




Research Article

Phylogeny, classification, and biogeography of *Afrotrichloris*, *Apochiton*, *Coelachyrum*, *Dinebra*, *Eleusine*, *Leptochloa*, *Schoenefeldia*, and a new genus, *Schoenefeldiella* (Poaceae: Chloridoideae: Cynodonteae: Eleusininae)

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Received 30 April 2021; Accepted 1 July 2021; Article first published online 6 July 2021

Abstract To investigate the evolutionary relationships among species of *Afrotrichloris*, *Apochiton*, *Coelachyrum*, *Dinebra*, *Eleusine*, *Leptochloa*, and *Schoenefeldia* of subtribe Eleusininae, a phylogeny based on DNA sequences from nine gene regions (ITS, *rps16-trnK*, *rps3*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) is presented. Previous molecular phylogenies indicated that *Coelachyrum* was polyphyletic and *Schoenefeldia* was paraphyletic, with *Afrotrichloris* embedded within it. *Apochiton burttii* was embedded in the *Coelachyrum* clade paired with *C. longiglume*, *Coelachyrum poiflorum* was placed outside of *Coelachyrum* and sister to *Eleusine*, and *Schoenefeldia* is paraphyletic, with its two species forming a grade sister to *Afrotrichloris*. Our molecular phylogeny supports recognition of a new genus, *Schoenefeldiella*, and a new combination, *Schoenefeldiella transiens*. In addition, we provide generic emendations for *Coelachyrum*, which now includes five species including a new combination proposed here, *Coelachyrum burttii*, and *Eleusine*, which now includes 11 species.

Key words: Biogeography, *Coelachyrum*, grasses, ITS, molecular systematics, plastid DNA sequences, Poaceae, *Schoenefeldiella*, taxonomy.

1 Introduction

The tribe Cynodonteae currently includes 850 species in 94 genera and 21 subtribes, and it has received high support as a monophyletic lineage in recent molecular analyses (Peterson et al., 2014a, 2015a, 2016; Soreng et al., 2015, 2017). Within the subtribe Eleusininae (236 species in 27 genera), Peterson et al. (2015a) found *Coelachyrum* Hochst. & Nees to be polyphyletic because *C. lagopoides* (Burm.f.) Senaratna, *Apochiton burttii* C.E. Hubb., and *Coelachyrum poiflorum* Chiov. form a grade sister to *Eleusine* Gaertn., and *Schoenefeldia* Kunth is paraphyletic with respect to two samples of *Afrotrichloris martinii* Chiov.

Coelachyrum is a heterogeneous group of five annual or perennial semi-desert grasses that have been grouped together based on having paniculate inflorescences composed of loose to dense racemes, these often spaced (racemose) or clustered (digitate) on a central axis; 3-veined, broadly elliptic to ovate, rounded-on-the-back lemmas; and dorso-ventrally flattened caryopses with free pericarps that are highly ornamented and often rugulose (Phillips, 1974,

1995; Clayton et al., 2016; Cope, 2007). The genus was described by Hochstetter & Nees von Esenbeck based on *Coelachyrum brevifolium* Hochst. & Nees, the type species (Nees von Esenbeck & Schauer, 1842). Twelve years later, Steudel (1854) transferred this species into *Eleusine* along with 15 other species. Recently, *Coelachyrum yemenica* (Schweinf.) S.M. Phillips was transferred to *Disakisperma* Steud. based on the shared morphology and sequence similarity of five DNA markers (Snow et al., 2013). The most recent treatment of *Eleusine* includes 10 species, and eight of these were found in a strongly supported clade sister to *C. poiflorum* in a molecular DNA sequence study (Liu et al., 2011; Peterson et al., 2015a; Soreng et al., 2017).

Apochiton C.E. Hubb. is a monotypic genus known only from Tanzania and is characterized as having an annual habit, panicle branches often reduced to racemes; 3-veined, short-awned lemmas; awned palea keels; and trigonous caryopses with free pericarps (Hubbard, 1936, 1974a). The species has never been attributed to any other genus, and Hubbard

(1936) mentions in his description that the unusual grain (free pericarp) is only known in a few species of *Eragrostis* Wolf, *Sporoboleae* [=Sporobolinae], *Sclerodactylon* Stapf, *Dinebra* Jacq., *Eleusine*, *Dactyloctenium* Willd., and *Coelachyrum*. However, *Afrotrichloris*, *Austrochloris* Lazarides, *Daknopholis* Clayton, *Tetrapogon* Desf., and the Unioliinae Clayton also have grains with a free pericarp (Clayton & Renvoize, 1986).

For most of the 20th century, *Dinebra* was represented by three species (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). Based on results of molecular DNA sequence studies, many species formerly placed in *Leptochloa* s.l. were transferred to an expanded *Dinebra* now with ± 23 species, while *Leptochloa* s.s. was reduced to eight species with recognition of *Diplachne* P. Beauv. (2 spp.), *Disakisperma* (4 spp.), and *Trigonochloa* P.M. Peterson & N. Snow (2 spp.) (Peterson et al., 2012, 2014c, 2015a; Snow & Peterson, 2012; Snow et al., 2013, 2018, in prep.; Soreng et al., 2017).

Schoenefeldia includes two species, *S. gracilis* Kunth (the type) and *S. transiens* (Pilg.) Chiov., both characterized by having solitary, paired, or digitate racemes and spikelets with long-awned lemmas with the awns braided along the culm (Hubbard, 1974b; Cope, 2007). *Schoenefeldia transiens* can be separated from *S. gracilis* in having two-flowered spikelets, with the upper floret sterile and awned, perennial habit, and flat leaf blades 5–35 cm long.

Afrotrichloris Chiov. also includes two species: *A. martinii* and *A. hyaloptera* Clayton. *Afrotrichloris hyaloptera* can be separated from *A. martinii* by the presence of shorter lateral lemma lobes with a longer central awn and longer inflorescence spikes (Clayton, 1967). Clayton (1967) indicated that *Afrotrichloris* bears some similarity to *Trichloris* E. Fourn. ex Benth., although the two species traditionally placed in *Trichloris* now reside within *Leptochloa* P. Beauv. s.s. (Peterson et al., 2012, 2015a). Clayton also mentioned that *A. hyaloptera* is not unlike *Enteropogon* Nees and that *Afrotrichloris* probably represents different lines of divergence from a common *Chloris* Sw. stock.

Using plastid (*rps16-trnK*, *rps3*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) and nuclear ITS DNA sequence markers, we present a new phylogenetic analysis of 85 species in 24 genera of Eleusininae, emphasizing those species surrounding *Coelachyrum*, *Apochiton*, *Schoenefeldia*, and *Afrotrichloris*, along with *Dinebra*, *Leptochloa*, and *Eleusine*. We expand the number of species sampled to include all five accepted species of *Coelachyrum* and both species of *Afrotrichloris* (Clayton et al., 2016; Snow et al., 2013). In addition, we discuss the morphological and anatomical characteristics supporting relationships, discuss biogeography, and propose changes to the classification of studied taxa.

2 Material and Methods

2.1 Taxon sampling

Our sampling consists of 141 samples, representing 85 species of grasses, of which 84 are included in the Cynodonteae and one is included in the Zoysieae. In addition, we include all six species that have been attributed to *Coelachyrum* and two species of *Afrotrichloris* (Clayton et al.,

2006). Outside of the Cynodonteae, *Sporobolus indicus* (L.) R. Br. was chosen as the out group. A complete list of taxa, voucher information, and GenBank numbers can be found in Appendix S1. All collections gathered by PMP after 1998 were collected in silica, but the majority of samples used in this study were obtained from herbarium specimens.

2.2 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 the *rpl32-trnL* spacer and the *ndhA* intron (small single-copy region); the *rps16-trnK* spacer and the *rps16* intron (large single-copy region); *ndhF*, *ccsA*, *rpoC2*, and *rps3* (encoding region); and ITS were accomplished following the procedures outlined in Peterson et al. (2010a, 2010b, 2012, 2014c). We specifically targeted plastid regions that proved to be most informative in our previous studies on chloridoid grasses (Peterson et al., 2010a, 2010b, 2011, 2012, 2014a, 2014b, 2014c, 2015a, 2015b, 2016; Liu et al., 2011).

2.3 Phylogenetic analyses

We used Geneious 5.3.4 (Drummond et al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *ndhA*, *ndhF*, *rps3*, *rps16*, *rps16-trnK*, *rpoC2*, *ccsA*, and ITS regions, and Muscle (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 data sets were partitioned in accordance with the number of markers used. Nucleotide substitution models selected according to Akaike's information criterion, as implemented in jModelTest v.0.1.1, were specified for each partition (Table 1). The ML analysis was conducted using GARLI 0.951 (Zwickl, 2006). The ML bootstrap analysis was performed with 1000 replicates, with 10 random additional sequences per replicate. The output file containing trees of ML found for each bootstrap data set 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 support, and 50%–69% as weak support.

Bayesian posterior probabilities (PP) were estimated using a parallel version of MrBayes v3.1.2 (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 four million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences decreased 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. PP of 0.95–1.00 were considered to indicate strong support.

In the phylogram (Fig. 1), the native distribution of each species is indicated by color as follows: North America (red), South America (tan), Africa (dark green), Australia + Pacific (dark purple), and Eurasia (light purple).

Table 1 Characteristics of the nine regions, *rps3*, *rps16-trnK*, *rps16* intron, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA* intron, *ccsA*, and ITS, and parameters used in Bayesian analyses indicated by the Akaike information criterion (AIC)

	<i>rps3</i>	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpoC2</i>	<i>rpl32-trnL</i>	<i>ndhF</i>	<i>ndhA</i> intron	<i>ccsA</i>	Combined plastid data	ITS	Overall
Total aligned characteristics	612	1079	898	808	884	765	1150	954	6949	746	7695
Number of sequences	77	101	92	77	120	73	80	70	690	135	825
Number of new sequences	47 (61%)	5 (5%)	3 (3%)	43 (56%)	10 (8%)	30 (41%)	3 (4%)	13 (19%)	154 (22%)	15 (11%)	167 (20%)
Likelihood score (-lnL)	1804.51	4012.8	3463.46	3041.68	4562.75	3779.90	4493.11	3048.45		11973.22	
Number of substitution types	6	6	6	6	6	6	6	6		6	
Model for among-site rate variation	gamma	gamma	gamma	gamma	gamma	gamma	gamma	gamma		gamma	
Substitution rates	1.67364	1.37867	1.17620	3.50734	0.97820	2.18640	1.38202	1.48282		1.26970	
	3.41539	2.83812	1.13839	5.16054	1.93638	3.03867	3.41070	3.95747		3.24444	
	0.48663	0.47934	0.25602	0.30343	0.36141	0.52675	0.70511	0.59455		1.92507	
	0.76892	1.70272	1.00798	2.04551	1.03125	1.65272	2.76200	1.27255		0.95472	
	4.82223	2.86646	1.92645	10.40906	1.52720	3.94143	3.61463	3.97891		4.87150	
	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000	1.00000		1.00000	
Characteristic state frequencies	0.43286	0.30958	0.39282	0.39745	0.37470	0.32680	0.36119	0.30032		0.23398	
	0.15127	0.14992	0.10761	0.14583	0.13243	0.12869	0.13661	0.15882		0.20819	
	0.16885	0.14703	0.16687	0.23401	0.12790	0.17034	0.14784	0.16227		0.25067	
	0.24701	0.39348	0.33271	0.22272	0.36497	0.37417	0.35436	0.37860		0.30716	
Proportion of invariable sites	0.68799	0.10426	0.33335	0.00000	0.18741	0.29544	0.34523	0.54699		0.23903	
Substitution model	TVM+G	TVM+G	GTR+I+G	TIM3+I+G	GTR+G	TPM3uf+G	TVM+I+G	TPM3uf+G		GTR+I+G	
Gamma shape parameter (α)	0.792707	1.05499	0.97074	0.57086	0.99039	0.78355	0.95969	0.96672		0.97093	

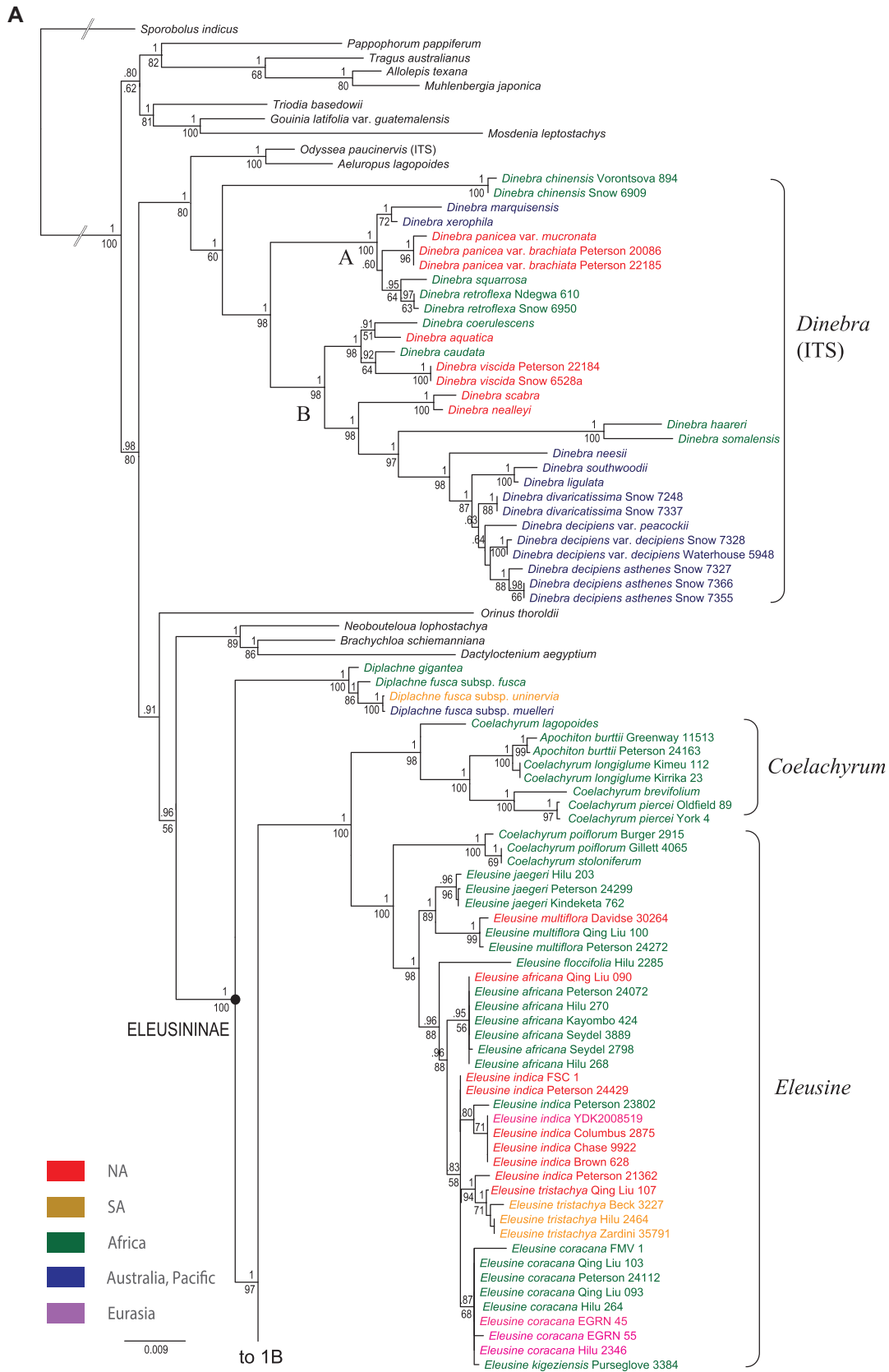


Fig. 1. A and B Maximum-likelihood tree inferred from combined plastid (*rps16-trnK*, *rps3*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) and ITS sequences. Numbers above branches show posterior probabilities; numbers below branches show bootstrap values; color indicates where the sample was collected, usually indicative of native status; and vertical bars indicate our classification. Scale bar = 0.9% substitutions/site.

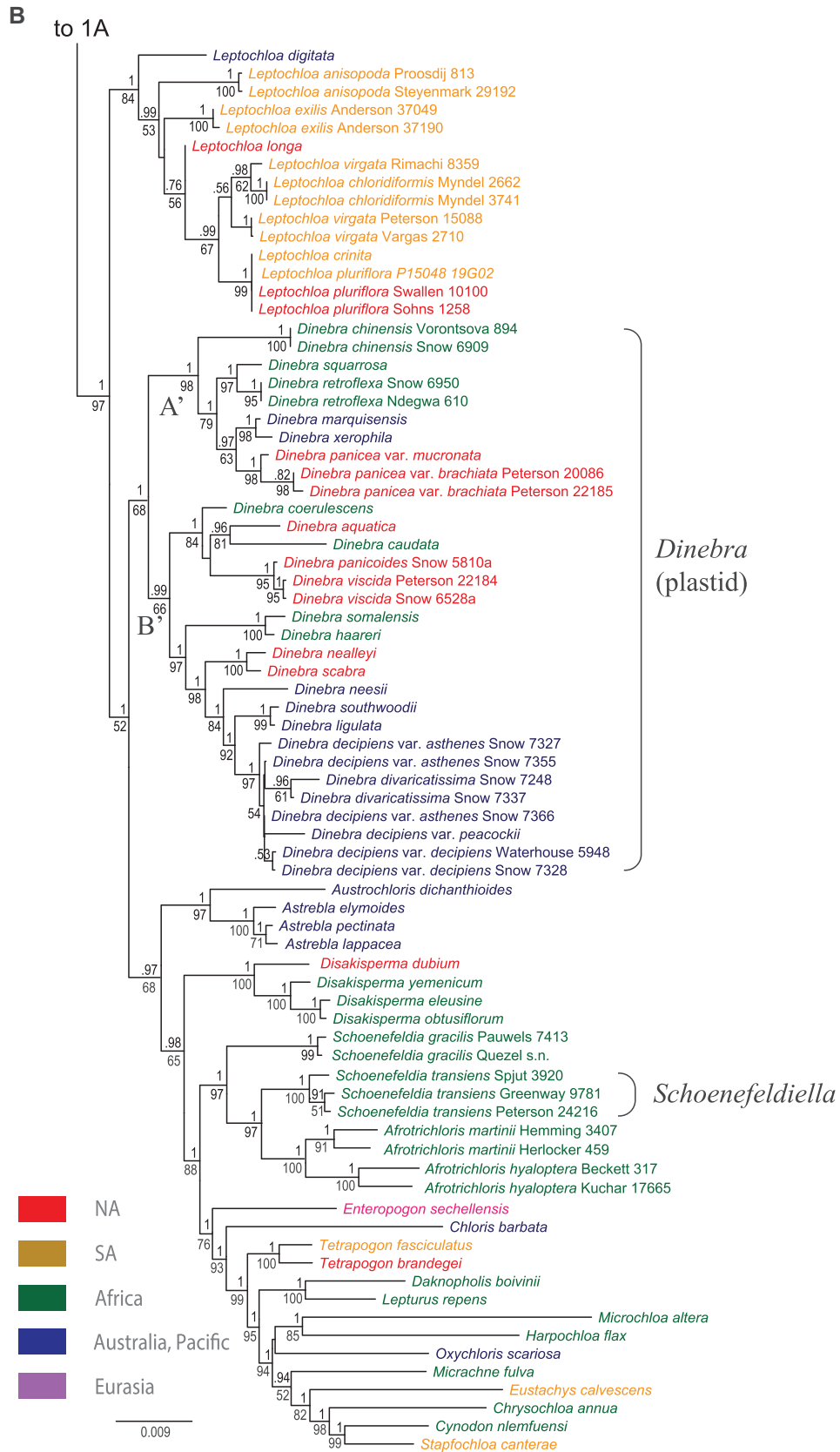


Fig. 1. Continued

2.4 Assessment of incongruence and data combining strategy

The resulting plastid and ITS topologies were inspected for conflicting nodes (see Fig. 1) with $\geq 80\%$ bootstrap support (BS) and/or PP ≥ 0.95 . If no supported conflict was found, plastid and ITS sequences were combined. Where conflicting topologies were found, the data sets for inconsistently placed taxa were duplicated in the matrix. One set of the taxon was represented by the corresponding plastid sequences only and the other taxon set by only ITS sequences. The remaining positions for the truncated data sets were then coded as missing data. We use this “taxon duplication” approach (Pirie et al., 2008; Pelsner et al., 2010; Peterson et al., 2015b, 2016) to resolve our phylogenetic tree minimizing the diffusing effects of taxa with strongly supported incongruence between the plastid and ITS data, and to represent their alternative placements in relation to the remaining phylogenetic groups among which relationships are congruent (see Fig. 1). The combination of data is advantageous because it can provide better backbone support for nodes through the use of plastid data and improve resolution for terminal nodes within the main phylogenetic groups using ITS sequences.

3 Results

3.1 Phylogenetic analyses

Twenty percent (167/823) of the sequences used in our study are newly reported here (Appendix S1). The characteristics of the nine regions are presented in Table 1. Forty-seven sequences of *rps3* (61%), 43 for *rpoC2* (56%), and 30 for *ndhF* (41%), 13 for *ccsA* (19%), 15 for ITS (11%), 10 for *rpl32-trnL* (8%), 5 for *rps16-trnK* (5%), 3 for *ndhA* (4%), and 3 for *rps16* (3%) are newly reported. Sequence alignment length for *ndhA* is 1150 bp, that for *rps16-trnK* is 1079 bp, that for *ccsA* is 954 bp, that for *rps16* is 898, that for *rpl32-trnK* is 884 bp, that for *rpoC2* is 808 bp, that for *ndhF* is 765 bp, that for ITS is 746 bp, and that for *rps3* is 612 bp. Four hundred and forty-six sequences or 35% (446/1269) were missing.

3.2 Incongruence between ITS and combined plastid phylograms

The ITS signal places the *Dinebra* clade as sister to *Aeluropus lagopoides*–*Odysea paucinervis* (PP = 1, BS = 80 in the Aeluropodinae) outside the Eleusininae, whereas the combined plastid signal places the *Dinebra* clade within Eleusininae (PP = 1, BS = 68). The topology among the species of *Dinebra* in the ITS- and plastid-derived trees is also different (Figs. 1A and 1B).

In the ITS-derived tree, *Dinebra chinensis* (L.) P.M. Peterson & N. Snow are sister to all remaining species in the genus that forms two clades (labeled A and B on Fig. 1A). Clade A (PP = 1, BS = 100) contains two varieties of *D. panicea* (Retz.) P.M. Peterson & N. Snow (PP = 1, BS = 96) that are sister to *D. squarrosa* (Pilg.) P.M. Peterson & N. Snow–*D. retroflexa* (Vahl.) Panz. (PP = 0.95, BS = 64), and these are sister to *D. marquisensis* (F. Br.) P.M. Peterson & N. Snow–*D. xerophila* (P.M. Peterson & Judz.) P.M. Peterson & N. Snow. Clade B contains an Australian clade with a monophyletic *D. decipiens* (R. Br.) P.M. Peterson & N. Snow, with three varieties sister

to *D. divaricatissima* (S.T. Blake) P.M. Peterson & N. Snow. Sister to *D. decipiens*–*D. divaricatissima* is *D. ligulata* (Lazarides) P.M. Peterson & N. Snow–*D. southwoodii* (N. Snow & B.K. Simon) P.M. Peterson & N. Snow (PP = 1, BS = 100). The basal member of the Australian clade is *D. neesii* (PP = 1, BS = 87), and sister to the Australian clade *D. haareri* (Stapf & C.E. Hubb.) P.M. Peterson & N. Snow–*D. somalensis* (Stapf) P.M. Peterson & N. Snow (PP = 1, BS = 98). Sister to *D. haareri*–*D. somalensis* + the Australian clade is *D. nealleyi* (Vasey) P.M. Peterson & N. Snow–*D. scabra* (Nees) P.M. Peterson & N. Snow (PP = 1, BS = 97). Sister to *D. nealleyi*–*D. scabra* + *D. haareri*–*D. somalensis* + the Australian clade is *D. aquatica* (Scribn. & Merr.) P.M. Peterson & N. Snow–*D. coerulescens* (Steud.) P.M. Peterson & N. Snow + *D. caudata* (K. Schum.) P.M. Peterson & N. Snow–*D. viscida* (Scribn.) P.M. Peterson & N. Snow (PP = 1, BS = 98).

In the plastid-derived tree, there are also two clades (labeled A' and B' in Fig. 1B). In clade A', the two varieties of *D. panicea* (PP = 1, BS = 98) are sister to *D. marquisensis*–*D. xerophila* (PP = 1, BS = 98). Sister to *D. panicea* + *D. marquisensis*–*D. xerophila* is *D. retroflexa*–*D. squarrosa* (PP = 1, BS = 97), and all of these are sister to *D. chinensis* (PP = 1, BS = 79). In clade B', the monophyletic Australian clade includes *D. divaricatissima* embedded with the three varieties of *D. decipiens* and this is sister to *D. nealleyi*–*D. scabra* (PP = 1, BS = 84). *Dinebra haareri*–*D. somalensis* (PP = 1, BS = 100) is sister (PP = 1, BS = 98) to *D. nealleyi*–*D. scabra* + the Australian clade, and all of these form a clade (PP = 0.99, BS = 66) with *D. panicoides* (J. Presl) P.M. Peterson & N. Snow–*D. viscida* + *D. aquatica*–*D. caudata* sister to *D. coerulescens* (PP = 1, BS = 84).

3.3 Phylogenetic tree of Eleusininae

The ML tree from the combined plastid and ITS regions is well resolved, with strong support (PP = 1, BS ≥ 98) for the Eleusininae and the following genera: *Afrotrichloris*, *Astrebla* F. Muell., *Ceolachyrum* s.s., *Diplachne*, *Disakisperma*, and *Eleusine* (Figs. 1A and 1B).

Diplachne is sister to all remaining genera in the Eleusininae (PP = 1, BS = 97). *Coelachyrum* is polyphyletic because *C. poiflorum* is sister to all species of *Eleusine* (PP = 1, BS = 98). *Apochiton burttii* C.E. Hubb. is embedded within *Coelachyrum* and sister to *C. longiglume* Napper, and this pair is sister to *C. brevifolium* Hochst. & Nees + *C. piercei* (Benth.) Bor (PP = 1, BS = 100). *Coelachyrum lagopoides* (type) is sister to the rest of the *Coelachyrum* s.s. clade. *Eleusine* is monophyletic with *E. jaegeri* Pilg. + *E. multiflora* Hochst. ex A. Rich. sister to remaining species in the genus. *Eleusine floccifolia* (Forssk.) Spreng. is sister (PP = 0.96, BS = 88) to *E. africana* Kenn.-O'Byrne + *E. indica* (L.) Gaertn. + *E. tristachya* (Lam.) Lam. + *E. coracana* (L.) Gaertn. + *E. kigeziensis* S.M. Phillips. Seven accessions of *E. africana* form a clade (PP = 0.95, BS = 56) and these are sister to a polytoma that includes *E. indica* (polyphyletic), *E. tristachya* (PP = 1, BS = 71), and *E. coracana* + *E. kigeziensis* (PP = 87, BS = 68).

The *Leptochloa* clade is moderately supported (PP = 1, BS = 84), with *L. crinita* (Lag.) P.M. Peterson & N. Snow and *L. pluriflora* (E. Fourn.) P.M. Peterson & N. Snow forming a clade showing little variation sister to a clade containing *L. chloridiformis* Parodi–*L. virgata* (L.) P. Beauv. (PP = 0.56), where a single individual of *L. virgata* (*Rimachi* 8359) is sister

to two accessions of *L. chloridiformis*, rendering *L. virgata* polyphyletic. *L. longa* Griseb. is sister to the *L. crinita*–*L. pluriflora* + *L. chloridiformis*–*L. virgata* clade. *Leptochloa digitata* (R. Br.) Domin is the first split, followed by two accessions of *L. anisopoda* (Scribn. ex B.L. Rob.) P.M. Peterson, and *L. exilis* (Renvoize) P.M. Peterson.

Austrochloris Lazarides + *Astreba* F. Muell. (PP = 1, BS = 97) are sister to the remaining Eleusininae genera (PP = 0.98, BS = 65; Fig. 1B). The next split includes the *Disakisperma* clade (PP = 1, BS = 100) sister to remaining Eleusininae. *Schoenefeldia* appears polyphyletic, with its two species in a grade sister to a monophyletic *Afrotrichloris* (PP = 1, BS = 100). *Schoenefeldia gracilis* is basal and sister to *S. transiens* + *Afrotrichloris*.

4 Discussion

4.1 Phylogeny

We found strong support for the following lineages recognized as genera: *Afrotrichloris*, *Astreba*, *Coelachyrum*, *Dinebra*, *Diplachne*, *Disakisperma*, *Eleusine*, and *Leptochloa*. However, our *Coelachyrum* clade is paraphyletic because it includes *Apochiton burttii* in a subclade with *C. longiglume*. These two species share morphological synapomorphies of an annual habit, a paniculate inflorescence, and pedicelled spikelets, whereas the other three species of *Coelachyrum* are perennial and have a raceme inflorescence (the branches inserted digitally or along the main axis), and nearly sessile spikelets. Therefore, we create the new combination for *Apochiton* below and emend *Coelachyrum* to include short-awned lemmas and paleas, and trigonous caryopses.

Chiovenda (1915) was the first to recognize the affinities of *C. poiflorum* by placing it in *Eleusine*. However, he mentions two other species, *Eleusine somalensis* Hack. and *E. yemensis* (Schweinf) Chiov., that, based on our earlier molecular studies, are placed in *Dinebra* and *Disakisperma*, respectively (Peterson et al., 2012; Snow et al., 2013). *Coelachyrum poiflorum* [\equiv *Eleusine poiflora* (Chiov.) Chiov.] has hairy florets, villous lemmas villous with spreading hairs on the midvein and flanks below, and villous palea keels (Phillips, 1995). The only distinguishing characteristic separating *C. poiflorum* from other species of *Eleusine* is hairy florets. Therefore, it seems best to align *C. poiflorum* within *Eleusine*, splitting at the same hierarchical level as *Coelachyrum* in our tree (Fig. 1A), rather than erect a new genus.

Our new phylogeny of *Eleusine* is topologically similar to that found in Liu et al. (2011) in their investigation of low-copy nuclear genes. However, we found a moderately supported *E. jaegeri* + *E. multiflora* clade (PP = 1, BS = 89), whereas Liu et al. (2011) found a strongly supported *E. jaegeri* + *E. floccifolia* clade (BS = 90–100, PP = 1) for both nuclear trees derived from *EF-1a* and *Pepc4* markers. We did not include *E. intermedia* (Chiov.) S.M. Phillips in our current study, and this may have affected our topology.

We verify for the first time using molecular data that *Leptochloa longa* aligns within *Leptochloa* and the number of species within the genus increases to eight. However, the exact placement of *L. longa* within the *Leptochloa* clade is tentative because we were only able to sequence the *rps3* marker for this species, although morphologically, *L. longa* fits easily into the

genus. The overall topology among the species of *Leptochloa* in our phylogeny is similar to that found in Peterson et al. (2015a). There are still three species that have historically been placed in *Leptochloa*: *L. malayana* (C.E. Hubb.) Jansen ex Veldkamp, *L. monticola* Chase, and *L. tectoneticola* (Backer) Jansen ex Veldkamp, that have not been included in a molecular DNA phylogeny and need further study.

The unresolved placement of the *Dinebra* clade (inside or outside of the Eleusininae) has been documented previously in Peterson et al. (2012, 2015a, 2016). Incongruence between the plastid and nuclear DNA signal is common, especially within the Poaceae, and more study of *Dinebra* is necessary to untangle its evolutionary history, although it appears to be another case of hybridization and subsequent genomic introgression (Peterson et al., 2016). In addition, there are four species currently placed in *Dinebra*, *D. perrieri* (A. Camus) Bosser., *D. polycarpha* S.M. Phillips, *D. simoniana* (N. Snow) P.M. Peterson & N. Snow, and *D. srilankensis* (N. Snow) P.M. Peterson & N. Snow, that have not been included in a molecular DNA phylogeny and require further study.

The inclusion of *Afrotrichloris hyaloptera* in our current study as a strongly supported sister to *A. martinii* provides evidence for retaining *Afrotrichloris* as a separate genus characterized by having a racemose inflorescence, 3- to 5-veined upper glumes shorter than the lemma, and deeply cleft lemma apices that can be awned (Watson & Dallwitz, 1992; Phillips, 1995; Clayton et al., 2016). *Afrotrichloris* shares many morphological features with *Schoenefeldia*, including racemose inflorescences, long-awned lemmas, and caryopses with free pericarps. However, in our phylogeny, *Schoenefeldia* is paraphyletic, with the two species of *Schoenefeldia* in a grade sister to *Afrotrichloris*. We are left with two options to interpret the taxonomy of these four species: (A) recognize all four species in *Schoenefeldia* or (B) erect a new genus for *S. transiens* because it does not pair with the type, *S. gracilis*. We chose B and describe a new genus, *Schoenefeldiella* below.

4.2 Biogeography

The Eleusininae (crown age of 25.85 Ma), a diverse assemblage now consisting of 28 genera with addition of *Schoenefeldiella*, may have originated in Africa because it shares a common ancestor with subtribe Dactylocteniiinae P.M. Peterson, Romasch. & Y. Herrera, also of African origins (Peterson et al., 2015a, 2016; Gallaher et al., 2022). Both species of *Afrotrichloris* (African), five species of *Coelachyrum* (primarily African, spreading to Asia), 10 of the 11 species of *Eleusine* Gaertn. (primarily African, Asian, and Australasian; only *E. tristachya* radiated to South America), and a single species each of *Schoenefeldia* and *Schoenefeldiella* occur in Africa (Liu et al., 2011; Clayton et al., 2016). *Dinebra* (± 23 species, African, Australasian, and North American) also seems to have African origins as shown in our analyses. *Dinebra chinensis* (native to east Africa, Asia, Malaysia, Papua New Guinea, Philippines, and Japan) is depicted as the basal split in our ITS-derived clade and in the plastid-derived A' clade, whereas in the plastid-derived B' clade, the first bifurcation *D. coerulescens* (African) is sister to the remaining species and the second bifurcation *D. haareri* + *D. somalensis* (African) is sister to the remaining species in the genus. The origins of *Leptochloa* are more difficult to speculate about because the basal species *L. digitata* is endemic to

Australia and shares a common ancestor with the remaining species of *Leptochloa*, many of which are widespread in the western hemisphere (4 spp.) or restricted to South America and/or the Caribbean (2 spp.), and Panama and Trinidad (1 spp.) (Snow et al., in prep). As mentioned previously, there are still three species only tentatively placed in *Leptochloa*; two of these, *L. malayana* and *L. tectoneticola* from tropical Asia, Indo-China, and Malaysia, were initially placed in *Diplachne* (Veldkamp, 1971; Clayton et al., 2016).

5 Taxonomy

5.1 *Coelachyrum* Hochst. & Nees, *Linnaea* 16(2): 221. 1842. **gen. emend.** Type: *Coelachyrum brevifolium* Hochst. & Nees

Description: Annuals or perennials, tufted, sometimes stoloniferous. Culms 7–90 cm long, geniculately ascending or decumbent, usually rooting at the lower nodes. Leaf sheaths glabrous; ligules membranous, sometimes with a ciliate fringe, apex usually truncate; and blades linear or lanceolate, occasionally rounded or cordate near base, flat. Inflorescence a panicle with pedicelled spikelets (*C. burttii* & *C. longiglume*) or composed of racemes; these either digitately inserted or racemously inserted along a main axis with nearly sessile spikelets. Spikelets 3- to 14-flowered, ovate, elliptic, or oblong, laterally compressed; disarticulation below the glumes, the spikelet falling as a unit; glumes shorter than the spikelet, 1–3 (–7)-veined, membranous, persistent, apex obtuse to acute, sometimes mucronate, and occasionally short-awned (*C. burttii*); lemmas 3-veined, membranous, glabrous, asperulous, or hairy, apex truncate, obtuse or acute to mucronate, occasionally short-awned (*C. burttii*); paleas shorter than the lemma, two-keeled, the keels ciliate or glabrous, occasionally the keels extending into awns (*C. burttii*); stamens 3. Caryopses ellipsoid, ovoid, oblong, or reniform, concavo–convex flattened or trigonous (*C. burttii*), the surface granular or rugose, pericarp free.

Distribution: Five species comprise *Coelachyrum*, which are found in west and east tropical Africa and tropical Asia in Arabia, Pakistan, and India (Phillips, 1995; Cope, 2007).

5.2 *Coelachyrum burttii* (C.E. Hubb.) P.M. Peterson, **comb. nov.** \equiv *Apochiton burttii* C.E. Hubb., *Hooker's Icon. Pl.* 34: t. 3319. 1936. Type: Tanzania, Tanganyika Territory, Kondoa Irangi District near Sambala, 19 May 1929, B.D. Burtt 2602 (holotype: K000366648 [image!]; isotype: US-1646885!).

5.3 *Eleusine* Gaertn., *Fruct. Sem. Pl.* 1:7. 1788. **gen. emend.** Type: *Eleusine coracana* (L.) Gaertn. (\equiv *Cynosurus coracanus* L.)

Description: Tufted annuals or perennials, sometimes rhizomatous or stoloniferous. Culms 10–200 cm tall, erect, geniculately ascending or decumbent; internodes flattened and elliptical in cross section. Leaf sheaths usually shorter than the internodes, keeled; ligules membranous, apex truncate, ciliate; blades smooth, occasionally with scattered papillose-based hairs, mostly flat. Inflorescence with digitate, subdigitate, or with a main axis of racemes, the spikelets biserial on one side of the triangular rachis, sessile. Spikelets 6- to 18-flowered, ovate, laterally compressed; disarticulation above the glumes and between the

florets; glumes shorter than the spikelets, usually 1-veined, but occasionally 2- to 7-veined, ovate, membranous, apex acute to obtuse, occasionally mucronate; lemmas 3-veined, membranous, the veins usually glabrous or occasionally with shaggy hairs below (*E. poiflora*), margins glabrous or sometimes hairy, apex acute, obtuse or truncate, occasionally mucronate; paleas shorter than the lemmas, 2-veined, the veins glabrous or occasionally with hairs (*E. poiflora*); stamens 3. Caryopses mostly trigonous, but occasionally dorsally or laterally compressed or concavo-convex, the surface granular, striate or rugose, hilum punctiform, and pericarp free.

Distribution: With the inclusion of *Eleusine poiflora* (\equiv *Coelachyrum poiflorum* Chiov. = *Coelachyrum stoloniferum* C.E. Hubb.), there are now 11 species of *Eleusine*, of which nine are found in Africa; of these nine, *E. indica* is a pantropical weed and *E. poiflora* extends into Somalia, Djibouti, Saudi Arabia, Yemen, and Oman; *E. tristachya* is native to South America; and *E. coracana* (finger millet) is known only from cultivation (Phillips, 1972, 1995; Peterson et al., 2001, 2015a; Cope, 2007).

5.4 *Schoenefeldiella* P.M. Peterson, **gen. nov.** – Type: *Schoenefeldiella transiens* (Pilg.) P.M. Peterson [\equiv *Schoenefeldia transiens* (Pilg.) Chiov.]

Diagnosis: *Schoenefeldiella* differs from *Schoenefeldia* in having 2-flowered spikelets with the upper floret sterile and awned, perennial habit, and flat leaf blades 5–35 cm long.

Description: Plants perennial, tufted. Culms 70–120 cm tall, erect, or geniculately ascending. Leaf blades 5–35 cm long, 1–5 mm wide, flat, scaberulous, or smooth below, glabrous, or loosely pilose. Inflorescence with 2–4 racemes digitately inserted; racemes 10–20 cm long, straight or flexuous, one-sided and two-rowed with sessile spikelets, rachis 0.5–0.8 mm wide; and disarticulation below the spikelets. Spikelets 3.5–5 mm long, 2-flowered, laterally compressed, the lower floret perfect, the upper floret reduced (vestigial) and sterile; glumes 2–5 mm long, 1-veined; lower glume 1.5–3 mm long, awned, the awn 1–2.5 mm long; upper glumes 3.5–5 mm long, unawned; perfect lemmas 3–4 mm long, 3-veined, membranous, awned, margins ciliate, the awns 25–45 mm long usually twisting and closely appressed to the raceme, apically inserted between a minutely bifid apex; sterile lemmas 0.4–1 mm long, awned, the awn 10–25 mm long; callus pilose, obtuse; paleas hyaline, 2-veined; stamens 3, anthers 0.5–1 mm long. Caryopses ellipsoid, laterally compressed, hilum punctiform, and pericarp free.

Distribution: *Schoenefeldiella transiens* is found in Eastern Africa from Ethiopia, South Sudan, Somalia, Uganda, Kenya, Tanzania, Zimbabwe, Mozambique, and South Africa (Hubbard, 1974b; Phillips, 1974, 1995; Russell et al., 1990; Cope, 1995, 1999; Mashau & Götze, 2014)

Schoenefeldiella transiens (Pilg.) P.M. Peterson, **comb. nov.** \equiv *Chloris transiens* Pilg., *Bot. Jahrb. Syst.* 51: 418. 1914 \equiv *Schoenefeldia transiens* (Pilg.) Chiov., *Res. Sci. Somal. Ital.* 1: 186. 1916 – Lectotype (designated by C.E. Hubbard in *Fl. Trop. E. Afr., Gramineae* 2: 309. 1974): TANZANIA. Pare District, Kwa Sengiwa-Maji ya juu, steppe below Kilimanjaro, 900 m, 14 Dec 1901, C. Uhlig 882 (B10 0002186 [image!]; isolectotype: EA00000056 [image!]).

Etymology: The name is derived from *Schoenefeldia* because both genera share many morphological features.

Acknowledgements

We thank the National Geographic Society Committee for Research and Exploration (Grant No. 8848–10, 8087–06) for field and laboratory support, the Smithsonian Institution's Restricted Endowments Fund, the Scholarly Studies Program, Research Opportunities, Atherton Seidell Foundation, Biodiversity Surveys and Inventories Program, Small Grants Program, the Laboratory of Analytical Biology, and the United States Department of Agriculture for financial support. We would also like to acknowledge Robert J. Soreng for many extended discussions pertinent to the manuscript and Jeffery M. Saarela and Neil Snow for providing helpful comments on the manuscript.

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Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12803/supinfo>:

Appendix S1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of rps3, rps16-trnK, rps16 intron, rpoC2, rpl32-trnL, ndhF, ndhA intron, ccsA, and ITS regions (bold indicates new accession); a dash (–) indicates missing data; and an asterisk (*) indicates sequences not generated in our lab.

Appendix S1: Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps3*, *rps16-trnK*, *rps16 intron*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA intron*, *ccsA*, and ITS; regions in **bold** indicate new accession; a dash (–) indicates missing data; an asterisk (*) indicates sequences not generated in our lab.

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-trnK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-trnL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Aeluropus lagopoides</i> (L.) Trin. ex Thwaites	Weinert s.n. & Mosawi (US)	Iraq	GU360085	GU360576	GU360284	KX582739	GU360013	GU359591	GU359391	KX582252	GU359261
<i>Afrotrichloris hyaloptera</i> Clayton	Beckett 317 (US)	Somalia	–	KX582950	–	–	MK530921	–	–	–	MK514298
<i>Afrotrichloris hyaloptera</i> Clayton	Kuchar 17665 (MO)	Somalia	–	–	–	–	MK530922	–	–	–	MK514299
<i>Afrotrichloris martinii</i> Chiov.	Hemming 3407 (FT)	Somalia, Mudug	–	KP873645	KP873962	–	KP873428	KX582503	KP873827	MK530788	KP873212
<i>Afrotrichloris martinii</i> Chiov.	Herlocker 459 (MO)	Somalia	–	–	–	–	–	MK530805	–	MK530789	KP873213
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F. Decker	Hitchcock 7541 (US)	Mexico, Durango	GU360088	GU360573	GU360318	MK530832	GU360015	GU359577	GU359388	JQ345048	GU359264
<i>Apochiton burtii</i> C.E. Hubb.	Peterson 24163, Soreng, Romaschenko & Abeid (US)	Tanzania, Dodoma	MK530873	KP873646	KP873963	KX582741	KP873429	KX582504	KP873828	–	KP873214
<i>Apochiton burtii</i> C.E. Hubb.	Greenway 11513, & Polhill (US)	Tanzania	GU360090	GU360571	–	–	–	GU359594	–	–	GU359266
<i>Astrebla elymoides</i> F. Muell. ex F.M. Bailey	Hubbard 7976 (US)	Australia	GU360093	–	GU360313	MK530833	KP873430	GU359587	GU359414	–	GU359269
<i>Astrebla lappacea</i> (Lindl.) Domin	McKinlay s.n. (US)	Australia	GU360094	GU360568	GU360312	KX582742	GU360009	GU359586	GU359395	KX582254	GU359270
<i>Astrebla pectinata</i> (Lindl.) F. Muell. ex Benth.	Chalmers 5 (US)	Australia	GU360095	GU360567	GU360311	KX582743	GU359861	GU359585	GU359421	JQ345050	GU359286
<i>Austrochloris dichanthioides</i> (Everist) Lazarides	Anson s.n. (US)	Australia, Queensland	GU360113	GU360566	GU360310	KX582744	GU359860	GU359584	GU359420	JQ345051	GU359272
<i>Brachychloa schiemaniana</i> (Schweick.) S.M.Phillips	Schweickerdt 1911 (US)	South Africa	GU360117	GU360582	–	KX582749	GU359881	GU359776	–	JQ345060	GU359256
<i>Chloris barbata</i> Sw.	Saarela 1830, Peterson, Soreng & Judziewicz (CAN)	Australia, Northern Territory	MK530874	KP873659	KP873977	KX582751	KP873443	KX582508	KP873838	KX582256	KP873228
<i>Chrysochloa annua</i> C.E. Hubb.	Arkrok 20417 (US)	Ghana, Yapei Ferri	–	KP873718	KP874002	KX582752	KP873515	KX582509	KP873880	KX582257	KP873300

Taxa	Voucher	Country	rps3	rps16-tr nK	rps16 intron	rpoC2	rpl32-tr nL	ndhF	ndhA intron	ccsA	ITS
<i>Coelachyrum brevifolium</i> Hochst. & Nees	Golding 37 (US)	Nigeria, Arege	-	-	-	-	MK530923	-	-	-	MK514300
<i>Coelachyrum lagopoides</i> (Burm. f.) Senaratna	Saldanha 15334 (US)	India	-	GU360602	-	-	GU359844	GU359572	-	-	-
<i>Coelachyrum longiglume</i> Napper	Kimeu 112 (K)	Kenya	-	MK530930	-	-	MK530924	-	-	-	MK514301
<i>Coelachyrum longiglume</i> Napper	Kirrika 23 (K)	Kenya, Isiolo					XX000000				XX000000
<i>Coelachyrum piercei</i> (Benth.) Bor	Oldfield 89		-	-	-	-	MK530925	-	-	-	MK514302
<i>Coelachyrum piercei</i> (Benth.) Bor	York 4		-	-	-	-	MK530926	-	-	-	MK514303
<i>Coelachyrum poiflorum</i> Chiov.	Burger 2915 (US)	Ethiopia	GU360129	GU360601	GU360457	KX582757	GU359843	-	-	-	GU359236
<i>Coelachyrum poiflorum</i> Chiov.	Gillett 4065 (US)	Somalia, Hargeisa	-	-	-	-	MK530927	-	-	-	MK514304
<i>Coelachyrum stoloniferum</i> C.E. Hubb.	Archer 10150 (US)	Ethiopia, Erer	-	-	-	-	MK530928	-	-	-	MK514305
<i>Cynodon nlemfuensis</i> Vanderyst	Peterson 24058, Soreng, Romaschenko & Abeid (US)	Tanzania, Mbeya	MK530875	KP873742	KP874024	KX582760	KP873542	KX582513	KP873900	KX582262	KP873324
<i>Dactyloctenium aegyptium</i> (L.) Willd.	Peterson 22283 & Saarela (US)	Mexico, Oaxaca	GU360122	GU360587	GU360432	KX582762	GU359886	GU359713	GU359351	JQ345070	GU359251
<i>Daknopholis boivinii</i> (A. Camus) Clayton	Ranaivojaona 1441, Andrianjafy, Phillipson & Lubke (MO)	Madagascar, Toliara	MK530876	KP873750	KP874032	KX582765	KP873548	KX582514	KP873907	KX582263	KP873332
<i>Dinebra aquatica</i> (Scribn. & Merr.) P. M. Peterson & N. Snow	Soderstrom 650 (US)	Mexico, Jalisco	-	KP873751	KP874033	-	KP873549	-	KP873908	-	KP873333
<i>Dinebra caudata</i> (K. Schum.) P. M. Peterson & N. Snow	Kuchar 24265 (MO)	Tanzania, Singida District	MK530877	JQ345239	JQ345282	MK530834	JQ345324	MK530806	JQ345210	JQ345096	JQ345170
<i>Dinebra chinensis</i> (L.) P. M. Peterson & N. Snow	Snow 6909 (MO)	Botswana	MK530878	JQ345240	-	-	JQ345325	-	-	JQ345097	JQ345171
<i>Dinebra chinensis</i> (L.) P. M. Peterson & N. Snow	Vorontsova 894 (K)	Kenya	MK530879	MK530931	-	-	MK530929	-	-	MK530790	MK514306

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Dinebra coerulescens</i> (Steud.) P. M. Peterson & N. Snow	Harris 289 & Fay (MO)	Central African Republic, Sangha Economiq ue	-	-	JQ345283	MK530835	-	-	-	-	JQ345172
<i>Dinebra decipiens</i> subsp. <i>asthenes</i> (Roem. & Schult.) P. M. Peterson & N. Snow	Snow 7327 (MO)	Australia	MK530880	JQ345241	JQ345284	MK530836	JQ345326	-	-	JQ345098	JQ345173
<i>Dinebra decipiens</i> subsp. <i>asthenes</i> (Roem. & Schult.) P. M. Peterson & N. Snow	Snow 7355 (MO)	Australia	MK530882	JQ345243	JQ345286	MK530838	JQ345328	MK530808	JQ345212	JQ345100	JQ345175
<i>Dinebra decipiens</i> subsp. <i>asthenes</i> (Roem. & Schult.) P. M. Peterson & N. Snow	Snow 7366 (MO)	Australia	MK530883	-	-	-	-	-	-	-	MK514307
<i>Dinebra decipiens</i> subsp. <i>decipiens</i> (R. Br.) P. M. Peterson & N. Snow	Snow 7328 & Simon (MO)	Australia, Queensland	MK530881	JQ345242	JQ345285	MK530837	JQ345327	MK530807	JQ345211	JQ345099	JQ345174
<i>Dinebra decipiens</i> subsp. <i>peacockii</i> (Maiden & Betche) P. M. Peterson & N. Snow	Snow 7361 & Simon (MO)	Australia, Queensland	-	JQ345244	JQ345287	MK530839	JQ345329	-	MF353842	-	JQ345176
<i>Dinebra decipiens</i> subsp. <i>decipiens</i> (R. Br.) P. M. Peterson & N. Snow	Waterhouse 5948 (MO)	Australia	MK530884	JQ345245	JQ345288	MK530840	JQ345330	-	-	JQ345101	JQ345177
<i>Dinebra divaricatissima</i> (S.T. Blake) P. M. Peterson & N. Snow	Snow 7248, Jacobs & Snow (NSW)	Australia, Queensland	-	-	-	-	MF353850	-	-	-	MF353830
<i>Dinebra divaricatissima</i> (S.T. Blake) P. M. Peterson & N. Snow	Snow 7337 & Simon (BRI)	Australia, Queensland	-	-	-	-	MF353851	-	-	-	MF353831
<i>Dinebra haareri</i> (Stapf & C.E. Hubb.) P. M. Peterson & N. Snow	Peterson 24231, Soreng, Romaschenko & Mbago (US)	Tanzania, Tanga	-	KP873753	KP874034	-	KP873551	-	KP873910	-	KP873335
<i>Dinebra ligulata</i> (Lazarides) P. M. Peterson & N. Snow	Snow 7402 (MO)	Australia, Queensland	MK530885	JQ345251	JQ345294	MK530841	JQ345336	MK530809	JQ345218	JQ345108	JQ345183

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Dinebra marquisensis</i> (F. Br.) P. M. Peterson & N. Snow	Wood 10145 (MO)	French Polynesia, Marquesas.	MK530886	JQ345252	JQ345295	MK530842	JQ345337	MK530810	JQ345219	JQ345109	JQ345184
<i>Dinebra nealleyi</i> (Vasey) P. M. Peterson & N. Snow	Snow 5806 (MO)	USA, Texas	MK530887	JQ345253	JQ345296	MK530843	JQ345338	MK530811	JQ345220	JQ345110	JQ345185
<i>Dinebra neesii</i> (Thwaites) P. M. Peterson & N. Snow	Snow 7380 & Simon (BRI)	Australia, Queensland	MK530888	JQ345254	JQ345297	MK530844	JQ345339	MK530812	JQ345221	JQ345111	JQ345186
<i>Dinebra panicea</i> subsp. <i>brachiata</i> (Steud.) P. M. Peterson & N. Snow	Peterson 20086, Alvarez Marvan & Dejesos (US)	Mexico, Guerrero	-	-	-	-	JQ345341	-	-	-	MK514308
<i>Dinebra panicea</i> subsp. <i>brachiata</i> (Steud.) P. M. Peterson & N. Snow	Peterson 22185 & Saarela (US)	Mexico, Sinaloa	GU360130	-	GU360389	MK530845	GU359810	-	GU359431	-	GU359146
<i>Dinebra panicea</i> subsp. <i>mucronata</i> (Michx.) P. M. Peterson & N. Snow	Peterson 9546, Annable & Herrera (US)	Mexico, Louisiana	MK530889	JQ345256	JQ345299	MK530846	JQ345342	MK530813	JQ345222	JQ345113	JQ345188
<i>Dinebra panicoides</i> (J. Presl) P. M. Peterson & N. Snow	Snow 5810a (MO)	USA, Arkansas	MK530890	JQ345257	JQ345300	MK530847	JQ345343	MK530814	-	JQ345114	-
<i>Dinebra retroflexa</i> (Vahl) Panz.	Ndegwa 610 (US)	Kenya	GU360052	GU360503	GU360479	MK530848	GU359778	GU359692	GU359355	JQ345077	GU359332
<i>Dinebra retroflexa</i> (Vahl) Panz.	Snow 6950 & Burgoyne (MO)	Swaziland	-	-	-	-	KP873552	-	-	MK530792	KP873336
<i>Dinebra scabra</i> (Nees) P. M. Peterson & N. Snow	Snow 5788 (MO)	USA, Louisiana	MK530891	JQ345258	JQ345301	MK530849	JQ345344	-	JQ345223	JQ345115	JQ345189
<i>Dinebra somalensis</i> (Stapf) P. M. Peterson & N. Snow	Faden 74-991 & Faden (MO)	Kenya, K7-Tana River District	MK530892	JQ345236	JQ345278	KX582770	JQ345321	KX582520	-	-	JQ345166
<i>Dinebra southwoodii</i> (N. Snow & B.K. Simon) P. M. Peterson & N. Snow	Snow 7362 (MO)	Australia	MK530893	JQ345259	JQ345302	MK530850	JQ345345	MK530815	JQ345224	JQ345116	JQ345190
<i>Dinebra squarrosa</i> (Pilg.) P. M. Peterson & N. Snow	Kayombo 5196 (MO)	Tanzania, Lindi. Kilwa	MK530894	JQ345260	JQ345303	MK530851	JQ345346	MK530816	JQ345225	JQ345117	JQ345191

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Eleusine africana</i> Kenn.-O'Byrne	Kayombo 424 (MO)	Tanzania, Iringa	MK530901	KP873756	KP874037	MK530858	KP873562	MK530822	KP873913	MK530794	KP873346
<i>Eleusine africana</i> Kenn.-O'Byrne	Peterson 24072, Soreng, Romaschenko & Abeid (US)	Tanzania, Rukwa	MK530902	KP873757	KP874038	MK530859	KP873563	MK530823	KP873914	MK530795	KP873347
<i>Eleusine africana</i> Kenn.-O'Byrne	Qing Liu 090 (US)	Mexico	-	HQ202632*	HQ202640*	-	HQ202625*	-	HQ202648*	-	-
<i>Eleusine africana</i> Kenn.-O'Byrne	Seydel 2798 (US)	Namibia, Midgard State	MK530903	MK530932	MK530919	MK530860	KP873564	MK530824	MK530802	MK530796	KP873348
<i>Eleusine africana</i> Kenn.-O'Byrne	Seydel 3889 (US)	Namibia, Windhoek City	MK530904	MK530933	MK530920	MK530861	KP873565	MK530825	MK530803	MK530797	KP873349
<i>Eleusine coracana</i> (L.) Gaertn.	EGRN45	India	-	-	-	-	-	-	-	-	KC201694*
<i>Eleusine coracana</i> (L.) Gaertn.	EGRN55	India	-	-	-	-	-	-	-	-	KC201686*
<i>Eleusine coracana</i> (L.) Gaertn.	FMV-1	South Africa	-	-	-	-	-	-	-	-	AJ272185*
<i>Eleusine coracana</i> (L.) Gaertn.	Hilu 2346 (CLEMS)	India, Himachal Pradesh	-	-	-	-	-	-	-	-	AY515200*
<i>Eleusine coracana</i> (L.) Gaertn.	Hilu 264 (CLEMS)	Kenya, Homa Bay	-	-	-	-	-	-	-	-	AY515204*
<i>Eleusine coracana</i> (L.) Gaertn.	Peterson 24112, Soreng, Romaschenko & Abeid (US)	Tanzania, Rukwa	-	KP873758	KP874039	-	KP873566	-	KP873915	-	KP873350
<i>Eleusine coracana</i> (L.) Gaertn.	Qing Liu 093 (US)	Ethiopia	-	-	-	-	KP873567	-	-	-	KP873351
<i>Eleusine coracana</i> (L.) Gaertn.	Qing Liu 103 (US)	Ethiopia	-	-	-	-	KP873568	-	-	-	KP873352
<i>Eleusine floccifolia</i> (Forssk.) Spreng.	Hilu 2285 (VPI)	Ethiopia,	-	-	-	-	-	-	-	-	AY515208*
<i>Eleusine indica</i> (L.) Gaertn.	FSC-1 (CLEMS)	USA, South Carolina	-	-	-	-	-	-	-	-	AY515210*
<i>Eleusine indica</i> (L.) Gaertn.	YDK2008519	Korea (South)	-	-	-	-	-	-	-	-	FJ766160*
<i>Eleusine indica</i> (L.) Gaertn.	Brown 628 & Clebsch (US)	USA, Tennessee	-	-	-	-	KP873569	-	-	-	KP873353

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Eleusine indica</i> (L.) Gaertn.	Chase 9922 (US)	USA, Arkansas	-	-	-	-	KP873570	-	-	-	KP873354
<i>Eleusine indica</i> (L.) Gaertn.	Columbus 2875 (RSA)	USA	-	-	-	-	-	-	-	-	EF153042*
<i>Eleusine indica</i> (L.) Gaertn.	Peterson 21362, Saarela & Flores Villegas (US)	Mexico	GU360031	GU360496	GU360472	MK530862	GU359797	GU359698	GU359473	JQ345081	GU359338
<i>Eleusine indica</i> (L.) Gaertn.	Peterson 23802, Soreng & Romaschenklo (US)	Tanzania, Dar Es Salaam	-	KP873759	KP874040	-	KP873571	-	KP873916	-	KP873355
<i>Eleusine indica</i> (L.) Gaertn.	Peterson 24429, Romaschenko & Knapp (US)	USA, Maryland	-	KP873760	KP874041	-	KP873572	-	MK530804	-	KP873356
<i>Eleusine jaegeri</i> Pilg.	Hilu 203 (VPI)	Kenya, Central Province	-	-	-	-	-	-	-	-	AY515213*
<i>Eleusine jaegeri</i> Pilg.	Kindeketa 762 (MO)	Tanzania, Arusha	MK530905	KP873761	KP874042	MK530863	KP873573	MK530826	KP873917	MK530798	KP873357
<i>Eleusine jaegeri</i> Pilg.	Peterson 24299, Soreng, Romaschenko & Mbago (US)	Tanzania, Arusha	-	KP873762	KP874043	-	KP873574	-	KP873918	-	KP873358
<i>Eleusine kigeziensis</i> S.M. Phillips	Purseglove 3384 (K)	Uganda	-	-	-	-	-	-	-	-	AY515216*
<i>Eleusine multiflora</i> Hochst. ex A. Rich.	Davidse 30264 & Davidse (MO)	Mexico, Distrito Federal	MK530906	-	-	MK530864	KP873575	MK530827	-	-	KP873359
<i>Eleusine multiflora</i> Hochst. ex A. Rich.	Peterson 24272, Soreng, Romaschenko & Mbago (US)	Tanzania, Shinyanga	-	KP873763	KP874044	KX582779	KP873576	KX582529	KP873919	KX582268	KP873360
<i>Eleusine multiflora</i> Hochst. ex A. Rich.	Qing Liu 100 (US)	Kenya	HQ202660*	HQ202638*	HQ202646*	-	HQ202630*	HQ202623	HQ202653*	-	-
<i>Eleusine tristachya</i> (Lam.) Lam.	Beck 3227 (US)	Bolivia, Ballivian	-	-	-	-	KP873577	-	-	-	KP873361
<i>Eleusine tristachya</i> (Lam.) Lam.	Hilu 2464 (VPI)	Uruguay, Cerro Largo Dep.	-	-	-	-	-	-	-	-	AY515224*
<i>Eleusine tristachya</i> (Lam.) Lam.	Qing Liu 107 (US)	Mexico	-	HQ202639*	HQ202647*	-	HQ202631*	-	HQ202654*	-	-
<i>Eleusine tristachya</i> (Lam.) Lam.	Zardini 35791 & Tillería (MO)	Paraguay, Misiones	MK530907	KP873764	KP874045	MK530865	KP873578	MK530828	KP873920	MK530799	KP873362

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Enteropogon sechellensis</i> (Baker) T. Durand & Schinz	Peterson 23815, Soreng & Romaschenko (US)	Tanzania, Dar Es Salaam	MK530908	KP873787	KP874064	KX582783	KP873602	KX582531	KP873934	-	KP873386
<i>Eustachys calvescens</i> (Hack.) Caro & E.A. Sánchez	Chase 10971 (US)	Brazil, Mato Grosso State	-	KP873789	KP874066	-	KP873604	-	KP873936	KX582272	KP873388
<i>Gouinia latifolia</i> var. <i>guatemalensis</i> (Hack.) J.J. Ortíz	Martinez S. 29764, Alvarez & Ramirez (MO)	Mexico, Campeche	MK530909	KF827774	KF827709	KX582792	KF827638	KX582534	KF827583	KX582274	KF827520
<i>Harpochloa falx</i> (L. f.) Kuntze	Zietsman 4015, Peyper, Avenant & van der Walt (MO)	South Africa, Mpumalanga	MK530910	KP873799	KP874072	KX582797	KP873613	KX582536	-	KX582276	KP873400
<i>Leptochloa anisopoda</i> (Scribn. ex B.L. Rob.) P.M. Peterson	Proosdij 813, van de Riet & Zauder (US)	Aruba	-	KP873777	-	-	KP873593	-	KP873928	-	KP873377
<i>Leptochloa anisopoda</i> (Scribn. ex B.L. Rob.) P.M. Peterson	Steyermark 29192 (US)	Guatemala	-	KP873778	-	-	KP873594	-	-	-	MK514310
<i>Leptochloa chloridiformis</i> Parodi	Myndel-Pedersen 2662 (US)	Argentina, Corrientes	-	KP873800	KP874073	-	KP873614	-	-	-	KP873401
<i>Leptochloa chloridiformis</i> Parodi	Myndel-Pedersen 3741 (US)	Argentina, Corrientes	-	KP873801	-	-	KP873615	-	-	-	KP873402
<i>Leptochloa crinita</i> (Lag.) P. M. Peterson	Renvoize 1987 (US)	Bolivia,	-	JQ345273	JQ345315	MK530866	JQ345359	-	JQ345231	JQ345152	JQ345203
<i>Leptochloa digitata</i> (R.Br.) Domin	Risler 476 & Kerrigan (MO)	Australia, Northern Territory	MK530911	JQ345246	JQ345289	MK530867	JQ345331	MK530829	JQ345213	JQ345102	JQ345178
<i>Leptochloa exilis</i> (Renvoize) P.M. Peterson	Anderson 37049, Stieber & Kirkbride (US)	Brazil, Bahia State	-	KP873676	-	-	KP873464	-	-	-	KP873250
<i>Leptochloa exilis</i> (Renvoize) P.M. Peterson	Anderson 37190, Stieber & Kirkbride (US)	Brazil, Minas Gerais State	-	KP873677	-	-	KP873465	-	-	-	KP873251
<i>Leptochloa longa</i> Griseb.	Croat 16903 (MO)	Panama, San Blas	MK530912	-	-	-	-	-	-	-	-
<i>Leptochloa pluriflora</i> (E. Fourn.) P. M. Peterson & N. Snow	Peterson 15048 & Refulio-Rodriguez (US)	Peru, Cajamarca	GU360192	GU360623	GU360334	MK530868	GU359905	GU359680	GU359554	JQ345153	GU359212
<i>Leptochloa pluriflora</i> (E. Fourn.) P. M. Peterson & N. Snow	Sohns 1258 (US)	Mexico	GU360160	GU360653	GU360374	MK530869	GU359934	GU359679	GU359553	MK530800	GU359214

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Leptochloa pluriflora</i> (E. Fourn.) P. M. Peterson & N. Snow	Swallen 10100 (US)	USA, Texas	MK530913	KP873802	KP874074	MK530870	KP873616	-	KP873942	MK530801	KP873403
<i>Leptochloa virgata</i> (L.) P.Beauv.	Peterson 15088 & Refulio-Rodriguez (US)	Peru, Cajamarca	-	JQ345262	JQ345304	MK530871	JQ345349	MK530830	-	JQ345119	JQ345193
<i>Leptochloa virgata</i> (L.) P.Beauv.	Rimachi 8359 (US)	Peru	MK530914	JQ345263	JQ345305	MK530872	JQ345350	MK530831	-	JQ345120	JQ345194
<i>Leptochloa virgata</i> (L.) P.Beauv.	Seidel 2710 (US)	Bolivia, La Paz	MK530915	JQ345264	JQ345306	KX582803	JQ345351	KX582543	JQ345226	JQ345121	JQ345195
<i>Lepturus repens</i> (G. Forst.) R. Br.	Peterson 23835, Soreng, Romaschenko & Abeid (US)	Tanzania, Lindi Reg.	MK530916	KP873804	KP874076	KX582805	KP873618	KX582545	KP873944	KX582282	KP873405
<i>Micrachne fulva</i> (Stapf) P.M. Peterson	Robson 1122 (US)	Mozambique	GU360120	GU360585	GU360444	KX582810	GU359884	-	GU359348	JQ345056	GU359253
<i>Microchloa altera</i> (Rendle) Stapf	Robinson 6362 (US)	Zambia, Central Prov.	MK530917	KP873807	KP874079	KX582811	KP873621	KX582548	KP873947	KX582284	KP873408
<i>Mosdenia leptostachys</i> (Ficalho & Hiern) Clayton	Schweickerdt 1542 (US)	South Africa	GU360216	GU360681	GU360420	KX582813	GU359967	GU359750	GU359458	JQ345131	GU359159
<i>Muhlenbergia japonica</i> Steud.	Soreng 5301, Peterson & Sun Hang (US)	China, Yunnan	HM143288	HM143668	HM143572	KX582814	HM143184	HM143476	HM143389	JQ345132	HM143082
<i>Neobouteloua lophostachya</i> (Griseb.) Gould	Peterson 11515 & Annable (US)	Argentina, San Juan	GU360262	GU360725	GU360273	KX582819	GU360004	GU359635	GU359396	JQ345134	GU359123
<i>Odyssea paucinervis</i> (Nees) Stapf	Peterson 24312, Soreng, Romaschenko & Mbago	Tanzania, Arusha	-	-	-	-	-	-	-	-	KX582388
<i>Orinus thoroldii</i> (Stapf ex Hemsely) Bor	Soreng 5529, Peterson & Sun Hang (US)	China, Xizang	GU360249	GU360714	GU360268	KX582825	GU359997	GU359595	GU359401	KX582290	GU359112
<i>Oxychloris scariosa</i> (F. Muell.) Lazarides	Forster 20737 & Holland (MEL)	Australia, Queensland	-	KP873813	KP874086	-	KP873631	KX582556	KP873952	-	KP873414
<i>Pappophorum pappiferum</i> (Lam.) Kuntze	Peterson 21689, Soreng, La Torre & Rojas Fox (US)	Peru, Ancash	GU360248	GU360700	GU360276	KX582829	GU359996	GU359596	GU359402	JQ345138	GU359128
<i>Schoenefeldia gracilis</i> Kunth	Pauwels 7413 (MO)	Benin, Borgou	-	KP873814	KP874087	-	KJ768981	XX000000	-	-	KJ768886

Taxa	Voucher	Country	<i>rps3</i>	<i>rps16-tr nK</i>	<i>rps16 intron</i>	<i>rpoC2</i>	<i>rpl32-tr nL</i>	<i>ndhF</i>	<i>ndhA intron</i>	<i>ccsA</i>	ITS
<i>Schoenefeldia gracilis</i> Kunth	Quezel s.n. & Bourreil (US)	Sudan, Darfur	GU360169	XX000000	XX000000	-	-	XX000000	-	-	XX000000
<i>Schoenefeldia transiens</i> (Pilg.) Chiov.	Greenway 9781 (US)	Kenya	GU360168	GU360636	GU360349	-	GU360007	GU359610	KP873953	-	GU359202
<i>Schoenefeldia transiens</i> (Pilg.) Chiov.	Peterson 24216, Soreng, Romaschenko & Mbago (US)	Tanzania, Tanga	MK530918	KP873815	KP874088	KX582837	KP873632	KX582565	KP873954	-	KP873415
<i>Schoenefeldia transiens</i> (Pilg.) Chiov.	Spjut 3920 (BRY)	Kenya	XX000000	JQ345270	JQ345312	-	JQ345357	XX000000	JQ345230	-	JQ345201
<i>Sporobolus indicus</i> (L.) R. Br.	Peterson 22025 & Saarela (US)	Mexico, Chihuahua	GU360161	GU360630	GU360355	KX582841	GU359913	GU359637	GU359504	KX582297	GU359209
<i>Stapfochloa canterae</i> (Arechav.) P.M. Peterson	Pedersen 9597 (US)	Paraguay, Misiones	-	KP873661	KP873978	-	KP873444	-	KP873839	-	KP873230
<i>Tetrapogon brandegeei</i> (Vasey) P.M. Peterson	Carter 2897 & Kellog (US)	Mexico, Baja California	-	KP873767	KP874048	-	KP873581	-	KP873922	-	KP873365
<i>Tetrapogon fasciculatus</i> (Hitchc. & Chase) P.M. Peterson	Ekman s.n. (US)	Dominican Republic	GU360171	GU360638	GU360317	KX582846	GU359982	GU359608	GU359528	JQ345142	GU359156
<i>Tragus australianus</i> S.T. Blake	Symon 13792 (US)	Australia	GU360150	GU360618	GU360368	KX582847	GU359900	GU359673	GU359515	KX582299	GU359222
<i>Triodia basedowii</i> Pritz.	Peterson 14437, Soreng & Rosenberg (US)	Australia, Western Australia	GU360205	GU360666	GU360322	KX582859	GU359946	GU359683	GU359550	KX582306	GU359174