

A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae)

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Abstract The subtribe Eleusininae (Poaceae: Chloridoideae: Cynodonteae) is a diverse group containing about 212 species in 31 genera found primarily in low latitudes in Africa, Asia, Australia, and the Americas, and the classification among these genera and species is poorly understood. Therefore, we investigated the following 28 Eleusininae genera: *Acrachne*, *Afrotrichloris*, *Apochiton*, *Astrebla*, *Austrochloris*, *Brachyachne*, *Chloris*, *Chrysochloa*, *Coelachyrum*, *Cynodon*, *Daknopholis*, *Dinebra*, *Diplachne*, *Disakisperma*, *Eleusine*, *Enteropogon*, *Eustachys*, *Harpochloa*, *Leptochloa*, *Lepturus*, *Lintonia*, *Microchloa*, *Ochthochloa*, *Oxychloris*, *Saugetia*, *Schoenefeldia*, *Stapfchloa*, and *Tetrapogon*. The goals of our study were to reconstruct the evolutionary history of the subtribe Eleusininae using molecular data with increased species sampling compared to earlier studies. A phylogenetic analysis was conducted on 402 samples, of which 148 species (342 individuals) were in the Eleusininae, using four plastid (*rpl32-trnL* spacer, *ndhA* intron, *rps16-trnK* spacer, *rps16* intron) and nuclear ITS 1 & 2 (ribosomal internal transcribed spacer) sequences to infer evolutionary relationships and revise the classification. We found strong support for the following Eleusininae lineages: *Acrachne*, *Apochiton*, *Astrebla*, *Austrochloris*, *Chloris*, *Chrysochloa*, *Cynodon*, *Daknopholis*, *Dinebra*, *Diplachne*, *Disakisperma*, *Eleusine*, *Enteropogon*, *Eustachys*, *Leptochloa*, *Lepturus*, *Micrachne* gen. nov., *Stapfchloa*, and *Tetrapogon*, and moderate support for *Harpochloa* and *Microchloa*. Four species of *Brachyachne*, including the type, are imbedded within *Cynodon*; *Oxychloris scariosa* (monotypic) is sister to *Harpochloa-Microchloa*; *Coelachyrum* is polyphyletic since *C. lagopoides*, *Apochiton burttii*, and *C. poiflorum* form a grade, with the latter species sister to *Eleusine*; *Schoenefeldia* appears paraphyletic since *Afrotrichloris martinii* and *Schoenefeldia transiens* together are sister to *Schoenefeldia gracilis*; *Saugetia fasciculata*, *Enteropogon brandegeei*, and *E. chlorideus* are embedded within *Tetrapogon*; *Lintonia nutans* and *Ochthochloa compressa* are embedded in *Chloris*; and *Enteropogon mollis* and *Chloris exilis* are embedded in *Leptochloa*. Our plastid and ITS analyses show rearrangement of lineages within *Acrachne* and *Chloris*, indicating possible hybridization events or evidence for multiple origins. The molecular results support recognition of a new genus, *Micrachne* with five species and emendation of *Stapfchloa* with six species. We provide 22 new combinations, *Chloris flagellifera*, *Ch. nutans*, *Cynodon ambiguus*, *C. prostratus*, *Diplachne divaricatissima*, *Leptochloa anisopoda*, *L. exilis*, *Micrachne fulva*, *M. obtusiflora*, *M. patentiflora*, *M. pilosa*, *M. simonii*, *Stapfchloa berroi*, *S. canerae*, *S. ciliata*, *S. elata*, *S. parvispicula*, *Tetrapogon brandegeei*, *T. chlorideus*, *T. fasciculatus*, *T. pleistachyus*, and *T. roxburghiana*; a new name, *Cynodon simonii*; and lectotypify *Eleusine flagellifera*.

Keywords *Brachyachne*; *Chloris*; *Cynodon*; *Diplachne*; *Enteropogon*; ITS; *Leptochloa*; *Micrachne*, plastid DNA sequences; *Stapfchloa*; systematics; *Tetrapogon*

Supplementary Material Electronic Supplement (Figs. S1–S2) and alignment are available in the Supplementary Data section of the online version of this article at <http://www.ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

The subtribe Eleusininae Dumort. (Poaceae: Chloridoideae: Cynodonteae) is a morphologically diverse group, characterized by having racemose inflorescences (with a few exceptions) and contains about 212 species in 31 genera found primarily in low latitudes in Africa, Asia, Australia, and the Americas. Ten of the genera are currently monotypic

(*Apochiton* C.E.Hubb., *Austrochloris* Lazarides, *Daknopholis* Clayton, *Harpochloa* Kunth, *Ochthochloa* Edgew., *Oxychloris* Lazarides, *Pommereulla* L.f., *Rheochloa* Filg. & al., *Sclerodactylon* Stapf, *Stapfchloa* H.Scholz), 16 genera contain 10 or fewer species: *Acrachne* Wight & Arn. ex Chiov. (3 spp.), *Afrotrichloris* Chiov. (2 spp.), *Astrebla* F.Muell. (4 spp.), *Brachyachne* (Benth.) Stapf (9 spp.), *Chrysochloa* Swallen (4 spp.), *Coelachyrum* Hochst. & Nees (5 spp.), *Cynodon* Rich.

(9 spp.), *Diplachne* P.Beauv. (2 spp.), *Disakisperma* Steud. (4 spp.), *Eleusine* Gaertn. (10 spp.), *Leptochloa* P.Beauv. (5 spp.), *Lintonia* Stapf (2 spp.), *Microchloa* R.Br. (6 spp.), *Saugetia* Hitchc. & Chase (2 spp.), *Schoenefeldia* Kunth (2 spp.), and *Tetrapogon* Desf. (5 spp.), and 5 genera contain 13 or more species: *Chloris* Sw. (59 spp.), *Dinebra* Jacq. (23+ spp.), *Enteropogon* Nees (18 spp.), *Eustachys* Desv. (13 spp.), and *Lepturus* R.Br. (15 spp.) (Clayton & al., 1974, 2006; Peterson & al., 2010a, 2012, 2014a; Soreng & al., 2014, 2015).

In a large phylogenetic study of the Chloridoideae Kunth ex Beilschm. based on seven DNA sequence markers (ITS, *ndhA* intron, *ndhF*, *rps16-trnK*, *rps16* intron, *rps3*, *rpl32-trnL*) Eleusininae was monophyletic in the ITS, plastid, and combined plastid/ITS phylograms (Peterson & al., 2010a). In the combined plastid/ITS tree, *Cynodon* appeared paraphyletic with at least two species of *Brachyachne* embedded within it; an additional strongly supported clade of three species of *Brachyachne* was found outside of *Cynodon*; *Chloris*, *Lepturus*, *Microchloa*, and *Tetrapogon* were monophyletic, although *Chloris* appeared polyphyletic in the ITS tree; *Astrebala* was paraphyletic with *Schoenefeldia gracilis* Kunth embedded within (but not in the plastid analysis); and *Enteropogon*, *Eustachys*, *Leptochloa*, and *Tetrapogon* were polyphyletic (Peterson & al., 2010a). Based on five DNA sequence markers (*rpl32-trnL*, *ndhA* intron, *rps16* intron, *ccsA*, ITS) the species of *Leptochloa* were realigned into four genera (*Dinebra*, *Diplachne*, *Disakisperma*, *Leptochloa*) in the Eleusininae and a new genus, *Trigonochloa* P.M.Peterson & N.Snow, was erected to accommodate two species in the subtribe Perotidinae P.M.Peterson & al. (Peterson & al., 2012, 2014a; Snow & Peterson, 2012a). Emphasizing possession of an ovoid Caryopsis that is broadly concave on the hilar (dorsal) side, Scholz & Müller (2004) placed *Chloris lamproparia* Stapf in a monotypic genus, *Stapfochloa*. Other members of Anderson's (1974) "Chloris ciliata Sw. complex", of which *C. lamproparia* is a member, have trigonous Caryopses without a concave surface. *Stapfochloa* and members of the *Chloris ciliata* complex have never been sampled in a molecular study.

The aim of our paper is to discern the evolutionary relationships, test the monophyly, and present a new classification of genera in the Eleusininae, excluding only *Pommereulla*, *Rheochloa* and *Sclerodactylon* of which we have no good material. To accomplish the immediate goal of understanding the evolutionary history of the Eleusininae we are using a large dataset of species of Chloridoideae. Here, we present a new phylogenetic analysis for 148 of the 212 species that are part of the Eleusininae based on analysis of ITS and four plastid regions (*rpl32-trnL*, *ndhA*, *rps16*, *rps16-trnK*). The number of species sampled within many of these 28 Eleusininae genera is expanded compared to earlier studies and for the first time we are including species of *Afrotrichloris*, *Daknopholis*, *Harpochloa*, *Ochthochloa*, and *Oxychloris* (Peterson & al., 2007, 2010a, 2012, 2014a). We discuss morphological and anatomical characters supporting relationships and propose changes to the classification. In addition, we include a description of a new genus, *Micrachne*, and emend the description of *Stapfochloa*.

■ MATERIALS AND METHODS

Taxon sampling. — Our sampling consists of 402 samples, representing 224 species of grasses, of which 148 species are included in the Eleusininae and 70 species are included in five other tribes and subtribes: Centropodieae with a single species, Triraphideae with two species, Eragrostideae with ten species, Zoysieae with seven species; and within the Cynodonteae we include the Tripogoninae with six species, Pappophorinae with three species, Tragineae with three species, Hilariinae with two species, Muhlenbergiinae with two species, Scleropogoninae with two species, Boutelouinae with a single species, Monanthochloinae with three species, Orcuttiinae with two species, Gouiniinae with three species, Cteniinae with a single species, Trichoneurinae with a single species, Gymnopogoninae with six species, Farragininae with two species, Perotidinae with four species, Triodiinae with a single species, and Aeluropodinae with three species (see Appendix 1). Our ingroup sampling was primarily focused on 28 morphologically similar genera (*Acrachne*, *Afrotrichloris*, *Apochiton*, *Astrebala*, *Austrochloris*, *Brachyachne*, *Chloris*, *Chrysochloa*, *Coelachyrum*, *Cynodon*, *Daknopholis*, *Dinebra*, *Diplachne*, *Disakisperma*, *Eleusine*, *Enteropogon*, *Eustachys*, *Harpochloa*, *Leptochloa*, *Lepturus*, *Lintonia*, *Microchloa*, *Ochthochloa*, *Oxychloris*, *Saugetia*, *Schoenefeldia*, *Stapfochloa*, *Tetrapogon*), most of which have been previously included in the Eleusininae (Peterson & al., 2010a). The dataset for these 28 genera includes 71% (148/209) of the species currently placed in these genera by Clayton & al. (2006–). In addition, we include two species of *Neobouteloua* Gould and three species of *Dactyloctenium* Willd. that are currently in the Cynodonteae, incertae sedis. Outside of the Chloridoideae, three species of Danthonioideae (*Capeochloa cincta* subsp. *sericea* (N.P.Barker) N.P.Barker & H.P.Linder, *Danthonia compressa* Austin, *Rytidosperma pallidum* (R.Br.) A.M.Humphreys & H.P.Linder), one species of Aristidoideae (*Aristida gypsophila* Beetle), and one species of Panicoideae (*Chasmanthium latifolium* (Michx.) H.O.Yates, phylogenetic root) were chosen as the outgroup. A complete list of taxa, voucher information, and GenBank numbers can be found in Appendix 1. All collections gathered by PMP after 1998 were collected in silica but the majority of samples used in this study were taken from herbarium specimens.

To compare ITS and combined plastid incongruence among species of the *Chloris* clade we provide a tanglegram using *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth. and *Leptochloa digitata* (R.Br.) Domin. as outgroups. Since there is hard incongruence involving the placement of *Acrachne* outside of the Eleusininae in the ITS tree and within the Eleusininae in the plastid tree, we removed all ITS sequences from this genus in our combined plastid+ITS tree.

DNA extraction, amplification, and sequencing. — All procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA isolation, amplification, and sequencing of *rpl32-trnL* spacer and *ndhA* intron (small single-copy region), *rps16-trnK* spacer and *rps16* intron (large single-copy region), and ITS was accomplished

following procedures outlined in Peterson & al. (2010a, b). We specifically targeted four of the plastid regions that proved to be most informative in our previous studies on chloridoid grasses (Peterson & al., 2010a, b, 2011, 2012, 2014a, b).

Phylogenetic analyses. — We used Geneious v.5.3.4 (Drummond & al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *ndhA* intron, *rps16* intron, *rps16-trnK*, and ITS regions, and MUSCLE v.3.5 (Edgar, 2004) to align consensus sequences and adjust the final alignment. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModelTest (Posada, 2008) and applied maximum likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined datasets were partitioned in accordance with the number of the markers used. Nucleotide substitution models selected by Akaike's information criterion, as implemented in jModelTest v.0.1.1, were specified for each partition (Table 1). The ML analysis was conducted with GARLI v.0.951 (Zwickl, 2006). The ML bootstrap analysis was performed with 1000 replicates, with 10 random addition sequences per replicate. The output file containing trees of ML found for each bootstrap dataset was then read into PAUP where the majority-rule consensus tree was constructed. Bootstrap (BS) values of 90%–100% were interpreted as strong support, 70%–89% as moderate, and 50%–69% as weak.

Bayesian posterior probabilities (PP) were estimated using a parallel version of MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis was initiated with random starting trees and was initially run for 4 million

generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences dropped below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn-in was set at 0.25. Posterior probabilities of 0.95–1.00 were considered to be strong support.

RESULTS

Phylogenetic analyses. — Fifty-four percent (893/1639) of the sequences used in our study are newly reported here, 46% (746/1639) are from previous studies, and 18.5% (371/2010) are missing (Appendix 1). Total aligned characters for individual regions are noted in Table 1. Plastid *rpl32-trnL* and ITS had the highest sequencing success of 93.8% and 92.6%, respectively, whereas recovery of other regions across the entire dataset ranged from 66.3% to 82.6%.

Incongruences between the ITS and combined plastid phylograms. — Summary plastid, ITS, and combined plastid+ITS abbreviated trees are compared (Fig. 1). Separate expanded trees for ITS and combined plastid markers are given in Figs. S1–S2 (Electr. Suppl.). All three trees provide strong support (BS 93–96/PP 1.00) for the monophyly of the Eleusininae (in part). Within Eleusininae, the order of divergence is: *Diplachne*, *Acrachne*, *Dinebra*, *Coelachyrum lagopoides* (Burm.f.) Senaratna–*Apochiton*–*C. poiflorum* Chiov.–*Eleusine*, and remaining genera (plastid tree); *Apochiton*–*Coelachyrum poiflorum*–*Eleusine*, *Diplachne*, and remaining genera (ITS tree); and *Acrachne*, *Dinebra*, *Coel-*

Table 1. Characteristics of *rpl32-trnL*, *ndhA* intron, *rps16* intron, *rps16-trnK* and ITS, and parameters used in Bayesian analyses indicated by Akaike information criterion.

	<i>rpl32-trnL</i>	<i>ndhA</i> intron	<i>rps16</i> intron	<i>rps16-trnK</i>	Combined plastid data	ITS	Overall
Total aligned characters	1117	1373	1110	1146	4746	857	5603
Sequencing success (%)	93.8	66.3	70.7	82.6	78.3	92.6	81.2
Number of new sequences	219 (58%)	135 (51%)	137 (48%)	181 (54%)	672 (53%)	221 (59%)	893 (54%)
Likelihood score (–lnL)	8149.6	7692.53	5965.44	7383.91		20188.86	
Number of substitution types	6	6	6	6	–	6	–
Model for among-site rate variation	gamma	gamma	gamma	gamma	–	gamma	–
Substitution rates	0.7009 1.6018 0.3286 1.0772 1.0554 1.0000	1.4804 2.9329 0.6893 2.4887 3.2724 1.0000	1.1730 1.2242 0.3295 1.3903 1.9526 1.0000	1.2472 2.6893 0.4504 1.9104 2.6182 1.0000	–	1.2221 3.0333 1.6482 0.9412 4.9300 1.0000	–
Character state frequencies	0.3809 0.1400 0.1136 0.3654	0.3652 0.1336 0.1448 0.3563	0.4022 0.0972 0.1630 0.3374	0.3094 0.1364 0.1399 0.4142	–	0.2403 0.1908 0.2416 0.3272	–
Proportion of invariable sites	0.1336	0.3039	0.2059	0.1640	–	0.2380	–
Substitution model	GTR+I+G	TVM+G	TIM3+I+G	TIM3+G	–	GTR+I+G	–
Gamma shape parameter (α)	0.7828	1.0849	0.9792	1.5740	–	1.0171	–

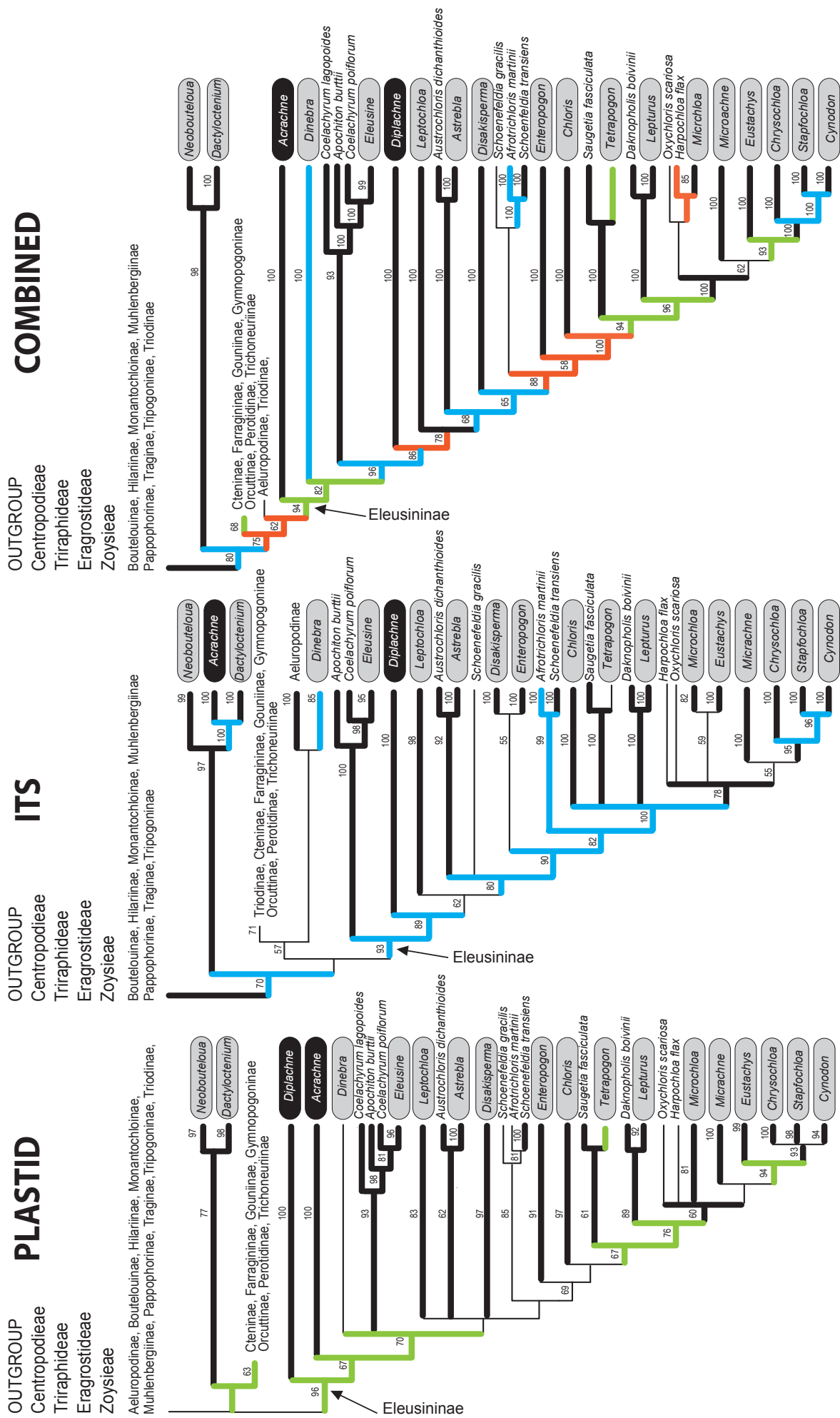


Fig. 1. A summary comparison of the plastid, ITS, and combined (plastid + ITS) maximum-likelihood trees. Numbers above branches are bootstrap values; thick branches represent statistically supported relationships (high bootstrap of 89–100 and/or posterior probability of 0.95–1.00); thin branches indicate unsupported relationships; green branches are derived from the plastid analysis; blue branches are derived from the ITS analysis; red branches indicate support not found in either the ITS or the plastid phylogeny; black branches are found in all three analyses; arrow indicates the Eleusininae clade.

achyrum lagopoides–*Apochiton*–*C. poiflorum*–*Eleusine*, *Diplachne*, and remaining genera (plastid & ITS tree). In the ITS tree *Dinebra* is sister to the Aeluropodinae (–/0.58) and *Acrachne* is sister to *Dactyloctenium* (100/1.00), both outside the Eleusininae.

Two clades, *Acrachne* and *Diplachne*, showed “hard” incongruence and were excluded from the datasets. We refer to hard incongruence as clades with strong bootstrap and posterior probability, while soft incongruence are clades with weak or no bootstrap and posterior probability less than 95%. We used only plastid sequences to represent the *Acrachne* clade in the combined analysis (Fig. 2). However, we retained the full set of sequences for *Dinebra* and *Diplachne* where the ITS signal completely overrides plastid signal. Due to differences in rates of evolution in plastid and nuclear DNA as well as a notoriously high rate of homoplasy in ITS data, our separate plastid and ITS phylogenetic trees have different patterns of resolution (Fig. 1). Combination of the ITS and plastid data improves branch support significantly within the Eleusininae tree by providing resolution for 54 major nodes with moderate to strong support compared to 39 with only plastid data and 38 with only ITS data. Seven of those nodes gained support in the combined analysis.

Phylogenetic trees of Eleusininae. — The ML tree from the combined plastid (*rpl32-trnL*, *ndhA*, *rps16-trnK*, *rps16*) and ITS regions (Fig. 2) is well resolved with strong support (99–100/1.00) for clades of the following genera: *Acrachne*, *Dinebra*, *Apochiton*, *Eleusine*, *Diplachne* (including *Dinebra divaricatissima* (S.T.Blake) P.M.Peterson & N.Snow), *Leptochloa* (including *Chloris exilis* Renvoize and *Enteropogon mollis* (Nees) Clayton), *Astrebla* sister to *Austrochloris*, *Disakisperma*, *Enteropogon*, *Chloris*, *Tetrapogon* (including *Chloris roxburghiana* Schult., *Enteropogon brandegeei* (Vasey) Clayton, *E. chlorideus* (J.Presl) Clayton, and *Saugetia fasciculata* Hitchc. & Chase), *Lepturus* sister to *Daknopholis boivinii* (A.Camus) Clayton, four species of *Brachyachne* that do not include the type (= *Micrachne*, gen. nov.), *Eustachys*, *Chrysochloa*, three species of *Chloris* (*C. canterae* Arechav., *C. ciliata*, *C. elata* Desv.) with *Stapfochloa lamproparia* (Stapf) H.Scholz, and *Cynodon* (including four species of *Brachyachne*, of which one is the type). Three species of *Microchloa* are in a moderately supported (85/1.00) clade that is sister to *Harpochloa falx* (L.f.) Kuntze, and together these are sister to *Oxychloris scariosa* (F.Muell.) Lazarides. *Coelachyrum* appears polyphyletic since *C. lagopoides* and *C. poiflorum* do not form a clade. The latter species, *C. poiflorum*, is sister to *Eleusine* (100/1.00) whereas *C. lagopoides* is basal to the *Apochiton*–*C. poiflorum*–*Eleusine* clade (98/1.00). *Schoenefeldia* appears paraphyletic since *Afrotrichloris martinii* Chiov. (type) and *Schoenefeldia transiens* (Pilg.) Chiov. form a strongly supported clade (100/1.00) that is sister to *Schoenefeldia gracilis* (type). Together these three species form an unsupported clade (–/0.72). Deeper clades with maximum support (100/1.00) include: *Chloris*–*Tetrapogon*–*Lepturus*–*Microchloa*–*Micrachne*–*Eustachys*–*Chrysochloa*–*Stapfochloa*–*Cynodon*, *Microchloa*–*Micrachne*–*Eustachys*–*Chrysochloa*–*Stapfochloa*–*Cynodon*, *Chrysochloa*–*Stapfochloa*–*Cynodon*, and *Stapfochloa*–*Cynodon*.

Within the *Chloris* s.str. clade there was hard incongruence between the combined plastid and ITS datasets; therefore, we did not combine them but provide a detailed tanglegam (Fig. 3). Both the ITS and combined plastid trees are well resolved and the monophyly of *Chloris* is strongly supported (100/1.00) but their interrelationships differ in each data partition. The four strongly supported clades (100/1.00) in the ITS tree labeled A–D nearly correspond to the clades with the same letters in the combined plastid tree. In the combined plastid tree clades A and C are each strongly supported (91, 100/1.00), clade D is moderately supported (87/1.00), and clade B is poorly supported (–/0.69). In the ITS tree, species in A–B and C–D form strongly supported clades (95/1.00) whereas in the combined plastid tree, species in A–C form a strongly supported clade (99/1.00) and species in B–D form a moderately supported clade (71/0.99). *Lintonia nutans* Stapf and *Ochthochloa compressa* (Forssk.) Hilu are included within *Chloris* in the ITS tree and are sister to *Chloris* s.str. in the plastid tree. In the combined plastid tree *Ochthochloa* is sister to the remaining members of *Chloris* and *Lintonia* is sister to clade A–C (99/1.00). In the ITS tree *Ochthochloa* is sister to *Lintonia* and two samples of *Chloris mossambicensis* K.Schum. (66/0.75), and all of these are sister to clade A–B (95/1.00). In the ITS and combined plastid tree clade A (*C. barbata* Sw. and *C. prieurii* Kunth) and B (*C. amethystea* Hochst., *C. andropogonoides* E.Fourn., *C. cucullata* Bisch., *C. latisquamea* Nash, *C. mossambicensis*, *C. × subdolichostachya* Müll.Hal., *C. verticillata* Nutt.) are each composed of the same species, although their interrelationships differ. In the ITS tree clade C contains three species (*C. gayana* Kunth, *C. pilosa* Schumach., *C. virgata* Sw.) whereas in the combined plastid tree *C. orthonoton* Döll and *C. rufescens* Lag. are additional members of clade C; these two species are sister to clade C in the ITS tree, but support for this topology is weak. In the combined plastid tree clade D contains nine species (*C. cruciata* (L.) Sw., *C. cubensis* Hitchc. & Ekman, *C. divaricata* R.Br., *C. ekmanii* Hitchc., *C. halophila* Parodi, *C. pectinata* Benth., *C. pycnothrix* Trin., *C. sagraeana* A.Rich., *C. submutica* Kunth) whereas in the ITS tree clade D contains these nine species plus three additional species (*C. orthonoton*, *C. rufescens*, *C. texana* (Vasey) Nash). *Chloris castilloniana* Lillo & Parodi is sister to the B–D clade in the combined plastid tree (71/0.99) and is sister to clade C in the ITS tree (100/1.00).

■ DISCUSSION

Within the Eleusininae we found strong support for the following lineages recognized as genera: *Acrachne*, *Apochiton*, *Astrebla*, *Austrochloris*, *Chloris*, *Chrysochloa*, *Cynodon*, *Daknopholis*, *Dinebra*, *Diplachne*, *Disakisperma*, *Eleusine*, *Enteropogon*, *Eustachys*, *Leptochloa*, *Lepturus*, *Micrachne*, *Stapfochloa*, and *Tetrapogon*; and moderate support for *Harpochloa* and *Microchloa*. Four species of *Brachyachne*, including the type, are embedded within *Cynodon*; *Oxychloris scariosa* (monotypic) is sister to *Harpochloa*–*Microchloa*; *Coelachyrum* appears polyphyletic since *C. lagopoides*, *Apochiton burttii*

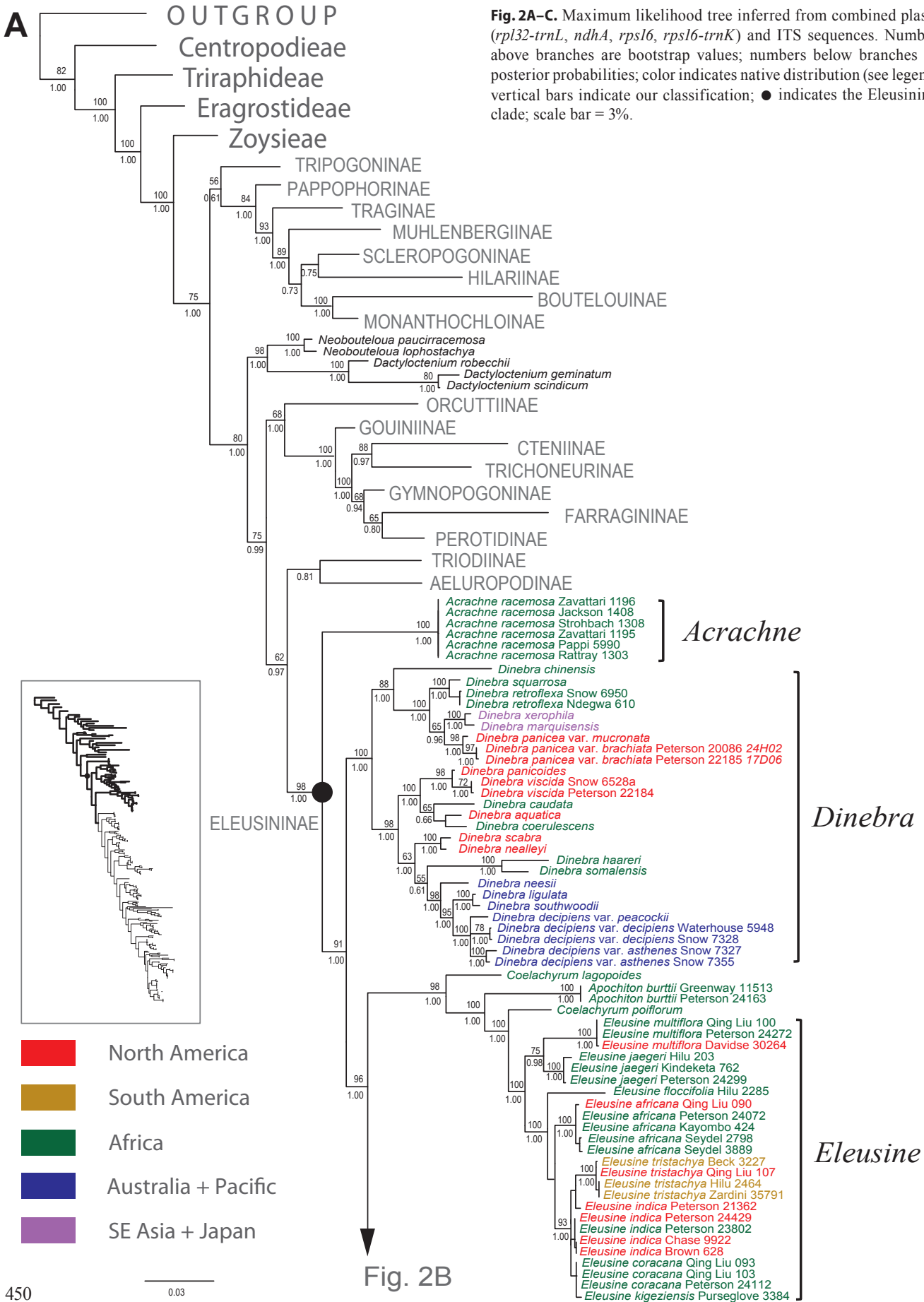
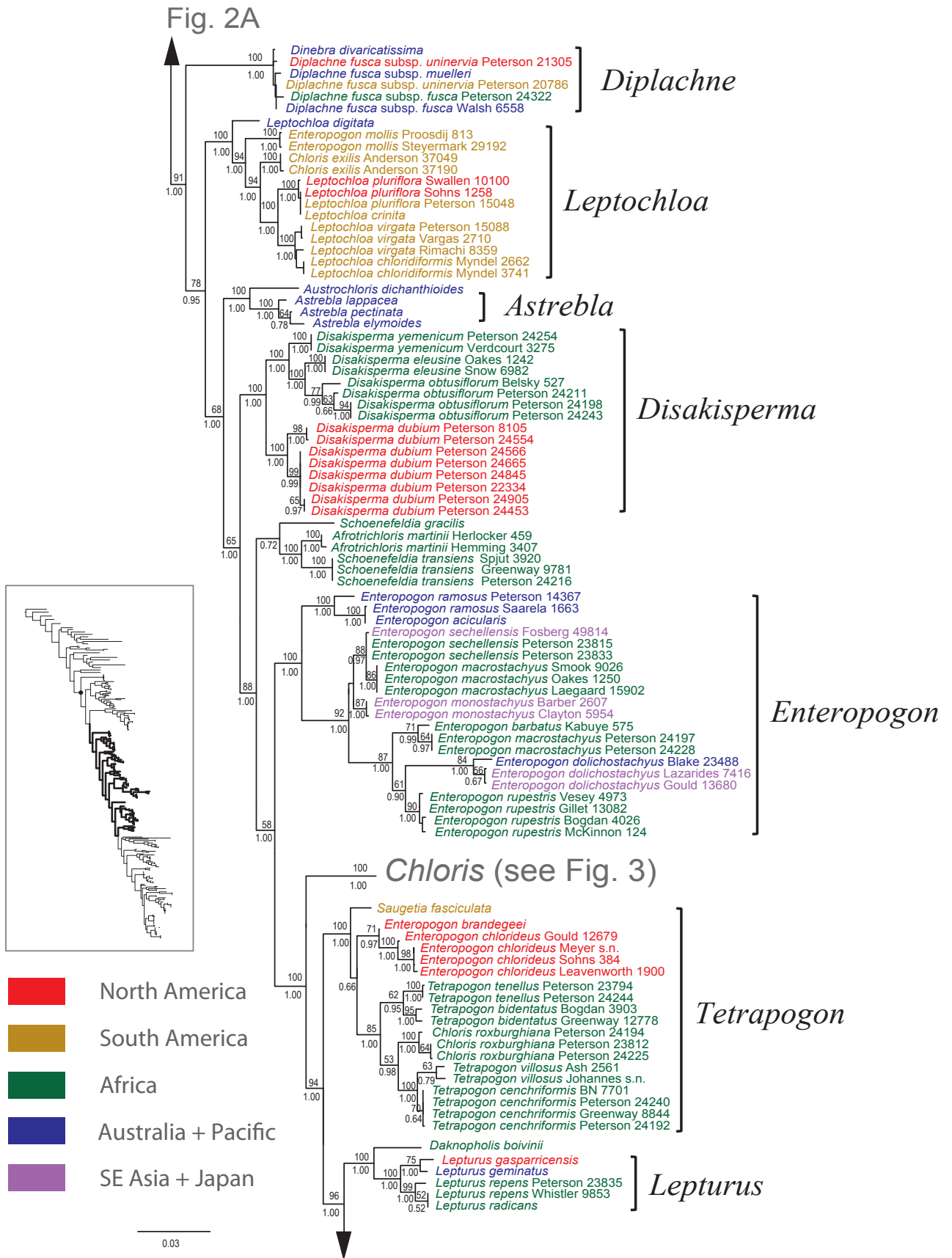


Fig. 2A–C. Maximum likelihood tree inferred from combined plastid (*rpl32-trnL*, *ndhA*, *rps16*, *rps16-trnK*) and ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; color indicates native distribution (see legend); vertical bars indicate our classification; ● indicates the Eleusininae clade; scale bar = 3%.

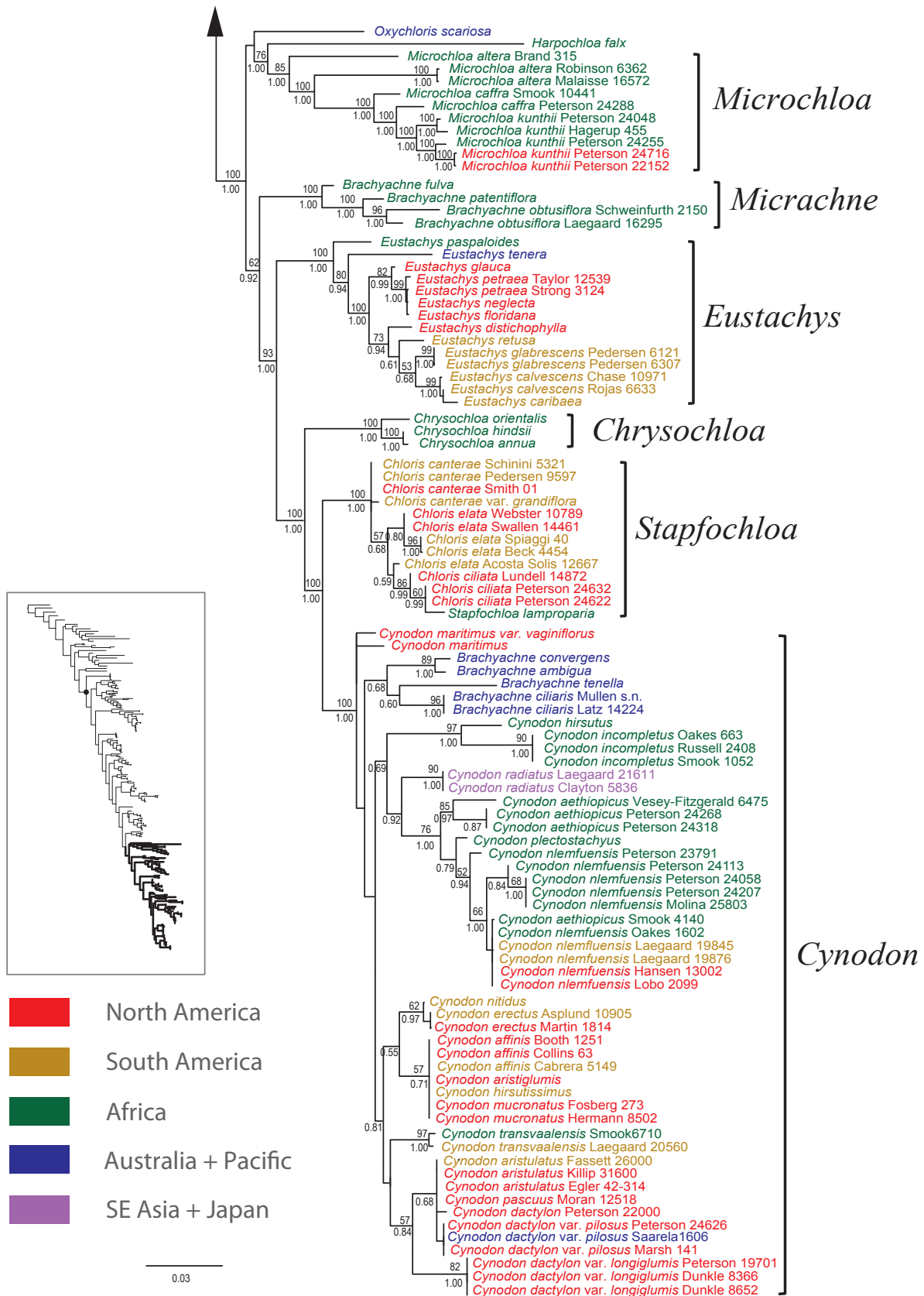
Fig. 2B

B



C

Fig. 2B



C.E.Hubb, and *C. poiflorum* appear in a grade, with the latter species sister to *Eleusine*; *Schoenefeldia* appears paraphyletic since *Afrotrichloris martinii* and *Schoenefeldia transiens* together are sister to *Schoenefeldia gracilis*; *Saugetia fasciculata* (monotypic), *Enteropogon brandegeei*, and *E. chlorideus* are embedded within *Tetrapogon*; and *Lintonia nutans* (monotypic) and *Ochthochloa compressa* (monotypic) are embedded in *Chloris*.

***Acrachne*, *Apochiton*, *Coelachyrum*, *Dactyloctenium*, *Dinebra*, and *Eleusine*.** — In order to detect different plastid haplotypes and to test the consistency of phylogenetic signal provided by plastid DNA markers, we included six samples of *Acrachne racemosa* from five countries in east and southern Africa, and these form a highly supported clade with no genetic variability (Fig. 2A). Based on possessing ornamented fruits with free pericarps, Phillips (1995) considered *Eleusine*, *Acrachne*, and *Dactyloctenium* to be closely related. Additionally, the species in these three genera share inflorescences with digitately to subdigitately arranged racemes usually with biseriate and secund spikelets (Watson & Dallwitz, 1992; Clayton & al., 2006–). Our data support this assumption, at least in part, since *Acrachne* is strongly supported sister of *Dactyloctenium* in the ITS tree outside of the Eleusininae, but in the combined plastid tree *Acrachne* is the second basal split in the Eleusininae (Fig. 1). Phillips (1972) noted that species of *Acrachne* can sometimes be mistaken for *Eleusine multiflora* Hochst. ex A.Rich. and that the latter species is somewhat intermediate between the two genera by sharing acropetal floret maturation (from the base upwards), mucronate lemmas, and a delicate pericarp that ruptures shedding the grain from the floret. However, *Eleusine* does not share a recent common ancestor with *Acrachne* in any of our trees and *E. multiflora* is clearly part of *Eleusine* suggesting that these characters are homoplasious. Further investigation of *Acrachne* and *Dactyloctenium* using low-copy nuclear genes is needed to test for hybridization and subsequent genomic exchange or introgression, given their discordant positions in the plastid and ITS trees (Romaschenko & al., 2014).

In our ITS tree, *Dinebra* is unresolved outside of the Eleusininae, a result also found in Peterson & al. (2012). We verify the placement of two additional species of *Dinebra* (see Fig. 2A) for the first time using molecular data: *D. aquatica* (Scribn. & Merr.) P.M.Peterson & N.Snow and *D. haareri* (Stapf & C.E.Hubb.) P.M.Peterson & N.Snow, where the former is an unsupported sister to *D. coerulescens* (Steud.) P.M.Peterson & N.Snow in a larger strongly supported clade that includes *D. caudata* (K.Schum.) P.M.Peterson & N.Snow, *D. panicoides* (J.Presl) P.M.Peterson & N.Snow, and *D. viscida* (Scribn.) P.M.Peterson & N.Snow; and the latter is a strongly supported sister to *D. somalensis* (Stapf) P.M.Peterson & N.Snow, a clade whose deep relationships are unclear.

Based on plastid markers, previous studies of *Eleusine* indicated that *E. africana* Kenn.-O’Byrne and *E. coracana* (L.) Gaertn. (finger millet) share a recent common ancestor (Liu & al., 2011, 2013). We here offer one new insight within *Eleusine* because our results differ from these. Based on five samples of *E. africana*, five samples of *E. indica* (L.) Gaertn., and three samples of *E. coracana* our ITS/

combined plastid tree (Fig. 2A) indicates that the *E. coracana*–*E. indica*–*E. kigeziensis* S.M.Phillips–*E. tristachya* (Lam.) Lam. clade is sister to five accessions of *E. africana*. In the plastid tree of Liu & al. (2011) *E. africana*, *E. kigeziensis*, and *E. coracana* share a recent common ancestor and these are sister to *E. indica*–*E. tristachya*. The ITS sequence marker in our study seems to be the primary marker responsible for this incongruence since *E. africana*, *E. coracana*, and *E. indica* form a clade based solely on plastid sequences (see Electr. Suppl.; Fig. S2). However, after realignment of the *rpl32-trnL* sequences for accessions of Liu 090 (*E. africana*) and Liu 093, 103 (*E. coracana*) used here and in Liu & al. (2011), we found that they still aligned with our *E. africana* and *E. coracana*–*E. indica*–*E. kigeziensis*–*E. tristachya* clades, respectively. Our results support the recognition of *E. africana* at the specific level, rather than as a subspecies of *E. coracana* or *E. indica* (Phillips, 1995; Cope, 1999).

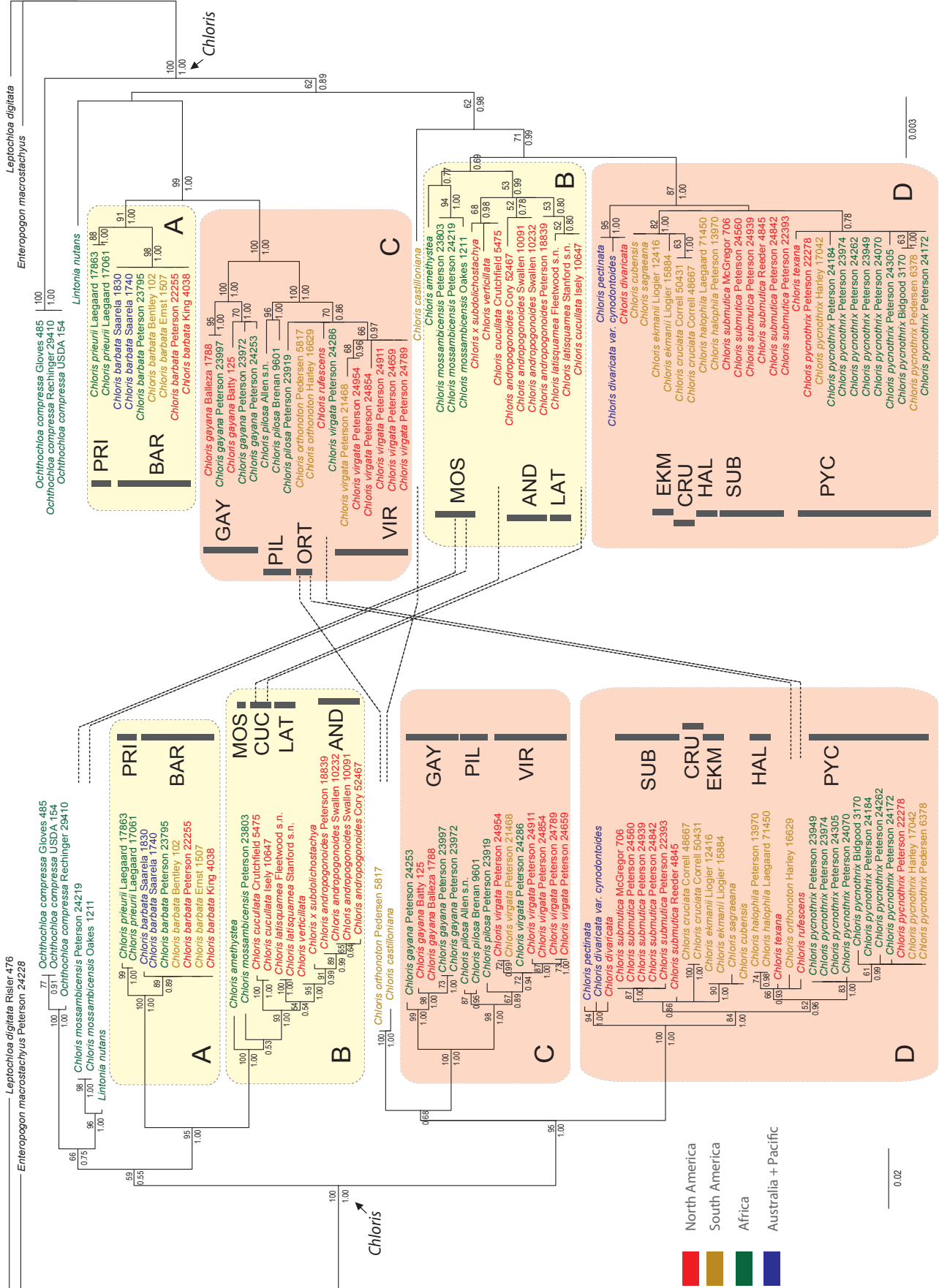
Sister to *Eleusine* is *Coelachyrum poiflorum*, a relationship that has been found in previous studies (Peterson & al. 2010a, 2012, 2014a; Liu & al. 2011; Snow & al., 2013). *Coelachyrum lagopoides* and *C. poiflorum* do not form a clade but are in a grade separated by two samples of *Apochiton burttii* Phillips (1995) indicated, “*Coelachyrum* is a rather heterogeneous assemblage ... the species vary considerably in inflorescence structure and hairiness of the spikelets.” Emilio Chiovenda, who first described *C. poiflorum*, later transferred the species into *Eleusine* (Chiovenda, 1898, 1912). There are quite a few morphological differences between *C. poiflorum* and species of *Eleusine*, such as dorsiventrally compressed caryopses (versus ellipsoid to trigonous) and lemmas with long shaggy hairs (versus glabrous; Cope, 2007). We still lack samples for three species of *Coelachyrum* (*C. brevifolium* Hochst. & Nees [type], *C. longiglume* Napper, *C. piercei* (Benth.) Bor) so we hesitate to make any taxonomic changes at the moment. The heterogeneous nature of *Coelachyrum* was observed in Snow & al. (2013), in which *C. yemenicum* (Schweinf.) S.M.Phillips was resolved within the *Disakisperma* clade, prompting the combination *Disakisperma yemenicum* (Schweinf.) P.M.Peterson & N.Snow.

***Afrotrichloris*, *Astrebala*, *Austrochloris*, *Daknopholis*, *Diplachne*, *Disakisperma*, *Enteropogon*, *Leptochloa*, *Lepturus*, *Saugetia*, *Schoenefeldia*, and *Tetrapogon*.** — Within *Disakisperma*, we include a larger sample of *D. dubium* (Kunth) P.M.Peterson & N.Snow (eight versus two individuals, see Snow & al., 2013) in order to test intraspecific variation in the species (Fig. 2B). There appear to be no gross morphological features or geographic components separating Peterson 8105 and Peterson 24554 from the other six accessions even though they form a strongly supported clade (phylogenetic signal in ITS) sister to the other six accessions. Three species, *D. eleusine* (Nees) P.M.Peterson & N.Snow, *D. obtusiflorum* (Hochst.) P.M.Peterson & N.Snow, and *D. yemenicum*, which form a strongly supported clade, have clavicorniculate hairs on the lemmas whereas *D. dubium*, the sister species to this clade, has acute or rounded lemmatal hairs (Snow & al., 2013).

Within the *Diplachne* clade we include two samples of *D. fusca* (L.) P.Beauv. ex Roem. & Schult. subsp. *fusca* and

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these differ little genetically from the two other subspecies of *D. fusca*. Contrary to our best guess in Snow & Peterson (2012b), we report that *Dinebra divaricatissima* aligns within the *Diplachne* clade, again with very little genetic variation between it and *D. fusca*.

We include for the first time a full complement of DNA markers for *Enteropogon mollis* (Columbus & al., 2007) and *Chloris exilis*, and confirm their placement in *Leptochloa* s.str. Anderson (1974) mentioned that “*Chloris mollis* Nees (= *Enteropogon mollis*) is unique in the genus [*Chloris*] in having sterile florets with a prominently pubescent callus and long awns”, and that it has many characters similar to *Gymnopogon* P.Beauv. Possession of long-awned (4–12 mm) florets is a common feature of *Leptochloa* s.str., although this trait was only recently found important after viewing a molecular phylogeny (Peterson & al., 2012). Only the Australian endemic, *Leptochloa digitata*, which is sister to the rest of *Leptochloa*, has entire to aristulate lemmas (Nightingale & al., 2005b). Anderson (1974) was correct in assuming *Chloris mollis* was misplaced in *Chloris* but the characters he mentions as being intermediate between *Gymnopogon* and *Chloris*, i.e., short, stiff leaf blades and sterile florets, seem to have arisen in parallel, since the *Gymnopogoninae* is far removed from Eleusininae (Peterson & al., 2014a). Renvoize (1984) indicated that *Chloris exilis* may be confused with *Enteropogon mollis*, although the latter has 2(–3)-flowered spikelets and strongly dorsally compressed lower lemmas. In our tree these two species are in a grade between *Leptochloa digitata* (basal) and *L. chloridiformis* (Hack.) Parodi–*L. crinita* (Lag.) P.M.Peterson & N.Snow–*L. pluriflora* (E.Fourn.) P.M. Peterson & N.Snow–*L. virgata* (L.) P.Beauv. (derived). We also verify that *Leptochloa chloridiformis* is included in *Leptochloa* s.str., as previously suggested (Peterson & al., 2012), bringing the genus to seven species.

This study corroborates the strong support found by Peterson & al. (2010a) for a monophyletic *Astrebla* sister to *Austrochloris dichanthioides* (Everist) Lazarides, and we confirm that in our study using three species of *Astrebla*, including *A. pectinata* (Lindl.) F.Muell. ex Benth. (type). Jozwick (1969) prepared an excellent morphological, anatomical, and hybridization study of the four species of *Astrebla* but there is no mention of their affinity with other genera, other than Tateoka (1957) placing the genus in the Chlorideae based on chromosome number. Clayton & Renvoize (1986) indicate *Astrebla* has “no obvious relatives ... but some resemblance to *Tetrapogon*”. Lazarides (1972), the author of *Austrochloris*, felt that *Chloris* was somehow related to *A. dichanthioides* but noted that dorsally compressed florets and caryopses in *Austrochloris* were important features not found in *Chloris*. In our tree the *Austrochloris*–*Astrebla* clade lies between *Leptochloa* (basal) and *Disakisperma* (derived), two splits (*Afrotrichloris*–*Schoenefeldia* and *Enteropogon*) removed from the derived *Chloris* clade. *Astrebla* and *Austrochloris* have dorsally compressed to terete caryopses with

free pericarps and inflorescences with biseriate racemes (2 or 3 in *Austrochloris* and 1 in *Astrebla*; Watson & Dallwitz, 1992; Clayton & al., 2006–). Geography seems to have played a large role in the evolution of these grasses since the *Austrochloris*–*Astrebla* lineage is an Australian endemic clade.

Our tree depicts *Schoenefeldia* paraphyletic with a clade of two samples of *Afrotrichloris martinii* embedded within. At this time it would be premature to submerge *Afrotrichloris martinii* (type) within *Schoenefeldia* because we have not sampled *A. hyaloptera* Clayton and we have no support for the *Schoenefeldia gracilis* (type)–*S. transiens*–*A. martinii* clade in the ITS tree where *Schoenefeldia* appears paraphyletic (see Electr. Suppl.: Fig. S1). However, we have moderate support (85/–, see Fig. 1A) for the *Schoenefeldia gracilis*–*S. transiens*–*A. martinii* clade in the plastid tree. Further study may indicate hybridization and introgression with members of this clade and other species in the Eleusininae.

We found strong support for a monophyletic *Enteropogon* in its current circumscription, which includes eight species, contrary to earlier reports of polyphyly of the genus (Hilu & Alice, 2001; Columbus & al., 2007; Peterson & al. 2010a; GPWG, 2011). None of these previous studies included more than two species of the genus, whereas Columbus & al. (2007) studied two species, *Enteropogon chlorideus* and *E. mollis*, which are here treated in *Tetrapogon* and *Leptochloa*, respectively. Peterson & al. (2010a) depicted a clade with two species of *Enteropogon* (*E. macrostachyus*, *E. ramosus* B.K.Simon) treated here in the genus and one species of *Eustachys*. Traditionally, *Enteropogon* was separated from *Chloris* by having a single, rarely two, spikelike racemes and fertile lemmas that are strongly dorsally compressed with raised midveins (Clayton, 1967; Anderson, 1974). However, *Enteropogon acicularis* (Lindl.) Lazarides from Australia and *E. dolichostachyus* (Lag.) Keng ex Lazarides from Southeast Asia have many (3–14) digitate to subdigitately arranged spikelike racemes and dorsally compressed lemmas with raised midveins, and our data confirm these are part of *Enteropogon*. Tateoka (1962) found simple, angular starch grains in *Enteropogon* while *Chloris* had compound starch grains, and both *E. acicularis* and *E. dolichostachyus* have simple, angular starch grains (Anderson, 1974). Delimitation of *E. macrostachyus* is problematic (Fig. 2B) where there are two separate clades of *E. macrostachyus*, implying a polyphyletic origin (or one of these clades may represent an undescribed taxon). Diploids and tetraploids have been documented in individuals of *E. macrostachyus* (Roodt & Spies, 2002, 2003a, b). There is little ITS variation among all accessions of *E. barbatus* C.E.Hubb., *E. macrostachyus*, *E. monostachyus* (Vahl) K.Schum., and *E. sechellensis* (Baker) T. Durand & Schinz (see Electr. Suppl.: Fig. S1) suggesting homogenization or simply recent, rapid radiation (i.e., they form a clade). However, moderate genetic variation occurs among the plastid markers in these four species, and their

◀ **Fig. 3.** A comparison (tanglegram) of the ITS and combined plastid phylograms for species of *Chloris* s.str. (see Fig. 2). Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; major clades are labeled A–D; abbreviation for species uses the first three letters; dashed lines indicate changed positions of species between and within clades; arrow indicates the *Chloris* clade; color indicates native distribution (see legend); scale bars = 2% (ITS) and 0.3% (plastid).

alignment appears to be congruent with geography (a clade of three accessions of *E. macrostachyus* from southern Africa and a clade of *E. barbatus* and two accessions of *E. macrostachyus* from east Africa; see Electr. Suppl.: Fig. S2). Traditional characters used to differentiate among the species of *Enteropogon*, such as leaf sheaths margins (glabrous versus hairy and strongly keeled versus not strongly keeled), callus hair length (<2 mm versus 3–4 mm), and lemma awn length (1–5 mm versus 10–18 mm) are inconsistent (Clayton, 1967). For instance, *E. macrostachyus* is characterized by having glabrous leaf sheaths that are not strongly keeled but *Oakes 1250* from South Africa has hairy sheaths that are strongly keeled like *E. sechellensis* (Renvoize, 1974a; Phillips, 1995) whereas *Smook 9026* and *Laegaard 15902* have glabrous sheaths.

We sampled four species traditionally treated in *Tetrapogon* and lack only *T. ferrugineus* (Renvoize) S.M.Phillips, known from Ethiopia, Kenya, and Somalia (Phillips, 1995). We have moderate support (85/1.00, Fig. 2B) for these four species previously included in *Tetrapogon* plus *Chloris roxburghiana*. *Tetrapogon* includes species with 2–5 fertile florets per spikelet whereas *Chloris* generally has a single fertile floret (Renvoize, 1974b; Phillips, 1995; Cope, 1999). *Chloris roxburghiana* has spikelets with a single perfect floret with 2 or 3 progressively smaller, reduced or sterile florets above but is unusual in *Chloris* in possessing 30–50 or more (1–3 in *Tetrapogon*), spikelike racemes, racemously inserted along a short axis (Anderson, 1974; Renvoize, 1974c). Sister to *Tetrapogon* (including *C. roxburghiana*) is a moderately supported clade with *Enteropogon brandegeei* and *E. chlorideus* (71/0.99; Fig. 2B). These two species have never been attributed to *Tetrapogon* but together have at one time been placed in seven other genera (*Chloris*, *Dinebra*, *Diplachne*, *Eutriana*, *Gouinia*, *Gymnopogon*, *Leptochloa*). It seems most parsimonious to recognize *E. brandegeei*, *E. chlorideus*, and *Saugetia fasciculata* (type) in a strongly supported (100/1.00) *Tetrapogon* s.l. Clayton & Renvoize (1986), who published a designation (invalid name) for *Enteropogon fasciculatus* and, never formally, made a combination for this or the sister species, *Saugetia pleiostachya* Hitchc. & Ekman (not sampled here), both of which are treated in *Enteropogon* in their online World Grass Flora (Clayton & al., 2006–) as forsan (“perhaps” in Latin). Similar to *Chloris roxburghiana*, *E. brandegeei*, *E. chlorideus*, *S. fasciculata*, and *S. pleiostachya* have spikelets with a single fertile floret and a single sterile floret (Hitchcock & Chase, 1917; Anderson, 1974). However, the inflorescences of *E. brandegeei* and *E. chlorideus* have 3–20 spike-like racemes, racemously to subverticillately arranged along the peduncle, whereas *S. fasciculata* and *S. pleiostachya* have a single raceme (Watson & Dallwitz, 1992; Clayton & al., 2006–). The alternative hypothesis would be to place *E. brandegeei* and *E. chlorideus* in a new genus and retain *Saugetia*.

We include the monotypic, *Daknopholis boivinii* for the first time in our analysis, which is strongly supported as sister to four species of *Lepturus*. This is surprising since no morphological characters suggest a link between these two genera. Clayton (1967) separated *Daknopholis boivinii* from *Chloris* by possessing a naked rachilla extension and suggested it was linked to *Cynodon* (Clayton & Renvoize, 1986). Clayton & al.

(2006) reconsidered and placed *D. boivinii* back in *Chloris*. Our results confirm that *D. boivinii* is not related to *Chloris* s.str. nor *Cynodon* but is sister to *Lepturus*.

***Brachyachne*, *Chrysochloa*, *Cynodon*, *Eustachys*, *Harpochloa*, *Micrachne*, *Microchloa*, *Oxychloris*, and *Stapfochloa*.**

— Within the *Microchloa* clade considerable genetic variation exists among individuals of each of the three species, as *M. altera* (Rendle) Stapf and *M. caffra* Nees appear in grades, and *M. kunthii* Desv. forms a clade with strongly supported substructure. Launert (1966) revised *Microchloa* because “specimens were often indiscriminately attributed to any of the described taxa”. Currently, six species are placed in *Microchloa* since *Rendlia altera* Rendle (= *Microchloa altera*) with 2 or 3-flowered spikelets (spikelets 1-flowered in *Microchloa* s.str.) was subsumed in *Microchloa* (Clayton, 1967; Clayton & Renvoize, 1986; Cope, 1999). *Harpochloa falx* is sister to our moderately supported *Microchloa* clade (85/1.00), differing from the latter genus by having shorter glumes not completely enclosing the florets (Cope, 1999). Clayton (1967) suggested that since *Harpochloa*, *Microchloa*, and *Rendlia* share many morphological similarities, the “three genera might well be united”. Our data clearly support this idea since these three taxa all lie in a moderately supported clade (76/1.00, Fig. 2C). Sister to the *Harpochloa-Microchloa* clade is an Australian endemic, *Oxychloris scariosa*, although this relationship is poorly supported. Clayton (1967), Lazarides (1972), and Anderson (1974) suggested the unique features, i.e., broadly winged fertile lemmas with a sharp, elongated callus and upper reduced sterile florets, of *Chloris scariosa* F.Muell. (= *Oxychloris scariosa*) might warrant generic status (Lazarides, 1985), which our results support.

Brachyachne fulva Stapf, *B. obtusifolia* (Benth.) C.E.Hubb., and *B. patentiflora* (Stent & J.M.Ratray) C.E.Hubb. form a strongly supported clade that we are describing as a new genus below since the type, *B. convergens* (F.Muell.) Stapf, lies within *Cynodon*. *Micrachne* gen. nov. differs from *Cynodon* in having golden brown to bronze spikelets (at least in herbarium specimens) bearing a rachilla extension and glumes that completely enclose the floret with the lower glume being slightly asymmetrical. Although not sampled in our study, we include a Zambia endemic, *B. simonii* Kupicha & Cope and *B. pilosa* Van der Veken from the Democratic Republic of the Congo in *Micrachne*, and provide a complete description of all five African species below (Van der Veken, 1958; Kupicha & Cope, 1985). Cope (1999) in the *Flora Zambesiaca* included a key to easily differentiate these four species (excluding *B. pilosa*).

We sampled 11 species of *Eustachys* and there is a strongly supported American clade (100/1.00, Fig. 2C) containing two separate subclades, each with a geographic component: (1) one comprising five species from North America (82/0.99) and (2) the other comprising four species from South America (73/0.94). The American *Eustachys* clade is sister to (in reverse order of divergence) the African *E. tenera* (J.Presl) A.Camus and the Australian *E. paspaloides* (Vahl) Lanza & Matte. Nash (1898) was one of the first agrostologists to treat *Eustachys* at the generic level rather than a subgenus of *Chloris*, recognizing the strongly flattened, folded, equitant leaf sheaths; bilobed

upper glumes with a short awn borne between the lobes; and fertile florets that are commonly pale to dark brown or black with awnless or short-awned lemmas (Anderson, 1974).

The strongly supported *Chrysochloa* clade, consisting of three species, is sister to the *Stapfochloa-Cynodon* clade (Fig. 2C). Even though *Chrysochloa annua* C.E.Hubb. has been placed as a synonym of *C. hindsii* C.E.Hubb. by Zon (1992) and Clayton & al. (2006), we retain these accessions as a different species since they are genetically variable, but either circumscription is consistent with our data.

The *Chloris ciliata* complex as recognized by Anderson (1974) included five species that have elliptic, ovate or lanceolate fertile lemmas with densely ciliate margins (usually along the entire length). As pointed out earlier by Anderson (1974), the African *Chloris lamproparia* (= *Stapfochloa lamproparia*) is the only Old World member of the *Chloris ciliata* complex. The observation of Scholz & Müller (2004) that “their [species included in the *Chloris ciliata* complex] striking resemblance with *C. lamproparia* in lemma form and indument is surely a result of parallel evolution and does not reflect close genetic relationship” is not supported by our tree (Fig. 2C). Anderson (1974) mentioned that the *Chloris ciliata* complex “presents more interspecific taxonomic problems than any other group”, which we confirm based on high genetic variability among individuals of *C. ciliata* and *C. elata*. *Stapfochloa* has priority, and we make the necessary new combinations for the American species and emend the generic description below.

In our tree three of the four species of *Brachyachne* (*B. ciliaris* (Kuntze) C.E.Hubb., *B. convergens*, *B. tenella* (R.Br.) C.E.Hubb.) that are embedded in *Cynodon* are endemic to Australia, whereas *B. ambigua* Ohwi is native to Java, Lesser Sunda Islands, and New Guinea (Nightingale & al., 2005a). Traditionally, *Brachyachne* was separated from *Cynodon* by having glumes that are longer than the floret (versus at least one glume shorter than the floret) and lemmas that are long hairy on the veins or all over (versus hairy or not only along the midvein; Nightingale & al., 2005a). Clearly this poorly supported clade (k) arose within *Cynodon*, the most derived clade in the Eleusininae. Few morphological differences separate the species in *Cynodon* s.l., and several species do not form monophyletic clades. For instance, *C. aethiopicus* Clayton & Harlan (*Smook 4140*) from South Africa is placed in an unresolved clade (clearly differentiated from a clade with three accessions of *C. aethiopicus*) with five other accessions of *C. nlemfuensis* Vanderyst from South Africa, United States, Costa Rica, and two from Ecuador. Morphological features used to differentiate *C. aethiopicus* from *C. nlemfuensis* are: lemma keel densely pubescent (former) versus glabrous or only with a few hairs (latter); plants robust, often woody and coarse, 60–100 cm tall versus plants fairly slender to robust, not woody, 30–60 cm tall (Gibbs Russell & al., 1991). Likewise, many species have been placed as synonyms or as varieties of *C. dactylon* (L.) Pers., such as *C. aristiglumis* Caro & E.A.Sánchez, *C. erectus* J.Presl, and *C. pascuus* Nees (Salariano & Zanotti, 2012), and these appear in a large clade at the base of the tree with *C. transvaalensis* Burt Davy, a morphologically distinct species with strong support (97/1.00; Fig. 2C). The species of *Cynodon* s.l.

appear to be undergoing rapid speciation since many morphological forms do not always segregate in a shared lineage. We agree with Cope (1999), who stated in the *Flora Zambesiaca*, “The taxonomy of *Cynodon* is the most difficult problem among southern African Cynodonteae.”

Chloris. — In the plastid tree *Ochthochloa compressa* is sister to the remaining species of *Chloris*. This species was initially described in *Panicum* L. by Forsskål (1775), transferred to *Eleusine* by Ascherson & Schweinfurth (1922) before being placed in a monotypic genus by Hilu (1981). Even though *O. compressa* has 3–6 fertile florets per spikelet (versus 1 or 2 fertile florets in *Chloris*) and caryopses with free pericarps (occasionally found in *Chloris*) we place this enigmatic taxon in *Chloris* and make the new combination below. Likewise, *Lintonia nutans* has never been associated with *Chloris* but it is clearly a member in our ITS and plastid tree (Fig. 3). *Lintonia nutans* has 2–5 fertile florets per spikelet with 5–11-veined (confluent at the base), cartilaginous lemmas (versus 3-veined and membranous to cartilaginous) with clavicorniculate hairs and dorsally flattened caryopses with free pericarps (versus usually subterete or trigonous caryopses; Watson & Dallwitz, 1992). Clavicorniculate lemmatal hairs have arisen twice in the Eleusininae since they appear in *Lintonia* and *Disakisperma*.

The major phylogenetic problem in *Chloris*, however, is the presence of the C-D clade in the ITS tree that encompasses species representing two distant plastid lineages. The most probable scenario underlying the formation of the C-D clade in the ITS tree could be ancient hybridization between the lineages in the early stages of speciation with subsequent alternation and homogenization of the ITS signal.

The subgeneric classification of *Chloris* by Varadarajan & Gilmartin (1983a, b) based on phenetic and cladistic analyses of morphological features does not coincide with our work. Their *Chloris* subg. *Phacalaria* (Steud.) Varadarajan & Gilmartin included species we place in *Leptochloa*, *Micrachne*, and *Stapfochloa* (Peterson & al., 2012) and their *Chloris* subg. *Chloris* includes species we place in *Tetrapogon* (Peterson & al., 2012). Within *Chloris* we found four separate strongly supported clades in the ITS tree (A–D, Fig. 3), which correspond to four clades in the plastid tree, two of which are strongly supported (A and C), one is moderately supported (D), and one is poorly supported (B, PP = 0.69).

Clades A and C contain species in the *Chloris inflata* Link complex (= *C. barbata*, see Kartesz & Gandhi, 1992), where most species have single-celled microhairs, *Chloris*-type silica cells (cuboidal to saddle-shaped), and fertile lemmas with a tuft of hairs on the upper margins (Anderson, 1974). *Chloris prieurii*, which is sister to *C. barbata* in clade A (ITS and plastid tree), and *C. orthonoton*, which is included in clade C (plastid tree only), lacks a tuft of hairs on the upper margins of the fertile lemma but instead has a row of clavate glandular hairs along the sides of the lemma (Anderson, 1974). *Chloris rufescens* (attributed by Anderson to the *C. verticillata* complex) also occurs in the plastid tree only and it has been indicated as a close relative of *C. orthonoton* but differs in having short-ciliate less than 1 mm long ligules (versus long ciliate, about

2 mm long), shorter hairs along the lemma margins (versus hairs >1.5 mm), and lemmas without clavate glandular hairs (Anderson, 1974).

Clade B (Fig. 3) contains *Chloris amethystea*, *C. andropogonoides*, *C. cucullata*, *C. latisquamea*, *C. × subdolichostachya*, *C. verticillata*, and *C. mossambicensis*, although two individuals of the latter species are sister to *Lintonia nutans* in the ITS tree, suggesting a past hybridization event. Anderson (1974, 1975) referred to most members of this clade as the *C. verticillata* complex and suggested that *C. andropogonoides*, *C. cucullata*, *C. verticillata*, and *C. × subdolichostachya*, form a hybridization complex that “seem to blend and recombine in various ways”. Anderson (1974) found that the lemmatal awn length and the sterile lemma width are best to differentiate among the three former (see preceding sentence) species while the latter taxon is perhaps a hybrid of *C. cucullata* crossed with *C. verticillata* or *C. andropogonoides* (Brown, 1969).

Anderson (1974) included *Chloris cubensis*, *C. ekmanii*, *C. halophila*, and *C. sagraeana* in his *C. radiata* (L.) Sw. complex, all of which appear in clade D in both the ITS and plastid trees (Fig. 3). These species have comparatively narrow spikelets, reduced sterile florets, and relatively long-awned lemmas (Anderson, 1974). In addition to these core species our trees include *C. cruciata* (mentioned by Anderson as having similar overall spikelet structure to the *C. radiata* complex), *C. divaricata*, *C. pectinata*, *C. pycnothrix*, *C. submutica*, and *C. texana*. *Chloris texana* is a possible hybrid (listed as a synonym of what we now call *Stapfochloa ciliata* ≡ *C. ciliata*; Anderson, 1974; Soreng & al., 2014). In the ITS tree, *C. texana* is found in a weakly supported clade with *C. halophila*, *C. orthonoton*, and *C. rufescens* and then is an unresolved member in a poorly supported *C. pycnothrix* clade in the plastid tree, possibly indicating hybridization.

■ TAXONOMY

Because our molecular analysis renders *Chloris* s.l. and *Brachyachne* polyphyletic, we describe a new genus, *Micrachne*, found in a separate, strongly supported clade with five species and emend *Stapfochloa* to include six species. In addition, we provide new combinations in *Chloris* (2), *Cynodon* (2), *Diplachne* (1), *Leptochloa* (2), *Micrachne* (5), *Stapfochloa* (5), and *Tetrapogon* (5); provide a new name in *Cynodon*; and lectotypify *Eleusine flagellifera*.

Chloris flagellifera (Nees) P.M.Peterson, **comb. nov.** ≡ *Eleusine flagellifera* Nees in *Linnaea* 16(2): 220. 1842 – **Lectotype (designated here):** SAUDI ARABIA. In planitie deserti prope Dscheddam, 10 Jan 1836, *W. Schimper 800* (US No. 3298791!; isoelectotypes: REG barcode 000227 [image!], US Nos. 88428! & 1535370!).

= *Panicum compressum* Forssk., *Fl. Aegypt.-Arab.*: 18. 1775 ≡ *Eleusine compressa* (Forssk.) Asch. & Schweinf. ex C. Chr. in *Dansk Bot. Ark.* 4(3): 12. 1922 ≡ *Ochthochloa compressa* (Forssk.) Hilu in *Kew Bull.* 36(3): 560. 1981, non *Chloris compressa* DC., *Cat. Pl. Horti Monsp.*: 94. 1813.

Chloris nutans (Stapf) P.M.Peterson, **comb. nov.** ≡ *Lintonia nutans* Stapf in *Hooker's Icon. Pl.* 30: t. 2949. 1911 – Holotype: KENYA. Nairobi, *A. Linton 193* (K barcode K000365107 [image!]).

Cynodon ambiguus (Ohwi) P.M.Peterson, **comb. nov.** ≡ *Brachyachne ambigua* Ohwi in *Bull. Tokyo Sci. Mus.* 18: 11. 1947 – Holotype: JAVA. Gersik, E Java, on low rocky hill, Dec 1924, *J.D. Dorzelo 3169* (BO; isotype: L).

Cynodon prostratus (C.A.Gardner & C.E.Hubb.) P.M.Peterson, **comb. nov.** ≡ *Brachyachne prostrata* C.A.Gardner & C.E. Hubb. in *Hooker's Icon. Pl.* 34: t. 3362. 1938 – Holotype: AUSTRALIA. Western Australia, Ereman Prov., 1 mi N of Meekatharra, 2 Aug 1927, *C.A. Gardner s.n.* (PERTH; isotypes: K barcodes K000885870 & K000885871 [images!]).

Cynodon simonii P.M.Peterson, **nom. nov.** ≡ *Cynodon ciliaris* Benth., *Fl. Austral.* 7: 610. 1878, non (L.) Raspail in *Ann. Sci. Nat., Bot.* 5: 302. 1825 ≡ *Capriola ciliaris* Kuntze, *Revis. Gen. Pl.* 2: 764. 1891 ≡ *Microchloa ciliaris* (Kuntze) Domin in *Biblioth. Bot.* 85: 364. 1915 ≡ *Brachyachne ciliaris* (Kuntze) C.E.Hubb. in *Bull. Misc. Inform. Kew* 1934: 448. 1934 – Holotype: AUSTRALIA. Northern Territory, central Australia, Charlotte Waters, *W.E.P. Giles s.n.* (K barcode K000885872 [image!]; isotype: MEL).

Etymology. – Named in honor of Bryan Kenneth Simon (1943–2014), an outstanding Australian agrostologist.

Diplachne divaricatissima (S.T.Blake) P.M.Peterson, **comb. nov.** ≡ *Leptochloa divaricatissima* S.T.Blake in *Contr. Queensland Herb.* 14: 8, fig. 5. 1972 ≡ *Dinebra divaricatissima* (S.T.Blake) P.M.Peterson & N.Snow in *Phytoneuron* 2012-71: 1. 2012 – Holotype: AUSTRALIA. Queensland, Goondiwindi, *S.T. Blake 10517* (BRI No. 131665-6; isotypes: CANB, K barcodes K000899894 & K000899895 [images!], MO, NSW, PRE).

Leptochloa anisopoda (Scribn. ex B.L.Rob.) P.M.Peterson, **comb. nov.** ≡ *Chloris anisopoda* Scribn. ex B.L.Rob. in *Proc. Amer. Acad. Arts* 38: 118. 1902 – Lectotype (designated by Hitchcock in *N. Amer. Fl.* 17: 596. 1939): ECUADOR. Galapagos Islands, Charles (Santa Maria) Island, Jun 1891, *G. Baur 333* (GH barcode GH00023358 [image!]; isoelectotype: US No. 2830885! fragm.)

= *Gymnopogon mollis* Nees in *Martius & al., Fl. Bras. Enum. Pl.* 2(1): 427. 1829 ≡ *Chloris mollis* (Nees) Swallen in *N. Amer. Fl.* 17: 596. 1939 ≡ *Enteropogon mollis* (Nees) Clayton in *Kew Bull.* 37: 419. 1982, non *Leptochloa mollis* Kunth, *Révis. Gramin.* 2: 443, t. 135. 1831.

= *Gymnopogon rupestris* Ridl. in *J. Linn. Soc., Bot.* 27: 73. 1890. ≡ *Chloris rupestris* (Ridl.) Hitchc., *Man. Grasses W. Ind.*: 126. 1936, non *Leptochloa rupestris* C.E.Hubb. in *Bull. Misc. Inform. Kew* 1941(2): 195–196. 1941.

Leptochloa exilis (Renvoize) P.M.Peterson, **comb. nov.** ≡ *Chloris exilis* Renvoize in *Kew Bull.* 37(2): 323, fig. 2.

1982 – Holotype: BRAZIL. 49 km N of Senhor do Bonfim on BA Hwy 130 to Juazeiro, W 40°13' S 10°05', 500 m, 26 Feb 1974, R.M. Harley 16363, Renvoize, Erskine, Brighton & Pinheiro (CEPEC; isotypes: K barcode K000003260 [image!], US No. 2955111!).

Micrachne P.M.Peterson, Romasch. & Y.Herrera, **gen. nov.**
– Type: *Micrachne fulva* (Stapf) P.M.Peterson (≡ *Brachyachne fulva* Stapf).

Diagnosis. – *Micrachne* differs from *Cynodon* sect. *Brachyachne* Benth. in having golden brown to bronze spikelets (at least in herbarium specimens) bearing a rachilla extension, glumes that completely enclose the floret, and the lower glume being slightly asymmetrical.

Description. – Plants perennial, occasionally annual, caespitose to geniculately ascending to erect. Culms 10–60(–70) cm tall. Leaf sheaths glabrous above, occasionally densely pilose below, often forming a cushion of fibers near base; ligule a short ciliate membrane; blades 0.5–15(–25) cm long, 0.5–3 mm wide, flat or involute, glabrous or sparsely hairy, strait or recurved, occasionally setaceous and rigid. Inflorescences paniculate usually with a single terminal spikelike branch or sometimes with (2–)3–5(–7) digitately inserted branches; the 1-sided spikelike branches 1.5–12 cm long, erect or somewhat curved and bearing imbricate spikelets. Spikelets 1-flowered, laterally compressed, golden brown to bronze (at least in herbarium specimens), the single fertile floret bearing a rachilla extension; glumes 2–5.3 mm long, longer than the floret, 1-veined, chartaceous to thinly coriaceous, glabrous or sparsely hairy, completely enclosing the floret, the lower glume slightly asymmetrical, apex obtuse to acute; lemmas 1.6–4 mm long, 3-veined, hyaline to membranous, delicate, oblong-elliptic, ovate to oblong-lanceolate, folded along the midvein, hairy along the midvein and marginal veins, apex obtuse to truncate or slightly emarginated, often short mucronate; paleas a little shorter than the lemmas, hairy or glabrous along the veins; stamens 3, anthers 0.8–2.3 mm long. Caryopses ellipsoid.

Distribution and habitat. – The five species are distributed in central and eastern Africa, often on rock outcrops with thin soils, sandy washes, laterite pans to open woodlands; 700–2130 m.

Micrachne fulva (Stapf) P.M.Peterson, **comb. nov.** ≡ *Brachyachne fulva* Stapf in Hooker's Icon. Pl. 31: t. 3099. 1922 – Holotype: ZAIRE. Katanga, *Homble 21* (K barcode K000365033 [image!]; isotypes: BR barcodes BR0000008756374 & BR0000008756411 [images!]).

Micrachne obtusiflora (Benth.) P.M.Peterson, **comb. nov.** ≡ *Microchloa obtusiflora* Benth., Niger Fl.: 565. 1849 ≡ *Brachyachne obtusiflora* (Benth.) C.E.Hubb. in Bull. Misc. Inform. Kew 1933: 503. 1933 – Holotype: NIGERIA. *Vogel 189* (K barcode K000365032 [image!]).

Micrachne patentiflora (Stent & J.M.Ratray) P.M.Peterson, **comb. nov.** ≡ *Microchloa patentiflora* Stent & J.M.Ratray in Proc. & Trans. Rhodesia Sci. Assoc. 32: 59. 1933 ≡

Brachyachne patentiflora (Stent & J.M.Ratray) C.E.Hubb. in Bull. Misc. Inform. Kew 1933: 503. 1933 – Holotype: ZIMBABWE. Harare, Dec 1919, F. Eyles 1955 (BM; isotypes: EA barcode EA000000464 [image!], K barcodes K000365039, K000365040 & K000365041 [images!], PRE barcode PRE0664092-0 [image!], SRGH barcode SRGH0106276 [image!]).

Micrachne pilosa (Van der Veken) P.M.Peterson, **comb. nov.** ≡ *Microchloa pilosa* Van der Veken in Bull. Jard. Bot. État. Bruxelles 24(1): 84. 1958 – Holotype: DEMOCRATIC REPUBLIC OF THE CONGO. District de Haut-Katanga, Parc National de l'Upemba, region de Kanongo, petit ruisseau tributaire de la riv. Lukanga, sur larges dalles de laterite, Feb 1949, *Van Meel in de G.F. Witte 5458* (BR barcode BR0000008756367 [image!]; isotype K barcode K000365034 [image!]).

Micrachne simonii (Kupicha & Cope) P.M.Peterson, **comb. nov.** ≡ *Brachyachne simonii* Kupicha & Cope in Kew Bull. 40(1): 89. 1985 – Holotype: ZAMBIA. 3 km E of Chizela, 27 Dec 1969, B.K. Simon & Williamson 2068 (K barcode K000365038 [image!]; isotypes: BM, BR barcode BR0000005628681 [image!], MO No. 2154714-1660917 [image!], PRE barcodes PRE0592099-0 & PRE0664091-0 [images!], SRGH).

Stapfochloa H.Scholz – Type: *Stapfochloa lamproparia* (Stapf) H.Scholz (≡ *Chloris lamproparia* Stapf).

Diagnosis. – *Stapfochloa* differs from *Chloris* in having elliptic, ovate or lanceolate fertile lemmas with lemma margins that are densely ciliate, usually along the entire length.

Description. – Plants perennial, occasionally annual, caespitose, rhizomatous or stoloniferous. Culms 5–80 cm tall. Leaf sheaths glabrous; ligule a short ciliate crown or lacking; blades 1–28 cm long, 1–8 mm wide, flat or folded, glabrous to pilose. Inflorescences paniculate with 1–12(–28) terminal spikelike branches, usually digitately or subdigitately inserted; the spikelike branches 3–20 cm long, erect to widely spreading and bearing spikelets in two rows on one side of the branch. Spikelets with 1 basal fertile floret with 2 or 3 reduced, sterile florets above; fertile lemmas 1.3–4.2 mm long, 0.5–1.7 mm wide, elliptic, ovate or lanceolate, with a single apical or subapical awn 1.4–6 mm long, the keel and margins with spreading ciliate hairs usually along the entire length, the hairs 0.5–3 mm long. Caryopses 1–2 mm wide, 0.5–1 mm wide, ovoid to ellipsoid to trigonous.

Distribution and habitat. – Five species are distributed in the New World and a single species, *S. lamproparia*, is native to Africa. Plants occur in open grasslands to wet savannahs, often on rocky slopes.

Stapfochloa berroi (Arechav.) P.M.Peterson, **comb. nov.** ≡ *Chloris berroi* Arechav. in Anales Mus. Nac. Montevideo 1: 388, t. 44. 1896 – Holotype: URUGUAY. Dept. Soriano, Estancia Vera, 5 Jan 1895, M.B. Berro 962 (MVFA barcode MVFA0000272 [image!]; isotypes: BAA No. 655-00001714

[image!], CORD No. 879335, K barcode K000308975 [image!], W No. 19160034138 [image!]).

Stapfochloa canterae (Arechav.) P.M.Peterson, **comb. nov.** ≡ *Chloris canterae* Arechav. in *Anales Mus. Nac. Montevideo* 1: 385. 1896 – Lectotype (designated by Rosengurt & Izaguirre in *Bol. Soc. Argent. Bot.* 12: 124. 1968): URUGUAY. Paysandú, *J. Arechavaleta s.n.* (MVM; isolectotypes: BAA barcode BAA00001717 [image!], CORD barcode CORD00001558 [image!], US No. 879336! fragm. ex MVM).

Stapfochloa ciliata (Sw.) P.M.Peterson, **comb. nov.** ≡ *Chloris ciliata* Sw., *Prodr.*: 25. 1788 ≡ *Cynodon ciliatus* (Sw.) Raspail in *Ann. Sci. Nat. (Paris)* 5: 303. 1825 – Holotype: JAMAICA. *O.P. Swartz s.n.* (S No. 06-646 [image!]; isolectotypes: BAA No. 661-00001719 [image!], US No. 80821! fragm. ex S).

Stapfochloa elata (Desv.) P.M.Peterson, **comb. nov.** ≡ *Chloris elata* Desv. in *Mém. Soc. Agric. Angers* 1: 177. 1831 – Holotype: BRAZIL. *s.coll., s.n.* (P).
= *Chloris dandyana* C.D.Adams in *Phytologia* 21: 408. 1971.

Stapfochloa lamproparia (Stapf) H.Scholz in *Willdenowia* 34: 131, fig. 1–2. 2004 ≡ *Chloris lamproparia* Stapf in *Mém. Soc. Bot. France* 2, mém. 8: 220. 1912 – Holotype: CHAD. Baguirmi, emplacement de la ville de Massenia, Aug 1903, *A.J.B. Chevalier 9633 bis* (P barcode P00439460 [image!]; isotype: K barcode K000365096 [image!]).

Stapfochloa parvispicula (Caro & E.A.Sánchez) P.M.Peterson, **comb. nov.** ≡ *Chloris parvispicula* Caro & E.A.Sánchez in *Kurtziana* 6: 227, fig. 3. 1971 – Holotype: ARGENTINA. La Rioja, Los Llanos, Los Cerrillos, 15 Feb 1940, *A. Castellanos s.n.* (BAA No. 33416-00000082 [image!]; isotype: LIL No. 42941-000028 [image!]).

Tetrapogon brandegeei (Vasey) P.M.Peterson, **comb. nov.** ≡ *Diplachne brandegeei* Vasey in *Proc. Calif. Acad. Sci.*, ser. 2: 213. 1889 (“*brandegei*”) ≡ *Gouinia brandegeei* (Vasey) Hitchc. in *Bull. Bur. Pl. Industr. U.S.D.A.* 33: 21. 1903 (“*brandegei*”) ≡ *Leptochloa brandegeei* (Vasey) Hitchc. in *Bull. Bur. Pl. Industr. U.S.D.A.* 33: 21. 1903 (“*brandegei*”) ≡ *Chloris brandegeei* (Vasey) Swallen in *Amer. J. Bot.* 22: 41. 1935 (“*brandegei*”) ≡ *Enteropogon brandegeei* (Vasey) Clayton in *Kew Bull.* 37: 419. 1982 (“*brandegei*”) – Lectotype (designated by Hitchcock in *Contr. U.S. Natl. Herb.* 17: 352. 1913): MEXICO. Baja California Sur, Magdalena Island, 18 Jan 1889, *T.S. Brandegee II* (US No. 78812!).
Etymology. – Originally named by Vasey to honor Townshend Stith Brandegee (1843–1925) and is therefore to be spelled “*brandegeei*” as per Art. 60.12 and Rec. 60C.1(a).

Tetrapogon chloridea (J.Presl) P.M.Peterson, **comb. nov.** ≡ *Dinebra chloridea* J.Presl in *C. Presl, Reliq. Haenk.* 1(4–5): 291. 1830 ≡ *Eutriana chloridea* (J.Presl) Kunth, *Enum.*

Pl. 1: 280. 1833 ≡ *Chloris chloridea* (J.Presl) Hitchc. in *Proc. Biol. Soc. Wash.* 41: 162. 1928 ≡ *Enteropogon chlorideus* (J.Presl) Clayton in *Kew Bull.* 37: 419. 1982 – Holotype: MEXICO. *Haenke s.n.* (PR; isotypes: MO, US No. 865870!).

Tetrapogon fasciculatus (Hitchc. & Chase) P.M.Peterson, **comb. nov.** ≡ *Saugetia fasciculata* Hitchc. & Chase in *Contr. U.S. Natl. Herb.* 18(7): 378. 1917 – Holotype: CUBA. Pinar del Río, in small wood savanna San Julián, S of Guane, 28 Dec 1916, *Leon 6901 & M. Roca* (US No. 950204!; isotypes: BAA barcode BAA00002812 [image!], NY barcode 00071123 [image!]).

Tetrapogon pleiostachyus (Hitchc. & Ekman) P.M.Peterson, **comb. nov.** ≡ *Saugetia pleiostachya* Hitchc. & Ekman in *Hitchcock, Man. Grasses W. Ind.*: 123. 1936 – Holotype: CUBA. Prov. Pinar del Río, Mendoza Municipio, Cerro de Mendoza, 26 Jun 1920, *E.L. Ekman 11483* (US No. 1296127!; isotype: NY barcode 00071124).

Tetrapogon roxburghiana (Schult.) P.M.Peterson, **comb. nov.** ≡ *Chloris roxburghiana* Schult., *Mant.* 2: 339. 1824 ≡ *Chloris polystachya* Roxb., *Fl. Ind.* 1: 332. 1820, nom. illeg., non Lag., *Gen. Sp. Pl.* 4. 1816 – Holotype: INDIA. Based on a fairly complete description and Roxburgh painting (K No. 2023).

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Appendix 1. List of specimens sampled.

Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rpl32-trnL*, *ndhA*, *rps16*, *rps16-trnK* and ITS regions (**bold** indicates new accession); a dash (–) indicates missing data; an asterisk (*) indicates sequences not generated in our lab.

OUTGROUP: *Aristida gypsophila* Beetle, *Peterson 15839 & Valdes-Reyna* (US), Mexico, GU359977, GU359386, GU360286, GU360570, GU359267; *Chasmanthium latifolium* (Michx.) H.O.Yates, *Peterson 22463* (US), U.S.A., GU359891, GU359379, GU360438, GU360517, GU359319; *Danthonia compressa* Austin, *Peterson 21986 & Levine* (US), U.S.A., GU359865, GU359370, GU360483, GU360521, GU359345; *Capeochloa cincta* subsp. *sericea* (N.P.Barker) N.P.Barker & H.P.Linder, *Barker 1545* (GRA), South Africa, JF729173, JF729163, JF729181, JF729074, –, *Rytidosperma pallidum* (R.Br.) A.M.Humphreys & H.P.Linder, *Peterson 19685, Saarela & Sears* (US), U.S.A., GU359984, GU359518, GU360291, GU360671, GU359183; **CENTROPODIEAE:** *Ellisochloa rangei* (Pilg.) P.M.Peterson & N.P.Barker, *Barker 960* (BOL), Namibia, –, JF729166, JF729184, JF729079, JQ345167; **TRIRAPHIDEAE:** *Neyraudia reynaudiana* (Kunth) Keng ex Hitchcock, *Soreng 5318, Peterson & Sun Hang* (US), China, GU360003, GU359397, GU360272, –, GU359124; *Triraphis ramosissima* Hack., *Seydel 4278* (US), South Africa, GU359931, GU359541, GU360338, GU360651, GU359188; **ERAGROSTIDEAE:** *Cottea pappophoroides* Kunth, *Peterson 21463, Soreng, LaTorre & Rojas Fox* (US), Peru, GU359842, GU359363, GU360456, GU360600, GU359237; *Ectrosia scabrada* C.E.Hubb., *Lazarides 4772* (US), Australia, GU359799, GU359476, GU360459, GU360497, GU359317; *Enneapogon desvauxii* P.Beauv., *Peterson 21999 & Saarela* (US), Mexico, GU359796, GU359474, GU360486, GU360495, GU359339; *Entoplocamia aristulata* (Hack. & Rendle) Stapf, *Seydel 187* (US), South Africa, GU359793, GU359469, GU360468, GU360492, GU359342; *Eragrostis desertorum* Domin, *Peterson 14358, Soreng & Rosenberg* (US), Australia, GU359787, GU359471, GU360462, GU360545, GU359289; *Eragrostis nigricans* (Kunth) Steud., *Peterson 21623, Soreng, LaTorre & Rojas Fox* (US), Peru, GU359790, GU359491, GU360398, GU360520, GU359299; *Harpachne harpachnoides* (Hack.) B.S.Sun & S.Wang, *Soreng 5288, Peterson & Sun Hang* (US), China, GU359815, GU359435, GU360382, GU360611, GU359113; *Psammagrostis wiseana* C.A.Gardner & C.E.Hubb., *Peterson 14345, Soreng & Rosenberg* (US), Australia, GU359986, GU359533, GU360288, GU360703, GU359137; *Tetrachne dregei* Nees, *Jarman 120* (US), South Africa, GU359904, GU359513, GU360365, GU360622, GU359218; *Uniola condensata* Hitchc., *Peterson 9342 & Judziewicz* (US), Ecuador, GU359927, GU359534, GU360340, GU360649, GU359191; *Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., *Hatch 5738 & Bearden* (US), U.S.A., GU359880, GU359357, GU360441, GU360548, GU359300; *Crypsis aculeata* (L.) Aiton, *Soreng 7940, Johnson, Johnson, Dzyubenko, Dzyubenko & Schilnikov* (US), Russia, JQ345316, JQ345205, JQ345275, JQ345233, JQ345163; *Spartina densiflora* Brongn., *Peterson 19154, Soreng, Salariato & Panizza* (US), Argentina, GU359916, GU359510, GU360352, JQ345271, GU359206; *Sporobolus indicus* (L.) R.Br., *Peterson 22025 & Saarela* (US), Mexico, GU359913, GU359504, GU360355, GU360630, GU359209; *Sporobolus lasiophyllus* Pilg., *Peterson 21879, Soreng & Sanchez Vega* (US), Peru, GU359912, GU359505, GU360356, GU360629, GU359210; *Sporobolus virginicus* (L.) Kunth, *Peterson 15683 & Soreng* (US), Chile, GU359892, GU359502, GU360362, GU360610, GU359215; *Zoysia macrantha* subsp. *walshii* M.E.Nightingale, *Loch 435* (US), Australia, GU359922, GU359548, GU360345, GU360642, GU359197; **CYNODONTEAE:** **Tripogoninae:** *Tripogon multiflorus* Miré & H.Gillet,

Appendix 1. Continued.

Spellenberg 7441 (MO), Yemen, JQ345360, JQ345232, JQ345315, JQ345274, JQ345204; *Tripogon trifidus* Munro ex Hook.f., *Laegaard 21668 & Norsangri* (MO), Thailand, **KP873641**, **KP873957**, **KP874094**, **KP873822**, **KP873422**; *Eragrostiella leioptera* (Stapf) Bor, *Chand 7961* (US), India, GU359827, GU359486, JQ345280, GU360529, GU359305; *Oropetium capense* Stapf, *Venter 9939 & Venter* (MO), South Africa, KM010692, KM010533, KM010917, KM011120, KM010324; *Melanocenchris abyssinica* (R.Br. ex Fresen.) Hochst., *DeWilde 6912* (MO), Ethiopia, JQ345355, JQ345228, JQ345310, JQ345268, JQ345198; *Desmostachya bipinnata* (L.) Stapf, *Dwyer 13120* (MO), Saudi Arabia, JQ345319, JQ345207, JQ345277, JQ345235, JQ345165; **CYNODONTEAE: Pappophorinae: Neesiochloa barbata** (Nees) Pilg., *Swallen 4491* (US), Brazil, GU360005, –, GU360279, GU360724, GU359122; *Pappophorum pappiferum* (Lam.) Kuntze, *Peterson 21689*, *Soreng*, *La Torre & Rojas Fox* (US), Peru, GU359996, GU359402, GU360276, GU360700, GU359128; *Tridens flavus* var. *chapmanii* (Small) Shinnars, *McCauley 438* (MO), U.S.A., KF827689, KF827615, KF827751, KF827817, KF827568; **CYNODONTEAE: Traginae: Monechrym luederitzianum** Hack., *Smook 10031* (US), South Africa, GU359969, GU359459, GU360421, GU360682, GU359158; *Tragus berteronianus* Schult., *FLSP 457* (US), Peru, GU359898, GU359503, GU360370, GU360616, GU359224; *Willkommia sarmentosa* Hack., *Schweickerdt 2181* (US), South Africa, GU359924, GU359545, GU360343, GU360645, GU359194; **CYNODONTEAE: Scleropogoninae: Blepharidachne benthamiana** (Hack.) Hitchc., *Melix 570 & Cherobini* (US), Argentina, GU359857, –, –, GU360579, GU359275; *Scleropogon brevifolius* Phil., *Peterson 19280*, *Soreng*, *Salariato & Panizza* (US), Argentina, GU359919, GU359530, –, GU360635, GU359203; **CYNODONTEAE: Hilarinae: Hilaria cenchroides** Kunth, *Peterson 22339 & Saarela* (US), Mexico, GU359813, GU359424, GU360380, GU360697, GU359143; *Pleuraphis rigida* Thurber, *Boyd 11566* (BRY), U.S.A., JQ345356, JQ345229, JQ345311, JQ345269, JQ345200; **CYNODONTEAE: Monanthochloinae: Distichlis eludens** (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Peterson 24864 & Romaschenko* (US), Mexico, **KP873561**, –, –, **KP873345**; *Distichlis eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Reeder 6430 & Reeder* (US), Mexico, JQ345320, –, GU360290, GU360701, GU359139; *Distichlis humilis* Phil., *Peterson 19362*, *Soreng*, *Salariato & Panizza* (US), Argentina, GU359835, GU359430, GU360478, GU360502, GU359333; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Moran 10570* (US), Mexico, GU359970, GU359460, GU360422, GU360699, GU359157; **CYNODONTEAE: Boutelouinae: Bouteloua simplex** Lag., *Peterson 21289*, *Saarela & Flores Villegas* (US), Mexico, GU359834, GU359406, GU360297, GU360607, GU359231; **CYNODONTEAE: Muhlenbergiinae: Muhlenbergia japonica** Steud., *Soreng 5301*, *Peterson & Sun Hang* (US), China, HM143184, HM143389, HM143572, HM143668, HM143082; *Muhlenbergia schreberi* J.F.Gmel., *Peterson 19443*, *Soreng*, *Salariato & Panizza* (US), Argentina, GU359950, GU359456, GU360404, GU360679, GU359161; **CYNODONTEAE: Aeluropodinae: Aeluropus lagopoides** (L.) Trin. ex Thwaites, *Weinert s.n. & Mosawi* (US), Iraq, GU360013, GU359391, GU360284, GU360576, GU359261; *Aeluropus littoralis* (Gouan) Parl., *Ferguson 634* (US), Greece, GU360018, GU359390, GU360308, GU360575, GU359262; *Aeluropus pungens* (M.Bieb.) K.Koch, *Yunatov 124*, *Li Shyin & Yuan Y-fen* (US), China, GU360014, GU360389, GU359319, GU360574, GU359263; **CYNODONTEAE: Triodiinae: Triodia intermedia** Cheel, *Peterson 14384*, *Soreng & Rosenberg* (US), Australia, GU359941, GU359563, GU360327, GU360661, GU359179; **CYNODONTEAE: Orcuttiinae: Orcuttia tenuis** Hitchc., *Stone 771* (US), U.S.A., GU360001, GU359398, GU360271, GU360727, JQ345199; *Tuctoria greenii* (Vasey) Reeder, *Reeder 6656 & Reeder* (US), U.S.A., GU359928, –, –, GU359190; **CYNODONTEAE: Gouiniinae: Gouinia paraguayensis** (Kuntze) Parodi, *Peterson 11526 & Annable* (US), Argentina, GU359817, GU359437, GU360584, GU360504, GU359314; *Triplasis purpurea* (Walter) Chapm., *Peterson 14238*, *Weakley & LeBlond* (US), U.S.A., GU359921, GU359536, GU360347, GU360656, GU359184; *Vaseyochloa multinervis* (Vasey) Hitchc., *Swallen 10041* (US), U.S.A., GU359925, GU359544, GU360342, GU360646, GU359193; **CYNODONTEAE: Cteniinae: Ctenium brevispicatum** J.G.Sm., *Filgueiras 3251 & Oliviera* (US), Brazil, JQ345317, JQ345206, JQ345276, JQ345234, JQ345164; **CYNODONTEAE: Trichoneurinae: Trichoneura eleusinoides** (Rendle) Ekman, *Seydel 448* (US), South Africa, GU359988, GU359522, GU360277, GU360705, GU359135; **CYNODONTEAE: Farragoinae: Craspedorhachis rhodesiana** Rendle, *Strohbach 5699* (US), Namibia, KF827623, KF827574, KF827696, KF827760, KF827504; *Farrago racemosa* Clayton, *Peterson 23851*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, KF827634, KF827582, KF827706, KF827772, KF827516; **CYNODONTEAE: Perotidinae: Mosdenia leptostachys** (Ficalho & Hiern) Clayton, *Schweickerdt 1542* (US), South Africa, GU359967, GU359458, GU360420, GU360681, GU359159; *Perotis arenacea* (Judz.) P.M.Peterson, *Phillipson 4117 & Raharilala* (MO), Madagascar, JQ345358, –, JQ345313, JQ345272, JQ345202; *Perotis hordeiformis* Nees, *Soreng 5717*, *Peterson & Sun Hang* (US), China, GU359991, GU359520, GU360283, GU360708, GU359132; *Trigonochloa uniflora* (Hochst. ex A.Rich.) P.M.Peterson & N.Snow, *Greenway 14075* (MO), Tanzania, JQ345347, –, –, JQ345261, –, *Trigonochloa uniflora* (Hochst. ex A.Rich.) P.M.Peterson & N.Snow, *Snow 6978*, *Burgoyne & Gumbi* (MO), South Africa, JQ345348, –, –, JQ345192; **CYNODONTEAE: Gymnopogoninae: Bewisia biflora** (Hack.) Gooss., *Peterson 23905*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, KF827617, KF827570, KF827692, KF827754, KF827498; *Dignathia hirtella* Stapf, *McCallum-Webster 5251* (US), Kenya, –, GU359368, GU360481, GU360490, GU359316; *Gymnopogon grandiflorus* Roseng., B.R.Arrill. & Izag., *Peterson 16642 & Refulio-Rodriguez* (US), Peru, GU359816, GU359436, GU360383, GU360581, GU359200; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Mboya 565* (MO), Tanzania, KF827658, KF827593, KF827723, KF827790, KF827537; *Leptothrium rigidum* Kunth, *Davidse 3281* (MO), Jamaica, KF827662, KF827596, KF827727, KF827794, KF827541; *Lophacme digitata* Stapf, *Smook 1453* (MO), South Africa, JQ345309, JQ345267, JQ345197; **CYNODONTEAE: Eleusininae: Acrachne racemosa** (B.Heyne ex Roem. & Schult.) Ohwi, *Jackson 1408* (US), Malawi, **KP873423**, **KP873823**, –, –, **KP873206**; *Acrachne racemosa* (B.Heyne ex Roem. & Schult.) Ohwi, *Pappi 5990* (US), Eritrea, –, –, –, **KP873207**; *Acrachne racemosa* (B.Heyne ex Roem. & Schult.) Ohwi, *Strohbach 1308* (US), Namibia, **KP873425**, **KP873959**, **KP873824**, **KP873642**, **KP873209**; *Acrachne racemosa* (B.Heyne ex Roem. & Schult.) Ohwi, *Zavattari 1195* (FT), Ethiopia, **KP873426**, **KP873825**, **KP873960**, **KP873643**, **KP873210**; *Acrachne racemosa* (B.Heyne ex Roem. & Schult.) Ohwi, *Zavattari 1196* (FT), Ethiopia, **KP873427**, **KP873826**, **KP873961**, **KP873644**, **KP873211**; *Afrotrichloris martinii* Chiov., *Hemming 3407* (FT), Somalia, **KP873428**, **KP873827**, **KP873962**, **KP873645**, **KP873212**; *Afrotrichloris martinii* Chiov., *Herlocker 459* (MO), Somalia, –, –, –, **KP873213**; *Apochiton burttii* C.E.Hubb., *Greenway 11513 & Polhill* (US), Tanzania, –, –, GU360571, GU359266; *Apochiton burttii* C.E.Hubb., *Peterson 24163*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, **KP873429**, **KP873828**, **KP873963**, **KP873646**, **KP873214**; *Astrelba elymoides* F.Muell. ex F.M.Bailey, *Hubbard 7976* (US), Australia, **KP873430**, GU359414, GU360313, –, GU359269; *Astrelba lappacea* (Lindl.) Domin, *McKinlay s.n.* (US), Australia, GU360009, GU359395, GU360312, GU360568, GU359270; *Astrelba pectinata* (Lindl.) F.Muell. ex Benth., *Chalmers 5* (US), Australia, GU359861, GU359421, GU360311, GU360567, GU359286; *Austrochloris dichanthioides* (Everist) Lazarides, *Anson s.n.* (US), Australia, GU359860, GU359420, GU360310, GU360566, GU359272; *Brachyachne ambigua* Ohwi, *Leach 3996* (MEL), Australia, **KP873431**, **KP873829**, **KP873964**, **KP873647**, **KP873215**; *Brachyachne ciliaris* (Kuntze) C.E.Hubb., *Latz 14224* (MEL), Australia, **KP873432**, **KP873830**, **KP873965**, **KP873648**, **KP873216**; *Brachyachne ciliaris* (Kuntze) C.E.Hubb., *Mullen s.n.* (US), Australia, –, –, **KP873966**, **KP873649**, –, *Brachyachne convergens* (F.Muell.) Stapf, *Adams 851* (US), Australia, GU359885, GU359349, –, GU360586, GU359252; *Brachyachne fulva* Stapf, *Robson 1122* (US), Mozambique, GU359884, GU359348, GU360444, GU360585; *Brachyachne obtusiflora* (Benth.) C.E.Hubb., *Laegaard 16295* (US), Zimbabwe, GU359883, GU359374, GU360458, GU360584, GU359254; *Brachyachne obtusiflora* (Benth.) C.E.Hubb., *Schweinfurth 2150* (US), South Sudan, **KP873433**, –, **KP873967**, **KP873650**, **KP873217**; *Brachyachne patensiflora* (Stent & J.M.Ratray) C.E.Hubb., *Bogdan 7075* (US), Kenya, GU359862, GU359350, GU360295, GU360605, GU359233; *Brachyachne tenella* (R.Br.) C.E.Hubb., *Lazarides 4281* (US), Australia, GU359882, GU359376, GU360442, GU360583, GU359255; *Chloris amethystea* Hochst., *Archer 8650* (US), Ethiopia, **KP873434**, **KP873831**, **KP873968**, **KP873651**, **KP873218**; *Chloris andropogonoides* E.Fourn., *Cory 52467* (US), U.S.A., **KP873435**, –, –, **KP873219**; *Chloris andropogonoides* E.Fourn., *Peterson 18839*, *Valdés-Reyna & Sifuentes* (US), Mexico, **KP873436**, **KP873832**, **KP873969**, **KP873652**, **KP873220**; *Chloris andropogonoides* E.Fourn., *Swallen 10091* (US), U.S.A., **KP873437**, **KP873833**, **KP873970**, **KP873653**, **KP873221**; *Chloris andropogonoides* E.Fourn., *Swallen 10232* (US), U.S.A., –, –, **KP873971**, **KP873654**, **KP873222**; *Chloris barbata* Sw., *Bentley 102* (US), Ecuador, **KP873438**, –, **KP873972**, –, **KP873223**; *Chloris barbata* Sw., *Ernst 1507* (US), Dominica, **KP873439**, **KP873834**, **KP873655**, **KP873224**; *Chloris barbata* Sw., *King 4038* (US), Mexico, **KP873440**, **KP873835**, **KP873974**, **KP873656**, **KP873225**; *Chloris barbata* Sw., *Peterson 22255 & Saarela* (US), Mexico, GU359873, GU359377, GU360435, GU360514, GU359320; *Chloris barbata* Sw., *Peterson 23795*, *Soreng & Romaschenko* (US), Tanzania, **KP873441**, **KP873836**, **KP873975**, **KP873657**, **KP873226**; *Chloris barbata* Sw., *Saarela 1740*, *Peterson*, *Soreng & Judziewicz* (CAN), Australia, **KP873442**, **KP873837**, **KP873976**, **KP873658**, **KP873227**; *Chloris barbata* Sw., *Saarela 1830*, *Peterson*, *Soreng & Judziewicz* (CAN), Australia, **KP873443**, **KP873838**, **KP873977**, **KP873659**, **KP873228**;

Appendix 1. Continued.

Chloris cantherae var. *grandiflora* (Roseng. & Izag.) D.E. Anderson, *Izaguirre de Artucio* 2642 (US), Uruguay, –, –, –, **KP873660, KP873229**; *Chloris cantherae* Arechav., *Pedersen* 9597 (US), Paraguay, **KP873444, KP873839, KP873978, KP873661, KP873230**; *Chloris cantherae* Arechav., *Schinini* 5321 (US), Argentina, –, **KP873840, KP873979**, –, –, *Chloris cantherae* Arechav., *Smith* 01 (US), U.S.A., **KP873445, KP873841, KP873980, KP873662, KP873231**; *Chloris castilloniana* Lillo & Parodi, *Gallinal H. 5542*, Aragone, Bergalli, *Campal & Rosengurt* (US), Uruguay, **KP873446**, –, **KP873981, KP873663, KP873232**; *Chloris ciliata* Sw., *Lundell* 14872 (US), U.S.A., **KP873447, KP873842, KP873982, KP873664, KP873233**; *Chloris ciliata* Sw., *Peterson* 24622 & *Romaschenko* (US), Mexico, **KP873448**, –, –, **KP873234**; *Chloris ciliata* Sw., *Peterson* 24632 & *Romaschenko* (US), Mexico, **KP873449**, –, –, **KP873235**; *Chloris cruciata* (L.) Sw., *Correll* 48667 & *Proctor* (US), Bahamas, **KP873450**, –, –, **KP873236**; *Chloris cruciata* (L.) Sw., *Correll* 50431 & *Correl* (US), Bahamas, **KP873451**, –, **KP873983, KP873665, KP873237**; *Chloris cubensis* Hitchc. & Ekman, *Box* 35 (US), Antigua and Barbuda, **KP873452**, –, –, **KP873238**; *Chloris cucullata* Bisch., *Crutchfield* 5475 & *Johnston* (US), Mexico, **KP873453, KP873843**, –, **KP873666, KP873239**; *Chloris cucullata* Bisch., *Isely* 10647 (US), U.S.A., **KP873454, KP873844**, –, **KP873667, KP873240**; *Chloris divaricata* var. *cynodontoides* (Balansa) Lazarides, *Greenwood* 226C (US), Fiji, **KP873455**, –, –, **KP873668, KP873241**; *Chloris divaricata* R.Br., *Swallen* 10572 (US), U.S.A., **KP873456**, –, –, **KP873669, KP873242**; *Chloris ekmanii* Hitchc., *Liogier* 12416 (US), Dominican Republic, **KP873457, KP873845**, –, **KP873670, KP873243**; *Chloris ekmanii* Hitchc., *Liogier* 15884 (US), Dominican Republic, **KP873458, KP873846**, –, **KP873671, KP873244**; *Chloris elata* Desv., *Acosta-Solis* 12667 (US), Ecuador, **KP873459**, –, –, **KP873245**; *Chloris elata* Desv., *Beck* 4454 (US), Bolivia, **KP873460, KP873847**, –, **KP873672, KP873246**; *Chloris elata* Desv., *Spiaggi* 40 (US), Bolivia, **KP873461, KP873848**, –, **KP873673, KP873247**; *Chloris elata* Desv., *Swallen* 14461 (US), U.S.A., **KP873462, KP873849**, –, **KP873674, KP873248**; *Chloris elata* Desv., *Webster* 10789, *Samuel & Williams* (US), Bahamas, **KP873463**, –, –, **KP873675, KP873249**; *Chloris exilis* Renvoize, *Anderson* 37049, *Stieber & Kirkbride* (US), Brazil, **KP873464**, –, –, **KP873676, KP873250**; *Chloris exilis* Renvoize, *Anderson* 37190, *Stieber & Kirkbride* (US), Brazil, **KP873465**, –, –, **KP873677, KP873251**; *Chloris gayana* Kunth, *Balleza* 1788 (US), Mexico, **KP873466**, –, –, **KP873678, KP873252**; *Chloris gayana* Kunth, *Batty* 125 (US), U.S.A., **KP873467, KP873850**, –, **KP873679, KP873253**; *Chloris gayana* Kunth, *Peterson* 23972, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873468**, –, **KP873984, KP873680, KP873254**; *Chloris gayana* Kunth, *Peterson* 23997, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873469, KP873851, KP873985, KP873681, KP873255**; *Chloris gayana* Kunth, *Peterson* 24253, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873470, KP873852, KP873986, KP873682, KP873256**; *Chloris halophila* Parodi, *Laegaard* 71450 (US), Ecuador, **KP873471, KP873853**, –, **KP873683, KP873257**; *Chloris halophila* Parodi, *Peterson* 13970 & *Refulio-Rodriguez* (US), Peru, **KP873472, KP873854**, –, **KP873684, KP873258**; *Chloris lamproparia* Stapf, *Sherif* 3945 (K), Sudan, **KP873473**, –, –, **KP890054**; *Chloris latisquamea* Nash, *Fleetwood* s.n. (US), U.S.A., **KP873474, KP873855**, –, **KP873685, KP873259**; *Chloris latisquamea* Nash, *Stanford* s.n., *Lauber & Taylor* (US), Mexico, **KP873475, KP873856**, –, **KP873686, KP873260**; *Chloris mossambicensis* K. Schum., *Oakes* 1211 (US), South Africa, GU359903, –, –, GU360621, GU359219; *Chloris mossambicensis* K. Schum., *Peterson* 23803, *Soreng & Romaschenko* (US), Tanzania, **KP873476, KP873857, KP873987, KP873687, KP873261**; *Chloris mossambicensis* K. Schum., *Peterson* 24219, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873477, KP873858, KP873988, KP873688, KP873262**; *Chloris orthonoton* Döll, *Harley* 16629, *Renvoize, Erskine, Brighton & Pinheiro* (US), Brazil, **KP873478**, –, –, **KP873689, KP873263**; *Chloris orthonoton* Döll, *Pedersen* 5817 (US), Argentina, **KP873479**, –, –, **KP873690, KP873264**; *Chloris pectinata* Benth., *Saarela* 1699, *Peterson, Soreng & Judziwicz* (CAN), Australia, **KP873480, KP873859, KP873989, KP873691, KP873265**; *Chloris pilosa* Schumach., *Allen* s.n. & *Baumgartner* (US), France, **KP873481, KP873860**, –, **KP873692, KP873266**; *Chloris pilosa* Schumach., *Brenan* 9601 (US), Nigeria, **KP873482**, –, –, **KP873693, KP873267**; *Chloris pilosa* Schumach., *Peterson* 23919, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873483, KP873861, KP873694, KP873268**; *Chloris prieurii* Kunth, *Laegaard* 17061 & *Traore* (US), Senegal, **KP873484, KP873862**, –, **KP873695, KP873269**; *Chloris prieurii* Kunth, *Laegaard* 17863 & *Traore* (US), Senegal, **KP873485**, –, –, **KP873696, KP873270**; *Chloris pycnothrix* Trin., *Bidgood* 3170 & *Vollesen* (US), Tanzania, **KP873486, KP873863, KP873697, KP873271**; *Chloris pycnothrix* Trin., *Harley* 17042 (US), Brazil, **KP873487, KP873864**, –, **KP873698, KP873272**; *Chloris pycnothrix* Trin., *Pedersen* 6378 (US), Argentina, **KP873488**, –, –, **KP873699, KP873273**; *Chloris pycnothrix* Trin., *Peterson* 22278 & *Saarela* (US), Mexico, GU359872, GU359366, GU360434, GU360513, GU359321; *Chloris pycnothrix* Trin., *Peterson* 23949, *Soreng & Romaschenko* (US), Tanzania, **KP873489, KP873865, KP873991, KP873700, KP873274**; *Chloris pycnothrix* Trin., *Peterson* 23974, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873490**, –, **KP873992, KP873701, KP873275**; *Chloris pycnothrix* Trin., *Peterson* 24070, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873491, KP873866, KP873993, KP873702, KP873276**; *Chloris pycnothrix* Trin., *Peterson* 24172, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873492, KP873867, KP873994, KP873703, KP873277**; *Chloris pycnothrix* Trin., *Peterson* 24184, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873493, KP873868, KP873995, KP873704, KP873278**; *Chloris pycnothrix* Trin., *Peterson* 24262, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873494, KP873869, KP873996, KP873705, KP873279**; *Chloris pycnothrix* Trin., *Peterson* 24305, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873495, KP873870, KP873997, KP873706, KP873280**; *Chloris roxburghiana* Schult., *Peterson* 23812, *Soreng & Romaschenko* (US), Tanzania, **KP873496, KP873871, KP873998, KP873707, KP873281**; *Chloris roxburghiana* Schult., *Peterson* 24194, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873497, KP873872, KP873999, KP873708, KP873282**; *Chloris roxburghiana* Schult., *Peterson* 24225, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873498, KP873873, KP874000, KP873709, KP873283**; *Chloris rufescens* Lag., *McVaugh* 19517 (US), Mexico, **KP873499, KP873874**, –, **KP873710, KP873284**; *Chloris sagraeana* A. Rich., *McKee* 10539 (US), Guadeloupe, **KP873500, KP873875**, –, **KP873711, KP873285**; *Chloris subdolichostachya* C. Müll., *Trouart* 17 (US), U.S.A., **KP873501, KP873876**, –, **KP873712, KP873286**; *Chloris submutica* Kunth, *McGregor* 706, *Harms, Robinson, Rosario & Seagal* (US), Mexico, **KP873502, KP873877**, –, **KP873713, KP873287**; *Chloris submutica* Kunth, *Peterson* 22393 & *Saarela* (US), Mexico, GU359871, GU359375, GU360471, GU360512, GU359322; *Chloris submutica* Kunth, *Peterson* 24560 & *Romaschenko* (US), Mexico, **KP873503**, –, –, **KP873288**; *Chloris submutica* Kunth, *Peterson* 24842 & *Romaschenko* (US), Mexico, **KP873504**, –, –, **KP873289**; *Chloris submutica* Kunth, *Peterson* 24939, *Romaschenko & González-Elizondo* (US), Mexico, **KP873505**, –, –, **KP873290**; *Chloris submutica* Kunth, *Reeder* 4845 & *Reeder* (US), Mexico, **KP873506, KP873878**, –, **KP873714, KP873291**; *Chloris texana* (Vasey) Nash, *Silvens* 423 (US), U.S.A., **KP873507**, –, –, **KP873715, KP873292**; *Chloris verticillata* Nutt., *Reeder* 5787 & *Reeder* (US), U.S.A., **KP873508**, –, –, **KP873716, KP873293**; *Chloris virgata* Sw., *Peterson* 21468, *Soreng, LaTorre & Rojas Fox* (US), Peru, GU359869, GU359373, GU360445, GU360510, GU359324; *Chloris virgata* Sw., *Peterson* 24286, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873509, KP873879, KP874001, KP873717, KP873294**; *Chloris virgata* Sw., *Peterson* 24659 & *Romaschenko* (US), Mexico, **KP873510**, –, –, **KP873295**; *Chloris virgata* Sw., *Peterson* 24789, *Romaschenko, Rodriguez Avalos, Herrera-Simoni & Garcia Rodriguez* (US), Mexico, **KP873511**, –, –, **KP873296**; *Chloris virgata* Sw., *Peterson* 24854 & *Romaschenko* (US), Mexico, **KP873512**, –, –, **KP873297**; *Chloris virgata* Sw., *Peterson* 24911 & *Romaschenko* (US), Mexico, **KP873513**, –, –, **KP873298**; *Chloris virgata* Sw., *Peterson* 24954 & *Romaschenko* (US), Mexico, **KP873514**, –, –, **KP873299**; *Chrysochloa annua* C.E. Hubb., *Arkrok* 20417 (US), Ghana, **KP873515, KP873880, KP874002, KP873718, KP873300**; *Chrysochloa hindsii* C.E. Hubb., *Reekmans* 11068 (US), Burundi, GU359868, –, GU360485, GU360509, GU359325; *Chrysochloa orientalis* (C.E. Hubb.) Swallen, *Burtt* 5666 (US), Tanzania, **KP873516**, –, **KP874003, KP873719, KP873301**; *Coelachyrum lagopoides* (Burm.f.) Senaratna, *Saldanha* 15334 (US), India, GU359844, –, –, GU360602, –, *Coelachyrum poiflorum* Chiov., *Burger* 2915 (US), Ethiopia, GU359843, –, GU360457, GU360601, GU359236; *Cynodon aethiopicus* Clayton & J.R. Harlan, *Peterson* 24268, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873517, KP873881, KP874004, KP873720, KP873302**; *Cynodon aethiopicus* Clayton & J.R. Harlan, *Peterson* 24318, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873518, KP873882, KP874005, KP873721, KP873303**; *Cynodon aethiopicus* Clayton & J.R. Harlan, *Smook* 4140 (US), South Africa, **KP873519, KP873883, KP874006, KP873722, KP873304**; *Cynodon aethiopicus* Clayton & J.R. Harlan, *Vesey-Fitzgerald* 6475 (US), Tanzania, **KP873520**, –, –, **KP873305**; *Cynodon affinis* Caro & E.A. Sánchez, *Booth* 1251 (US), U.S.A., **KP873521, KP873884, KP874007, KP873723, KP873306**; *Cynodon affinis* Caro & E.A. Sánchez, *Cabrera* 5149 (US), Argentina, **KP873522, KP873885, KP874008, KP873724, KP873307**; *Cynodon affinis* Caro & E.A. Sánchez, *Collins* 63 (US), U.S.A., –, **KP873886, KP874009, KP873725, KP873308**; *Cynodon aristiglus* Caro & E.A. Sánchez, *Beetle* 2731 (US), U.S.A., **KP873523, KP873887, KP874010, KP873726, KP873309**; *Cynodon aristulatus* Caro & E.A. Sánchez, *Egler* 42-314 (US), Guatemala, **KP873524, KP873888, KP874011, KP873727, KP873310**; *Cynodon aristulatus* Caro & E.A. Sánchez, *Fassett* 26000 (US), Colombia, **KP873525, KP873889, KP874012, KP873728, KP873311**; *Cynodon aristulatus* Caro & E.A. Sánchez, –

Appendix 1. Continued.

Killip 31600 (US), U.S.A., **KP873526, KP873890, KP874013, KP873729, KP873311**; *Cynodon dactylon* var. *longiglumis* Caro & E.A.Sánchez, *Dunkle 8366* (US), U.S.A., **KP873527**, –, –, –, *Cynodon dactylon* var. *longiglumis* Caro & E.A.Sánchez, *Dunkle 8652* (US), U.S.A., **KP873528**, –, –, –, *Cynodon dactylon* var. *pilosus* Caro & E.A.Sánchez, *Marsh 141* (US), U.S.A., **KP873529**, –, –, –, *Cynodon dactylon* var. *longiglumis* (L.) Pers., *Peterson 19701*, *Saarela & Sears* (US), U.S.A., **KP873530**, –, –, –, *Cynodon dactylon* (L.) Pers., *Peterson 22000 & Saarela* (US), Mexico, GU359836, GU359359, GU360453, GU360580, GU359243; *Cynodon dactylon* var. *pilosus* (L.) Pers., *Peterson 24626 & Romaschenko* (US), Mexico, **KP873531**, –, –, –, **KP873312**; *Cynodon dactylon* var. *pilosus* (L.) Pers., *Saarela 1606*, *Peterson*, *Soreng & Judziewicz* (CAN), Australia, **KP873532, KP873891, KP874014, KP873730, KP873313**; *Cynodon erectus* J.Presl, *Asplund 10905* (US), Peru, –, –, **KP874015, KP873731, KP873314**; *Cynodon erectus* J.Presl, *Martin 1814* (US), U.S.A., **KP873533, KP873892, KP874016, KP873732, KP873315**; *Cynodon hirsutissimus* (Litard. & Maire) Caro & E.A.Sánchez, *Parodi 15066* (US), Argentina, –, –, –, **KP873316**; *Cynodon hirsutus* Stent, *Smook 6616* (US), South Africa, GU359876, GU359358, GU360452, GU360594, GU359229; *Cynodon incompletus* Nees, *Oakes 663* (US), South Africa, **KP873534**, –, –, –, *Cynodon incompletus* Nees, *Smook 10152* (US), South Africa, GU359847, GU359347, GU360451, GU360609, GU359245; *Cynodon incompletus* Nees, *Smook 2408 & Gibbs-Russell* (US), South Africa, GU359849, **KP873893**, GU360450, **KP873733**, GU359246; *Cynodon maritimus* Kunth, *Howard 10214 & Howard* (US), Bahamas, GU359889, GU359365, GU360448, GU360591, GU359248; *Cynodon maritimus* var. *vaginiflorus* Caro, *Martindale s.n.* (US), U.S.A., **KP873535**, –, –, –, *Cynodon mucronatus* Caro & E.A.Sánchez, *Fosberg 273 & Batts* (US), U.S.A., **KP873536, KP873894, KP874017, KP873734, KP873317**; *Cynodon mucronatus* Caro & E.A.Sánchez, *Hermann 8502* (US), U.S.A., **KP873537, KP873895, KP874018, KP873735, KP873318**; *Cynodon nitidus* Caro & E.A.Sánchez, *Macbride 524 & Featherstone* (US), Peru, –, –, **KP874019, KP873736, KP873319**; *Cynodon nlemfuensis* Vanderyst, *Hansen 13002* (US), U.S.A., **KP873538, KP873896, KP874020, KP873737, KP873320**; *Cynodon nlemfuensis* Vanderyst, *Laegaard 19845* (US), Ecuador, **KP873539, KP873897, KP874021, KP873738, KP873321**; *Cynodon nlemfuensis* Vanderyst, *Laegaard 19876* (US), Ecuador, **KP873540, KP873898, KP874022, KP873739, KP873322**; *Cynodon nlemfuensis* Vanderyst, *Lobo 2099*, *Cascante, Quesada & Prieto* (CR), Costa Rica, KJ768976, **KP873899, KP874023, KP873740**, KJ768881; *Cynodon nlemfuensis* Vanderyst, *Molina 25803* (US), Honduras, –, GU359353, –, GU360589, –, *Cynodon nlemfuensis* Vanderyst, *Peterson 24058*, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873541**, –, –, **KP873741, KP873323**; *Cynodon nlemfuensis* Vanderyst, *Peterson 24113*, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873543, KP873901, KP874025, KP873743, KP873325**; *Cynodon nlemfuensis* Vanderyst, *Peterson 24207*, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873544, KP873902, KP874026, KP873744, KP873326**; *Cynodon pascuus* Nees, *Moran 12518* (US), Mexico, GU359888, GU359354, GU360447, GU360590, GU359247; *Cynodon plectostachyus* (K.Schum.) Pilg., *Troupin 11610* (US), Rwanda, GU359890, GU359356, GU360449, GU360592, GU359247; *Cynodon radiatus* Roth, *Clayton 5836* (US), Sri Lanka, GU359837, GU359360, GU360454, GU360596, GU359257; *Cynodon radiatus* Roth, *Laegaard 21611* (US), Thailand, **KP873545, KP873903, KP874027, KP873745, KP873327**; *Cynodon transvaalensis* Burtt Davy, *Laegaard 20560* (US), Ecuador, –, –, **KP874028, KP873746, KP873328**; *Cynodon transvaalensis* Burtt Davy, *Smook 6710* (US), South Africa, GU359887, GU359352, GU360446, GU360588, GU359250; *Daknopholis boivinii* (A.Camus) Clayton, *Ranaivojaona 1441*, *Andrianjafy, Phillipson & Lubke* (MO), Madagascar, **KP873548, KP873907, KP874032, KP873750, KP873332**; *Dinebra aquatica* (Scribn. & Merr.) P.M.Peterson & N.Snow, *Soderstrom 650* (US), Mexico, **KP873549, KP873908, KP874033, KP873751, KP873333**; *Dinebra caudata* (K.Schum.) P.M.Peterson & N.Snow, *Kuchar 24265* (MO), Tanzania, JQ345324, JQ345210, JQ345282, JQ345239, JQ345170; *Dinebra chinensis* (L.) P.M.Peterson & N.Snow, *Snow 6909* (MO), Botswana, JQ345325, –, –, JQ345240, JQ345171; *Dinebra coeruleascens* (Steud.) P.M.Peterson & N.Snow, *Harris 289 & Fay* (MO), Central African Republic, –, –, JQ345283, –, JQ345172; *Dinebra decipiens* subsp. *asthenes* (Roem. & Schult.) P.M.Peterson & N.Snow, *Snow 7327* (MO), Australia, JQ345326, –, JQ345284, JQ345241, JQ345173; *Dinebra decipiens* subsp. *decipiens* (R.Br.) P.M.Peterson & N.Snow, *Snow 7328 & Simon* (MO), Australia, JQ345327, JQ345211, JQ345285, JQ345242, JQ345174; *Dinebra decipiens* subsp. *asthenes* (Roem. & Schult.) P.M.Peterson & N.Snow, *Snow 7355* (MO), Australia, JQ345328, JQ345212, JQ345286, JQ345243, JQ345175; *Dinebra decipiens* subsp. *peacockii* (Maiden & Betche) P.M.Peterson & N.Snow, *Snow 7361 & Simon* (MO), Australia, JQ345329, –, JQ345287, JQ345244, JQ345176; *Dinebra decipiens* subsp. *decipiens* (R.Br.) P.M.Peterson & N.Snow, *Waterhouse 5948* (MO), Australia, JQ345330, –, JQ345288, JQ345245, JQ345177; *Dinebra divaricatissima* (S.T.Blake) P.M.Peterson & N.Snow, *Brown 253* (MEL), Australia, **KP873550, KP873909**, –, **KP873752, KP873334**; *Dinebra haareri* (Stapf & C.E.Hubb.) P.M.Peterson & N.Snow, *Peterson 24231*, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873551, KP873910, KP874034, KP873753, KP873335**; *Dinebra ligulata* (Lazarides) P.M.Peterson & N.Snow, *Snow 7402* (MO), Australia, JQ345336, JQ345218, JQ345294, JQ345251, JQ345183; *Dinebra marquisensis* (F.Br.) P.M.Peterson & N.Snow, *Wood 10145* (MO), French Polynesia, JQ345337, JQ345219, JQ345295, JQ345252, JQ345184; *Dinebra nealleyi* (Vasey) P.M.Peterson & N.Snow, *Snow 5806* (MO), U.S.A., JQ345338, JQ345220, JQ345296, JQ345253, JQ345185; *Dinebra neesii* (Thwaites) P.M.Peterson & N.Snow, *Snow 7380 & Simon* (MO), Australia, JQ345339, JQ345221, JQ345297, JQ345254, JQ345186; *Dinebra panicea* subsp. *brachiata* (Steud.) P.M.Peterson & N.Snow, *Peterson 20086*, *Alvarez Marvan & Dejesos* (US), Mexico, JQ345341, –, –, –, *Dinebra panicea* subsp. *brachiata* (Steud.) P.M.Peterson & N.Snow, *Peterson 22185 & Saarela* (US), Mexico, GU359810, GU359431, GU360389, –, GU359146; *Dinebra panicea* subsp. *mucronata* (Michx.) P.M.Peterson & N.Snow, *Peterson 9546*, *Annable & Herrera* (US), Mexico, JQ345342, JQ345222, JQ345299, JQ345256, JQ345188; *Dinebra panicoides* (J.Presl) P.M.Peterson & N.Snow, *Snow 5810a* (MO), U.S.A., JQ345343, –, JQ345300, JQ345257, –, *Dinebra retroflexa* (Vahl) Panz., *Ndegwa 610* (US), Kenya, GU359778, GU359355, GU360479, GU360503, GU359332; *Dinebra retroflexa* (Vahl) Panz., *Snow 6950 & Burgoyne* (MO), Swaziland, **KP873552**, –, –, **KP873336**; *Dinebra scabra* (Nees) P.M.Peterson & N.Snow, *Snow 5788* (MO), U.S.A., JQ345344, JQ345223, JQ345301, JQ345258, JQ345189; *Dinebra somalensis* (Stapf) P.M.Peterson & N.Snow, *Faden 74-991 & Faden* (MO), Kenya, JQ345321, –, JQ345278, JQ345236, JQ345166; *Dinebra southwoodii* (N.Snow & B.K.Simon) P.M.Peterson & N.Snow, *Snow 7362* (MO), Australia, JQ345345, JQ345224, JQ345302, JQ345259, JQ345190; *Dinebra squarrosa* (Pilg.) P.M.Peterson & N.Snow, *Kayombo 5196* (MO), Tanzania, JQ345346, JQ345225, JQ345303, JQ345260, JQ345191; *Dinebra viscidula* (Scribn.) P.M.Peterson & N.Snow, *Peterson 22184 & Saarela* (US), Mexico, GU359808, GU359429, GU360430, GU360693, GU359148; *Dinebra viscidula* (Scribn.) P.M.Peterson & N.Snow, *Snow 6528a & Prinzie* (MO), Mexico, JQ345352, –, JQ345307, JQ345265, –, *Dinebra xerophila* (P.M.Peterson & Judz.) P.M.Peterson & N.Snow, *Perlman 18438* (MO), French Polynesia, JQ345353, JQ345227, JQ345308, JQ345266, JQ345196; *Diplachne fusca* var. *muelleri* (Benth.) J.M.Black, *Badman 1282* (MO), Australia, JQ345334, JQ345216, JQ345292, JQ345249, JQ345181; *Diplachne fusca* var. *uniervia* (J.Presl) P.M.Peterson & N.Snow, *Peterson 20786*, *Soreng, Romaschenko & Gonzalez-Elizondo* (US), Peru, JQ345335, JQ345217, JQ345293, JQ345250, JQ345182; *Diplachne fusca* var. *uniervia* (J.Presl) P.M.Peterson & N.Snow, *Peterson 21305*, *Saarela & Flores Villegas* (US), Mexico, GU359809, GU359461, GU360391, GU360694, GU359147; *Diplachne fusca* var. *fusca* (L.) P.Beauv. ex Roem. & Schult., *Peterson 24322*, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873553, KP873911, KP874035, KP873754, KP873337**; *Diplachne fusca* var. *fusca* (L.) P.Beauv. ex Roem. & Schult., *Walsh 6558* (MEL), Australia, **KP873554, KP873912, KP874036, KP873755, KP873338**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 22334 & Saarela* (US), Mexico, GU359811, GU359442, GU360416, GU360695, GU359145; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24453*, *Romaschenko & Valdés-Reyna* (US), Mexico, **KP873555**, –, –, **KP873339**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24554 & Romaschenko* (US), Mexico, **KP873556**, –, –, **KP873340**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24566*, *Romaschenko & Valdés-Reyna* (US), Mexico, **KP873557**, –, –, **KP873341**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24665 & Romaschenko* (US), Mexico, **KP873558**, –, –, **KP873342**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24845 & Romaschenko* (US), Mexico, **KP873559**, –, –, **KP873343**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 24905 & Romaschenko* (US), Mexico, **KP873560**, –, –, **KP873344**; *Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 8105 & Annable* (US), Mexico, JQ345332, JQ345214, JQ345290, JQ345247, JQ345179; *Disakisperma eleusine* (Nees) P.M.Peterson & N.Snow, *Snow 6982* (MO), South Africa, JQ345333, JQ345215, JQ345291, JQ345248, JQ345180; *Disakisperma obtusiflorum* (Hochst.) P.M.Peterson & N.Snow, *Belsky 527* (MO), Kenya, JQ345340, –, JQ345298, JQ345255, JQ345187; *Disakisperma obtusiflorum* (Hochst.) P.M.Peterson & N.Snow, *Peterson 24198*, *Soreng, Romaschenko & Mbago* (US), Tanzania, KF574411, KF574405, KF574417, KF574423, KF574400; *Disakisperma obtusiflorum* (Hochst.) P.M.Peterson & N.Snow, *Peterson 24211*, *Soreng, Romaschenko & Mbago* (US), Tanzania, KF574412, KF574406, KF574418, KF574424, KF574401; *Disakisperma obtusiflorum* (Hochst.) P.M.Peterson & N.Snow, *Peterson 24243*,

Appendix 1. Continued.

Soreng, Romaschenko & Mbago (US), Tanzania, KF574413, KF574407, KF574419, KF574425, KF574402; *Disakisperma yemenicum* (Schweinf.) P.M.Peterson & N.Snow, Peterson 24254, Soreng, Romaschenko & Mbago (US), Tanzania, KF574414, KF574408, KF574420, KF574426, KF574403; *Disakisperma yemenicum* (Schweinf.) P.M.Peterson & N.Snow, Verdcourt 3275 (US), Kenya, KF574415, KF574409, KF574421, KF574427, KF574404; *Eleusine africana* Kenn.-O'Byrne, Kayombo 424 (MO), Tanzania, KP873562, KP873913, KP874037, KP873756, KP873346; *Eleusine africana* Kenn.-O'Byrne, Peterson 24072, Soreng, Romaschenko & Abeid (US), Tanzania, KP873563, KP873914, KP874038, KP873757, KP873347; *Eleusine africana* Kenn.-O'Byrne, Peterson, Qing Liu 090 (US), Mexico, HQ202625, HQ202648, HQ202640, HQ202632, -, *Eleusine africana* Kenn.-O'Byrne, Seydel 2798 (US), Namibia, KP873564, -, -, -, KP873348; *Eleusine africana* Kenn.-O'Byrne, Seydel 3889 (US), Namibia, KP873565, -, -, -, KP873349; *Eleusine coracana* (L.) Gaertn., Peterson 24112, Soreng, Romaschenko & Abeid (US), Tanzania, KP873566, KP873915, KP874039, KP873758, KP873350; *Eleusine coracana* (L.) Gaertn., Qing Liu 093 (US), Ethiopia, KP873567, -, -, -, KP873351; *Eleusine coracana* (L.) Gaertn., Qing Liu 103 (US), Ethiopia, KP873568, -, -, -, KP873352; *Eleusine floccifolia* (Forssk.) Spreng., Hilu s.n. (VPI), Ethiopia, -, -, -, AY15208*; *Eleusine indica* (L.) Gaertn., Brown 628 & Clebsch (US), U.S.A., KP873569, -, -, -, KP873353; *Eleusine indica* (L.) Gaertn., Chase 9922 (US), U.S.A., KP873570, -, -, -, KP873354; *Eleusine indica* (L.) Gaertn., Peterson 21362, Saarela & Flores Villegas (US), Mexico, GU359797, GU359473, GU360472, GU360496, GU359338; *Eleusine indica* (L.) Gaertn., Peterson 23802, Soreng & Romaschenko (US), Tanzania, KP873571, KP873916, KP874040, KP873759, KP873355; *Eleusine indica* (L.) Gaertn., Peterson 24429, Romaschenko & Knapp (US), U.S.A., KP873572, -, KP874041, KP873760, KP873356; *Eleusine jaegeri* Pilg., Hilu 203 (VPI), Kenya, -, -, -, AY151213*; *Eleusine jaegeri* Pilg., Kindeketa 762 (MO), Tanzania, KP873573, KP873917, KP874042, KP873761, KP873357; *Eleusine jaegeri* Pilg., Peterson 24299, Soreng, Romaschenko & Mbago (US), Tanzania, KP873574, KP873918, KP874043, KP873762, KP873358; *Eleusine kigeziensis* S.M. Phillips, Purseglove 3384 (K), Uganda, -, -, -, AY151216*; *Eleusine multiflora* Hochst. ex A.Rich., Davidse 30264 & Davidse (MO), Mexico, KP873575, -, -, -, KP873359; *Eleusine multiflora* Hochst. ex A.Rich., Peterson 24272, Soreng, Romaschenko & Mbago (US), Tanzania, KP873576, KP873919, KP874044, KP873763, KP873360; *Eleusine multiflora* Hochst. ex A.Rich., Qing Liu 100 (US), Kenya, HQ202630, HQ202653, HQ202646, HQ202638, -, *Eleusine tristachya* (Lam.) Lam., Beck 3227 (US), Bolivia, KP873577, -, -, -, KP873361; *Eleusine tristachya* (Lam.) Lam., Hilu 2464 (VPI), Uruguay, -, -, -, AY151224*; *Eleusine tristachya* (Lam.) Lam., Qing Liu 107 (US), Mexico, HQ202631, HQ202654, HQ202647, HQ202639, -, *Eleusine tristachya* (Lam.) Lam., Zardini 35791 & Tilleria (MO), Paraguay, KP873578, KP873920, KP874045, KP873764, KP873362; *Enteropogon acicularis* (Lindl.) Lazarides, Cochrane 521B (MEL), Australia, KP873579, KP873921, KP874046, KP873765, KP873363; *Enteropogon barbatus* C.E. Hubb., Kabuye 575, Luke, Robertson, Mungai & Mathegne (US), Kenya, KP873580, -, KP874047, KP873766, KP873364; *Enteropogon brandegeei* (Vasey) Clayton, Carter 2897 & Kellogg (US), Mexico, KP873581, KP873922, KP874048, KP873767, KP873365; *Enteropogon chlorideus* (J.Presl) Clayton, Gould 12679 (US), Mexico, KP873582, KP873923, KP874049, KP873768, KP873366; *Enteropogon chlorideus* (J.Presl) Clayton, Leavenworth 1900 (US), Mexico, KP873583, -, KP874050, KP873769, KP873367; *Enteropogon chlorideus* (J.Presl) Clayton, Meyer s.n. (US), U.S.A., KP873584, -, KP874051, KP873770, KP873368; *Enteropogon chlorideus* (J.Presl) Clayton, Sohns 384 (US), Mexico, KP873585, -, -, -, KP873369; *Enteropogon dolichostachyus* (Lag.) Keng ex Lazarides, Blake 23488 (MEL), Australia, KP873586, -, -, -, KP873370; *Enteropogon dolichostachyus* (Lag.) Keng ex Lazarides, Gould 13680 & Cooray (US), Sri Lanka, KP873587, -, KP874052, KP873771, KP873371; *Enteropogon dolichostachyus* (Lag.) Keng ex Lazarides, Lazarides 7416 (US), Thailand, KP873588, -, -, KP873772, KP873372; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., Laegaard 15902 (US), Zimbabwe, GU359795, GU359472, GU360470, GU360494, GU359340; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., Oakes 1250 (US), South Africa, KP873589, KP873924, KP874053, KP873773, KP873373; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., Peterson 24197, Soreng, Romaschenko & Mbago (US), Tanzania, KP873590, KP873925, KP874054, KP873774, KP873374; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., Peterson 24228, Soreng, Romaschenko & Mbago (US), Tanzania, KP873591, KP873926, KP874055, KP873775, KP873375; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., Smook 9026 (US), Namibia, KP873592, KP873927, KP874056, KP873776, KP873376; *Enteropogon mollis* (Nees) Clayton, Proosidj 813, van de Riet & Zauder (US), Aruba, KP873593, KP873928, -, KP873777, KP873377; *Enteropogon mollis* (Nees) Clayton, Steyermark 29192 (US), Guatemala, KP873594, -, -, KP873778, KP873378; *Enteropogon monostachyus* (Vahl) K.Schum., Barber 2607 (US), India, KP873595, KP873929, KP874057, KP873779, KP873379; *Enteropogon monostachyus* (Vahl) K.Schum., Clayton 5954 (US), Sri Lanka, KP873596, -, KP874058, KP873780, KP873380; *Enteropogon ramosus* B.K.Simon, Peterson 14367, Soreng & Rosenberg (US), Australia, GU359794, GU359470, GU360469, GU360493, GU359341; *Enteropogon ramosus* B.K.Simon, Saarela 1663, Peterson, Soreng & Judziewicz (CAN), Australia, KP873597, KP873929, KP873781, KP873381; *Enteropogon rupestris* (J.A.Schmidt) A.Chev., Bogdan 4026 (US), Kenya, KP873598, -, KP874060, KP873782, KP873382; *Enteropogon rupestris* (J.A.Schmidt) A.Chev., Gillet 13082 (US), Kenya, KP873599, KP873931, KP874061, KP873783, KP873383; *Enteropogon rupestris* (J.A.Schmidt) A.Chev., Vesey-Fitzgerald 4973 (US), Kenya, KP873601, KP873932, KP873942, KP873785, KP873384; *Enteropogon sechellensis* (Baker) T.Durand & Schinz, Peterson 49814 (US), Seychelles, -, KP873933, KP874063, KP873786, KP873385; *Enteropogon sechellensis* (Baker) T.Durand & Schinz, Peterson 23815, Soreng & Romaschenko (US), Tanzania, KP873602, KP873934, KP874064, KP873787, KP873386; *Enteropogon sechellensis* (Vahl) K.Schum., Peterson 23833, Soreng, Romaschenko & Abeid (US), Tanzania, KP873603, KP873935, KP874065, KP873788, KP873387; *Eustachys calvescens* (Hack.) Caro & E.A.Sánchez, Chase 10971 (US), Brazil, KP873604, KP873936, KP874066, KP873789, KP873388; *Eustachys calvescens* (Hack.) Caro & E.A.Sánchez, Rojas 6633 (US), Paraguay, KP873605, -, KP874067, KP873790, KP873389; *Eustachys caribaea* (Spreng.) Herter, Renvoize 4022 & Cope (US), Bolivia, KP873606, KP873937, KP874068, KP873791, KP873390; *Eustachys distichophylla* (Lag.) Nees, Harris s.n. (US), U.S.A., KP873607, KP873938, -, KP873792, KP873391; *Eustachys floridana* Chapm., Kral 44355 (US), U.S.A., KP873608, KP873939, -, KP873793, KP873392; *Eustachys glabrescens* (Hack.) Caro & E.A.Sánchez, Pedersen 6121 (US), Argentina, -, -, KP874069, KP873794, KP873393; *Eustachys glabrescens* (Hack.) Caro & E.A.Sánchez, Pedersen 6307 (US), Argentina, KP873610, KP873940, KP874070, KP873795, KP873394; *Eustachys glauca* Chapm., Swallen 8221 (US), U.S.A., KP873610, KP873941, -, KP873796, KP873395; *Eustachys neglecta* (Nash) Nash, Chase 4499 (US), U.S.A., KP873611, -, -, KP873797, KP873396; *Eustachys paspaloides* (Vahl) Lanza & Mattei, Ndegway 741 (US), Kenya, GU359819, GU359439, GU360386, GU360522, GU359312; *Eustachys petraea* (Sw.) Desv., Strong 3124 (US), U.S.A., GU359833, GU359438, GU360385, GU360637, GU359313; *Eustachys petraea* (Sw.) Desv., Taylor 12539 (US), Mexico, -, -, -, KP873397; *Eustachys retusa* (Lag.) Kunth, Krapovickas 22799 & Cristobal & Quarin (US), Brazil, -, -, -, KP873398; *Eustachys tenera* (J.Presl) A.Camus, Strong 10564 & Clemens (US), Papua New Guinea, KP873612, -, KP874071, KP873798, KP873399; *Harporchloa falx* (L.f.) Kuntze, Zietsman Peyper, Avenant & Van der Walt (MO), South Africa, KP873613, -, KP874072, KP873799, KP873400; *Leptochloa chloridiformis* Parodi, Myndel-Pedersen 2662 (US), Argentina, KP873614, -, KP874073, KP873800, KP873401; *Leptochloa chloridiformis* Parodi, Myndel-Pedersen 3741 (US), Argentina, KP873615, -, -, KP873801, KP873402; *Leptochloa crinita* (Lag.) P.M.Peterson, Renvoize 1987 (US), Bolivia, JQ345359, JQ345231, JQ345315, JQ345273, JQ345203; *Leptochloa digitata* (R.Br.) Domin, Risler 476 (MO), Australia, JQ345331, JQ345213, JQ345289, JQ345246, JQ345178; *Leptochloa pluriflora* (E.Fourn.) P.M.Peterson & N.Snow, Peterson 15048 & Refulio-Rodriguez (US), Peru, GU359905, GU359554, GU360334, GU360623, GU359212; *Leptochloa pluriflora* (E.Fourn.) P.M.Peterson & N.Snow, Sohns 1258 (US), Mexico, GU359934, GU359553, GU360374, GU360693, GU359214; *Leptochloa pluriflora* (E.Fourn.) P.M.Peterson & N.Snow, Swallen 10100 (US), U.S.A., KP873616, KP873942, KP873403, KP873802, KP873403; *Leptochloa virgata* (L.) P.Beauv., Peterson 15088 & Refulio-Rodriguez (US), Peru, JQ345349, -, JQ345304, JQ345262, JQ345193; *Leptochloa virgata* (L.) P.Beauv., Rimachi 8359 (US), Peru, JQ345350, -, JQ345305, JQ345263, JQ345194; *Leptochloa virgata* (L.) P.Beauv., Vargas 2710 (US), Bolivia, JQ345351, JQ345226, JQ345306, JQ345264, JQ345195; *Lepturus gasparricensis* Fosberg, Herbst 9687 (US), U.S.A. Wake Isl., GU359807, GU359477, GU360427, GU360690, GU359151; *Microchloa altera* (Rendle) Stapf, Brand 315, Kay, Logie & Logie (MO), South Africa, KP873617, KP873943, KP873803, KP873404; *Lepturus radicans* (Steud.) A.Camus, Gilleopie 38 (US), Kenya, GU359806, -, -, -, *Lepturus repens* (G.Forst.) R.Br., Peterson 23835, Soreng, Romaschenko & Abeid (US), Tanzania, KP873618, KP873944, KP874076, KP873804, KP873405; *Lepturus repens* R.Br., Whistler 9853 (US), Chagos Archipelago, Diego Garcia Isl., GU359893, GU359427, GU360428, GU360691, GU359150; *Lintonia nutans* Stapf, Mwasumbi 14374 (US), Tanzania, GU359980, GU359426, GU360427, GU360690, GU359151; *Microchloa altera* (Rendle) Stapf, Brand 315, Kay, Logie & Logie (MO), South Africa, KP873619, KP873945, KP874077, -

Appendix 1. Continued.

KP873805, KP873406; *Microchloa altera* (Rendle) Stapf, *Malaisse 16572* (MO), Congo (Kinshasa) Dem. Rep., **KP873620, KP873946, KP874078, KP873806, KP873407;** *Microchloa altera* (Rendle) Stapf, *Robinson 6362* (US), Zambia, **KP873621, KP873947, KP874079, KP873807, KP873408;** *Microchloa caffra* Nees, *Peterson 24288, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873622, KP873948, KP874080, KP873808, KP873409;** *Microchloa caffra* Nees, *Smook 10441* (US), South Africa, GU359972, GU359453, GU360424, GU360670, GU359155; *Microchloa kunthii* Desv., *Hagerup 455 & Olufsen* (US), Mali, **KP873623, KP873949, KP874081, KP873809, –;** *Microchloa kunthii* Desv., *Peterson 22152 & Saarela* (US), Mexico, GU359971, GU359434, GU360423, GU360684, GU359141; *Microchloa kunthii* Desv., *Peterson 24048, Soreng, Romaschenko & Abeid* (US), Tanzania, **KP873624, KP873950, KP874082, KP873810, KP873410;** *Microchloa kunthii* Desv., *Peterson 24255, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873625, KP873951, KP874083, KP873811, KP873411;** *Microchloa kunthii* Desv., *Peterson 24716, Romaschenko & Zamudio Ruiz* (US), Mexico, **KP873626, –, –, –, KP873412;** *Ochthochloa compressa* (Forssk.) Hilu, *Gloves 48 & Gilliband* (US), Somalia, **KP873628, –, –, –, KP890055;** *Ochthochloa compressa* (Forssk.) Hilu, *Rechinger 29410* (US), Pakistan, **KP873629, –, KP874084, –, KP890056;** *Ochthochloa compressa* (Forssk.) Hilu, *USDA 154-57* (US), Pakistan, **KP873630, –, KP874085, –, KP890057;** *Oxychloris scariosa* (F.Muell.) Lazarides, *Forster 20737 & Holland* (MEL), Australia, **KP873631, KP873952, KP874086, KP873813, KP873414;** *Saugetia fasciculata* Hitchc. & Chase, *Ekman s.n.* (US), Dominican Republic, GU359982, GU359528, GU360317, GU360638, GU359156; *Schoenefeldia gracilis* Kunth, *Pauwels 7413* (MO), Benin, KJ768981, –, **KP874087, KP873814, KJ768886;** *Schoenefeldia transiens* (Pilg.) Chiov., *Greenway 9781* (US), Kenya, GU360007, **KP873953, GU360349, GU360636, GU359202;** *Schoenefeldia transiens* (Pilg.) Chiov., *Peterson 24216, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873632, KP873954, KP874088, KP873815, KP873415;** *Schoenefeldia transiens* (Pilg.) Chiov., *Spjut 3920* (BRY), Kenya, JQ345357, JQ345230, JQ345312, JQ345270, JQ345201; *Tetrapogon bidentatus* Pilg., *Bogdan 3903* (US), Kenya, **KP873633, –, KP874089, KP873816, KP873416;** *Tetrapogon bidentatus* Pilg., *Greenway 12778 & Kanuri* (US), Kenya, **KP873634, –, KP874090, –, KP873417;** *Tetrapogon cenchriformis* (A.Rich.) Clayton, *BN 7701* (US), Ethiopia, **KP873635, –, KP874091, KP873817, –;** *Tetrapogon cenchriformis* (A.Rich.) Clayton, *Greenway 8844* (US), Kenya, **KP873636, –, –, –, –;** *Tetrapogon cenchriformis* (A.Rich.) Clayton, *Peterson 24192, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873637, –, –, KP873818, KP873418;** *Tetrapogon cenchriformis* (A.Rich.) Clayton, *Peterson 24240, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873638, KP873955, KP874092, KP873819, KP873419;** *Tetrapogon tenellus* (J.Koenig ex Roxb.) Chiov., *Peterson 23794, Soreng & Romaschenko* (US), Tanzania, **KP873639, KP873956, KP874093, KP873820, KP873420;** *Tetrapogon tenellus* (J.Koenig ex Roxb.) Chiov., *Peterson 24244, Soreng, Romaschenko & Mbago* (US), Tanzania, **KP873640, –, –, KP873821, KP873421;** *Tetrapogon villosus* Desf., *Ash 2561* (US), Ethiopia, GU359902, –, GU360366, GU360620, GU359220; *Tetrapogon villosus* Desf., *Johannes s.n.* (US), Canary Islands, GU359901, GU359514, GU360367, GU360619, GU359221; **Incertae sedis:** *Pogononeura biflora* Napper, *Greenway 10091* (US), Tanzania, KM010694, –, –, –, –; *Neobouteloua lophostachya* (Griseb.) Gould, *Peterson 11515 & Annable* (US), Argentina, GU360004, GU359396, GU360273, GU360725, GU359123; *Neobouteloua pauciracemosa* M.G.López & Biurrun, *Porter 11968 & Columbus* (US), Argentina, **KP873627, –, –, KP873812, KP873413;** *Dactyloctenium geminatum* Hack., *Peterson 23808, Soreng & Romaschenko* (US), Tanzania, **KP873546, KP873904, KP874029, KP873747, KP873329;** *Dactyloctenium robecchii* Chiov., *Puccioni 626 & Stefanini* (FT), Somalia, **KP873547, KP873905, KP874030, KP873748, KP873330;** *Dactyloctenium scindicum* Boiss., *Hemming 2358* (US), Somalia, –, **KP873906, KP874031, KP873749, KP873331.**

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**A molecular phylogeny and classification of the
Eleusininae with a new genus, *Micrachne* (Poaceae:
Chloridoideae: Cynodonteae)**

Paul M. Peterson, Konstantin Romaschenko, & Yolanda Herrera Arrieta

***Taxon* 64: 445–467**

Fig. S2. Maximum-likelihood tree from analysis of 4 plastid markers (*rp132-trnL*, *ndhA* intron, *rps16* intron, *rps16-trnK*). Numbers above branches are posterior probabilities; numbers below branches are bootstrap values.

