 1.00); strong support for *M. subg. Muhlenbergia* that includes two species of *Aegopogon*, three species of *Pereilema*, *M. appressa*, *M. brandegei*, *M. racemosa*, and *M. schreberi* (BS = 100, PP = 0.99); strong support for *M. subg. Clomena* that includes *M. flaviveta*, *M. montana*, and *M. peruviana*; and strong support for a *M. unranked Pseudosporobolus* clade that contains three species of *Chaboissaea*, two species of *Lycurus*, *Redfieldia*, *Schaffnerella*, *Schedonnardus*, *M. arenacea*, *M. richardsonis*, and *M. uniflora* (BS = 92, PP = 0.66).

Sister to the Muhlenbergiinae–*Lepturidium*–*Sohnsia* clade is the Scleropogoninae that consists of the following six genera: *Blepharidachne*, *Dasyochloa*, *Erioneuron*, *Munroa*, *Scleropogon*, and *Swallenia*. In a combined ITS and *trnL-F* tree, Columbus et al. (2007) obtained strong support for a clade of *Dasyochloa*, *Erioneuron*, and *Munroa*. In this same tree Columbus et al. (2007) recovered an unsupported clade containing *Blepharidachne*, *Scleropogon*, and *Swallenia*. Morphologically, these species share lemmas that are often chartaceous to coriaceous with ciliate margins and usually narrow and condensed inflorescences (Watson and Dallwitz, 1992a). Florets are perfect in *Dasyochloa*, *Erioneuron*, and *Swallenia*, can be unisexual in *Blepharidachne* and *Munroa*, while individual plants of *Scleropogon* are male or female (dioecious) or sometimes of both sexes (monoecious). We provide the

first molecular support for including *Blepharidachne*, *Scleropogon*, and *Swallenia* in the Scleropogoninae, hence placing Munroinae in synonymy (Peterson et al., 1995).

In our study the Monanthochloinae and Boutelouinae are sister (BS = 67, PP = 1.00 in Fig. 3) and both subtribes have been the subject of molecular studies. Based on ITS and *trnL-F* sequences Columbus (1999) and Columbus et al. (1998, 2000) subsumed nine genera (many of these were unisexual) to accommodate a monophyletic *Bouteloua*. We also support this view since at least three (*Buchloe*, *Cathetecum*, and *Opizia*) were included in our analysis and all our trees depict a strongly supported Boutelouinae (excluding *Neobouteloua*). In a three gene study (ITS, *ndhF*, and *trnL-F*) of the Monanthochloinae, Bell and Columbus, 2008b proposed expanding *Distichlis* to include two species of *Monanthochloa* and *Reederchloa eludens* (= *Distichlis eludens* (Soderstr. & H. F. Decker) H. L. Bell & Columbus). Our data does not refute this decision and we agree with their interpretation even though our combined and plastid trees placed *M. littoralis* and *Reederchloa* in a clade as sister to the remaining three species of *Distichlis*. Our analysis did not include *M. acerosa* (Griseb.) Speg. (= *Distichlis acerosa* (Griseb.) H. L. Bell & Columbus) or *Distichlis australis* (Speg.) Villamil, both members of a clade with *M. littoralis* (= *Distichlis littoralis* (Engelm.) H. L. Bell & Columbus) and *Reederchloa* that was sister to all other species of *Distichlis* (Bell and Columbus, 2008b).

The Traginae in our study includes a polyphyletic *Tragus* and *Willkommia* with a single species of *Monelytrum* (ditypic) and *Polevansia* (monotypic) imbedded within. Clayton and Renvoize (1986) indicate that *Polevansia* is “like *Willkommia*” in that both have inflorescences with several racemes on an elongated axis and dorsally compressed spikelets; while *Tragus* and *Monelytrum* have cylindrical false racemes with each branch short pedunculate, dorsally compressed spikelets, and lower glumes that are usually reduced to small scales. Columbus et al. (2007) was first to link *Willkommia* with *Tragus* where they were aligned as a pair with strong support. Our study is the first molecular evidence to link *Monelytrum* and *Polevansia* with *Tragus*–*Willkommia*. Six out of eight possible species of *Tragus* and three of the four species of *Willkommia* are included in our study (Clayton et al. 2008). This is very strong evidence for placing *Willkommia* within *Tragus* and it appears that *Monelytrum* and *Polevansia* should also be subsumed within *Tragus*. Species of this tribe are distributed in Africa and only *Willkommia texana* is endemic to the New World in USA and Argentina.

We provide the first molecular support for including *Neesiochloa* (monotypic) in the Pappophorinae. All nine species of *Pappophorum* and *Neesiochloa barbata* are from the New World. The alignment of this subtribe is interesting since it is not part of the New World clade of Hilariinae–*Jouvea*–*Allolepis*–Monanthochloinae–Boutelouinae–Scleropogoninae–*Sohnsia*–*Lepturidium*–Muhlenbergiinae clade but is found in a different position in each of the three trees.

We have moderate support (BS = 83, PP = 1.00 in the combined tree) for the Tripogoninae where *Tripogon* is polyphyletic with two species of *Eragrostiella* embedded within. Sister to this are two species of *Melanocenthris*. This is the first time that *Eragrostiella* and *Tripogon* have been linked and they are morphologically similar since both have winged paleas, strongly keeled and glabrous lemmas that are 1–3-nerved, and spike to racemose inflorescences (Watson and Dallwitz, 1992a). We recommend realignment of *Tripogon* to include *Eragrostiella*. Columbus et al. (2007) found *Melanocenthris* sister to *Tripogon* in their strict consensus tree based on *trnL-F* and ITS sequences. Most species in this subtribe are from the Old World tropics to Australia and a single species is found in tropical America (Clayton et al., 2008).

We have low bootstrap values (BS = 78 in ITS tree) but high posterior probability (PP = 1.00 in combined tree) for the Eleusininae and we have pretty good structure for this large and enigmatic subtribe. The Eleusininae as here recognized is a combination of the Pommereullinae, Chloridinae, and Eleusininae sensu Clayton and Renvoize (1986) and earlier authors. Morphologically and geographically this is a very diverse group although most species have racemose inflorescences and many species are found in tropical environments in Africa, Southeast Asia, the Americas, and Australia. Our trees lend support for the monophyly of *Lepturus*, *Microchloa*, and *Trichloris*; and support the expansion of the following: *Astrebla* (*Schoenefeldia gracilis* embedded in overall tree only), *Chloris* (*Lintonia* and *Tetrapogon mossambicensis* as sister or embedded within), *Cynodon* (*Brachyachne convergens* and *B. tenella* embedded), and *Enteropogon* (*Eustachys distichophylla* embedded in plastid and combined trees). *Brachyachne*, *Eustachys*, *Leptochloa*, and *Tetrapogon* are all clearly polyphyletic, although there is strong support for three species of *Brachyachne* (BS = 100, PP = 1.00 in all trees), two species of *Eustachys* (BS = 100, PP = 1.00 in all trees), and two species of *Tetrapogon* (BS = 100, PP = 1.00 in all trees). Clearly there is more work to be done to sort out relationships among these genera and to determine monophyletic lineages. This subtribe recovered by Roodt-Wilding and Spies (2006) whose strict consensus trees obtained from ITS and the combined ITS–*trnL-F* sequences indicates moderate to strong support for a clade containing *Chloris*, *Cynodon*, *Eustachys*, *Harpochloa*, *Microchloa*, and *Rendlia*.

The identical four genera (*Gouinia*, *Tridens*, *Triplasis*, and *Vaseyochloa*) in the Tridentinae were found to have moderate support (BS = 84) by Columbus et al. (2007) in their *trnL-F* + ITS strict consensus tree. Our results are concordant with theirs and we used *Gouinia paraguayensis* and *Triplasis purpurea*, two different species in our study. Members of the Tridentinae usually have pubescent lemma nerves, a line of hairs for the ligule, and keeled florets, although the monotypic *Vaseyochloa* has dorsally rounded florets (Clayton and Renvoize, 1986; Watson and Dallwitz, 1992a). Based on data reported in Columbus et al. (2007), Peterson et al. (2007) erected the subtribe Gouiniinae to include *Gouinia* and *Vaseyochloa*; this name is now placed in synonymy to accommodate the larger assemblage.

The Orcuttiinae is a small group of nine annuals known from California, Baja California, and Baja California Sur whose unusual features of glandular hairs, leaves without ligules, and mushroom-button bicellular microhairs were first noted by Crampton (1959) and later recognized as a tribe by Reeder (1965). We have not sampled *Neostapfia* in our study but we still have strong support for two species of *Tuctoria* being sister to three species of *Orcuttia* (BS = 100, PP = 1.00 in the combined tree). This subtribe was recovered with strong support (BS = 100) in Columbus et al. (2007) in their *trnL-F* + ITS strict consensus tree and by Bouchenak-Khelladi et al. (2008) in their Bayesian consensus tree. Roalson and Columbus (1999) presented a phylogeny based on morphological characteristics that depict *Tuctoria* as a grade. Even though we lack one species of *Tuctoria* and two species of *Orcuttia* it appears that these two genera warrant recognition.

We have strong support for the monophyly of *Aeluropus* (BS = 99, PP = 1.00 in combined tree) and *Triodia* (BS = 96, PP = 1.00 in combined tree), and for their treatment in separate subtribes, the Aeluropodinae and Triodiinae, respectively. We indicate that these two subtribes could be sister (PP = 0.99 in our ITS tree) to one another; and we have weak support for Aeluropodinae as sister to the *Orinus*–Triodiinae clade (BS = 54, PP = 1.00 in our combined tree). A molecular study of ITS, *trnL-F*, and *ndhF* sequences indicated that *Aeluropus* was related to the African *Odysea* Stapf (not sampled in our study) and the Australian *Troidia* (Bell 2007).

4.1.2. *Incertae sedis* genera

In the ITS tree species of *Orinus* and *Cleistogenes* form a clade (PP = 0.99) but in the plastid and combined trees they are not aligned near one another. Morphologically, these species although at first appearing very similar, have quite a few distinguishing characteristics with the former having long scaly rhizomes, pungent leaf blade apices, membranous ligules, and rachilla extensions beyond the upper floret, whereas the latter genus is composed of tufted perennials with unarmed leaf blades, a line of hairs for a ligule, and the occurrence of cleistogamous spikelets. *Orinus* contains four species from the Himalayas to western China (three spp. endemic) while *Cleistogenes* contains 13 species with 10 species occurring in China (five spp. endemic) (Chen and Phillips, 2006a,b). The relationship between these two genera warrants further study since we report equivocal results.

In our study *Dactyloctenium* forms a strongly supported monophyletic genus with four species represented, including the Australian, *D. australe*. The genus contains about 13 species mainly from Africa to India and is characterized by digitate inflorescences composed of several linear to narrowly oblong secund spikes (Phillips, 1974). It has been linked to *Eleusine* but differs from the latter by having each raceme terminate in a bare rachis extension rather than a fertile floret (Clayton and Renvoize, 1986). We are the first to report *Brachyachloa* as sister with weak support (BS = 66 in combined tree) and sister to these is *Neobouteloua lophostachya* with moderate support (BS = 73 in combined tree). Columbus et al. (2007) found a weakly supported clade (BS = 59) containing *D. aegyptium* and *N. lophostachya* in their strict consensus tree based on *trnL-F* and ITS sequences.

We are first to provide molecular evidence for the polyphyletic origin of *Perotis* (primarily African in distribution with 13 species) since *Lopholepis ornithocephala* (monotypic) and *Craspedorhachis africana* are embedded within a weakly supported clade (BS = 51, PP = 0.68 in the combined tree) (Clayton et al., 2008). We have only a single sequence (*rps3*) for *Craspedorhachis* and therefore its placement within *Perotis* may be due to a lack of variation within this single marker. *Lopholepis* is morphologically similar to *Perotis* as both share narrow racemes with spikelets borne on a short pedicel and falling with it, flat leaf blades that are cordate near base, laterally compressed spikelets, glumes that are longer than the floret (in *Lopholepis* this is developed into an obliquely constricted structure resembling a birds head), and awnless lemmas (Bor, 1960; Clayton and Renvoize, 1986; Watson and Dallwitz, 1992a). Sister to the *Perotis*–*Lopholepis* clade are *Mosdenia leptostachys* (PP = 1.00 in the combined tree) and *M. phleoides* (placed as a synonym of *M. leptostachys* in Clayton et al., 2008). Morphologically, *Mosdenia* is similar to *Perotis* but it has sessile spikelets and awnless glumes (Clayton and Renvoize, 1986). *Dignathia* (east African to India) appears monophyletic (BS = 94, PP = 1.00 in the combined tree) and these two species form a clade (BS = 83, PP = 1.00) with *Gymnopogon grandiflorus* (primarily New World in distribution; one species India to Thailand) and *Bewsia biflora* (monotypic from Africa) (Clayton and Renvoize, 1986). These species then form a clade with *Mosdenia*–*Perotis*–*Lopholepis* (PP = 0.72 in the combined tree). A monophyletic *Trichoneura* (distributed in Africa, Asia, and America) with two species forms a strongly supported clade (BS = 100, PP = 1.00 in the combined tree) and they are sister (BS = 67, PP = 0.79) to a monophyletic *Ctenium* (distributed in Africa, Madagascar, and America) with two species. Together, all these species form a clade (PP = 1.00) in the combined tree. Perhaps with greater sampling among species of *Ctenium*, *Gymnopogon*, *Trichoneura*, and all other genera not placed in a subtribe, we will be able to better resolve relationships and circumscribe other lineages within the Cynodonteae.

4.2. Biogeography

All three phylograms indicate that the Chloridoideae might have originated in Africa and/or Asia since the basal lineage, the tribe Triraphideae, includes sister genera, *Neyraudia* and *Triraphis*, both with African and Asian distribution. *Neyraudia* contains four species all native to Asia with *N. arundinacea* (L.) Henrard (not in our study) also occurring in tropical Africa (Chen and Phillips, 2006c; Clayton et al., 2008). *Triraphis* consists of 8 species with six of these native to Africa; *T. mollis* R. Br. native to Australia and *T. devia* Filg. & Zuloaga (not in our study) native to South America (Filgueiras and Zuloaga, 1999; Nightingale and Weiller, 2005b). The latter species is more than likely derived and recently dispersed to South America. Because more than half of the genera of Chloridoideae reside in Africa and the larger tribes, such as, the Eragrostideae, Zoysieae, and Cynodonteae, excluding the Muhlenbergiinae, have centers of diversity there, Hartley and Slater (1960) concluded that the subfamily probably originated on the African continent (during the Oligocene) and spread to other parts of the world. Our data is equivocal and we cannot satisfactorily choose Africa or Asia as the likely area for the origin of the subfamily.

Within the tribe Eragrostideae, the Cotteinae is sister to the Uniolinae–Eragrostidinae clade (Figs. 2 and 3) and includes three genera: *Cottea* with a single species distributed in the Americas; *Schmidia* (not in our study) with two species centered in Africa; and *Enneapogon* with 16 species native to Australia (15 of these endemic), 8 species native to Africa, and one species, *E. desvauxii*, distributed worldwide (Weiller and Lazarides, 2005; Clayton et al., 2008). Therefore, it seems likely that the tribe Eragrostideae might have originated in Australia and/or Africa and then radiated to all parts of the world. *Eragrostis*, the largest chloridoid genus estimated to have 423 species in the derived subtribe Eragrostidinae, has 212 species in Africa, 153 species in the Americas, 74 species in Australasia, 56 in tropical Asia, and 51 in temperate Asia (Clayton et al., 2008; Simon et al., 2009).

Zoysia, the basal lineage within the tribe Zoysieae includes 11 species, six species in Asia, four in Australasia, one in Africa, one in the Pacific, and three introduced in the Americas (Peterson et al., 2001; Clayton et al., 2008). The Zoysieae might have originated in Asia where it is most speciose today and subsequently radiated. *Sporobolus* with 200 species in the derived subtribe Sporobolinae, includes 86 species in the Americas, 83 species in Africa, 59 species in Asia, and 23 species in Australasia (18 native to Australia) (Simon, 2005; Clayton et al., 2008; Simon et al., 2009).

Even though we have rather poor backbone support for the derivation of subtribes within the tribe Cynodonteae, the total evidence phylogram (Fig. 3) suggests that Asia and/or Africa might have been the area of origin. The basal lineage, subtribe Aeluropodinae, consists of 5–10 species, five distributed in Asia (two endemic to China), two in Africa, and two in Europe (Chen and Phillips, 2006d; Clayton et al., 2008). Sister to the Aeluropodinae is *Orinus* with all four species from Asia and subtribe Triodiinae with 68 species in three genera (*Monodia* S.W.L. Jacobs and *Symplectrodia* Lazarides (not in our study) and *Triodia*) all endemic to Australia (Lazarides et al., 2005; Nightingale and Weiller, 2005c; Nightingale et al., 2005).

As mentioned earlier, the derived clade containing the Hilariinae with *Allolepis* and *Jouvea*, Monanthochloinae, Boutelouinae, Scleropogoninae, *Sohnsia*, *Lepturidium*, and Muhlenbergiinae is almost entirely distributed in the Americas. Only six species of *Muhlenbergia* and one species of *Distichlis* are known to be disjunct in southeastern Asia and Australia, respectively. Earlier population studies of *Chaboissaea*, *Lycurus*, *Scleropogon*, and *Muhlenbergia torreyi* indicate that the subtribe Muhlenbergiinae probably originated in North America and has since radiated to South America

multiple times (Peterson and Herrera Arrieta, 1995; Peterson and Columbus, 1997; Sykes et al., 1997; Peterson and Morrone, 1998; Peterson and Ortiz-Diaz, 1998; Peterson et al. in review). Based on four Asian species studied within *Muhlenbergia*, there is evidence for a single colonization event from the Americas to south-eastern Asia (Peterson et al., in review).

Three other subtribes, the Tridentinae, Orcuttiinae, and Pappophorinae are also entirely New World in distribution but these are usually aligned near Old World-African subtribes and incertae sedis genera in our tree where there is little deep support among the nodes (see Fig. 3). The subtribe Tripogoninae contains three genera: *Eragrostiella* with six species, five distributed in tropical Asia, one in Australasia, and one in Africa; *Melanocenchris* with three species, two known in Africa and two from Asia; and *Tripogon* with approximately 30 species, 22 of these species from tropical Asia, nine from Africa, and three from the Americas. The subtribe Traginae is composed of four genera: *Monelytrum* and *Polevansia* each with a single species from Africa; *Tragus* with nine species, six in Africa, five in Asia, one endemic to Australia, and four introduced in the Americas (Peterson et al., 2001; Nightingale and Weiller, 2005d; Clayton et al., 2008). The subtribe Eleusininae is a diverse assemblage of at least 25 genera (as treated here) and is widely distributed.

4.3. Cytology

Within the subfamily Chloridoideae there is a high frequency of polyploids ranging from diploid to 20-ploid (*Pleuraphis mutica* Buckley, not sampled in our study) and many of these are thought to be allopolyploids suggesting extensive hybridization (Roodt and Spies, 2003). The common base chromosome number for all chloridoid tribes treated here is $x = 10$ and this is the predominant number found in the Triraphideae, Eragrostideae, Zoysieae, and Cynodonteae. Lower base numbers are common in the Cotteinae ($x = 9, 10$), Sporobolinae ($x = 7, 8, 9, 10$), Eleusininae ($x = 9, 10$), Hilariinae ($x = 9$), Scleropogoninae ($x = 7, 8, 10$), and Muhlenbergiinae ($x = 8, 9, 10$) (Watson and Dallwitz, 1992a).

4.4. C_4 evolution

According to molecular dating C_4 photosynthesis in the subfamily Chloridoideae originated between 32 and 25 mya in the early Miocene–late Oligocene (Christin et al., 2008; Vicentini et al., 2008; Bouchenak-Khelladi et al., 2009). The genetic changes responsible for the evolution of C_4 PCK subtype are still unidentified (Christin et al., 2009) and the development of this subtype is probably not identical, i.e., not analogous, in all lineages (Kellogg, 1999). In the Chloridoideae approximately 68% of the species are NAD-ME and as many as 31% have been estimated to be PCK (Taub, 2000). Based on a list of genera containing C_4 grasses (Sage et al., 1999), within the Chloridoideae the PCK subtype has arisen many times and is found in the Triraphideae (*Neyraudia*), Eragrostideae, Zoysieae, and Cynodonteae. However, most of the PCK-like species were identified solely on their anatomical descriptions and very few species have actually been investigated biochemically to determine the predominant decarboxylating enzyme (Sage et al., 1999). In addition to being polyphyletic, the three largest genera: *Eragrostis* (Eragrostideae), *Muhlenbergia* (Cynodonteae), and *Sporobolus* (Zoysieae) apparently contain both PCK and NAD-ME species. With the exception of the Aeluropodinae, Triodiinae, and Orcuttiinae, all subtribes treated here at least one taxon that has been identified as having the PCK subtype. The Orcuttiinae with nine species in three genera (*Neostaphia*, *Orcuttia*, and *Tuctoria*), are the only members of the Chloridoideae that have been identified to be NADP-ME (nicotinamide adenine dinucleotide phosphate co-factor malic enzyme) (Keeley, 1998). The NADP-ME is the primary

decarboxylating enzyme in the Panicoideae and is found in over 90% of the species in this subfamily (Taub, 2000).

5. Conclusion

In this study we have performed a multi-gene phylogenetic analysis of the Chloridoideae with the largest sample size published to date at the species, generic, subtribal, and tribal levels. We have produced a robust classification of the tribes (Triraphideae, Eragrostideae, Zoysieae, and Cynodonteae) and subtribes (Cotteinae, Uniolinae and Eragrostidinae in the Eragrostideae; Zoysiinae and Sporobolinae in the Zoysieae; Aeluropodinae, Triodiinae, Orcuttiinae, Tridentinae, Eleusiniinae, Tripogoninae, Pappophorinae, Traginae, Hilariinae, Monanthochloinae, Boutelouinae, Scleropogoninae, and Muhlenbergiinae in the Cynodonteae) based on our phylogenetic inferences from six plastid and one nuclear DNA sequences (see Fig. 3, Table 3). We have moderate to strong support for all clades representing the tribes and subtribes (except subtribe Eleusiniinae where we have only posterior probability support, PP = 1.00) and all were resolved as monophyletic. The Chloridoideae might have originated in Africa and/or Asia since the basal lineage, the tribe Triraphideae, includes species with African and Asian distribution. In our study we have 20 incertae sedis genera (not placed within a subtribe) primarily within the Cynodonteae (19) and a single genus (*Urochondra*) in the Zoysieae. Based on our phylogenetic treatment the following 15 genera are polyphyletic: *Astrelba*, *Brachyachne*, *Chloris*, *Cynodon*, *Distichlis* (ITS tree only), *Enteropogon*, *Eragrostis*, *Eustachys*, *Leptochloa*, *Muhlenbergia*, *Perotis*, *Sporobolus*, *Tetrapogon*, *Tragus*, and *Tripogon*; and the following 22 genera with two or more species were always portrayed as monophyletic: *Aeluropus*, *Blepharidachne*, *Bouteloua*, *Cleistogenes*, *Ctenium*, *Dactyloctenium*, *Dignathia*, *Erioneuron*, *Lepturus*, *Melanocentris*, *Microchloa*, *Mosdenia*, *Munroa*, *Orcuttia*, *Orinus*, *Trichloris*, *Trichoneura*, *Triodia*, *Triraphis*, *Tuxetia*, *Uniola*, and *Zoysia*. Other genera depicted as monophyletic but found embedded within other genera were: *Aegopogon*, *Blepharoneuron*, *Chaboissaea*, *Lycurus* (all in *Muhlenbergia*), *Ectrosia* (in *Eragrostis*), and *Eragrostiella* (in *Tripogon*). Even though we have tried to sample as many chloridoid genera as possible (95) there are still approximately 46 (of these 30 are monotypic and 11 are ditypic) remaining that we have not yet included in our study. The majority of these unsampled genera are primarily distributed in Africa and we hope to gather these in the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2010.01.018.

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Appendix A. Specimens sampled, localities, vouchers, and GenBank accession numbers for DNA sequences. All accessions are newly submitted sequences to GenBank and all vouchers are deposited in the United States National Herbarium (US). Predominant native distribution indicated by taxon colour: American—red, African—green, Asian—blue, and Australian—purple.

Taxon	Locality	Voucher	<i>ITS</i>	<i>ndhA</i> intron	<i>ndhF</i>	<i>rpl32- trnL</i>	<i>rps3</i>	<i>rps16</i> intron	<i>rps16- trnK</i>
<i>Acrachne racemosa</i> (B. Heyne ex Roem. & Schult.) Ohwi	South Africa	Smook 9899					GU360099		
<i>Aegopogon cenchroides</i> Humb. & Bonpl. ex Willd.	Mexico	Peterson 22045 & Saarela	GU359259	GU359403	GU359613	GU360011	GU360143	GU360274	GU360578
<i>Aegopogon tenellus</i> (DC.) Trin.	Mexico	Peterson 22044 & Saarela	GU359260	GU359392	GU359592	GU360012	GU360128	GU360278	GU360577
<i>Aeluropus lagopoides</i> (L.) Trin. ex Thwaites	Iraq	Weinert s.n. & Mosawi	GU359261	GU359391	GU359591	GU360013	GU360085	GU360284	GU360576
<i>Aeluropus littoralis</i> (Gouan) Parl.	Greece	Ferguson 634	GU359262	GU359390	GU359590	GU360018	GU360086	GU360308	GU360575
<i>Aeluropus pungens</i> (M. Bieb.) K. Koch	China	Yunatov s.n., Li Shyin & Yuan Yfen	GU359263	GU359389	GU359589	GU360014	GU360087	GU360319	GU360574
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F. Decker ♀	Mexico	Hitchcock 7541	GU359264	GU359388	GU359577	GU360015	GU360088	GU360318	GU360573
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F. Decker ♂	Mexico	Le Roy 1412 & Harvey	GU359265	GU359387	GU359588	GU360016	GU360089	GU360306	GU360572
<i>Apochiton burtii</i> C.E. Hubb.	Tanzania	Greenway 11513 & Polhill	GU359266		GU359594		GU360090	GU360316	GU360571
<i>Aristida gypsophila</i> Beetle	Mexico	Peterson 15839 & Valdes-Reyna Peterson 15985 & Gonzalez-	GU359267	GU359386		GU359977	GU360091	GU360286	GU360570
<i>Aristida scribneriana</i> Hitchc.	Mexico	Elizondo	GU359268	GU359412		GU360010	GU360092	GU360314	GU360569
<i>Astrebla elymoides</i> F. Muell. ex F.M. Bailey	Australia	Hubbard 7976	GU359269	GU359414	GU359587		GU360093	GU360313	
<i>Astrebla lappacea</i> (Lindl.) Domin	Australia	McKinlay s.n.	GU359270	GU359395	GU359586	GU360009	GU360094	GU360312	GU360568
<i>Astrebla pectinata</i> (Lindl.) F. Muell. ex Benth.	Australia	Chalmers 5	GU359286	GU359421	GU359585	GU359861	GU360095	GU360311	GU360567
<i>Astrebla squarrosa</i> C.E. Hubb.	Australia	Hubbard 7940					GU360096		
<i>Austrochloris dichanthioides</i> (Everist) Lazarides	Australia	Anson s.n.	GU359272	GU359420	GU359584	GU359860	GU360113	GU360310	GU360566
<i>Bealia mexicana</i> Scribn.	Mexico	Peterson 7946, Annable & Herrera Davidse 6471, Simon, Drummond	GU359258			GU359859	GU360098	GU360309	GU360550
<i>Bewsia biflora</i> (Hack.) Gooss.	Africa	& Bennett	GU359274		GU359583	GU359858	GU360084	GU360294	GU360564
<i>Blepharidachne benthamiana</i> (Hack.) Hitchc.	Argentina	Melix 570 & Cherobini	GU359275		GU359582	GU359857	GU360100		GU360579
<i>Blepharidachne bigelovii</i> (S. Watson) Hack.	Mexico	Johanston 9401			GU359581	GU359856	GU360101	GU360307	GU360562
<i>Blepharidachne kingii</i> (S. Watson) Hack.	USA	Reeder 7347 & Reeder	GU359276			GU359855			GU360561
<i>Blepharoneuron shepherdii</i> (Vasey) P.M. Peterson & Annable	Mexico	Peterson 22452 & Saarela	GU359277	GU359419	GU359580	GU359854	GU360102	GU360320	GU360560
<i>Blepharoneuron tricholepis</i> (Torr.) Nash	Mexico	Peterson 22099 & Saarela	GU359278	GU359418	GU359576	GU359853	GU360103	GU360305	GU360559
<i>Bouteloua aristidoides</i> (Kunth) Griseb.	Mexico	Peterson 21994 & Saarela	GU359279	GU359417	GU359570	GU359852	GU360104	GU360304	GU360558
<i>Bouteloua barbata</i> Lag.	Mexico	Peterson 22002 & Saarela	GU359280	GU359416			GU360105	GU360303	GU360557
<i>Bouteloua curtipendula</i> (Michx.) Torr.	Mexico	Peterson 22005 & Saarela Peterson 21441, Saarela &	GU359281	GU359415			GU360106		GU360556
<i>Bouteloua dactyloides</i> (Nutt.) Columbus	Mexico	Stančik	GU359282	GU359404	GU359569	GU359851	GU360107	GU360302	GU360555
<i>Bouteloua dimorpha</i> Columbus	Mexico	Peterson 22281 & Saarela	GU359283	GU359413			GU360108	GU360301	GU360554

<i>Bouteloua diversispicula</i> Columbus	Mexico	Peterson 22254 & Saarela	GU359284	GU359423		GU360109		GU360553	
<i>Bouteloua gracilis</i> (Kunth) Lag. ex Griffiths	Mexico	Peterson 22015 & Saarela	GU359285	GU359411		GU360110		GU360552	
<i>Bouteloua hirsuta</i> Lag.	Mexico	Peterson 22203 & Saarela		GU359410		GU360111		GU360593	
<i>Bouteloua parryi</i> (E. Fourn.) Griffiths	Mexico	Peterson 22252 & Saarela	GU359244	GU359409		GU360112	GU360300	GU360563	
<i>Bouteloua reflexa</i> Swallen	Mexico	Peterson 22125 & Saarela	GU359242	GU359408		GU360176	GU360299	GU360565	
		Peterson 21232, Gonzalez							
<i>Bouteloua repens</i> (Kunth) Scribn.	Mexico	Elizondo, Rosen & Reid	GU359271	GU359407	GU359568	GU359850	GU360131	GU360298	GU360608
		Peterson 21289, Saarela & Flores							
<i>Bouteloua simplex</i> Lag.	Mexico	Villegas	GU359231	GU359406	GU359571	GU359834	GU360132	GU360297	GU360607
		Peterson 21423, Saarela &							
<i>Bouteloua uniflora</i> Vasey	Mexico	Stančik	GU359232	GU359383	GU359567	GU359848	GU360133	GU360296	GU360606
<i>Brachyachne convergens</i> (F. Muell.) Stapf	Australia	Adams 851	GU359252	GU359349	GU359714	GU359885	GU360121		GU360586
<i>Brachyachne fibrosa</i> C.E. Hubb.	Zambesia	Robson 1122	GU359253	GU359348		GU359884	GU360120	GU360444	GU360585
<i>Brachyachne patentiflora</i> (Stent & Rattray) C.E. Hubb.	Kenya	Bogdan 7075	GU359233	GU359350		GU359862	GU360134	GU360295	GU360605
<i>Brachyachne patentiflora</i> (Stent & Rattray) C.E. Hubb.	Zimbabwe	Laegaard 16295	GU359254	GU359374	GU359708	GU359883	GU360119	GU360458	GU360584
<i>Brachyachne tenella</i> (R. Br.) C.E. Hubb.	Australia	Lazarides 4281	GU359255	GU359376	GU359715	GU359882	GU360118	GU360442	GU360583
<i>Brachyachloa schiemaniana</i> (Schweick.) S.M. Phillips	Africa	Schweickerdt 1911	GU359256		GU359776	GU359881	GU360117		GU360582
<i>Calamovilfa longifolia</i> (Hook.) Hack. ex Scribn. & Southw.	USA	Hatch 5738 & Bearden	GU359300	GU359357	GU359716	GU359880	GU360116	GU360441	GU360548
<i>Chaboissaea atacamensis</i> (Parodi) P.M. Peterson & Annable	Argentina	Peterson 19626, Soreng, Salariato, & Panizza,	GU359344	GU359382	GU359729	GU359879	GU360115	GU360489	GU360595
<i>Chaboissaea ligulata</i> E. Fourn.	Mexico	Peterson 22416 & Saarela	GU359273	GU359381	GU359718	GU359863	GU360069	GU360440	GU360551
		Peterson 21158, Saarela, Rosen &							
<i>Chaboissaea subbiflora</i> (Hitcch.) Reeder & C. Reeder	Mexico	Reid	GU359318	GU359428	GU359707	GU359877	GU360036	GU360439	GU360518
<i>Chasmanthium latifolium</i> (Michx.) H.O. Yates	USA	Peterson 22463	GU359319	GU359379	GU359720	GU359891	GU360097	GU360438	GU360517
<i>Chasmanthium laxum</i> (L.) H.O. Yates	USA	Kanal 694		GU359405	GU359721	GU359875	GU360050	GU360437	GU360516
<i>Chasmanthium sessiliflorum</i> (Poir.) H.O. Yates	USA	Peterson 20823 & Saarela		GU359378	GU359722	GU359874		GU360436	GU360515
<i>Chloris barbata</i> Sw.	Mexico	Peterson 22255 & Saarela	GU359320	GU359377	GU359723	GU359873	GU360049	GU360435	GU360514
<i>Chloris radiata</i> (L.) Sw.	Mexico	Peterson 22278 & Saarela	GU359321	GU359366	GU359724	GU359872	GU360048	GU360434	GU360513
<i>Chloris submutica</i> Kunth	Mexico	Peterson 22393 & Saarela	GU359322	GU359375	GU359725	GU359871	GU360047	GU360471	GU360512
<i>Chloris virgata</i> Sw.	Mexico	Peterson 22179 & Saarela	GU359323	GU359384	GU359726	GU359870	GU360046	GU360443	GU360511
		Peterson 21468, Soreng, LaTorre							
<i>Chloris virgata</i> Sw.	Peru	& Rojas Fox	GU359324	GU359373	GU359727	GU359869	GU360045	GU360445	GU360510
<i>Chrysochloa hindsii</i> C.E. Hubb.	Burundi	Reekmans 11068	GU359325		GU359728	GU359868	GU360044	GU360485	GU360509
		Soreng 5406, Peterson & Sun							
<i>Cleistogenes mucronata</i> Keng ex P.C. Keng & L. Liu	China	Hang	GU359234	GU359422	GU359696	GU359846	GU360144	GU360351	GU360604
<i>Cleistogenes squarrosa</i> (Trinius) Keng	China	Soreng 5156 & Peterson	GU359235	GU359393	GU359566	GU359845	GU360136	GU360473	GU360603
<i>Coelachyrum lagopoides</i> (Burm. f.) Senaratna	India	Saldanha 15334		GU359364	GU359572	GU359844			GU360602
<i>Coelachyrum poiflorum</i> Chiov.	Ethiopia	Burger 2915	GU359236			GU359843	GU360129	GU360457	GU360601
		Peterson 21463, Soreng, LaTorre							
<i>Cottea pappophoroides</i> Kunth	Peru	& Rojas Fox	GU359237	GU359363	GU359579	GU359842	GU360138	GU360456	GU360600
<i>Craspedorhachis africana</i> Benth.	South Africa	Zohy 504 & Schweikeidt					GU360139		
<i>Crypsis aculeata</i> (L.) Aiton	China	Soreng 5469 & Peterson	GU359238	GU359362	GU359573	GU359841	GU360140	GU360402	GU360599

<i>Crypsis schoenoides</i> (L.) Lam.	USA	Peterson 19814, Saarela & Sears Peterson 14235, Weakley &	GU359239	GU359361	GU359574	GU359840	GU360141	GU360455	GU360598
<i>Ctenium aromaticum</i> (Walter) Alph. Wood	USA	LeBlond	GU359240		GU359575	GU359839			
<i>Ctenium cirrhosum</i> (Nees) Kunth	Brazil	Grola 1452 & Filgueiras	GU359241			GU359838	GU360142	GU360353	GU360597
<i>Cynodon arcuatus</i> J. Presl	Ceylon	Clayton 5836	GU359257	GU359360	GU359578	GU359837	GU360114	GU360454	GU360596
<i>Cynodon dactylon</i> (L.) Pers.	Mexico	Peterson 22000 & Saarela	GU359243	GU359359	GU359603	GU359836	GU360137	GU360453	GU360580
<i>Cynodon hirsutus</i> Stent	South Africa	Smook 6616	GU359229	GU359358	GU359751	GU359876	GU360135	GU360452	GU360594
<i>Cynodon incompletus</i> Nees	South Africa	Smook 2408 & Gussell	GU359246			GU359849		GU360450	
<i>Cynodon incompletus</i> Nees	South Africa	Smook 10152	GU359245	GU359347	GU359593	GU359847		GU360451	GU360609
<i>Cynodon maritimus</i> Kunth	Bahamas	Howard 10214 & Howard	GU359248	GU359365	GU359710	GU359889	GU360126	GU360448	GU360591
<i>Cynodon pascuus</i> Nees	Mexico	Morgan 12518	GU359249	GU359354	GU359711	GU359888	GU360125	GU360447	GU360590
<i>Cynodon plectostachyus</i> (K. Schum.) Pilg.	Ruwanda	Troupin 11610	GU359247	GU359356	GU359709	GU359890	GU360127	GU360449	GU360592
<i>Cynodon plectostachyus</i> (K. Schum.) Pilg.	Honduras	Morazan 25803		GU359353			GU360124		GU360589
<i>Cynodon transvaalensis</i> Burtt Davy	South Africa	Smook 6710	GU359250	GU359352	GU359712	GU359887	GU360123	GU360446	GU360588
<i>Dactyloctenium aegyptium</i> (L.) Willd.	Mexico	Peterson 22283 & Saarela	GU359251	GU359351	GU359713	GU359886	GU360122	GU360432	GU360587
<i>Dactyloctenium australe</i> Steud.	South Africa	Davidse 6945 Kabuye 714, Luke, Robertson,	GU359326	GU359372			GU360043		GU360508
<i>Dactyloctenium bogdanii</i> S.M. Phillips	Kenya Weissen	Mungai & Mathenge	GU359327	GU359371	GU359717	GU359867	GU360042	GU360484	GU360507
<i>Dactyloctenium giganteum</i> B.S. Fisher & Schweick.	Nossob	Seydel 2701	GU359328		GU359687	GU359866	GU360041		GU360491
<i>Danthonia compressa</i> Austin	USA	Peterson 21986 & Levine	GU359345	GU359370	GU359688	GU359865	GU360040	GU360483	GU360521
<i>Dasyochloa pulchella</i> (Kunth) Willd. ex Rydb.	Mexico	Peterson 21992 & Saarela	GU359330	GU359369	GU359689	GU359864	GU360039	GU360482	GU360505
<i>Dignathia hirtella</i> Stapf	Kenya	Welski 5251	GU359316	GU359368	GU359690		GU360023	GU360481	GU360490
<i>Dignathia villosa</i> C.E. Hubb.	Ethiopia	Ellis 204		GU359367	GU359691	GU359820	GU360037	GU360480	GU360519
<i>Dinebra retroflexa</i> (Vahl) Panz.	Kenya	Ndegwa 610	GU359332	GU359355	GU359692	GU359778	GU360052	GU360479	GU360503
<i>Distichlis humilis</i> Phil.	Argentina	Peterson 19362, Soreng, Salariato & Panizza	GU359333	GU359430	GU359693	GU359835	GU360035	GU360478	GU360502
<i>Distichlis scoparia</i> (Nees ex Kunth) Arechav.	Argentina	Peterson 17475, Soreng & Refulio-Rodriguez	GU359334	GU359480	GU359694	GU359803	GU360034	GU360477	GU360501
<i>Distichlis spicata</i> (L.) Greene	Argentina	Peterson 17484, Soreng & Refulio-Rodriguez	GU359335	GU359479	GU359706	GU359802	GU360033	GU360476	GU360500
<i>Distichlis spicata</i> (L.) Greene	Argentina	Peterson 19309, Soreng, Salariato & Panizza	GU359346	GU359478	GU359695	GU359801	GU360032	GU360475	GU360499
<i>Ectrosia leporina</i> R. Br.	Australia	Lazarides 3928	GU359336	GU359484	GU359685	GU359800		GU360474	GU360498
<i>Ectrosia scabrida</i> C.E. Hubb.	Australia	Lazarides 4772	GU359317	GU359476	GU359697	GU359799		GU360459	GU360497
<i>Ectrosia schultzii</i> Benth.	Australia	Latz 2237 Peterson 21362, Saarela & Flores	GU359337			GU359798			
<i>Eleusine indica</i> (L.) Gaetrn.	Mexico	Villegas	GU359338	GU359473	GU359698	GU359797	GU360031	GU360472	GU360496
<i>Enneapogon desvauxii</i> P. Beauv.	Mexico	Peterson 21999 & Saarela	GU359339	GU359474	GU359699	GU359796	GU360030	GU360486	GU360495
<i>Enteropogon macrostachyus</i> (Hochst. ex A.Rich.) Munro ex Benth.	Zimbabwe	Laegaard 15902	GU359340	GU359472	GU359700	GU359795	GU360029	GU360470	GU360494

<i>Enteropogon ramosus</i> B.K. Simon	Australia	Peterson 14367, Soreng & Rosenberg	GU359341	GU359470	GU359701	GU359794	GU360028	GU360469	GU360493
<i>Entoplocamia aristulata</i> (Hack. & Rendle) Stapf	SW Africa	Seydel 187	GU359342	GU359469	GU359702	GU359793	GU360027	GU360468	GU360492
<i>Eragrostiella bifaria</i> (Vahl) Bor	Ceylon	Clayton 5950				GU359828			
<i>Eragrostiella leioptera</i> (Stapf) Bor	India	Chand 7961	GU359305	GU359486	GU359769	GU359827	GU360066		GU360529
<i>Eragrostis barrelieri</i> Daveau	Mexico	Peterson 21429, Saarela & Flores Villegas	GU359295	GU359496	GU359759	GU359781	GU360075	GU360401	GU360539
<i>Eragrostis cilianensis</i> (Bellardi) Vignolo ex Janch.	Mexico	Peterson 21286, Saarela & Flores Villegas	GU359296	GU359495	GU359760	GU359780	GU360068	GU360488	GU360538
<i>Eragrostis curvula</i> (Schrad.) Nees	Peru	Peterson 20542, Soreng & Romaschenko	GU359306	GU359497		GU359826		GU360392	
<i>Eragrostis desertorum</i> Domin	Australia	Peterson 14358, Soreng & Rosenberg	GU359289	GU359471	GU359719	GU359787	GU360038	GU360462	GU360545
<i>Eragrostis dielsii</i> Pilg.	Australia	Peterson 14399, Soreng & Rosenberg	GU359297	GU359494	GU359761	GU359779	GU360077	GU360400	GU360537
<i>Eragrostis eriopoda</i> Benth.	Australia	Peterson 14321, Soreng & Rosenberg	GU359290	GU359485	GU359754	GU359786	GU360070	GU360461	GU360544
<i>Eragrostis intermedia</i> Hitchc.	Mexico	Peterson 22302 & Saarela	GU359298	GU359501	GU359762	GU359818	GU360078	GU360399	GU360536
<i>Eragrostis kennedyae</i> F.Turner	Australia	Peterson 14446, Soreng & Rosenberg	GU359291	GU359500	GU359755	GU359785	GU360071	GU360460	GU360543
<i>Eragrostis lanicaulis</i> Lazarides	Australia	Peterson 14288, Soreng, Rosenberg & Macfarlane	GU359292	GU359499	GU359756	GU359784	GU360072	GU360418	GU360542
<i>Eragrostis lugens</i> Nees	Peru	Peterson 21601, Soreng, LaTorre & Rojas Fox	GU359302	GU359467	GU359704	GU359791	GU360025	GU360466	GU360535
<i>Eragrostis lugens</i> Nees	Mexico	Peterson 21428, Saarela & Stančik	GU359343	GU359468	GU359703	GU359777	GU360026	GU360467	GU360533
<i>Eragrostis lurida</i> subsp. <i>contracta</i> (Pilg.) P.M. Peterson & Sánchez Vega	Peru	Peterson 21797 & Soreng	GU359293	GU359498	GU359757	GU359783	GU360073	GU360378	GU360541
<i>Eragrostis lurida</i> J. Presl <i>lurida</i>	Peru	Peterson 21798 & Soreng	GU359294	GU359492	GU359758	GU359782	GU360083	GU360433	GU360540
<i>Eragrostis mexicana</i> (Hornem.) Link	Peru	Peterson 21155, Saarela, Rosen & Reid	GU359307	GU359483	GU359770	GU359825		GU360377	GU360528
<i>Eragrostis minor</i> Host	USA	Peterson 19739, Saarela & Sears	GU359308	GU359475	GU359771	GU359824	GU360065	GU360390	GU360527
<i>Eragrostis nigricans</i> (Kunth) Steud.	Peru	Peterson 21623, Soreng, LaTorre & Rojas Fox	GU359299	GU359491	GU359775	GU359790	GU360079	GU360398	GU360520
<i>Eragrostis parviflora</i> (R.Br.) Trin.	Australia	Peterson 14445, Soreng & Rosenberg	GU359331	GU359466		GU359804	GU360024	GU360465	GU360506
<i>Eragrostis pastoensis</i> (Kunth) Trin.	Peru	Peterson 21690, Soreng, LaTorre & Rojas Fox	GU359315	GU359490	GU359764	GU359792	GU360080	GU360397	GU360534
<i>Eragrostis pectinacea</i> (Michx.) Nees	Mexico	Peterson 21431, Saarela & Stančik	GU359301	GU359489	GU359753	GU359832	GU360081	GU360396	GU360549
<i>Eragrostis pergracilis</i> S.T.Blake	Australia	Peterson 14347, Soreng & Rosenberg	GU359329	GU359465	GU359731	GU359789	GU360067	GU360464	GU360547

<i>Eragrostis pilgeri</i> subsp. <i>ancashensis</i> (P.M. Peterson, Refulio & Tovar) P.M. Peterson & Sánchez Vega	Peru	Peterson 21809 & Soreng	GU359288	GU359464	GU359686	GU359788	GU360082	GU360463	GU360546
<i>Eragrostis reptans</i> (Michx.) Nees	USA	Peterson 9545 Peterson 16274, Cano, LaTorre,	GU359309	GU359432	GU359772	GU359823	GU360064		GU360526
<i>Eragrostis soratensis</i> Jedwabn.	Peru	Ramire & Susanibar	GU359287	GU359488	GU359766	GU359831	GU360053	GU360395	GU360532
<i>Eragrostis tenuifolia</i> (A. Rich.) Hochst. ex Steud.	Mexico	Peterson 22279 & Saarela	GU359303	GU359487	GU359767	GU359830	GU360076	GU360394	GU360531
<i>Eragrostis weberbaueri</i> Pilg.	Peru	Peterson 21807 & Soreng Peterson 19329, Soreng, Salariato	GU359304	GU359482	GU359768	GU359829	GU360074	GU360393	GU360530
<i>Erioneuron avenaceum</i> (Kunth) Tateoka	Argentina	& Panizza	GU359310	GU359441	GU359773	GU359822	GU360063	GU360403	GU360525
<i>Erioneuron nealleyi</i> (Vasey) Tateoka	Mexico	Peterson 19964 & Lara Contreras	GU359311		GU359774	GU359821	GU360062	GU360388	GU360524
<i>Eustachys distichophylla</i> (Lag.) Nees	Indonesia	Fowler s.n.		GU359440	GU359742	GU359805	GU360061	GU360387	GU360523
<i>Eustachys paspaloides</i> (Vahl) Lanza & Mattei	Kenya	Ndegway 741	GU359312	GU359439	GU359740	GU359819	GU360060	GU360386	GU360522
<i>Eustachys petraea</i> (Sw.) Desv.	USA	Strong 3124	GU359313	GU359438	GU359763	GU359833	GU360059	GU360385	GU360637
<i>Gouinia paraguayensis</i> (Kuntze) Parodi	Argentina	Peterson 11526 & Annable Peterson 16642 & Refulio-	GU359314	GU359437	GU359732	GU359817	GU360058	GU360384	GU360504
<i>Gymnopogon grandiflorus</i> Roseng., B.R. Arill. & Izag.	Peru	Rodriguez Soreng 5288, Peterson & Sun	GU359200	GU359436	GU359733	GU359816	GU360057	GU360383	GU360581
<i>Harpachne harpachnoides</i> (Hack.) B.S. Sun & S. Wang	China	Hang	GU359113	GU359435	GU359734	GU359815		GU360382	GU360611
<i>Hilaria cenchroides</i> Kunth	Mexico	Peterson 22339 & Saarela Peterson 21326, Saarela & Flores	GU359143	GU359424	GU359736	GU359813	GU360055	GU360380	GU360697
<i>Hilaria cenchroides</i> Kunth	Mexico	Villegas	GU359230		GU359735	GU359814	GU360056	GU360381	GU360698
<i>Jouvea pilosa</i> (J. Presl) Scribn.	Mexico	Peterson 11017 & Annable	GU359144	GU359433	GU359737	GU359812	GU360173	GU360379	GU360696
<i>Leptochloa dubia</i> (Kunth) Nees	Mexico	Peterson 22334 & Saarela	GU359145	GU359442	GU359738	GU359811	GU360051	GU360416	GU360695
<i>Leptochloa filiformis</i> (Pers.) P. Beauv.	Mexico	Peterson 22185 & Saarela Peterson 21305, Saarela & Flores	GU359146	GU359431		GU359810	GU360130	GU360389	
<i>Leptochloa uninervia</i> (J. Presl) Hitchc. & Chase	Mexico	Villegas	GU359147	GU359461	GU359739	GU359809	GU360234	GU360391	GU360694
<i>Leptochloa viscida</i> (Scribn.) Beal	Mexico	Peterson 22184 & Saarela	GU359148	GU359429	GU359752	GU359808	GU360233	GU360430	GU360693
<i>Lepturidium insulare</i> Hitchc. & Ekman	Cuba	Ekman 12060					GU360232		
<i>Lepturus acutiglumis</i> Steud.	USA:Hawaii USA: Wake	Whistler 5756					GU360231		
<i>Lepturus gasparricensis</i> Fosberg	Is.	Herbst 9687	GU359149	GU359477	GU359741	GU359807	GU360230	GU360429	GU360692
<i>Lepturus radicans</i> (Steud.) A. Camus	Kenya Minni-Minni Diego Gracia	Gilleopie 38				GU359806	GU360229		
<i>Lepturus repens</i> R. Br.	Is.	Whistler 9853	GU359150	GU359427	GU359730	GU359893	GU360228	GU360428	GU360691
<i>Lepturus schlechteri</i> Pilg.	South Africa	Schlechter s.n.					GU360227		
<i>Lintonia nutans</i> Stapf	Tanzania	Mwasumbi 14374	GU359151	GU359426	GU359743	GU359980	GU360226	GU360427	GU360690
<i>Lopholepis ornithocephala</i> (Hook.) Steud.	Ceylon	Clayton 5582				GU359878	GU360225		GU360689
<i>Lycurus setosus</i> (Nutt.) C. Reeder	Mexico	Peterson 22008	GU359153	GU359451	GU359745	GU359975	GU360223	GU360425	GU360687

<i>Lycurus setosus</i> (Nutt.) C. Reeder	Mexico	Peterson 20960, Saarela, Lara Contreras & Reyna Alvarez	GU359152	GU359425	GU359744	GU359976	GU360224	GU360426	GU360688
<i>Melanocenchris monoica</i> (Rottler) C.E.C. Fisch.	Ceylon	Clayton 5634				GU359974			GU360686
<i>Melanocenchris royleana</i> Hook. f.	India	Wisner 24	GU359169			GU359973	GU360222		
<i>Microchloa caffra</i> Nees	South Africa	Smook 10441	GU359155	GU359453	GU359746	GU359972	GU360206	GU360424	GU360670
<i>Microchloa kunthii</i> Desv.	Mexico	Peterson 22152 & Saarela	GU359141	GU359434	GU359747	GU359971	GU360220	GU360423	GU360684
<i>Monanthochloe littoralis</i> Engelm.	Mexico	Moran 10570	GU359157	GU359460	GU359748	GU359970	GU360235	GU360422	GU360699
<i>Monelytrum luederitzianum</i> Hack.	South Africa	Smook 10031	GU359158	GU359459	GU359749	GU359969	GU360218	GU360421	GU360682
<i>Mosdenia leptostachys</i> (Ficalho & Hiern) Clayton	South Africa	Smook 1145				GU359968	GU360217		
<i>Mosdenia phleoides</i> (Hack.) Stent	South Africa	Schweickerdt 1542	GU359159	GU359458	GU359750	GU359967	GU360216	GU360420	GU360681
<i>Muhlenbergia appressa</i> C.O. Goodd.	USA	Peterson 4183 & Annable	GU359164	GU359443	GU359618	GU359962	GU360211	GU360415	GU360676
<i>Muhlenbergia arenacea</i> (Buckley) Hitchc.	Mexico	Peterson 10624 & Annable	GU359165	GU359452	GU359619	GU359961	GU360210	GU360414	GU360675
<i>Muhlenbergia arenicola</i> Buckley	Mexico	Peterson 19947 & LaraContreras	GU359166	GU359462	GU359620	GU359960	GU360209	GU360413	GU360674
<i>Muhlenbergia brandegeei</i> C. Reeder	Mexico	Peterson 4760 & Annable	GU359167	GU359450	GU359621	GU359959	GU360208	GU360412	GU360711
<i>Muhlenbergia emersleyi</i> Vasey	Mexico	Peterson 22096 & Saarela	GU359168	GU359449	GU359622	GU359958	GU360207	GU360411	GU360672
<i>Muhlenbergia flaviseta</i> Scribn.	Mexico	Peterson 22409 & Saarela	GU359127	GU359448	GU359623	GU359957	GU360250	GU360410	GU360685
<i>Muhlenbergia gigantea</i> (E. Fourn.) Hitchc.	Mexico	Peterson 22260 & Saarela	GU359160	GU359457	GU359663	GU359966	GU360215	GU360419	GU360680
<i>Muhlenbergia macroura</i> (Kunth) Hitchc.	Mexico	Peterson 22062 & Saarela	GU359125	GU359447	GU359624	GU359956	GU360265	GU360409	GU360683
<i>Muhlenbergia montana</i> (Nutt.) Hitchc.	Mexico	Peterson 22234 & Saarela	GU359162	GU359455	GU359705	GU359964	GU360213	GU360417	GU360678
<i>Muhlenbergia peruviana</i> (P. Beauv.) Steud.	Mexico	Peterson 22440 & Saarela	GU359154	GU359446	GU359625	GU359955	GU360221	GU360408	GU360713
<i>Muhlenbergia racemosa</i> (Michx.) Britton	USA	Peterson 20924, Saarela & Howard	GU359114	GU359445	GU359638	GU359954	GU360253	GU360407	GU360716
<i>Muhlenbergia ramulosa</i> (Kunth) Swallen	Mexico	Peterson 22447 & Saarela	GU359115	GU359444	GU359627	GU359953	GU360254	GU360406	GU360717
<i>Muhlenbergia richardsonis</i> (Trin.) Rydb.	USA	Peterson 19817, Saarela & Sears	GU359163	GU359454	GU359617	GU359978	GU360212	GU360431	GU360677
<i>Muhlenbergia rigens</i> (Benth.) Hitchc.	Mexico	Peterson 22129 & Saarela	GU359117	GU359481	GU359629	GU359951	GU360256	GU360357	GU360729
<i>Muhlenbergia rigida</i> (Kunth) Kunth	Peru	Peterson 21637, Soreng, LaTorre & Rojas Fox	GU359116	GU359380	GU359616	GU359952	GU360255	GU360405	GU360718
<i>Muhlenbergia schreberi</i> J.F. Gmel.	Argentina	Peterson 19443, Soreng, Salariato & Panizza	GU359161	GU359456	GU359765	GU359950	GU360214	GU360404	GU360679
<i>Muhlenbergia torreyi</i> (Kunth) Hitchc. ex Bush	Argentina	Peterson 19429, Soreng, Salariato & Panizza	GU359118		GU359630	GU359992	GU360266	GU360267	GU360720
<i>Muhlenbergia uniflora</i> (Muhl.) Fernald	USA	Peterson 20862 & Saarela	GU359119	GU359463	GU359631	GU359994	GU360258	GU360275	GU360715
<i>Munroa andina</i> Phil. var. <i>andina</i>	Argentina	Peterson 19552, Soreng, Salariato & Panizza	GU359120	GU359394	GU359632	GU359965	GU360251		GU360722
<i>Munroa argentina</i> Griseb.	Chile	Peterson 15505, Soreng & Judziewicz	GU359121	GU359385	GU359633	GU360006	GU360260		GU360723
<i>Neesiochloa barbata</i> (Nees) Pilg.	Brazil	Swallen 4491	GU359122		GU359634	GU360005	GU360261	GU360279	GU360724
<i>Neobouteloua lophostachya</i> (Griseb.) Gould	Argentina	Peterson 11515 & Annable	GU359123	GU359396	GU359635	GU360004	GU360262	GU360273	GU360725

<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchcock	China	Soreng 5318 & Peterson	GU359124	GU359397	GU359636	GU360003	GU360263	GU360272	
<i>Orcuttia inaequalis</i> Hoover	USA	Hoover 1256			GU359605	GU360002	GU360264		GU360726
<i>Orcuttia tenuis</i> Hitchc.	USA	Stone 771		GU359398		GU360001		GU360271	GU360727
<i>Orcuttia viscida</i> (Hoover) Reeder	USA	Reeder 6234 & Reeder Soreng 5447, Peterson & Sun				GU360000	GU360236		
<i>Orinus kokonorica</i> (K. S. Hao) Keng ex X. L. Yang	China	Hang Soreng 5515, Peterson & Sun	GU359140	GU359399	GU359628	GU359999	GU360259	GU360270	GU360728
<i>Orinus thoroldii</i> (Stapf ex Hemsely) Bor	China	Hang Soreng 5529, Peterson & Sun	GU359126	GU359400	GU359626	GU359998	GU360257	GU360269	GU360721
<i>Orinus thoroldii</i> (Stapf ex Hemsely) Bor	China	Hang Peterson 21689, Soreng, La Torre	GU359112	GU359401	GU359595	GU359997	GU360249	GU360268	GU360714
<i>Pappophorum pappiferum</i> (Lam.) Kuntze	Peru	& Rojas Fox Peterson 20366, Soreng &	GU359128	GU359402	GU359596	GU359996	GU360248	GU360276	GU360700
<i>Pereilema beyrichianum</i> (Kunth) Hitchc.	Peru	Romaschenko Peterson 20106, Hall, Alvarez	GU359129	GU359493	GU359597	GU359995	GU360247	GU360280	GU360712
<i>Pereilema ciliatum</i> E. Fourn.	Mexico	Marvan & Alvarez Jimenez	GU359130	GU359516	GU359598	GU359979	GU360246	GU360281	GU360719
<i>Pereilema crinitum</i> J. Presl	Mexico	Peterson 22191 & Saarela	GU359131	GU359519	GU359599	GU359993	GU360245	GU360282	GU360710
<i>Perotis hildebrandtii</i> Mez	Tanzania	Renvoize 1784 & Abdallah Soreng 5717, Peterson & Sun				GU360008	GU360244		GU360709
<i>Perotis hordeiformis</i> Nees	China	Hang	GU359132	GU359520	GU359600	GU359991	GU360243	GU360283	GU360708
<i>Perotis indica</i> (L.) Kuntze	South Africa	Godfrey 1661	GU359133	GU359521		GU359990	GU360242	GU360293	GU360707
<i>Perotis rara</i> R. Br.	Australia	Roc 1900 Greenway 10620, Turner &	GU359134			GU359989	GU360241	GU360285	GU360706
<i>Pogoneura biflora</i> Napper	Tanzania	Watson				GU359987	GU360239		GU360704
<i>Polevansia rigida</i> De Winter	South Africa	Smook 6000 Peterson 14345, Soreng &	GU359136	GU359523	GU359602		GU360238	GU360287	
<i>Psammagrostis wiseana</i> C.A. Gardner & C.E. Hubb.	Australia	Rosenberg	GU359137	GU359533	GU359615	GU359986	GU360237	GU360288	GU360703
<i>Redfieldia flexuosa</i> (Thurb. ex A. Gray) Vasey	USA	Peterson 7845 & Annable	GU359138	GU359525	GU359604	GU359985	GU360191	GU360289	GU360702
<i>Reederochloa eludens</i> Soderstr. & H.F. Decker	Mexico	Reed 6430	GU359139				GU360158	GU360290	GU360701
<i>Rytidosperma penicellatum</i> (Labill.) Connor & Edgar	USA	Peterson 19685, Saarela & Sears Peterson 19182, Soreng, Salariato	GU359183	GU359518	GU359606	GU359984	GU360219	GU360291	GU360671
<i>Rytidosperma pictum</i> (Nees & Meyen) Nicora var. <i>pictum</i>	Argentina Dominican	& Panizza	GU359227	GU359527	GU359607	GU359983	GU360172	GU360292	GU360655
<i>Saugetia fasciculata</i> Hitchc. & Chase	Republic	Ekman s.n.	GU359156	GU359528	GU359608	GU359982	GU360171	GU360317	GU360638
<i>Schaffnerella gracilis</i> (Benth.) Nash	Mexico	Schaffner 134				GU359981			
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	USA	Peterson 12070 & Annable	GU359201	GU359529	GU359609	GU359936	GU360170	GU360375	GU360673
<i>Schoenefeldia gracilis</i> Kunth	Darfur	Quezel & Bourreil s.n.					GU360169		
<i>Schoenefeldia transiens</i> (Pilg.) Chiov.	Kenya Seychelles, Aldabra	Greenway 9781	GU359202		GU359610	GU360007	GU360168	GU360349	GU360636
<i>Sclerodactylon macrostachyum</i> (Benth.) A.Camus	Island	Stoddart 741 Peterson 19280, Soreng,				GU359963			
<i>Scleropogon brevifolius</i> Phil.	Argentina	Salariato & Panizza	GU359203	GU359530	GU359611	GU359919	GU360167		GU360635

<i>Sohnsia filifolia</i> (E. Fourn.) Airy Shaw	Mexico	Peterson 11129 & Annable	GU359204	GU359531	GU359612	GU359918	GU360166	GU360350	GU360634
<i>Sohnsia filifolia</i> (E. Fourn.) Airy Shaw	Mexico	Reeder 4073 & Reeder Peterson 19154, Soreng, Salariado & Panizza	GU359205	GU359532	GU359614	GU359917	GU360165	GU360332	GU360633
<i>Spartina densiflora</i> Brongn.	Argentina		GU359206	GU359510	GU359640	GU359916	GU360164	GU360352	
<i>Sporobolus atrovirens</i> (Kunth) Kunth	Mexico	Peterson 22342 & Saarela	GU359207	GU359508		GU359915	GU360163	GU360315	GU360632
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	Mexico	Peterson 22003 & Saarela	GU359208	GU359524	GU359674	GU359914	GU360162	GU360354	GU360631
<i>Sporobolus indicus</i> (L.) R. Br.	Mexico	Peterson 22025 & Saarela Peterson 21879, Soreng & Sanchez Vega	GU359209	GU359504	GU359637	GU359913	GU360161	GU360355	GU360630
<i>Sporobolus lasiophyllus</i> Pilg.	Peru	Peterson 14233, Weakley & LeBlond	GU359210	GU359505	GU359664	GU359912	GU360145	GU360356	GU360629
<i>Sporobolus pinetorum</i> Weakley & P.M. Peterson	USA	Peterson 21163, Saarela, Rosen & Reid	GU359211	GU359506		GU359911	GU360159	GU360358	
<i>Sporobolus pyramidalis</i> P. Beauv.	Mexico	Peterson 19224, Soreng, Salariado & Panizza	GU359228	GU359507	GU359665	GU359910	GU360174	GU360359	GU360628
<i>Sporobolus rigens</i> (Trin.) Desv.	Argentina	Peterson 14232, Weakley & LeBlond	GU359213	GU359517	GU359666	GU359909	GU360157	GU360360	GU360627
<i>Sporobolus teretifolius</i> R.M. Harper	USA	Peterson 15683 & Soreng	GU359199	GU359509		GU359908	GU360156	GU360376	GU360626
<i>Sporobolus virginicus</i> (L.) Kunth	Chile		GU359215	GU359502	GU359667	GU359892		GU360362	GU360610
<i>Sporobolus wrightii</i> Munro ex Scribn.	Mexico	Peterson 19841 & LaraContreras	GU359216	GU359511	GU359668	GU359906	GU360155	GU360348	GU360624
<i>Swallenia alexandrae</i> (Swallen) Soderstr. & H.F. Decker	USA	Carter 2784	GU359217	GU359512	GU359669	GU359920	GU360154	GU360364	GU360639
<i>Tetrachne dregei</i> Nees	South Africa	Jarman 120	GU359218	GU359513	GU359670	GU359904		GU360365	GU360622
<i>Tetrapogon mossambicensis</i> (K. Schum.) Chippend. ex B. S. Fisher	South Africa	Oakes 1211	GU359219			GU359903	GU360153		GU360621
<i>Tetrapogon spathaceus</i> (Hochst. ex Steud.) Hack. ex T. Durand & Schinz	Ethiopia Gran	Ash 2561	GU359220		GU359671	GU359902	GU360152	GU360366	GU360620
<i>Tetrapogon villosus</i> Desf.	Canaria	Johannes s.n.	GU359221	GU359514	GU359684	GU359901	GU360151	GU360367	GU360619
<i>Tragus australianus</i> S.T. Blake	Australia	Symon 13792 Peterson 21615, Soreng, LaTorre & Rojas Fox	GU359222	GU359515	GU359673	GU359900	GU360150	GU360368	GU360618
<i>Tragus berteronianus</i> Schult.	Peru	FLSP 457	GU359223	GU359535	GU359662	GU359899	GU360149	GU360369	GU360617
<i>Tragus berteronianus</i> Schult.	Peru	Gillett 13019	GU359224	GU359503	GU359675	GU359898	GU360148	GU360370	GU360616
<i>Tragus heptaneuron</i> W.D.Clayton	Kenya		GU359225	GU359526	GU359676	GU359897	GU360147	GU360371	GU360615
<i>Tragus koelerioides</i> Asch.	South Africa	Smook 6844	GU359226	GU359551	GU359677	GU359896	GU360146	GU360372	GU360614
<i>Tragus mongolorum</i> Ohwi	Ceylon	Clayton 5229				GU359894	GU360204		GU360612
<i>Tragus pedunculatus</i> Pilg.	South Africa	Schweickerdt 2297	GU359185	GU359552	GU359678	GU359895	GU360189	GU360373	GU360613
<i>Trichloris crinita</i> (Lag.) Parodi	Bolivia	Bastian 341	GU359171	GU359555		GU359907	GU360193	GU360363	GU360625
<i>Trichloris pluriflora</i> E. Fourn.	Mexico	Sohns 1258 Peterson 15048 & Refulio- Rodriguez	GU359214	GU359553	GU359679	GU359934	GU360160	GU360374	GU360653
<i>Trichloris pluriflora</i> E. Fourn.	Peru		GU359212	GU359554	GU359680	GU359905	GU360192	GU360334	GU360623
<i>Trichoneura eleusinoides</i> (Rendle) Ekman	South Africa	Seydel 448	GU359135	GU359522	GU359601	GU359988	GU360240	GU360277	GU360705

<i>Trichoneura weberbaueri</i> Pilg.	Chile	Peterson 15686 & Soreng	GU359172	GU359565	GU359681	GU359948	GU360194	GU360361	GU360668
<i>Tridens muticus</i> (Torr.) Nash	Mexico	Peterson 21997 & Saarela Peterson 14437, Soreng & Rosenberg	GU359173	GU359557	GU359682	GU359947	GU360195	GU360321	GU360667
<i>Triodia basedowii</i> Pritz.	Australia	Peterson 14432, Soreng & Rosenberg	GU359174	GU359550	GU359683	GU359946	GU360205	GU360322	GU360666
<i>Triodia brizoides</i> N.T. Burb.	Australia	Peterson 14424, Soreng & Rosenberg	GU359175	GU359559	GU359651	GU359945	GU360197	GU360323	GU360665
<i>Triodia bynoei</i> (C.E. Hubb.) Lazarides	Australia	Rosenberg	GU359176	GU359560	GU359649	GU359944	GU360190	GU360324	GU360664
<i>Triodia desertorum</i> (C.E. Hubb.) Lazarides	Australia	Lepschi 4499 & Craven	GU359177	GU359561	GU359672	GU359943	GU360199	GU360325	GU360663
<i>Triodia fitzgeraldii</i> N.T. Burb.	Australia	Lazarides 3169	GU359178	GU359562	GU359641	GU359942	GU360200	GU360326	GU360662
<i>Triodia intermedia</i> Cheel	Australia	Peterson 14384, Soreng, & Rosenberg	GU359179	GU359563	GU359642	GU359941	GU360201	GU360327	GU360661
<i>Triodia irritans</i> var. <i>laxispicata</i> N.T. Burb.	Australia	Hind 5731, D'Aubert & Jones Peterson 14383, Soreng & Rosenberg	GU359180	GU359564	GU359643	GU359940	GU360202	GU360328	GU360660
<i>Triodia melvillei</i> (C.E. Hubb.) Lazarides	Australia	Rosenberg	GU359181	GU359542	GU359644	GU359939	GU360203	GU360329	GU360659
<i>Triodia pungens</i> R. Br.	Australia	Thompson BUC800 & Simon	GU359182	GU359540	GU359645	GU359938	GU360175	GU360330	GU360658
<i>Triodia rigidissima</i> (Pilg.) Lazarides	Australia	Spjut 7263, White, Phillips & Lacy Peterson 14238, Weakley & LeBlond	GU359198	GU359556	GU359646	GU359937	GU360198	GU360331	GU360657
<i>Triplasis purpurea</i> (Walter) Chapm.	USA	LeBlond	GU359184	GU359536	GU359647	GU359921	GU360196	GU360347	GU360656
<i>Tripogon spicatus</i> (Nees) Ekman	Peru	Peterson 21784 & Soreng	GU359170	GU359537	GU359648	GU359935	GU360188	GU360333	GU360640
<i>Tripogon yunnanensis</i> J.L. Yang ex S.M. Phillips & S.L. Chen	China	Soreng 5564, Peterson & Sun Hang	GU359186	GU359538			GU360187	GU360487	
<i>Triraphis andropogonoides</i> (Steud.) E. Phillips	South Africa	Mennell s.n. Peterson 14344, Soreng & Rosenberg			GU359661	GU359949	GU360186	GU360335	GU360654
<i>Triraphis mollis</i> R. Br.	Australia	Rosenberg	GU359187	GU359539	GU359650	GU359933	GU360185	GU360336	GU360669
<i>Triraphis purpurea</i> Hack.	South Africa	Schweickerdt 2115		GU359549	GU359639	GU359932	GU360184	GU360337	GU360652
<i>Triraphis ramosissima</i> Hack.	South Africa	Seydel 4278	GU359188	GU359541	GU359652	GU359931	GU360183	GU360338	GU360651
<i>Triraphis schinzii</i> Hack.	South Africa	Smook 1933			GU359653	GU359930		GU360339	GU360650
<i>Tuctoria fragilis</i> (Swallen) Reeder	Mexico	Reeder 7255 & Reeder	GU359189			GU359929	GU360182		
<i>Tuctoria greenei</i> (Vasey) Reeder	USA	Reeder 6656 & Reeder	GU359190			GU359928	GU360181		
<i>Uniola condensata</i> Hitchc.	Ecuador	Peterson 9342 & Judziewicz Peterson 11160, Annable & Valdes-Reyna	GU359191	GU359534	GU359654	GU359927	GU360180	GU360340	GU360649
<i>Uniola paniculata</i> L.	USA	Valdes-Reyna	GU359192	GU359543	GU359655	GU359926	GU360179	GU360341	GU360648
<i>Urochondra setulosa</i> (Trin.) C.E. Hubb.	Pakistan	Reichinger 27496					GU360178		GU360647
<i>Vaseyochloa multinervosa</i> (Vasey) Hitchc.	USA	Swallen 10041	GU359193	GU359544	GU359656	GU359925	GU360177	GU360342	GU360646
<i>Willkommia annua</i> Hack.	South Africa	Hackel s.n.					GU360019		
<i>Willkommia sarmentosa</i> Hack.	South Africa	Schweickerdt 2181	GU359194	GU359545	GU359657	GU359924	GU360252	GU360343	GU360645
<i>Willkommia texana</i> Hitchc. var. <i>texana</i>	USA	Gould 12525	GU359195	GU359546			GU360054	GU360344	GU360644
<i>Zoysia japonica</i> Steud.	Japan	Kuragadake s.n.	GU359196	GU359547	GU359658	GU359923	GU360022		GU360643
<i>Zoysia macrantha</i> Desv.	Australia	Soreng 5913 & Peterson	GU359142	GU359558	GU359660	GU360017	GU360020	GU360346	GU360641
<i>Zoysia macrantha</i> subsp. <i>walshii</i> M.E. Nightingale	Australia	Loch 435	GU359197	GU359548	GU359659	GU359922	GU360021	GU360345	GU360642