

A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaiqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaiqiqahinae; and a subgeneric classification of *Distichlis*

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Abstract Morphologically, the tribe Cynodonteae is a diverse group of grasses containing about 839 species in 96 genera and 18 subtribes, found primarily in Africa, Asia, Australia, and the Americas. Because the classification of these genera and species has been poorly understood, we conducted a phylogenetic analysis on 213 species (389 samples) in the Cynodonteae using sequence data from seven plastid regions (*rps16-trnK* spacer, *rps16* intron, *rpoC2*, *rpl32-trnL* spacer, *ndhF*, *ndhA* intron, *ccsA*) and the nuclear ribosomal internal transcribed spacer regions (ITS 1 & 2) to infer evolutionary relationships and refine the current classification. The phylogenetic tree from the combined plastid and nuclear region is well resolved depicting a strongly supported monophyletic Cynodonteae that includes 17 strongly supported clades corresponding to the subtribes Tripogoniinae, Pappophorinae, Traginae, Muhlenbergiinae, Hilariinae, Scleropogoniinae, Boutelouinae, Monanthochloinae, Dactylocteniinae, Eleusininae, Aeluropodinae, Triodiinae, Orcuttiinae, Zaiqiqahinae, Farragininae, Perotidinae, and Gouiniinae, and two moderately supported clades corresponding to the Orininae and Hubbardochloinae. The plastid data places *Odysea paucinervis* as sister to *Neobouteloua* in the Dactylocteniinae whereas the nuclear ITS data places it as sister to *Aeluropus* in the Aeluropodinae. *Odysea mucronata* is strongly supported sister to the Cteniinae, Trichoneurinae, Farragininae, Perotidinae, Hubbardochloinae, and the Gouiniinae, and not closely related to *Odysea paucinervis*. The nuclear data placed *Acrachne racemosa* as sister to *Dactyloctenium* in the Dactylocteniinae while the plastid data places it near the base of the Eleusininae. Our new classification recognizes three new subtribes (bringing the total to 21 subtribes): Dactylocteniinae that includes *Acrachne*, *Brachyachloa*, *Dactyloctenium*, and *Neobouteloua*; Orininae with *Cleistogenes* and *Orinus*; and Zaiqiqahinae with a single genus, *Zaiqiqah* gen. nov.; Hubbardochloinae (resurrected here) with seven genera; and describes four new genera: *Orthacanthus* (Traginae) with a single species, *Triplasiella* (Gouiniinae) with a single species, *Tripogonella* (Tripogoniinae) with three species, and *Zaiqiqah* with a single species. We additionally provide a subgeneric classification of *Distichlis* recognizing three sections: *D.* sect. *Monanthochloe*, *D.* sect. *Bajaenses*, and *D.* sect. *Spicatae*, the latter two representing new sections. The following nine new combinations are made: *Distichlis* sect. *Monanthochloe*, *Orthacanthus pedunculatus*, *Tridentopsis buckleyana*, *Tridentopsis mutica* var. *elongata*, *Triplasiella eragroides*, *Tripogonella loliiformis*, *Tripogonella minima*, *Tripogonella spicata*, and *Zaiqiqah mucronata*. We lectotypify the following five names: *Festuca loliiformis*, *F. minima*, *F. mucronata*, *Triodia eragroides*, and *Uralepis elongata*.

Keywords Dactylocteniinae; *Distichlis* sect. *Bajaenses*; *Distichlis* sect. *Monanthochloe*; *Distichlis* sect. *Spicatae*; ITS; Orininae; *Orthacanthus*; plastid DNA sequences; systematics; *Tridentopsis*; *Triplasiella*; *Tripogonella*; *Zaiqiqah*; Zaiqiqahinae

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

■ INTRODUCTION

In the most recent classification of the grasses, the subfamily Chloridoideae Kunth ex Beilschm. includes five tribes: Centropodieae P.M.Peterson & al., Triraphideae P.M.Peterson,

Eragrostideae Stapf, Zoysieae Benth., and the Cynodonteae Dumort. (Soreng & al., 2015, 2016; Peterson & al., in press). The Cynodonteae currently includes 839 species in 96 genera and 18 subtribes (Peterson & al., 2014a, 2015a, b, in press; Soreng & al., 2015), and it has received high support as a

monophyletic lineage in recent molecular analyses (Peterson & al., 2014a, 2015b). Eighty genera in the Cynodonteae are currently classified in one of the 18 subtribes and 16 genera are incertae sedis or unplaced (Soreng & al. 2015). The following 12 unplaced genera of Cynodonteae are included here: *Allolepis* Soderstr. & H.F.Decker, *Brachychloa* S.M.Phillips, *Cleistogenes* Keng, *Dactyloctenium* Willd., *Halopyrum* Stapf, *Hubbardochloa* Auquier, *Jouvea* E.Fourn., *Kalinia* H.L.Bell & Columbus, *Neobouteloua* Gould, *Orinus* Hitchc., *Pogononeura* Napper, and *Sohnsia* Airy Shaw. We have been unable to procure material for the four remaining unplaced Cynodonteae: *Decaryella* A.Camus, *Kampochloa* Clayton, *Lepeturidium* Hitchc. & Ekman, and *Vietnamochloa* Veldkamp & Nowack. Previous molecular studies in the Cynodonteae strongly support the monophyly (Peterson & al., 2014a) of subtribes Gouiniinae P.M.Peterson & Columbus (17 species in 5 genera, Western Hemisphere), Cteniinae P.M.Peterson & al. (20 species in 1 genus, African/Western Hemisphere), Trichoneurinae P.M.Peterson & al. (8 species in 1 genus, Western Hemisphere), Gymnopogoninae P.M.Peterson & al. (25 species in 6 genera, African), Farragininae P.M.Peterson & al. (4 species in 2 genera, African), and the Perotidinae P.M.Peterson & al. (20 species in 5 genera, African and Eurasian). The Orcuttiinae P.M.Peterson & Columbus (9 species in 3 genera, western North America) and the Eleusininae Dumort. (238 species in 30 genera, low latitudes in Africa, Asia, Australia, and the Americas) are successive sister lineages to these six subtribes (Peterson & al., 2015b; Soreng & al., 2015). The Aleuropodinae (11 species in 2 genera) and the Triodiinae (69 species in 3 genera) distributed in Australasia and Africa together comprise a clade that is sister to the eight previously named subtribes (Peterson & al., 2015b). Subtribes Tripogoninae Stapf (60 species in 5 genera, primarily Australasian and African), Pappophorinae Dumort. (28 species in 3 genera, Western Hemisphere), Traginae P.M.Peterson & Columbus (14 species in 4 genera, primarily African and Australasian), Hilariinae P.M.Peterson & Columbus (10 species in 1 genus), Muhlenbergiinae Pilg. (182 species in 1 genus), Scleropogoninae Pilg. (15 species in 6 genera), Boutelouinae Stapf (60 species in 1 genus), and Monanthochloinae Pilg. ex Potztl (10 species in 1 genus) form a clade that is sister to all the other chloridoids (Peterson & al., 2014a, 2015a, b; Soreng & al., 2015, 2016). The latter four subtribes are primarily distributed in the Western Hemisphere; only six species of *Muhlenbergia* Schreb. are known to occur in Asia (Peterson & al. 2010a, b).

Using plastid (*rps16-trnK*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) and nuclear ITS DNA sequence markers, we present a new phylogenetic analysis of 214 species in 88 genera of Cynodonteae. The number of species sampled within many of these genera is expanded and our study for the first time includes *Halopyrum mucronatum* (L.) Stapf, *Hubbardochloa gracilis* Auquier, and *Odysea mucronata* (Forssk.) Stapf. In addition, we discuss morphological and anatomical characters supporting relationships and propose changes to the classification.

■ MATERIALS AND METHODS

Taxon sampling. — Our sampling consists of 419 samples, representing 244 species of grasses, of which 213 species represent the Cynodonteae: the Tripogoninae with 22 species, Pappophorinae with 19 species, Traginae with 13 species, Hilariinae with 6 species, Muhlenbergiinae with 3 species, Scleropogoninae with 14 species, Boutelouinae with 3 species, Monanthochloinae with 11 species, Eleusininae with 29 species, Orcuttiinae with 9 species, Gouiniinae with 12 species, Cteniinae with 1 species, Trichoneurinae with 1 species, Gymnopogoninae with 7 species, Farragininae with 2 species, Perotidinae with 4 species, Triodiinae with 24 species, and Aleuropodinae with 3 species; and 27 species are included within the Chloridoideae: the Centropodieae with 1 species, Triraphideae with 3 species, Eragrostideae with 16 species, Zoysieae with 7 species. In addition, in the Cynodonteae we include *Allolepis texana* (Vasey) Soderstr. & H.F.Decker, 2 species of *Brachychloa*, 10 species of *Cleistogenes*, 8 species of *Dactyloctenium*, *Jouvea pilosa* (J.Presl) Scribn., *Kalinia obtusiflora* (E.Fourn.) H.L.Bell & Columbus, 2 species of *Neobouteloua*, 2 species of *Odysea* Stapf, 2 species of *Orinus*, and *Sohnsia filifolia* (E.Fourn.) Airy Shaw. For outgroups beyond the Chloridoideae, we chose 2 species of Danthoioideae (*Capeochloa cincta* subsp. *sericea* (N.P.Barker) N.P.Barker & H.P.Linder, *Danthonia compressa* Austin), 1 species of Aristidoideae (*Aristida gypsophila* Beetle), and 1 species of Panicoideae (*Chasmanthium latifolium* (Michx.) H.O.Yates) (Peterson & al. 2010a). 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.

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); *ndhF*, *ccsA*, and *rpoC2* (coding genes); and ITS followed procedures outlined in Peterson & al. (2010a, b, 2012). We specifically targeted plastid regions that proved to be most informative in our previous studies on chloridoid grasses (Peterson & al., 2010a, b, 2011, 2012, 2014a, b, c, 2015a, b). In addition, we included sequences from the variable grass-specific insert in the chloroplast gene *rpoC2* (RNA polymerase beta II subunit). The phylogenetic utility of this region was advocated by Cummings & al. (1994) and Barker & al. (1999). Based on sequences of the complete chloroplast genome of *Oryza* L., *Zea* L., *Hordeum* L., *Lolium* L., *Triticum* L., and *Agrostis* L. available from GenBank, we designed two primers, GI1730F-5'CGAAGAAATAGGYTCGYCATTCCAT3' (T = 57) and GI2540R-5'GATCTCGGCAAGATATGMAGTTTC3' (T = 54.5), to amplify and sequence 740 bp of the gene *rpoC2* (16.3% of entire gene).

Phylogenetic analyses. — We used Geneious v.5.3.4 (Drummond & al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *ndhA*, *ndhF*, *rps16*, *rps16-trnK*, *rpoC2*, *ccsA*, and ITS regions, and MUSCLE v.9.1.3 (Edgar, 2004) to

align consensus sequences and adjust the final alignment (see supplementary data for sequence alignments). We identified models of molecular evolution for the cpDNA and nrDNA regions using jModelTest v.0.1.1 (Posada, 2008) and applied maximum likelihood (ML) and Bayesian searches to infer the 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, 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 v.4.b10 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. All calculations were performed using the Smithsonian Institution high performance computing cluster, hydra.

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 eight 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.

In the phylogram (Fig. 1A–E) the native distribution of each Cynodonteae species is indicated by color as follows: North America (red), South America (tan), Africa (dark green), Australia+Pacific (dark blue), and Eurasia (light purple). We present each portion of the tree (A–E) in a “fish-eye” manner where each page includes a place name for every major clade or subtribe, emphasizing selected, linearly arranged clades (from top to bottom) with a complete complement of species (Peterson & al., 2010a, b).

Assessment of incongruence and data combining strategy.

— The resulting plastid and ITS topologies were inspected for conflicting nodes (see Fig. 1D) with BS ≥ 80% and/or PP ≥ 0.95. If no supported conflict was found, plastid and ITS sequences were combined. Where conflicting topologies were found, the datasets for inconsistently placed taxa were duplicated in the

Table 1. Characteristics of *rps16-trnK*, *rps16* intron, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA* intron, *ccsA*, and ITS; and parameters used in Bayesian analyses using Akaike information criterion.

	<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 characters	1079	1049	1085	1537	807	1445	1017	8019	849	8868	
Number of sequences	244	217	147	334	231	190	141	1504	383	1887	
Number of new sequences	74 (30%)	64 (29%)	147 (100%)	143 (43%)	95 (41%)	43 (23%)	74 (52%)	640 (42%)	133 (35%)	772 (41%)	
Likelihood score (–lnL)	9994.02	7629.24	7553.4	13002.08	8934.71	10818.14	6357.70		29976.54		
Number of substitution types	6	6	6	6	6	6	6	–	6	–	
Model for among-site rate variation	gamma	gamma	gamma	gamma	gamma	gamma	gamma	–	gamma	–	
Substitution rates	AC	1.2592	1.0868	1.7235	0.6738	2.3599	1.3977	1.5077	–	1.5560	–
	AG	2.9201	1.2403	2.7593	1.6791	3.5296	2.7092	4.4988	–	3.3358	–
	AT	0.4423	0.2829	0.2640	0.3667	0.6615	0.4612	0.6100	–	1.4641	–
	CG	1.5988	1.0876	1.2039	1.0386	1.4330	2.1889	1.4732	–	1.2414	–
	CT	2.4993	2.0879	5.8158	1.2275	4.4817	2.8118	4.1108	–	5.4734	–
	GT	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	–	1.0000	–
Character state frequencies	A	0.3018	0.4079	0.3928	0.3908	0.3324	0.3711	0.3014	–	0.2524	–
	C	0.1344	0.0965	0.1502	0.1395	0.1309	0.1227	0.1517	–	0.1701	–
	G	0.1427	0.1593	0.2348	0.1228	0.1672	0.1358	0.1553	–	0.2322	–
	T	0.4209	0.3361	0.2221	0.3467	0.3694	0.3703	0.3914	–	0.3451	–
Proportion of invariable sites	0.0832	0.2788	0.1049	0.0713	0.2940	0.2227	0.4194	–	0.2162	–	
Substitution model	TVM+G	GTR+I+G	TIM3+I+G	GTR+G	TPM3uf+G	TVM+I+G	TPM3uf+G	–	GTR+I+G	–	
Gamma shape parameter (α)	1.1523	1.1740	1.0935	0.7219	0.8826	1.0927	0.9759	–	1.0248	–	

matrix. One set of the taxon was represented by the corresponding plastid sequences only, the other taxon set by only ITS sequences. The remaining positions for the truncated datasets were then coded as missing data. We use this “taxon duplication” approach (Pirie & al., 2008; Pelser & al., 2010; Peterson & al., 2015a) 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. 1D). The combination of data has an obvious advantage since it can provide better backbone support for nodes and improve resolution for terminal nodes within the main phylogenetic groups. The individual ITS and combined plastid trees are found in the Electronic Supplement (Figs. S1, S2).

■ RESULTS

Phylogenetic analyses. — Forty-one percent (772/1887) of the sequences used in our study are newly reported here, 59% (1115/1887) are from previous studies, and 44% (1463/3350) are missing or failed (Appendix 1). Total aligned characters for individual regions are noted in Table 1. All of the *rpoC2* sequences are newly reported (147, 100%), followed by *rpl32-trnL* (143, 43%), ITS (133, 35%), *ndhF* (95, 41%), *ccsA* (74, 52%), *rps16-trnK* (74, 30%), *rps16* (64, 29%), and *ndhA* (43, 23%).

Incongruence between the ITS and combined plastid phylograms. — The ITS and combined plastid phylogenies rendered similar patterns overall. However, despite a high number of compatible characters between the two datasets (Table 1), the ITS phylogeny differed from the plastid phylogeny in three ways: *Acrachne racemosa* (B. Heyne ex Roem. & Schult.) Ohwi was strongly supported (BS = 98, PP = 1.00) sister to *Dactyloctenium* in the ITS tree but was included within the Eleusininae in the plastid tree; three species of *Dinebra* Jacq. were strongly supported (BS = 92, PP = 1.00) sister to the *Aeluropus-Odyssea* clade in the ITS tree but were included within the Eleusininae in the plastid tree; and *Odyssea paucinervis* (Nees) Stapf was strongly supported (BS = 100, PP = 1.00) sister to *Aeluropus* Trin. in the ITS tree but was strongly supported (BS = 99, PP = 1.00) sister to two species of *Neobouteloua* in the plastid tree.

Phylogenetic tree of Cynodonteae. — The ML tree from the combined plastid (*rps16-trnK*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) and ITS regions (Fig. 1A–E) is well resolved depicting a strongly supported monophyletic Cynodonteae (BS = 100, PP = 1.00) that includes 17 strongly supported clades (BS = 98–100, PP = 1.00) corresponding to the Tripogoninae, Pappophorinae, Traginae, Muhlenbergiinae, Hilariinae, Scleropogoninae, Boutelouinae, Monanthochloinae, Dactylocteniinae (newly described below), Eleusininae, Aeluropodinae, Triodiinae, Orcuttiinae, Zaqiqahinae (newly described below), Farragininae, Perotidinae, and Gouiniinae and two moderately supported clades (BS = 75–78, PP = 1.00) corresponding to the Orininae (newly described below) and Hubbardochoinae Auquier.

Within the Tripogoninae (Fig. 1A), *Tripogon* Roem. & Schult. is polyphyletic and *Tripogon* s.str. is sister to *Oropetium* Trin. (BS = 100, PP = 1.00); and together these are sister to *Eragrostiella* Bor (BS = 66, PP = 0.77) and a strongly supported clade containing *Tripogon loliiformis* (F. Muell.) C.E. Hubb., *T. minimus* Hochst. ex Steud., and *T. spicatus* (Nees) Ekman (BS = 100, PP = 1.00). *Halopyrum mucronatum* is sister to the *Eragrostiella-Oropetium-Tripogon* clade (BS = 100, PP = 1.00). *Melanocenchris* Nees is monophyletic with three species (BS = 100, PP = 1.00) and is sister to *Desmostachya bipinnata* (L.) Stapf.

The Pappophorinae (Fig. 1A) includes a poorly supported *Tridens* Roem. & Schult. s.str. clade (PP = 0.92) with 13 species sister to a strongly supported *Pappophorum* Schreb. clade (BS = 96, PP = 1.00) with 5 species. *Neesiochloa barbata* (Nees) Pilg. is sister to the *Pappophorum-Tridens* clade (BS = 100, PP = 1.00).

In the Traginae (Fig. 1B), *Tragus* Haller is polyphyletic with *T. pedunculatus* Pilg. sister to *Willkommia sarmentosa* Hack. (BS = 51, PP = 0.60). *Willkommia* Hack. appears polyphyletic since *Willkommia texana* Hitchc. is not an immediate sister of *W. sarmentosa*. The *Tragus* s.str. clade is strongly supported (BS = 100, PP = 1.00) and includes seven species. *Pogononeura biflora* Napper is sister to *Polesvansia rigida* De Winter (BS = 57, PP = 0.57). *Monelytrum luederitzianum* Hack. is sister to the strongly supported *Tragus* s.str. clade that includes six species.

The Muhlenbergiinae, Hilariinae, Scleropogoninae, Boutelouinae, Monanthochloinae, plus *Sohnsia*, *Allolepis*, *Jouvea*, and *Kalinia* form a moderately supported clade (BS = 85, PP = 1.00) that is composed of species from the Western Hemisphere, except for a few Asian species of *Muhlenbergia*.

The Hilariinae (Fig. 1B) consists of a single, strongly supported genus, *Hilaria* Kunth (BS = 100, PP = 1.00) that forms two separate strongly supported clades, *Hilaria* subg. *Pleura-phis* (Torr.) Columbus and *H.* subg. *Hilaria*, each with three species.

The Scleropogoninae (Fig. 1B) contains seven strongly supported genera (BS = 100, PP = 1.00), with the following order of divergence: *Scleropogon* Phil., *Swallenia* Soderstr. & H.F. Decker, *Blepharidachne* Hack., *Dasyochloa* Willd. ex Rydb. + *Munroa* Torr., and *Erioneuron* Nash.

The Boutelouinae (Fig. 1C) contains three strongly supported species (BS = 100, PP = 1.00) and is sister to the Monanthochloinae. The Monanthochloinae (Fig. 1C) includes 11 species that form two strongly supported clades (BS = 100, PP = 1.00) and one moderately supported clade (BS = 72, PP = 0.98). We recognize these three clades as sections within *Distichlis* Raf. and they are described below. *Monanthochloe* sect. *Monanthochloe* and sect. *Spicata* are moderately supported as sister taxa (BS = 73, PP = 0.99).

The Dactylocteniinae (Fig. 1D) includes five genera: *Dactyloctenium* with eight species in our analysis (BS = 100, PP = 1.00) that is sister to *Acrachne racemosa* (BS = 98, PP = 1.00) in the ITS tree, a strongly supported clade of two species of *Brachychloa* (BS = 100, PP = 1.00), and a strongly supported clade (BS = 100, PP = 1.00) of two species of *Neobouteloua*.

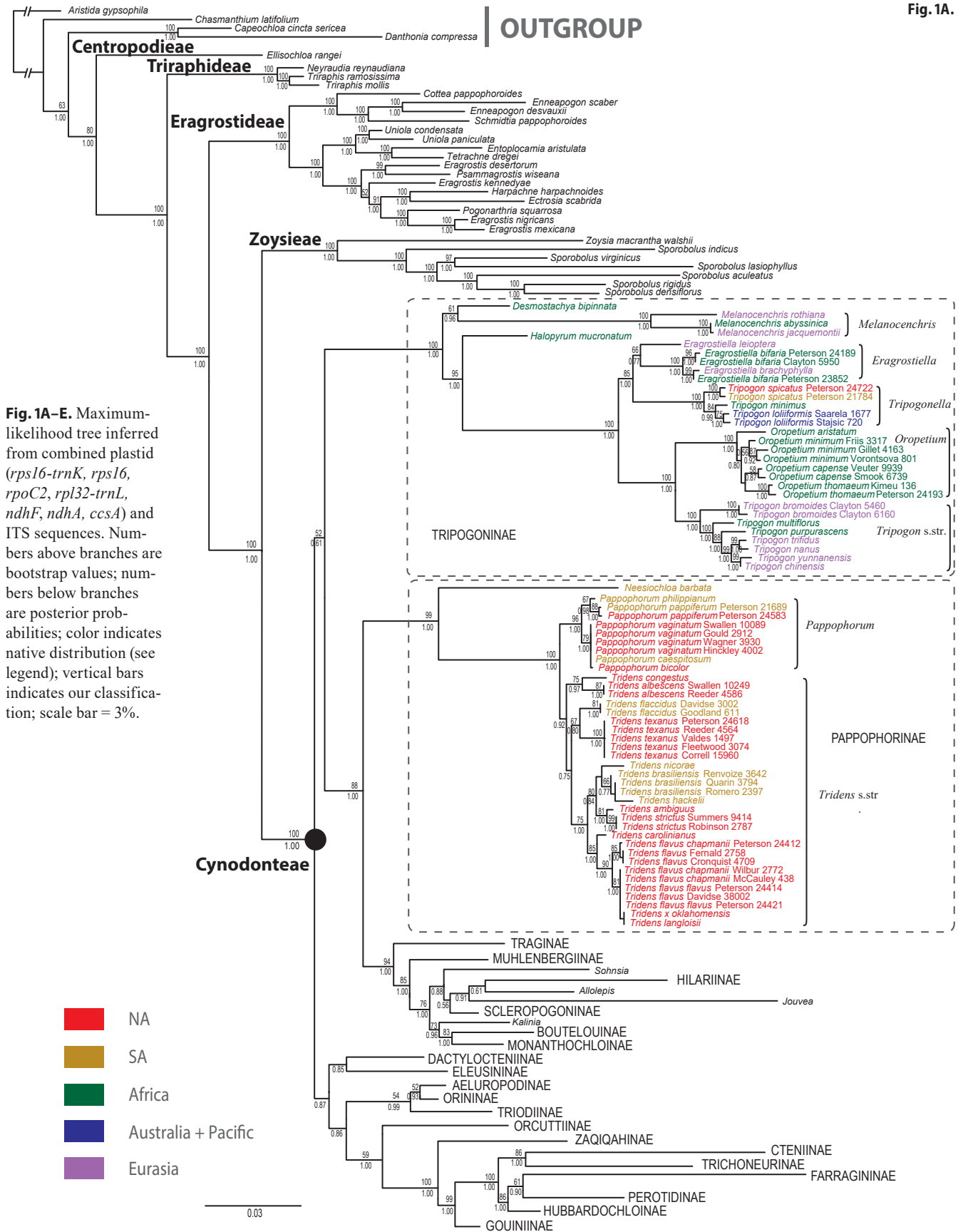


Fig. 1B.



The Eleusininae (Fig. 1D) contains 23 genera (excl. *Acrachne* and *Dinebra*) with *Coelachyrum* Hochst. & Nees appearing polyphyletic since *C. lagopoides* (Burm.f.) Senaratna is sister to *Apochiton burttii* C.E.Hubb. and *C. poiflorum* Chiov. is sister to *Eleusine multiflora* Hochst. ex A.Rich.

The Aeluropodinae (Fig. 1D) consists of a strongly supported *Aeluropus* clade (BS = 100, PP = 1.00) with three species sister to two accessions of *Odysea paucinervis*.

The Orininae (Fig. 1E), newly described below, includes two genera, a strongly supported *Cleistogenes* clade (BS = 100, PP = 1.00) represented by 10 species that is sister to a strongly supported *Orinus* clade (BS = 100, PP = 1.00) with two species.

The Triodiinae (Fig. 1E) includes a single genus, *Triodia* R.Br., and we have included 22 species that occur in five

groups. Lazarides (1997) and Lazarides & al. (2005) divided *Triodia* into nine infrageneric groups and we have placed these names on our tree at the appropriate clades. The Danthonioides group appears polyphyletic.

The Orcuttiinae includes all nine known species in the subtribe, and *Tuctoria* Reeder is clearly polyphyletic and lies in a grade between *Neostapfia* Burt Davy and strongly supported *Orcuttia* Vasey s.str. clade (BS = 100, PP = 1.00).

Three accessions of *Odysea mucronata* are strongly supported (BS = 100, PP = 1.00) and not closely related to two accessions of *O. paucinervis*. Therefore, we describe a new genus and erect a new subtribe below.

The Hubbardochoinae is moderately supported (BS = 75, PP = 1.00) and includes *Hubbardochoa* (for the first time), *Lophacme* Stapf, *Gymnopogon* P.Beauv., *Bewsia* Gooss.,

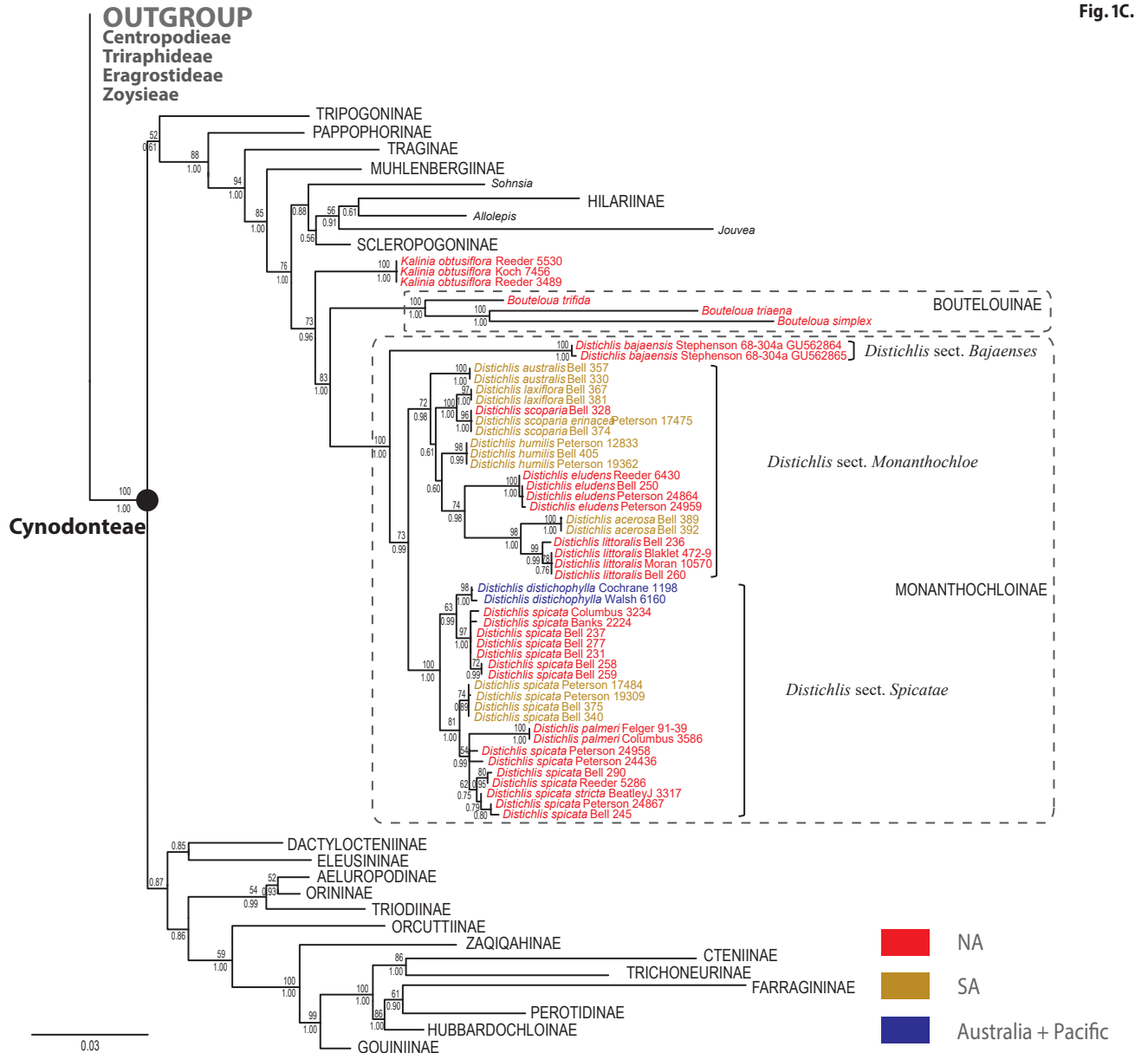


Fig. 1C.

Fig. 1D.

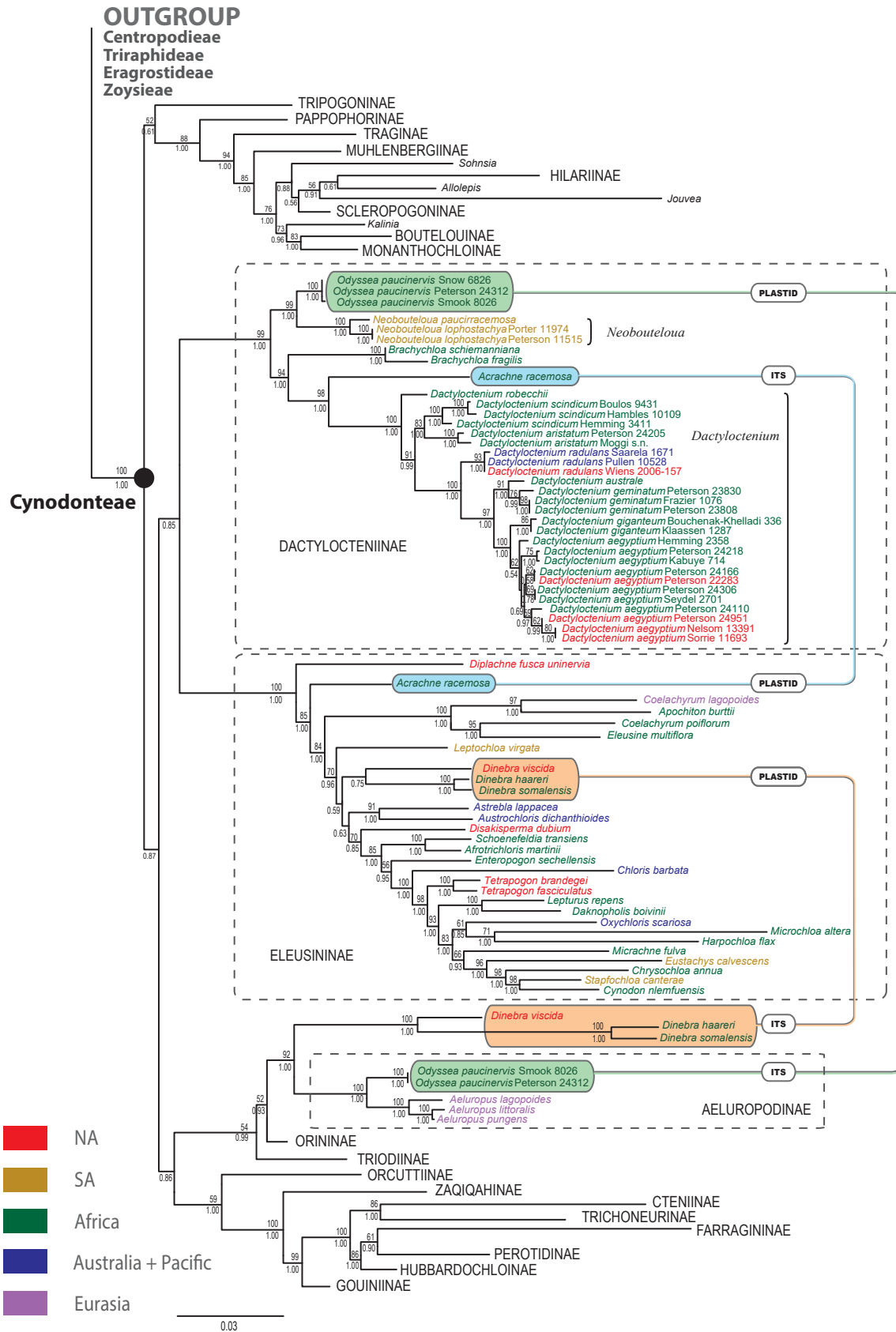
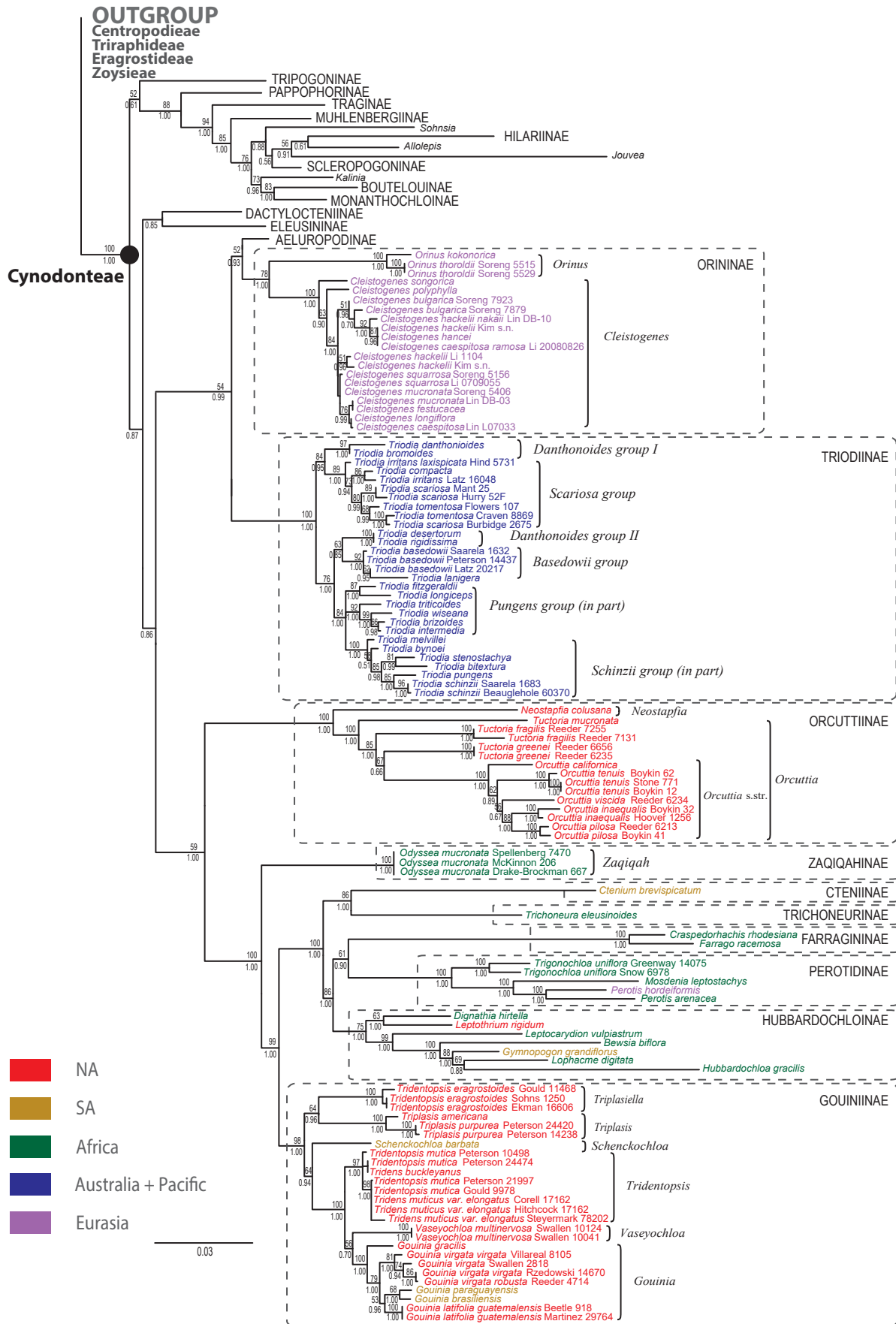


Fig. 1E.



Leptocarydion Hochst. ex Stapf, *Leptothrium* Kunth, and *Dignathia* Stapf.

The Gouiniinae includes strongly supported clades (BS = 100, PP = 1.00) of *Gouinia* E.Fourn. ex Benth. & Hook.f. with five species and *Triplasis* P.Beauv. with two species. *Tridentopsis* P.M.Peterson appears polyphyletic and we describe a new genus below for *T. eragrostoides* (Vasey & Scribn.) P.M.Peterson. *Vaseyochloa multinervosa* (Vasey) Hitchc. is sister to *Gouinia*, and *Schenckochloa barbata* (Hack.) J.J.Ortiz is sister to *Tridentopsis*+*Vaseyochloa* Hitchc.+*Gouinia*.

DISCUSSION

Our phylogenetic tree from the combined plastid and nuclear region provides strong support for a monophyletic Cynodonteae that includes 17 strongly supported clades corresponding to the subtribes Tripogoninae, Pappophorinae, Traginae, Muhlenbergiinae, Hilariinae, Scleropogoninae, Boutelouinae, Monanthochloinae, Dactylocteniinae, Eleusiniinae, Aeluropodinae, Triodiinae, Orcuttiinae, Zaqiqahinae, Faraginatae, Perotidinae, and Gouiniinae, and two moderately supported clades corresponding to the Orininae and Hubbardochloinae. Incongruent placement of *Odyssea paucinervis*, *Acrachne racemosa*, and three species of *Dinebra* was found in our combined phylogenetic tree. The plastid data places *Odyssea paucinervis* as sister to *Neobouteloua* in the Dactylocteniinae whereas the nuclear ITS data places it as sister to *Aeluropus* in the Aeluropodinae. The nuclear data placed *Acrachne racemosa* as sister to *Dactyloctenium* in the Dactylocteniinae while the plastid data places it near the base of the Eleusiniinae. The nuclear ITS data place the three species of *Dinebra* as sister to Aeluropodinae and the plastid data place these species within the Eleusiniinae. *Odyssea mucronata* is a strongly supported sister to the Cteniinae, Trichoneurinae, Faraginatae, Perotidinae, Hubbardochloinae, and the Gouiniinae, and not closely related to *Odyssea paucinervis*. We discuss the major clades or subtribes below.

Aeluropodinae (Fig. 1D). — Based on plastid *ndhF* and *rbcL* sequences, the Grass Phylogeny Working Group II (2012) found *Odyssea paucinervis* to be sister to *Neobouteloua lophostachya* (Griseb.) Gould. Our plastid results confirm this but our ITS data aligns *O. paucinervis* with *Aeluropus*. We have additional evidence from single-copy nuclear At103 COS gene sequences (Peterson & Romaschenko, unpub.) that confirm *O. paucinervis* as sister to *Aeluropus* (Li & al., 2008). Morphologically, *O. paucinervis* is similar to *Aeluropus* in having elongated rhizomes, stiff and pungent leaf blades, inflorescences composed of racemes born on a central axis, multiple-flowered spikelets, and mucronate lemmas (Clayton & al., 2006). However, *O. paucinervis* has some features that are similar to *Dactyloctenium*, i.e., 3-veined lemmas and caryopses with free pericarps. Since the genome of *O. paucinervis* has multiple origins we hypothesize that an ancient hybridization event and subsequent genomic introgression, most likely from paternal backcrossing, occurred. We hope to elaborate on the evolutionary history of *O. paucinervis* in the future.

Dactylocteniinae (Fig. 1D). — Earlier molecular phylogenetic studies of *Dactyloctenium*, using only a few species, suggested relationships with *Brachychloa* and *Neobouteloua* (Columbus & al., 2007; Peterson & al., 2010a, b). Our study includes 62% (8/13) of the species found in a monophyletic *Dactyloctenium*, two species of *Neobouteloua* (100%, 2/2), two species of *Brachychloa* (100%, 2/2), *Acrachne racemosa* (33%, 1/3), and *Odyssea paucinervis* (the other species in this genus is not related, see Zaqiqahinae). The latter two species have incongruent DNA data; *Acrachne* is found at the base of the Eleusiniinae (plastid) clade and *Odyssea* is sister to the *Aeluropus* (ITS) clade. We found no genetic variation among six accessions of *Acrachne racemosa* in an earlier study where it fell near the base of the Eleusiniinae in the plastid tree, but it was sister to *Dactyloctenium* in the ITS tree (Peterson & al., 2015b). We have additional evidence from At103 sequences (Peterson & Romaschenko, unpub.) that support placement of *Acrachne* in the Dactylocteniinae suggesting an ancient hybridization event and subsequent genomic introgression, most likely from paternal backcrossing.

Like *Dactyloctenium*, the species in this new subtribe have inflorescences composed of digitately arranged racemes or racemes borne on a central axis, caryopses usually with a free pericarp (excluding *Neobouteloua*), 1–9-flowered laterally compressed spikelets, glumes that are usually shorter than the spikelets (excluding a single species of *Dactyloctenium*), and (1–)3(–5)-veined lemmas (excluding a single species of *Dactyloctenium*) (Clayton & al., 2006). The considerable morphological variation within *D. aegyptium* (L.) Willd. is reflected among the 11 individuals included in our *Dactyloctenium* clade where support for the monophyly of this species is weak (BS = 62, PP = 0.54). It is interesting that two accessions of *D. aegyptium*, (Peterson & al. 24166 from Dodoma Region, Tanzania and Peterson & Saarela 22283 from Oaxaca, Mexico) form a tight pair. Since *D. aegyptium* is an introduced species in Mexico our results suggest that Peterson & Saarela 22283 was introduced from Africa. These two accessions have three noteworthy morphological characters, all within the broad limits of the species: inflorescences with only two or three racemes per culm and plumbeous spikelets with long-awned upper glumes (the awn twice as long as the body of the glume) as seen in African material (Phillips, 1974, 1995).

Eleusiniinae (Fig. 1D). — Thirty genera currently comprise the Eleusiniinae (Peterson & al., 2015b; Soreng & al., 2015), and we only include a brief survey of this subtribe in the current analysis and in this discussion. As in Peterson & al. (2015b), we note two hard incongruent patterns, that of *Acrachne racemosa* (discussed above) and *Dinebra*. Three species of *Dinebra* form a clade sister to the Aeluropodinae based on the ITS data. More study of *Dinebra* is necessary to untangle its evolutionary history, although it appears to be another case of hybridization and subsequent genomic introgression.

Gouiniinae (Fig. 1E). — We described *Tridentopsis* recently to include *T. mutica* (Torr.) P.M.Peterson and *T. eragrostoides* (Vasey & Scribn.) P.M.Peterson (Peterson & al., 2014a). In Peterson & al. (2014a), *Tridens eragrostoides* Vasey & Scribn. was transferred to *Tridentopsis* based on an unpublished

preliminary tree that included nine species of *Tridens* using only *Erioneuron pilosus* (Buckley) Nash as outgroup. In our current study using a larger sample of genera and species in the Gouiniinae, we find *Tridentopsis eragrostoides* to be weakly supported sister to *Triplasis*, and not included in the *Tridentopsis* clade with *T. mutica*, *Tridens muticus* var. *elongatus* (Buckley) Shinnery, and *Tridens buckleyanus* (Vasey ex L.H.Dewey) Nash. The latter species is endemic to Texas and is morphologically very similar to *Tridentopsis mutica* but differs in having longer, widely spaced primary branches that are usually spreading up to 80° from the culm axis (Valdés Reyna, 2003b; Hatch & Haile, 2012). We also include for the first time three accessions of *Tridens muticus* var. *elongatus*, which clearly aligns with the *Tridentopsis* clade. In the taxonomy section, we transfer *Tridens buckleyanus* and *T. muticus* var. *elongatus* into *Tridentopsis*, erect a new genus (*Triplasiella*) for *T. eragrostoides*, and emend the generic description of *Tridentopsis*.

Hilariinae (Fig. 1B). — *Hilaria* and *Pleuraphis* Torr. were recognized as separate genera until Bentham (1881) transferred *Pleuraphis jamesii* Torr. and *P. mutica* Buckley to *Hilaria*. Only three species are attributed to *Pleuraphis* and they form a strongly supported clade in our tree that is sister to three species of *Hilaria*. The three species of *Hilaria* subg. *Pleuraphis* have short or long rhizomes, whereas the remaining seven species of *Hilaria* subg. *Hilaria* are often stoloniferous but never rhizomatous (Clayton & al., 2006). Without the additional four species of *Hilaria* included in our analysis it is premature to suggest the resurrection of *Pleuraphis*. There appears to be a lot of genetic variation among individuals of *H. mutica* and *H. rigida* since neither species appears monophyletic in our tree.

Hubbardochloinae (Fig. 1E). — In our tree *Hubbardochloa gracilis* is weakly supported (BS = 69, PP = 0.88) sister to *Lophacme digitata* Stapf. When Auquier (1980) described *Hubbardochloa* he did not know what other grasses within the Chloridoideae might be closely related. Even though we have reported only an ITS sequence for *H. gracilis*, we have additional evidence from At103 sequences (Peterson & Romaschenko, unpub.) that support placement with these other genera. The enigmatic *H. gracilis*, known only from Burundi, Namibia, and Rwanda, is a delicate annual with small, 1-flowered spikelets 1.2–1.4 mm long with awned, hyaline lemmas that lack paleas and lodicules (Auquier, 1980; Cope, 1999). Peterson & al. (2014a) described the subtribe Gymnopogoninae (now subsumed in Hubbardochloinae) as having inflorescences with many racemes scattered along a central axis or subdigitally arranged with pedicelled spikelets. These characters are found in *Hubbardochloa* where none of the delicate branches ever re-branch (= racemes) and arise along the main axis in whorls or scattered along the central axis.

Lophacme digitata is endemic to South Africa and morphologically does not appear similar to *Hubbardochloa*. In *Lophacme* the 2-flowered spikelets are sessile or short-pedicellate with hairy 3-veined lemmas, relatively long 2-veined paleas, and somewhat fleshy and glabrous lodicules (Watson & Dallwitz, 1992).

Monanthochloinae (Fig. 1C). — This subtribe includes 11 primarily dioecious species with 3–11-veined lemmas, Kranz C₄ NAD-ME subtype leaf anatomy, blades with papillae, bulbous bicellular microhairs, a column of cells between vascular bundles, narrow metaxylem elements in the primary vascular bundles, presence of papillae on subsidiary cells of the lemma stomata, and all species occur in saline habitats (Bell, 2007, 2010; Bell & Columbus, 2008). *Kalina obtusiflora* (E.Fourn.) H.L.Bell & Columbus has been hypothesized to be most closely related to *Distichlis* (Bell & Columbus, 2008; Bell & al., 2013) but in our study *Bouteloua* Lag. and *Distichlis* are sister taxa with moderate support (BS = 83, PP = 1.00), and *Kalina* is the sister group of *Bouteloua*+*Distichlis*. Until recently, *K. obtusiflora* was placed in *Eragrostis* Wolf (= *E. obtusiflora* (E.Fourn.) Scribn.) even though Ogden (1896) had originally thought it was conspecific with *Jouvea* and near *Distichlis* (Peterson & Valdés Reyna, 2005). The improved resolution and support in our study compared to Bell & al. (2013) is likely attributed to a combination of increased taxon and gene sampling. Incidentally, adaptation to saline environments may be symplesiomorphic in *Kalina*, *Distichlis*, and *Bouteloua* since the basal clade of *Bouteloua* sect. *trifida* P.M.Peterson & al. includes *Bouteloua kayi* Warnock, a Texas endemic known from mountainous limestone-derived habitats along the Rio Grande River (Wipff, 2003; Herrera Arrieta & al., 2004; Peterson & al., 2015a).

Our study includes multiple accessions of all species with 18 individuals of the highly variable *D. spicata* (L.) Greene complex. Within *Distichlis* we have strong to moderate support for three major clades we describe below as sections. *Distichlis* sect. *Bajaenses* consists of a single species, *D. bajaensis* H.L.Bell, known only from one large population in alkaline seeps of Arroyo Rosarito, Baja California, Mexico. It is characterized by being yellowish, having short (8–15 mm long) leaf blades that have a slight bend towards the adaxial side with antrorse hairs along the margins and along the abaxial side of the median vascular bundle from the bend to the apex (Bell, 2010). *Distichlis* sect. *Monanthochloe* includes seven well-delineated species, each found in a strongly supported clade (BS = 96–100, PP = 0.99–1.00). As expected, *D. acerosa* (Griseb.) H.L.Bell & Columbus and *D. littoralis* (Engelm.) H.L.Bell & Columbus, both formerly described in *Monanthochloe*, are sister species (Bell, 2007; Bell & Columbus, 2008). These seven species are characterized in having conduplicate narrow leaf blades 0.2–2(–3) mm wide, spikelets with 1–9 fertile florets, and 1–8-veined glumes that are sometimes wanting or obscure (Clayton & al., 2006; Bell & Columbus, 2008). In contrast, *Distichlis* sect. *Spicatae* includes three species with flat to involute leaf blades 1–6 mm wide, spikelets with 5–15 fertile florets, and 3–9-veined glumes (Clayton & al., 2006; Bell & Columbus, 2008). In our tree two strongly supported clades of *Distichlis distichophylla* (Labill.) Fassett (three individuals) and *D. palmeri* (Vasey) Fassett (two individuals) fall within the large sample of *D. spicata* rendering it paraphyletic. Previously, only *D. palmeri* individuals were found embedded within the *D. spicata* complex (Bell & Columbus, 2008), and historically, these three taxa have been treated as conspecific (Beetle, 1943, 1945; Peterson & al., 2001).

Orcuttinae (Fig. 1E). — Our tree clearly supports *Neostapfia* as sister to a clade containing species of a paraphyletic *Tuctoria* (including three species) with five derived species of *Orcuttia*. We have included all species in this subtribe and hope to settle the classification quandary mentioned by Boykin (2010): (1) submerge (actually return) *Tuctoria* within *Orcuttia* as previously treated by Hoover (1941), (2) create a monotypic genus for *Tuctoria mucronata* (Crampton) Reeder and maintain *Tuctoria* with two species, or (3) maintain *Tuctoria* with three species as paraphyletic. Reeder (1982) erected *Tuctoria* and separated it from *Orcuttia* and *Neostapfia* by possessing spikelets that are spirally arranged on the axis (distichously arranged in *Orcuttia* and *Neostapfia*) and lemmas with entire or denticulate apices (deeply cleft into five mucronate or awn-tipped teeth in *Orcuttia* and *Neostapfia*). Our tree shows *Tuctoria* to be paraphyletic as all three species are successive sister lineages to *Orcuttia* s.str., and therefore our data clearly supports option one. Option 3 is taxonomically disruptive because, based on our data, two species of *Tuctoria*, *T. mucronata* and *T. greenei* (Vasey) Reeder, each would require a separate generic name. Reeder (1982) reported that seed proteins of the three species are not as similar to one another as they are to other species of *Orcuttia* and that relationships are more firmly established based on morphology and anatomy. This is clearly “old school” phenetic thinking, since proteins are genetically controlled and we now know that if we are to base our classification on descent, i.e., sharing a common ancestor, then the only adequately way to polarize and interpret morphological and anatomical features is with molecular data. Since *Neostapfia* is sister to a strongly supported clade with all remaining species in the subtribe, it seems best to retain *Orcuttia* s.l. and *Neostapfia*.

Orininae (Fig. 1E). — In an earlier DNA sequence-derived phylogeny, *Orinus* was weakly supported sister to *Triodia*, and *Cleistogenes* formed an unsupported grade between the Orcuttiinae and nine other subtribes (Peterson & al., 2010a). The reason why we have recovered a robust, although moderately supported clade comprising *Cleistogenes* and *Orinus* as sister taxa is that we have a much larger sample of species within the genera of all major clades. *Cleistogenes* includes 13 or 14 species ranging from southern Europe to Turkey and eastward through central Asia, China (10 species), Pakistan, northwest India, and Japan, and *Orinus* includes 6 species from the Himalayas from Kashmir to Nepal and China (Clayton & al., 2006; Shouling & Phillips, 2006a, b). The two genera are often difficult to separate morphologically, and have been linked historically since the basionym of *Orinus kokonorica* (K.S.Hao) Tzvelev was described as a *Cleistogenes* (Hao, 1938). However, *Cleistogenes* has hidden cleistogamous spikelets concealed within the upper sheaths (not found in *Orinus*), a caespitose habit or very short rhizomes (vs. elongated rhizomes in *Orinus*), and 3–7-veined lemmas (vs. 3-veined lemmas in *Orinus*) (Clayton & al., 2006; Shouling & al., 2006). Below, we describe Orininae as a new subtribe.

Pappophorinae (Fig. 1A). — Earlier molecular studies of the Pappophorinae examined a small number of species where the subtribe was shown to include three genera: *Neesiochloa*, *Pappophorum*, and *Tridens* (Columbus & al., 2007; Peterson & al.,

2010a, 2014a; Soreng & al., 2015). We expand our sample here to include 5 of 8 (63%) species of *Pappophorum* and 15 of 16 (94%) species in *Tridens* (Reeder & Toolin, 1989; Clayton & al., 2006; Peterson & al., 2014a). We find little genetic divergence in our tree among samples of *Pappophorum bicolor* E.Fourn., *P. caespitosum* R.E.Fr. (*J.C. Tivano 801* – Argentina), and *P. vaginatum* Buckley. These three species form a clade that is sister to *P. philippianum* Parodi and *P. pappiferum* (Lam.) Kuntze.

Even though we find poor support (PP = 0.92) for the monophyly of *Tridens*, some interesting conclusions can be drawn. However, the ITS tree (Electr. Suppl.: Fig. S1) does have slightly higher support for the *Tridens* clade (BS = 54, PP = 0.96). Ten accessions, five of *T. flavus* (L.) Hitchc., three of *T. flavus* var. *chapmanii* Small, one of *T. langloisii* (Nash) Nash, and one of *T. ×oklahomensis* (Feath.) Feath. form a strongly supported clade (BS = 90, PP = 1.00). *Tridens flavus* var. *chapmanii* has been treated as a species, *T. chapmanii* (Small) Chase while *T. ×oklahomensis* is thought to be a hybrid between *T. flavus* and *T. strictus*. *Tridens nicorae* Anton, also placed in *Antonella* Caro (1981), is sister to *T. brasiliensis* (Nees ex Steud.) Parodi and *T. hackelii* (Arechav.) Parodi. *Tridens flaccidus* (Döll) Parodi is sister to *T. texanus* (Döll) Parodi and the basal lineage consists of *T. congestus* (L.H.Dewey) Nash sister to *T. albescens* (Vasey) Wooton & Standl. We were unable to sequence DNA from a poorly preserved specimen (*Gossweiler 9858*) of *Gossweilerchloa delicatula* Renvoize, which Clayton & al. (2006) provisionally placed in *Tridens* (Antón, 1977; Renvoize, 1979; Acedo & Llamas, 2003; Valdés Reyna, 2003b).

Scleropogoninae (Fig. 1B). — Within this subtribe we include all species in the subtribe and a much larger sample of individuals than in our previous study (Peterson & al., 2010a) for the following species: *Scleropogon brevifolius* Phil. (6), *Blepharidachne bigelovii* (S.Watson) Hack. (2), *Dasyochloa pulchella* (Kunth) Willd. ex Rydb. (6), *Erioneuron avenaceum* (Kunth) Tateoka (7), *E. nealleyi* (Vasey) Tateoka (6), and *E. pilosum* (Buckley) Nash (10), *Munroa andina* Phil. (2), *M. argentina* Griseb. (2), *M. decumbens* Phil. (1), *M. mendocina* Phil. (1), and *M. squarrosa* (Nutt.) Torr. (2).

Our data clearly support *Dasyochloa pulchella* as sister to all species of *Munroa*, and we do not agree with Amarilla & al. (2013, 2015) that it should be subsumed within *Munroa*, a proposal they made based solely on morphological evidence. Both classification as separate genera (*Dasyochloa*, *Munroa*) or as a single genus (*Munroa*) is supported by both of our datasets. Historically, *Dasyochloa* has been used for the North American species and we feel to change the classification should require compelling support. *Dasyochloa* has two apomorphies (perennial habit and is restricted to North America), in addition to being a strongly supported sister (BS = 100, PP = 1.00) of *Munroa* in our molecular study. The morphological characters used by Amarilla & al. (2013) to support their *Dasyochloa-Munroa* clade are primarily based on size of structures, e.g., internode, stolon, sheath, blade, ligule, inflorescence, spikelet, lemma, palea, anther, caryopsis, lodicule, and there is at least one misinterpretation regarding caryopsis compression (caryopses are laterally compressed in both taxa, not dorsally compressed; Watson & Dallwitz, 1992).

Our sample of 22 *Erioneuron* individuals from North America plus one individual from Argentina gives us an opportunity to assess genetic variation among congeners (*E. avenaceum*, *E. nealleyi*, *E. pilosum*) in comparison with their current morphological circumscription. The sample of *E. avenaceum* (Peterson & al. 19329) from Argentina is clearly separated from other North American accessions in our tree (BS = 97, PP = 1.00). There appears to be limited taxonomic structure to the *Erioneuron* clade since accessions of the three species are rather randomly distributed. Although near the base of the tree there are five poorly resolved accessions of *E. pilosum*, the strongly supported Argentine *E. avenaceum*, and 17 accessions of all three species are poorly resolved. Embedded in the latter polytomy is a strongly supported (BS = 96, PP = 1.00) pair of accessions of *E. nealleyi*, both from northern Coahuila, Mexico in the Sierra El Jardin (Peterson & Lara Contreras 19866) and Madera del Carmen (Peterson & Romaschenko 24483). Clearly, there appears to be a complicated ancestry among these three species where traditional morphological features such as the depth of the apical notch of the lemma and length of the midvein awn, and length of the glumes compared to the lowermost floret have been used as key features for identification (Valdés-Reyna & Hatch, 1997; Valdés-Reyna, 2003a). One could argue that these three species do not exist because there is little genetic support for their recognition. However, our DNA markers seem to support clades from similar geographic areas. A much larger sample size is needed to test this hypothesis, and better resolution of specific boundaries would need to include the many South American varieties of *E. avenaceum* and *E. pilosum* (Nicora, 1973; Antón, 1977).

Traginae (Fig. 1B). — As in Peterson & al. (2010a), *Tragus* and *Willkommia* appear polyphyletic in a clade (BS = 94, PP = 1.00) with *Monelytrum luederitzianum* embedded. However, *Polevansia rigida* is no longer included in the *Tragus* s.l. clade as seen in Peterson & al. (2010a) but is removed with the addition of *Pogononeura biflora* in our study. Therefore, it seems most parsimonious to retain *Pogononeura* and *Polevansia* as separate genera since they form a weak clade (BS = 57, PP = 0.57) and together are sister to the *Tragus* clade. *Pogononeura* and *Polevansia* each have unique morphological features, the former with two fertile florets per spikelet and the latter with a single fertile floret per spikelet. *Willkommia*, *Monelytrum* Hack., and *Tragus* all have dorsally compressed or terete 1-flowered spikelets that are somewhat coriaceous (Clayton & al., 2006), so it is no surprise these three genera are related. We have missing data for *Willkommia annua* Hack. so we are unable to draw a definite conclusion for this genus. We feel it best to recognize the strongly supported *Tragus* s.str. clade and place *Tragus pedunculatus* in a new genus since it has two unique morphological characters: straight, tubercle-based hairs (versus hooked or curved in *Tragus* s.str.) on the veins of the upper glumes and inflorescences with widely diverging long-pedunculate racemose branches (vs. short peduncles), the peduncles 4–10 mm long. *Willkommia* and *Monelytrum* lack tubercle-based hairs on the glumes, although the latter genus has tubercle-based hairs on the margins of the leaf blades.

The eight species currently recognized in *Tragus* possess strongly veined (ribbed) upper glumes that bear stout prickles (Antón, 1981; Cope, 1999; Sulekic & Zapater, 2001; Clayton & al., 2006). These prickles are probably important in zoochory, as *T. berteronianus* Schult. spikelets were the most common disseminule found in the fur of Kenyan hares (Agnew & Flux, 1970). Our current study includes the type of *Tragus* (*T. racemosus* (L.) All.) and it clearly falls within the strongly supported *Tragus* s.str. clade (BS = 100, PP = 1.00). The morphological features separating *Tragus berteronianus*, *T. mongolorum* Ohwi, *T. racemosus*, and *T. heptaneuron* Clayton are small and this is reflected in our tree where they are genetically doubtfully distinct. *Tragus berteronianus* and *T. mongolorum* have 5-veined upper glumes with acute apices in the former and acuminate-attenuate apices in the latter whereas *T. racemosus* and *T. heptaneuron* have 7-veined upper glumes with 2–4 spikelets per branch (former) and paired spikelets (latter) (Clayton, 1972). Perhaps these characters are more a reflection of local phenotypic variation due to environmental differences rather than fixed genetic differences.

Triodiinae (Fig. 1E). — Early molecular DNA studies of *Triodia* s.str. suggesting that the genus is monophyletic (Mant & al., 2000; Peterson & al., 2010a) have been verified recently by extensive sampling that included 66 of the 69 species in the genus (Toon & al., 2015). We include 22 species in our strongly supported *Triodia* clade (BS = 100, PP = 1.00) that is sister to the Aeluropodinae and the Orininae. Lazarides (1997) and Lazarides & al. (2005) divided *Triodia* into nine infrageneric groups. In our tree the four species of the Scariosa group (BS = 89, PP = 1.00) and three accessions of *T. basedowii* Pritz. plus *T. lanigera* Domin. (BS = 92, PP = 1.00) form strongly supported clades. The Danthonioides group appears polyphyletic since there are two widely separated pairs: *T. bromoides* (F.Muell.) Lazarides–*T. danthonioides* (F.Muell.) Lazarides (BS = 97, PP = 1.00) and *T. desertorum* (C.E.Hubb.) Lazarides–*T. rigidissima* (Pilg.) Lazarides (BS = 100, PP = 1.00). The latter two species are morphologically similar, although *T. rigidissima* differs from *T. desertorum* in having shorter, few-flowered spikelets and a shorter panicle (Lazarides, 1997). Our tree includes (in part) a strongly supported Schinzii group (BS = 100, PP = 1.00) with six species; however, *T. pungens* R.Br. (a member of the Pungens group) is embedded within. A moderately supported pair (BS = 87, PP = 1.00), *T. fitzgeraldii* N.T.Burb.–*T. longiceps* J.M.Black form a clade, the former species attributed to the Angusta group and the latter species is unplaced (Lazarides, 1997). *Triodia brizoides* N.T.Burb., *T. intermedia* Cheel, and *T. wiseana* C.A.Gardner form a strongly supported clade (BS = 99, PP = 1.00) that was included in the Pungens group and these are sister to *T. triticoides* C.A.Gardner (Angusta group sensu Lazarides).

Tripogoninae (Fig. 1A). — With only two species each of *Eragrostiella*, *Tripogon*, and *Melanocenchris*, Peterson & al. (2010a) found moderate support (BS = 83, PP = 1.00) for the Tripogoninae. By including additional taxa (e.g., *Desmostachya bipinnata*, *Halopyrum mucronatum*, 3 species of *Melanocenchris*, 3 species of *Eragrostiella*, 4 species of *Oropetium*, 10 species of *Tripogon*), we now obtained strong support (BS = 100, PP = 1.00) for the subtribe.

Tripogon is clearly polyphyletic with two separate clades. The “*Tripogonella*” clade has three species with similar, if not identical morphologies, separated geographically (*Tripogon loliformis* from Australia, *T. minimus* from Africa, and *T. spicatus* from New World), which are sister to a weakly supported (BS = 66, PP = 0.77) *Eragrostiella* clade. Together they form a clade with moderate support (BS = 85, PP = 1.00). The remaining seven species of *Tripogon* (primarily from Asia) form a strongly supported clade sister to *Oropetium*. There are six species currently recognized in *Oropetium* and we have included the type, *O. thomaenum* (L.f.) Trin., in our study (Clayton & al., 2006). Morphologically, *Oropetium* is well delineated in having biserially arranged, 1-flowered spikelets embedded in cavities of the rachis with lower glumes reduced to small hyaline scales (Phillips, 1975). Likewise, *Eragrostiella* is morphologically well defined, although weakly supported in our tree (the type, *E. leioptera* (Stapf) Bor is sister to remaining species), in containing many-flowered, unawned, cartilaginous spikelets, these resembling species of *Eragrostis* (Lazarides, 1976; Phillips, 1995). It is interesting to note that *Eragrostiella bifaria* does not appear to be monophyletic, since one of our recent collections from Tanzania is sister to *E. brachyphylla* (Stapf) Bor from Sri Lanka. However, *E. bifaria* is morphologically variable (it contains at least three varieties) and it is possible that the Sri Lankan specimen of *E. brachyphylla* should be relegated to a variety of *E. bifaria* (Lazarides, 1976, 1994). At this point we have two options: expand the circumscription of *Eragrostiella* to include the three *Tripogon* species or place these three species in a new genus, *Tripogonella*. Even though our *Tripogon* sample includes less than 21% of the species in the genus (10/49), we chose to recognize *Tripogonella* as a new genus with three new combinations below (Phillips & Launert, 1971; Phillips & Chen, 2002; Clayton & al., 2006; Newmaster & al., 2008; Chorghé & al., 2013, 2015; Thoiba & Pradeep, 2014; Sunil & al., 2015; Thoiba & al., 2015). We realize additional species of *Tripogon* may need to be transferred to *Tripogonella*. However, the overall relationships presented here should not substantially change since *Tripogon* s.str. is strongly supported sister to *Oropetium*.

This is the first report of *Halopyrum mucronatum* belonging in the Tripogoninae, as earlier classifications indicated unknown affinity or “incertae sedis” within the Cynodonteae (Clayton & Renvoize, 1986; Soreng & al., 2015). This tough, stoloniferous perennial with culms up to 2 m tall was collected in 2012 by PMP, Robert J. Soreng, KR, and Yahia Abeid at the mouth of the Mbwemkuru River along the east coast of Tanzania. We were led to this site by the mayor of Rushungi who had taken the previous collector, Robert C. Wingfield to the same locality 35 years previously.

Zaqqahinae (Fig. 1E). — The other species of *Odyssea* included in our manuscript, *O. mucronata*, is a strongly supported sister to six subtribes (Cteniinae, Farragininae, Perotidinae, Trichoneurinae, Gouiniinae, Hubbardochloinae). All of these subtribes were discussed in Peterson & al. (2014a) where we included an expanded sample of the Gouiniinae. We completely understand why Stapf (1922) erected *Odyssea* with *O. mucronata* and *O. paucinervis*. Morphologically, the two species are

very similar in having short, rigid to pungent leaf blades; narrow and contracted panicles; several-flowered spikelets with 1-veined glumes; lemmas that are 3-veined with silky villous veins, apices dentate and mucronate; and caryopses with free pericarps (Stapf, 1922; Phillips, 1951, 1995; Cope, 1999, 2007). However, *O. mucronata* is a suffrutescent perennial with stiff, hard, much-branched culms up to 2 m tall, lemmas 4–5 mm long, and is found along the immediate coast bordering the Red Sea in sand dunes or plains whereas *O. paucinervis* is a low mat-forming, rhizomatous perennial with culms up to 35(–60) cm tall, lemmas 2.3–3.5(–4) mm long, and is found on inland, saline soils from Tanzania to South Africa (Phillips, 1995). In the generic description of *Odyssea* Stapf (1922) made these appropriate comments, “There are few grasses, if any, which have experienced as many and as varied generic transferences and corresponding combinations as the grass described here. In the course of time it has become connected with no fewer than nine mostly widely different genera—a veritable Odyssey, hence the name—but it may be hoped that it has at last reached a safe port.” Based on our results we place *O. mucronata* in a new genus, *Zaqqah* and subtribe, *Zaqqahinae* below.

■ TAXONOMY

Dactylocteniinae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.** – Type: *Dactyloctenium* Willd.

Description. – The subtribe is characterized by its annual or perennial habit, culms erect or geniculate ascending to decumbent, sometimes stoloniferous. Inflorescence composed of racemes, these borne along a central axis, more commonly digitately inserted, the spikelets inserted unilaterally along the unbranched racemes, the spikelets sessile or short pedicellate. Spikelets 1–9-flowered, laterally compressed; glumes usually shorter than the spikelets; lemmas (1–)3(–5)-veined; caryopses usually with a free pericarp.

Included genera. – *Acrachne*, *Brachychloa*, *Dactyloctenium*, *Neobouteloua*.

Distichlis* sect. *Bajaenses P.M.Peterson & Romasch., **sect. nov.** – Type: *Distichlis bajaensis* H.L.Bell in Madroño 57(1): 59, fig. 3–6, 8, 2010 – Holotype: MEXICO. Baja California, Municipio de Ensenada, salt marsh arroyo 1 km SW of Rosarito, Oct 1968, *Stephenson 68-304a* (MSC No. 216526).

Description. – Sprawling, decumbent yellowish-green perennials with rhizomes and stolons, 8–12 cm tall, intravaginal branching along stolons, culms 1 mm in diameter; leaf blades 8–15 mm long, spreading at collar, narrowing gradually to pungent tip, with slight bend toward adaxial side, antrorse hairs along margins and along the abaxial side of the median vascular bundle from the bend and above, male inflorescences a small panicle of racemes; inflorescences exerted above blade tips on peduncles of up to 1 cm, flattened pedicels 3–5 mm with toothed margins, 2–5 spikelets per inflorescence, 2–4 florets per spikelet, glumes hyaline with a single vein, lemmas with 7–11 indistinct nerves, hyaline, palea slightly shorter than

lemma, enclosed within lemma, anthers 2.5–3.5 mm, straw colored, some with purple tinge.

Species included. – *D. bajaensis* H.L.Bell.

Distichlis* sect. *Monanthochloe (Engelm.) P.M.Peterson & Romasch., **comb. & stat. nov.** ≡ *Monanthochloe* Engelm. in Trans. Acad. Sci. St. Louis 1: 436. 1859 – Type: *Monanthochloe littoralis* Engelm. in Trans. Acad. Sci. St. Louis 1: 437, pl. 13–14. 1859 ≡ *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus in Syst. Bot. 33: 548. 2008 – Lectotype (designated by Davidse & Pohl in Davidse & al., Fl. Mesoamer. 6: 258. 1994): U.S.A. Texas, Galveston, May 1843, *F.J. Lindheimer* 63 (MO barcode MO-197280 [No. 1837530; image!]; isolectotypes: MO barcode MO-197278 [No. 1837531; image!], MO barcode MO-197277 [No. 1837528; image!]).

Description. – Stoloniferous or rhizomatous perennials; leaf blades conduplicate, folded, 0.2–2(–3) mm wide; spikelets with 1–9 fertile florets, glumes 1–8-veined, sometimes wanting or obscure; lemmas 7–13-veined.

Species included. – *D. acerosa* (Griseb.) H.L.Bell & Columbus, *D. australis* (Speg.) Villamil, *D. eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *D. humilis* Phil., *D. laxiflora* Hack., *D. littoralis* (Engelm.) H.L.Bell & Columbus, *D. scoparia* (Nees ex Kunth) Arechav.

Distichlis* sect. *Spicatae P.M.Peterson & Romasch., **sect. nov.** – Type: *Uniola spicata* L., Sp. Pl.: 71. 1753 ≡ *Distichlis spicata* (L.) Greene in Bull. Calif. Acad. Sci. 2: 415. 1887 – Lectotype (designated by Hitchcock in Contr. U.S. Natl. Herb. 12: 121. 1908): U.S.A. America borealis maritimis, *Kalm s.n.*, Herb. Linn. No. 89.4 (LINN [image!]).

Description. – Rhizomatous perennials; leaf blades flat to involute upon drying, 1–6 mm wide; spikelets with 5–15 fertile florets, glumes 3–9-veined, lemmas 5–12-veined.

Species included. – *D. distichophylla* (Labill.) Fassett, *D. palmeri* (Vasey) Fassett, *D. spicata* (L.) Greene.

Hubbardochloinae Auquier in Bull. Jard. Bot. Natl. Belg. 50: 246. 1980 – Type: *Hubbardochloa* Auquier in Bull. Jard. Bot. Natl. Belg. 50: 246. 1980.

= ***Gymnopogoninae*** P.M.Peterson, Romasch. & Y.Herrera in Taxon 63: 283–284. 2014.

Description (emendation). – Perennials or annuals, culms erect or geniculate and decumbent; ligules membranous, ciliate or eciliate, sometimes a fringe of hairs; inflorescence of many racemes scattered along a central axis or sub-digitately arranged with pedicelled spikelets; fertile spikelets 1.2–11 mm long, 1–14-flowered, laterally compressed; glumes usually exceeding the florets, 1(3)-veined, membranous to coriaceous, apex often mucronate, sometimes awned; lemmas (1)3-veined, usually awned or mucronate.

Included genera. – *Bewsia*, *Dignathia*, *Gymnopogon*, *Hubbardochloa*, *Leptocarydion*, *Leptothrium*, *Lophacme*.

Orininae P.M.Peterson & Romasch. & Y.Herrera, **subtr. nov.** – Type: *Orinus* Hitchc. in J. Wash. Acad. Sci. 23: 136, fig. 2. 1933.

Description. – Caespitose or rhizomatous perennials. Culms 15–100 cm tall, erect or geniculately spreading. Upper leaf sheaths sometimes with cleistogamous spikelets; ligules membranous or a line of hairs. Inflorescence a panicle with racemose branches borne along a central axis. Spikelets 5–13 mm long, (1)2–8-flowered, laterally compressed; glumes shorter than adjacent floret; (0)1–7-veined; lemmas 3–7-veined, apices usually entire, mucronate or awned; paleas 2-veined. Caryopses with adherent pericarp.

Included genera. – *Cleistogenes*, *Orinus*.

Orthacanthus P.M.Peterson & Romasch., **gen. nov.** – Type: *Orthacanthus pedunculatus* (Pilg.) P.M.Peterson & Romasch. ≡ *Tragus pedunculatus* Pilg.

Diagnosis. – *Orthacanthus* differs from species of *Tragus* in having straight tubercle-based hairs on the veins of the upper glumes and inflorescences with widely diverging long-pedunculate racemose branches, the peduncles 4–10 mm long.

Description. – Mat-forming annuals. Culms 10–50 cm tall, erect or geniculate below. Leaf sheaths shorter than the internodes, glabrous; ligules 0.2–0.4 mm long, a line of hairs; blades (1.5–)2–6 cm long, 1.2–2.6 mm wide, flat, margins thickened and often whitish with a few tubercle-based hairs below. Inflorescence a panicle up to 7 cm long with 4–8 racemously arranged, widely diverging branches; branches with tubercle-based hairs; peduncles 4–10 mm long; disarticulation at base of branch; rachis triangular in cross section. Spikelets 6–10 mm long, 1-flowered, dorsally compressed; glumes unequal; lower glumes 1–2 mm long, unveined, hyaline; upper glumes 6–10 mm long, lanceolate, membranous, 7–9-veined, the veins bearing straight tubercle-based hairs, apex acuminate; lemmas 5–8 mm long, 3-veined, membranous, apex acuminate; paleas 2-keeled; stamens 3; anthers 0.9–1.3 mm long. Caryopses ellipsoid, dorsally compressed.

Distribution and habitat. – The single species is distributed in Botswana, Namibia, and South Africa; in sandy soils near calcareous rock outcrops and margins of pans on calcrete; ca. 1000 m.

Etymology. – The name of the new genus is derived from the Greek roots “ortho” meaning straight and “acanthus” meaning spine, alluding to the straight tubercle-based hairs on the veins of the upper glumes. *Orthacanthus* is also the generic name of a freshwater xenacanth shark that lived in Europe and North America during the Carboniferous and Permian (ca. 400–225 Ma) (Agassiz, 1833–1843).

Orthacanthus pedunculatus (Pilg.) P.M.Peterson & Romasch., **comb. nov.** ≡ *Tragus pedunculatus* Pilg. in Bot. Jahrb. Syst. 45: 208. 1910 – Holotype: NAMIBIA. Grootfontein, 11 Jan 1909, *Dinter* 689 (B barcode B 10 0168910 [image!]; isotype: M barcode M-0103713 [image!]).

Tridentopsis P.M.Peterson, emend. – Type: *Tridentopsis mutica* (Torr.) P.M.Peterson (≡ *Tricuspis mutica* Torr.).

Description (emendation). – Caespitose perennials sometimes with knotty, short rhizomatous bases. Culms 20–80 cm tall, nodes often with soft hairs up to 2 mm long. Leaf sheaths

glabrous, scabrous, often pilose; ligules 0.4–1.5 mm long, membranous, ciliate; blades up to 15 cm long, 1–4 mm wide, flat to involute. Panicles 7–28 × 1–6 cm, narrow spreading; branches up to 13 cm long, erect, appressed. Spikelets 7–13 mm long, 2–11-flowered, laterally compressed; disarticulation above the glumes; glumes 3–10 mm long, 1–7-veined, glabrous; lemmas 3.5–7 mm long, 3-veined, usually purple-tinged, midveins sometimes excurrent, pubescent to pilose along the veins; paleas 1.5–5 mm long, shorter than the lemmas, glabrous or hairy. Caryopses 1.5–2.6 mm long, dorsally flattened and deeply concave to folded on the dorsal or hilar surface and thickened towards the margin below, surface is reticulate, reddish-brown. $2n = 40$.

Tridentopsis buckleyana (Vasey ex L.H.Dewey) P.M.Peterson & Romasch., **comb. nov.** ≡ *Sieglingia buckleyana* Vasey ex L.H.Dewey in Contr. U.S. Natl. Herb. 2: 540. 1894 ≡ *Tridens buckleyanus* (Vasey ex L.H.Dewey) Nash in Small, Fl. S.E. U.S.: 143. 1903 ≡ *Triodia buckleyana* (Vasey ex L.H.Dewey) Vasey ex Hitchc. in J. Wash. Acad. Sci. 23: 452. 1933 – Holotype: U.S.A. Texas, 1883, *S.B. Buckley s.n.* (US No. 81808!; isotype: NY barcode 00431683 [image!]).

Tridentopsis mutica var. *elongata* (Buckley) P.M.Peterson & Romasch., **comb. nov.** ≡ *Uralespis elongata* Buckley in Proc. Acad. Nat. Sci. Philadelphia 14: 89. 1862 ≡ *Sieglingia elongata* (Buckley) Nash in Britton & Brown, Ill. Fl. N.U.S. 3: 504. 1898 ≡ *Tricuspis elongata* (Buckley) A.Heller, Cat. N. Amer. Pl., ed. 2: 28. 1900 ≡ *Triodia elongata* (Buckley) Scribn. in Bull. Div. Agrostol. U.S.D.A. 17 (ed. 2): 210, fig. 506. 1901, **comb. superfl.** ≡ *Triodia elongata* (Buckley) Bush in Trans. Acad. Sci. St. Louis 12: 76. 1902, **comb. superfl.** ≡ *Tridens elongatus* (Buckley) Nash in Small, Fl. S.E. U.S.: 143. 1903 ≡ *Tridens muticus* var. *elongatus* (Buckley) Shinnors in Rhodora 56: 28. 1954 – **Lectotype (designated here)**: U.S.A. Texas, northern Texas, May 1861, *S.B. Buckley s.n.* (PH barcode 00028567 [image!]; isoelectotype: US barcode 01165138 [image!]).

Triplasiella P.M.Peterson & Romasch., **gen. nov.** – Type: *Triplasiella eragrostoides* (Vasey & Scribn.) P.M.Peterson & Romasch. (≡ *Triodia eragrostoides* Vasey & Scribn.).

Diagnosis. – *Triplasiella* differs from the two species of *Triplasis* in having panicles 10–30 × 8–20 cm (versus 1–7 × 1–6 cm in *Triplasis*), palea keels smooth or scabrous (versus ciliate), and no cleistogamous spikelets in the upper sheaths.

Distribution and habitat. – *Triplasiella eragrostoides* is distributed in southern U.S.A., eastern and southern Mexico, the Caribbean, and Venezuela in shrubby grasslands, desert scrub, open ground, cliffs, and rocky sites; 0–2300 m.

Triplasiella eragrostoides (Vasey & Scribn.) P.M.Peterson & Romasch., **comb. nov.** ≡ *Triodia eragrostoides* Vasey & Scribn. in Contr. U.S. Natl. Herb. 1: 58–59. 1890 ≡ *Sieglingia eragrostoides* (Vasey & Scribn.) L.H.Dewey in Contr. U.S. Natl. Herb. 2: 539. 1894 ≡ *Tridens eragrostoides* (Vasey & Scribn.) Nash in Small, Fl. S.E. U.S.:

142. 1903 ≡ *Tridentopsis eragrostoides* (Vasey & Scribn.) P.M.Peterson in Taxon 63: 284. 2014 – **Lectotype (designated here)**: U.S.A. Texas, 1889, *G.C. Nealley 822* (US barcode 00141889 [No. 81811; image!]; isoelectotype: W No. 1916-0017781 [image!]).

Note. – An inaccurate (wrong Nealley specimen chosen) lectotype by Hitchcock in Contr. U.S. Natl. Herb. 17: 357. 1913 states, “the type specimen collected by Nealley in 1892 at San Diego”.

Tripogonella P.M.Peterson & Romasch., **gen. nov.** – Type: *Tripogonella spicata* (Nees) P.M.Peterson & Romasch. (≡ *Bromus spicatus* Nees).

Description. – Small, slender caespitose perennials. Culms 4–34(–55) cm tall, erect, wiry, with 1–3 nodes. Leaf sheaths mostly basal, glabrous to hairy; ligules 0.1–2 mm long, a ciliate membrane; blades 1–10 cm long, 0.2–1.3 mm wide, flat to involute and filiform, glabrous, pubescent or pilose. Inflorescence a spike-like raceme with a single spikelet per node, racemes (1.5–) 2–10(–17) cm long, straight, the biserially arranged spikelets sessile to short pedicellate on a flattened rachis, the pedicels usually less than 0.5 mm long. Spikelets 3.2–12(–15) mm long, 1–1.5 mm wide, 5–22-flowered, laterally compressed, membranous; callus pubescent or pilose; rachilla apex with a few hairs; glumes 1.2–3.5 mm long, unequal, 1-veined, rarely the upper glume 3-veined; lemmas (1.2–)1.6–3.4 mm long, 3-veined, apex emarginate with two small teeth, mucronate or short-awned from the sinus, the awn less than 1.4 mm long; paleas shorter than lemma, keels ciliate; stamens 2 or 3, anthers 0.2–0.5 mm long. Caryopses 0.8–2 mm long, narrowly lanceolate.

Distribution and habitat. – The three species are distributed throughout tropical and southern Africa and Madagascar (*T. minima*); Australia (*T. loliiformis*); and North America, Central America, South America, and the Caribbean (*T. spicata*); shallow soils, rock outcrops, margins of rivers, flood plains, open xerophytic grasslands; 0–3000 m.

Tripogonella loliiformis (F.Muell.) P.M.Peterson & Romasch., **comb. nov.** ≡ *Festuca loliiformis* F.Muell., Fragm. 8: 128. 1873 ≡ *Diplachne loliiformis* (F.Muell.) Benth., Fl. Austral. 7: 618. 1878 ≡ *Tripogon loliiformis* (F.Muell.) C.E.Hubb. in Bull. Misc. Inform. Kew 1934: 448. 1934 – **Lectotype (designated here)**: AUSTRALIA. Queensland, Swamps of Bokhara, Charley’s Creek, 3 Jan 1847, *F.W.L. Leichardt s.n.* (MEL barcode MEL 626901 [image!]; isoelectotypes: A barcode 00024513, plant on left of sheet [image!], MEL barcode MEL626900 [image!]).

Tripogonella minima (A.Rich.) P.M.Peterson & Romasch., **comb. nov.** ≡ *Festuca minima* A.Rich., Tent. Fl. Abyss. 2: 436. 1850 ≡ *Tripogon minimus* (A.Rich.) Hochst. ex Steud., Syn. Pl. Glumac. 1: 301. 1854 – **Lectotype (designated here)**: ETHIOPIA. Prope Djeladjeranne in montibus versus fluvium Tacaze, 3 Aug 1840, *G.W. Schimper 1652* (P barcode P00439486 [image!]; isoelectotypes: B barcode B 10 0168885 [image!], BR barcodes 000008255631 & 000008765666 [images!], FI, G barcodes G00022717,

G00022718 & G00022719 [images!], GOET barcode GOET006964 [image!], HAL barcode HAL0107211 [image!], K, L barcodes L 0050279, L 0050280, L 0050281, L 0050282 & L 0050283 [images!], LG [barcoded with BR barcode 000009003704; image!], MO No. 2108845!, MPU barcodes MPU012822 & MPU027842 [images!], P barcodes P00439489 & P00439487 [images!], S No. S11-11665 [image!], TUB barcodes TUB-006645 & TUB-006646 [images!], US Nos. 899302!, 3243713! & 1006682 ex herb. J. Gay!).

Tripogonella spicata (Nees) P.M.Peterson & Romasch., **comb. nov.** ≡ *Bromus spicatus* Nees, Fl. Bras. Enum. Pl. 2(1): 471. 1829 ≡ *Diplachne spicata* (Nees) Döll in Martius, Fl. Bras. 2(3): 160. 1878 ≡ *Leptochloa spicata* (Nees) Scribn. in Proc. Acad. Nat. Sci. Philadelphia 43(2): 304. 1891 ≡ *Rabdochloa spicata* (Nees) Kuntze ex Stuck. in Anales Mus. Nac. Buenos Aires 11: 121. 1904 ≡ *Sieglingia spicata* (Nees) Kuntze ex Stuck. in Anales Mus. Nac. Buenos Aires 11: 128. 1904 ≡ *Tripogon spicatus* (Nees) Ekman in Ark. Bot. 11(4): 36. 1912 – Type: BRAZIL. Piauí, *Martius s.n.* (holotype: not located; isotypes: LE [herb. Trinius] No. 2313.01!, M).

Zaqqahinae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.** – Type: *Zaqqah* P.M.Peterson & Romasch.

Diagnosis. – Zaqqahinae differs from Aeluropodinae in having erect, tall, suffrutescent culms up to 2 m tall, 1-veined glumes 2.6–3.6 mm long, and 3-veined lemmas 4–5 mm long. **Included genera.** – *Zaqqah*.

Zaqqah P.M.Peterson & Romasch., **gen. nov.** – Type: *Zaqqah mucronata* (Forssk.) P.M.Peterson & Romasch. (≡ *Festuca mucronata* Forssk.).

Description. – Suffrutescent, rhizomatous perennials. Culms up to 2 m tall, stiff, hard, much branched. Leaf blades up to 3 cm long, distichous, involute, stiff, rigid, apex pungent. Inflorescence a panicle 1.5–3 × 0.8–2.5 cm, globose, the racemose branches crowded on a central axis. Spikelets 8.5–13.3 mm long, 5–9-flowered, elliptic-oblong, laterally compressed; disarticulating between the florets; callus pilose; glumes 2.6–3.6 mm long, shorter than the lower floret, 1-veined; lemmas (3.8–)4–5 mm long, 3-veined, margins ciliate, the hairs 1–1.5 mm long, apex dentate and mucronate; paleas pubescent. Caryopses about 1.5 mm long, ellipsoid.

Distribution and habitat. – The single species is distributed on the coast of the Red Sea in Ethiopia, Saudi Arabia, Somalia, Socotra, and Yemen. Plants occur on dunes and sandy and gravelly plains near the coast; 0–10 m.

Etymology. – The name of the new genus is derived from zaqqah (زَقِقَة), the Yemenese Arabic name for the species, meaning “dart”, thus referring to its pungent leaf blades.

Zaqqah mucronata (Forssk.) P.M.Peterson & Romasch., **comb. nov.** ≡ *Festuca mucronata* Forssk., Fl. Aegypt.-Arab.: 22. 1775 ≡ *Festuca pungens* Vahl, Symb. Bot. 1: 10, t. 2. 1790, nom. illeg. superfl. ≡ *Triodia pungens* (Vahl) Roem. & Schult., Syst. Veg. 2: 598. 1817, nom. illeg.

superfl. ≡ *Calotheca arabica* Spreng., Syst. Veg. 1: 348. 1824 ≡ *Uralepis pungens* (Vahl) Kunth, Révis. Gramin. 1: 108. 1829, nom. illeg. superfl. ≡ *Aeluropus arabicus* (Spreng.) Steud., Nomencl. Bot., ed. 2, 1: 30. 1840, nom. illeg. superfl. ≡ *Dactylis mucronata* (Forssk.) Steud., Syn. Pl. Glumac. 1: 289. 1854 ≡ *Aeluropus mucronatus* (Forssk.) Asch. in Schweinfurth, Beitr. Fl. Aethiop.: 297, 310. 1867 ≡ *Aeluropus pungens* (Vahl) Boiss., Fl. Orient. 5: 595. 1884, nom. illeg. superfl. ≡ *Diplachne mucronata* (Forssk.) Hack. ex Schinz in Vierteljahrsschr. Naturf. Ges. Zürich 56: 81. 1911 ≡ *Odysea mucronata* (Forssk.) Stapf in Hooker's Icon. Pl. 31: t. 3100. 1922 – **Lectotype (designated here):** Yemen. Beit al Fakih, copiose in collibus arenosis, 1 Apr 1763, *Forsskål s.n.* (C barcode C10002274 [image!, reinstated in the Herb. Forsskål from the general herbarium at C and recorded as Addit. No. 1262, at one time from Herb. Vahl]); isolectotypes: BM barcode BM00095948 [image!], C barcode C10002275 [image!, the only specimen at C with a number 74 indicating the original description number in the protologue as indicated by P. Ascherson; 94 indicates Forsskål herbarium number], S No. S05-10117 [image!]).

■ CONCLUDING REMARKS

There remain many questions regarding the relationships among the 21 subtribes of the Cynodonteae. However, we can make some general observations. Highly supported clades that include more than one subtribe are: (1) Zaqqahinae, Cteniinae, Trichoneurinae, Farraginae, Perotidinae, Hubbardochloinae, and Gouiniinae and (2) Pappophorinae, Traginae, Muhlenbergiinae, Hilariinae, Scleropogoninae, Boutelouinae, and Monanthochloinae. The latter clade contains four orphan genera (*Allolepis*, *Jouvea*, *Kalinia*, *Sohnsia*) which may eventually be classified as monogeneric subtribes. The Cynodonteae may have originated via explosive or rapid radiation, so that deep relationships are not easily resolved. Genomic approaches seem appropriate here and could be applied to study the hypothesized introgression and hybridization events in *Acrachne racemosa*, *Odysea paucinervis*, and *Dinebra*.

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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 *rps16-trnK*, *rps16* intron, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA* intron, *ccsA*, 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, GU360570, GU360286, –, GU359977, –, GU359386, JQ345049, GU359267; *Chasmanthium latifolium* (Michx.) H.O.Yates, Peterson 22463 (US), U.S.A., Maryland, GU360517, GU360438, **KX582750**, GU359891, GU359720, GU359379, JQ345062, GU359319; *Danthonia compressa* Austin, Peterson 21986 & Levine (US), U.S.A., North Carolina, GU360483, **KX582766**, GU359865, GU359688, GU359370, JQ345074, GU359345; *Capeochloa cincta* subsp. *sericea* (N.P.Barker) H.P.Linder, Barker 1545 (GRA), South Africa, Eastern Cape, JF729074, JF729181, –, JF729173, JF729167, JF729163, –, –; **CENTROPODIEAE:** *Ellisochloa rangei* (Pilg.) P.M.Peterson & N.P.Barker, Barker 960 (BOL), Namibia, JF729079, JF729184, **KX582780**, –, JF729172, JF729166, JQ345082, JQ345167; **TRIRAPHIDEAE:** *Neyraudia reynaudiana* (Kunth) Keng ex Hitchcock, Soreng 5318, Peterson & Sun Hang (US), China, Yunnan, –, GU360272, **KX582820**, GU360003, GU359636, GU359397, JQ345135, GU359124; *Triraphis mollis* R.Br., Peterson 14344, Soreng & Rosenberg (US), Australia, Western Australia, GU360669, GU360336, **KX582879**, GU359933, GU359650, GU359539, JQ345158, GU359187; *Triraphis ramosissima* Hack., Seydel 4278 (US), South Africa, GU360651, GU360338, **KX582880**, GU359931, GU359652, GU359541, **KX582323**, GU359188; **ERAGROSTIDAE:** *Cottea pappophoroides* Kunth, Peterson 21463, Soreng, LaTorre & Rojas Fox (US), Peru, Ancash, GU360600, GU360456, **KX582758**, GU359842, GU359579, GU359363, JQ345065, GU359237; *Ectrosia scabrata* C.E.Hubb, Lazarides 4772 (US), Australia, GU360497, GU360459, **KX582778**, GU359799, GU359697, GU359476, JQ345080, GU359317; *Enneapogon desvauxii* P.Beauv, Peterson 21999 & Saarela (US), Mexico, Chihuahua, GU360495, GU360486, **KX582781**, GU359796, GU359699, GU359474, **KX582269**, GU359339; *Enneapogon scaber* Lehm, Sachse 008 (MO), South Africa, Western Cape, JQ345237, JQ345279, **KX582782**, JQ345322, **KX582530**, JQ345208, JQ345083, JQ345168; *Entoplocamia aristulata* (Hack. & Rendl) Stapf, Seydel 187 (US), South Africa, GU360492, GU360468, **KX582784**, GU359793, GU359702, GU359469, JQ345085, GU359342; *Eragrostis desertorum* Domin, Peterson 14358, Soreng & Rosenberg (US), Australia, Western Australia, GU360545, GU360462, **KX582787**, GU359933, GU359719, GU359471, –, GU359289; *Eragrostis kennedyae* F.Turner, Latz 13486 (MO), Australia, JQ345238, JQ345281, **KX582788**, JQ345323, **KX582532**, JQ345209, JQ345087, JQ345169; *Eragrostis mexicana* subsp. *mexicana* (Hornem.) Link, Peterson 21429, Saarela & Stancik (US), Mexico, Zacatecas, GU360539, GU360401, –, GU359781, GU359759, GU359496, –, GU359295; *Eragrostis nigricans* (Kunth) Steud, Peterson 21623, Soreng, LaTorre & Rojas Fox (US), Peru, Ancash, GU360520, GU360398, **KX582789**, GU359790, GU359775, GU359411, JQ345088, GU359299; *Harpachne harpachnoides* (Hack.) B.S.Sun & S.Wang, Soreng 5288, Peterson & Sun Hang (US), China, Yunnan, GU360611, GU360382, **KX582796**, GU359815, GU359734, GU359435, JQ345093, GU359113; *Pogonarthria squarrosa* (Roem. & Schult.) Pilg, Mawi 180, Majengo, Salum & Samwe (MO), Tanzania, Singida, KM011121, KM010918, **KX582833**, KM010693, **KX582563**, KM010534, **KX582294**, KM010325; *Psammodontis wiseana* C.A.Gardner & C.E.Hubb, Peterson 14345, Soreng & Rosenberg (US), Australia, Western Australia, GU360703, GU360288, **KX582835**, GU359986, GU359615, GU359533, JQ345140, GU359137; *Schmidtia pappophoroides* Steud. ex J.A.Schmidt, Smook 10558 (MO), South Africa, Northern Cape, KM011124, KM010921, **KX582836**, KM010697, **KX582564**, KM010537, **KX582296**, KM010328; *Tetrachne dregei* Nees, Jarman 120 (US), South Africa, GU360622, GU360365, –, GU359904, GU359670, GU359513, –, GU359218; *Uniola condensata* Hitchc., Peterson 9342 & Judziewicz (US), Ecuador, GU360649, GU360340, **KX582881**, GU359927, GU359654, GU359534, JQ345160, GU359191; *Uniola paniculata* L., Peterson 11160, Annable & Valdes-Reyna (US), U.S.A., Texas, GU360648, GU360341, –, GU359926, GU359655, GU359543, **KX582324**, GU359192; **ZOYSIEAE:** *Sporobolus aculeatus* (L.) P.M.Peterson, Soreng 7940, Johnson, Johnson, Dzyubenko, Dzyubenko & Schilnikov (US), Russia, Stavropol, JQ345233, JQ345275, –, JQ345316, **KX582571**, JQ345205, JQ345066, JQ345163; *Sporobolus densiflorus* (E.Fourn.) Vasey, Lomer 5723 (UBC), Canada, British Columbia, KM011137, KM010932, **KX582840**, KM010710, –, KM010547, –, KM010340; *Sporobolus indicus* (L.) R.Br., Peterson 22025 & Saarela (US), Mexico, Chihuahua, GU360630, GU360355, **KX582841**, GU359913, GU359637, GU359504, **KX582297**, GU359209; *Sporobolus lasiophyllus* Pilg, Peterson 21879, Soreng & Sanchez Vega (US), Peru, Cajamarca, GU360629, GU360356, **KX582842**, GU359912, GU359664, GU359505, **KX582298**, GU359210; *Sporobolus rigidus* (Buckley) P.M.Peterson, Hatch 5738 & Bearden (US), U.S.A., Colorado, GU360548, GU360441, **KX582843**, GU359880, GU359716, GU359357, JQ345061, GU359300; *Sporobolus virginicus* (L.) Kunth, Peterson 15683 & Soreng (US), Chile, Region I, GU360610, GU360362, **KX582844**, GU359892, GU359667, GU359502, JQ345147, GU359215; *Zoysia macrantha* subsp. *walshii* M.E.Nightingale, Loch 435 (US), Australia, GU360642, GU360345, **KX582885**, GU359922, GU359659, GU359548, JQ345162, GU359197; **CYNODONTEAE:** *Acrachne racemosa* (B.Heyne ex Roem. & Schult.) Ohwi, Strohbach 1308 (US), Namibia, KP873642, KP873959, –, KP873425, **KX582502**, KP873824, –, KP873209; *Aeluropus lagopoides* (L.) Trin. ex Thwaites, Weinert s.n. & Mosawi (US), Iraq, GU360576, GU360284, **KX582739**, GU360013, GU359591, GU359391, **KX582252**, GU359261; *Aeluropus littoralis* (Gouan) Parl, Ferguson 634 (US), Greece, GU360575, GU360308, –, GU360018, GU359590, GU359390, JQ345047, **KX582253**, GU359263; *Aeluropus pungens* (M.Bieb.) K.Koch, Yunatov 124, Li Shyin & Yuan Y-fen (US), China, GU360574, GU360319, **KX582740**, GU360014, GU359589, GU359389, **KX582253**, GU359263; *Afrotichloris martinii* Chiov, Hemming 3407 (FT), Somalia, Mudug Reg, KP873645, KP873962, –, KP873428, **KX582503**, KP873827, –, KP873212; *Allolepis texana* (Vasey) Soderstr. & H.F.Decker, Hitchcock 7541 (US), Mexico, Durango, GU360573, GU360318, –, GU360015, GU359577, GU359388, JQ345048, **KX582254**, GU359264; *Apoehiton burttii* C.E.Hubb, Peterson 24163, Soreng, Romaschenko & Abeid (US), Tanzania, Dodoma, KP873646, KP873963, **KX582741**, KP873429, **KX582504**, KP873828, –, KP873214; *Astrebla lappacea* (Lindl.) Domin, McKinlay s.n. (US), Australia, GU360568, GU360312, **KX582742**, GU360009, GU359586, GU359395, **KX582254**, GU359270; *Austrochloa dichanthioides* (Everist) Lazarides, Anson s.n. (US), Australia, GU360566, GU360310, **KX582744**, GU359860, GU359584, GU359420, JQ345051, GU359272; *Bewisia biflora* (Hack.) Gooss, Peterson 23905, Soreng, Romaschenko & Abeid (US), Tanzania, Ruvuma Region, KF827754, KF827692, **KX582745**, KF827617, **KX582505**, KF827570, **KX582255**, KF827498; *Blepharidachne benthamiana* (Hack.) Hitchc., Melix 570 & Cherobini (US), Argentina, GU360579, –, **KX582746**.

Appendix 1. Continued.

GU359857, GU359582, -, JQ345053, GU359275; *Blepharidachne bigelovii* (S.Watson) Hack, *Johnston 9401* (US), Mexico, Coahuila, GU360562, GU360307, **KX582747**, GU359856, GU359581, -, -, -, *Blepharidachne bigelovii* (S.Watson) Hack, *Johnston 9411* (US), Mexico, Coahuila, -, -, -, **KX582596**, **KX582506**, -, -, -, *Blepharidachne kingii* (S.Watson) Hack, *Reeder 7347 & Reeder* (US), U.S.A., Nevada, GU360561, -, -, GU359855, **KX582507**, -, -, GU359276; *Bouteloua simplex* Lag, *Peterson 21289*, *Saarela & Flores Villegas* (US), Mexico, Zacatecas, GU360607, GU360297, **KX582748**, GU359834, GU359716, GU359406, JQ345054, GU359231; *Bouteloua triaena* (Trin. ex Spreng.) Scribn, *Siqueiros Delgado 4510* (US), Mexico, Puebla, KR185295, **KX582886**, -, KR185136, -, **KX582459**, -, KR184961; *Bouteloua trifida* Thurb, *Peterson 24645a & Romaschenko* (US), Mexico, San Luis Potosí, KR185302, -, -, KR185143, -, -, -, KR184968; *Brachychloa fragilis* S.M. Phillips, *Snow 6979*, *Burgoyne & Gumbi* (MO), South Africa, KwaZulu-Natal, -, -, -, JN681722, -, -, -, *Brachychloa schiemaniana* (Schweick.) S.M. Phillips, *Schweickerdt 1911* (US), South Africa, GU360582, -, **KX582749**, GU359881, GU359776, -, JQ345060, GU359256; *Chloris barbata* Sw, *Saarela 1830*, *Peterson*, *Soreng & Judziewicz* (CAN), Australia, Northern Territory, KP873659, KP873977, **KX582751**, KP873443, **KX582508**, KP873838, **KX582256**, KP873228; *Chrysochloa annua* C.E. Hubb, *Arkkrok 20417* (US), Ghana, Yapei Ferri, KP873718, KP874002, **KX582752**, KP873515, **KX582509**, KP873880, **KX582257**, KP873300; *Cleistogenes bulgarica* (Bornm.) Keng, *Soreng 7879*, *Johnson*, *Johnson*, *Dzyubenko & Dzyubenko* (US), Russia, Stavropol, **KX582951**, **KX582887**, **KX582753**, **KX582597**, **KX582510**, **KX582460**, **KX582258**, **KX582326**; *Cleistogenes bulgarica* (Bornm.) Keng, *Soreng 7923*, *Johnson*, *Johnson*, *Dzyubenko*, *Dzyubenko & Schilnikov* (US), Russia, Stavropol, **KX582952**, **KX582888**, **KX582754**, **KX582598**, **KX582511**, **KX582461**, **KX582259**, **KX582327**; *Cleistogenes caespitosa* var. *ramosa* F.Z. Li & C.K. Ni, *Li 20080826* (SDNU), China, -, -, -, -, -, FJ548986*; *Cleistogenes caespitosa* Keng, *Lin L07033* (SDNU), China, -, -, -, -, -, FJ548978*; *Cleistogenes festucacea* Honda, *Lin DB-09 & Yan* (SDNU), China, -, -, -, -, -, FJ548977*; *Cleistogenes hackelii* (Honda) Honda, *Kim s.n.*, Korea (South), Jeon-nam, Gok-seong-gun, -, -, -, -, -, KP057012*; *Cleistogenes hackelii* (Honda) Honda, *Li 1104* (SDNU), China, -, -, -, -, -, FJ548975*; *Cleistogenes hackelii* var. *nakaii* (Keng) Ohwi, *Lin DB-10 & Yan*, Korea (South), -, -, -, -, -, FJ548976*; *Cleistogenes hancei* Keng, *Li 200509049 & Zhang* (SDNU), China, -, -, -, -, -, FJ548974*; *Cleistogenes longiflora* Keng ex Keng f. & L.Liou, *Lin L07041* (SDNU), China, -, -, -, -, -, FJ548979*; *Cleistogenes mucronata* Keng ex Keng f. & L.Liou, *Lin DB-03 & Yan* (SDNU), China, -, -, -, -, -, FJ548987*; *Cleistogenes mucronata* Keng ex Keng f. & L.Liou, *Soreng 5406*, *Peterson & Sun Hang* (US), China, Qinghai, GU360604, GU360351, **KX582755**, GU359846, GU359696, GU359422, **KX582260**, GU359234; *Cleistogenes polyphylla* Keng ex Keng f. & L.Liou, *Li 031005 & Lin* (SDNU), China, -, -, -, -, -, FJ548981*; *Cleistogenes songorica* (Roshev.) Ohwi, *Hilu 5760* (VPI), -, -, -, -, JN681739*, -, -, FJ548983*; *Cleistogenes squarrosa* (Trin.) Keng, *Li 0709055 & Lin* (SDNU), China, -, -, -, -, -, FJ548980*; *Cleistogenes squarrosa* (Trinius) Keng, *Soreng 5156*, *Peterson*, *Wang Zong-tao & Zhu Da-hai* (US), China, Nei Mongol, GU360603, GU360473, **KX582756**, GU359845, GU359566, GU359393, **KX582261**, GU359235; *Coelachyrum lagopoides* (Burm. f.) Senaratna, *Saldanha 15334* (US), India, GU360602, -, -, GU359844, GU359572, -, -, -, *Coelachyrum poiflorum* Chiov, *Burger 2915* (US), Ethiopia, GU360601, GU360457, **KX582757**, GU359843, -, -, -, GU359236; *Craspedorhachis rhodesiana* Rendle, *Sirohbach 5699* (US), Namibia, KF827760, KF827696, -, KF827623, -, KF827574, -, KF827504; *Ctenium brevispicatum* J.G.Sm, *Filgueiras 3251 & Oliveira* (US), Brazil, Goiás, JQ345234, JQ345276, **KX582759**, JQ345317, JQ345206, JQ345067, JQ345164; *Cynodon nlemfuensis* Vanderyst, *Peterson 24058*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, Mbeya, KP873742, KP874024, **KX582760**, KP873542, **KX582513**, KP873900, **KX582262**, KP873324; *Dactyloctenium aegyptium* (L.) Willd, *Hemming 2358* (US), Somalia, Lughaiya, KP873749, KP874031, **KX582760**, **KX582599**, -, KP873906, -, KP873331; *Dactyloctenium aegyptium* S.M. Phillips, *Kabuye 714*, *Luke*, *Robertson*, *Mungai & Mathenge* (US), Kenya, Tana River National Primate Reserve, GU360507, GU360484, **KX582761**, GU359867, GU359717, GU359371, JQ345072, GU359327; *Dactyloctenium aegyptium* (L.) Willd, *Nelson 13391 & Long* (US), U.S.A., South Carolina, -, -, -, **KX582600**, -, -, -, *Dactyloctenium aegyptium* (L.) Willd, *Peterson 22283 & Saarela* (US), Mexico, Oaxaca, GU360587, GU360432, **KX582762**, GU359886, GU359713, GU359351, JQ345070, GU359251; *Dactyloctenium aegyptium* (L.) Willd, *Peterson 24110*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, Rukwa, **KX582953**, **KX582889**, -, **KX582601**, -, **KX582462**, -, **KX582328**; *Dactyloctenium aegyptium* (L.) Willd, *Peterson 24166*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, Dodoma, **KX582954**, **KX582890**, -, **KX582602**, -, **KX582463**, -, **KX582329**; *Dactyloctenium aegyptium* (L.) Willd, *Peterson 24218*, *Soreng*, *Romaschenko & Mbago* (US), Tanzania, Tanga, **KX582955**, -, -, **KX582603**, -, -, **KX582330**; *Dactyloctenium aegyptium* (L.) Willd, *Peterson 24306*, *Soreng*, *Romaschenko & Mbago* (US), Tanzania, Arusha, **KX582956**, **KX582891**, -, **KX582604**, -, **KX582464**, -, **KX582331**; *Dactyloctenium aegyptium* (L.) Willd, *Peterson 24951 & Romaschenko* (US), Mexico, Durango, -, -, -, **KX582605**, -, -, -, **KX582332**; *Dactyloctenium aegyptium* (L.) Willd, *Seydel 2701* (US), Namibia, GU360491, -, **KX582763**, GU359866, GU359687, -, JQ345073, **KX582328**; *Dactyloctenium aegyptium* (L.) Willd, *Sorrie 11693* (US), U.S.A., North Carolina, -, -, -, **KX582606**, -, -, -, *Dactyloctenium aristatum* Link, *Moggi s.n.*, *Bavazzano & Tardelli* (FT), Somalia, Bay Region, **KX582957**, **KX582892**, -, **KX582607**, -, **KX582465**, -, -, *Dactyloctenium aristatum* Link, *Peterson 24205*, *Soreng*, *Romaschenko & Mbago* (US), Tanzania, Tanga, **KX582958**, **KX582893**, -, **KX582608**, -, **KX582466**, -, **KX582333**; *Dactyloctenium australe* Steud, *Davids 6945* (US), South Africa, GU360508, -, **KX582764**, JQ345318, -, GU359372, JQ345071, GU359326; *Dactyloctenium geminatum* Hack, *Frazier 1076* (US), Tanzania, Sadani, -, -, -, -, -, **KX582334**; *Dactyloctenium geminatum* Hack, *Peterson 23808*, *Soreng & Romaschenko* (US), Tanzania, Dar Es Salaam, KP873747, KP874029, -, KP873546, -, KP873904, -, KP873329; *Dactyloctenium geminatum* Hack, *Peterson 23830*, *Soreng*, *Romaschenko & Abeid* (US), Tanzania, Lindi Region, **KX582959**, -, -, **KX582609**, -, -, **KX582335**; *Dactyloctenium giganteum* B.S. Fisher & Schweick, *Bouchenak-Khelladi 336* (BOL), South Africa, Kruger National Park, -, -, -, -, -, HM347008*; *Dactyloctenium giganteum* B.S. Fisher & Schweick, *Klaassen 1287*, *Bartsch & Hochobes* (US), Namibia, Okavango, **KX582960**, -, -, **KX582610**, -, -, **KX582336**; *Dactyloctenium radulans* (R.Br.) P.Beauv, *Pullen 10528* (US), Australia, Central Australia, -, -, -, **KX582611**, -, -, -, *Dactyloctenium radulans* (R.Br.) P.Beauv, *Saarela 1671*, *Peterson*, *Soreng & Judziewicz* (CAN), Australia, Northern Territory, **KX582961**, **KX582894**, -, **KX582612**, -, **KX582467**, -, **KX582337**; *Dactyloctenium radulans* (R.Br.) P.Beauv, *Wiens 2006-157*, *Hemgingway & Hanson* (US), U.S.A., Arizona, -, -, -, **KX582613**, -, -, -, *Dactyloctenium robecchii* Chiov, *Puccioni 626 & Stefanini* (FT), Somalia, Migiriirtina, KP873748, KP874030, -, KP873547, -, KP873905, -, KP873330; *Dactyloctenium scindicum* Boiss, *Boulos 9431* (FT), Ethiopia, Afar Region, **KX582962**, **KX582895**, -, **KX582614**, -, **KX582468**, -, **KX582338**; *Dactyloctenium scindicum* Boiss, *Hemming 3411* (FT), Somalia, Mudugh Reg, -, -, -, **KX582615**, -, -, -, **KX582339**; *Dactyloctenium scindicum* Boiss, *Humbles 10109* (US), Saudi Arabia, Wadi Busel, **KX582963**, -, -, **KX582616**, -, -, -, **KX582340**; *Daknopholis boivinii* (A.Camus) Clayton, *Ranaivojaona 1441*, *Andrianjafy*, *Phillipson & Lubke* (MO), Madagascar, Toliara, KP873750, KP874032, **KX582765**, KP873548, **KX582514**, KP873907, **KX582263**, KP873332; *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Angulo 369 & Amarilla* (XAL), Mexico, Durango, KT273286*, -, -, KT273315*, KT273294*, KT273298*, -, KT273304*; *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Peterson 18832*, *Valdés-Reyna & Sifuentes* (US), Mexico, Coahuila, -, -, -, **KX582617**, **KX582515**, -, -, -, *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Peterson 21992 & Saarela* (US), Mexico, Chihuahua, GU360505, GU360482, **KX582767**, GU359864, GU359689, GU359369, **KX582264**, GU359330; *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Peterson 24481 & Romaschenko* (US), Mexico, Coahuila, -, -, -, **KX582618**, **KX582516**, -, -, **KX582341**; *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Peterson 24790*, *Romaschenko*, *Rodriguez Avalos*, *Herrera-Simoni & Garcia Rodriguez* (US), Mexico, Aguascalientes, -, -, -, **KX582619**, **KX582517**, -, -, **KX582342**; *Dasyochloa pulchella* (Kunth) Willd. ex Rydb, *Peterson 24878 & Romaschenko* (US), Mexico, San Luis Potosí, -, -, -, **KX582620**, **KX582518**, -, -, **KX582343**; *Desmostachya bipinnata* (L.) Stapf, *Dwyer 13120* (MO), Saudi Arabia, JQ345235, JQ345277, **KX582768**, **KX582519**, JQ345207, JQ345165; *Dignathia hirtella* Stapf, *McCallum-Webster 5251* (US), Kenya, GU360490, GU360481, **KX582769**, -, GU359690, GU359368, JQ345076, GU359316; *Dinebra haareri* (Stapf & C.E. Hubb.) P.M. Peterson & N.Snow, *Peterson 24231*, *Soreng*, *Romaschenko & Mbago* (US), Tanzania, Tanga, KP873753, KP874034, -, KP873551, -, KP873910, -, KP873335; *Dinebra somalensis* (Stapf) P.M. Peterson & N.Snow, *Faden 74-991 & Faden* (MO), Kenya, K7-Tana River District, JQ345236, JQ345278, **KX582770**, JQ345321, **KX582520**, -, -, JQ345166; *Dinebra viscidula* (Scribn.) P.M. Peterson & N.Snow, *Peterson 22184 & Saarela* (US), Mexico, Sinaloa, GU360693, GU360430, **KX582771**, GU359808, GU359752, GU359429, JQ345122, GU359148; *Diplachne fusca* var. *uninervia* (J.Presl) P.M. Peterson & N.Snow, *Peterson 21305*, *Saarela & Flores Villegas* (US), Mexico, GU360694, GU360391, **KX582772**, GU359809, GU359739, GU359461, JQ345118, GU359147; *Disakisperma dubium* (Kunth) P.M. Peterson & N.Snow, *Peterson 22334 & Saarela* (US), Mexico, Oaxaca, GU360695, GU360416, **KX582773**, GU359811, GU359738, GU359442, JQ345103, GU359145; *Distichlis acerosa* (Griseb.) H.L. Bell & Columbus, *Bell 389* (RSA), Argentina, La Rioja, -, -, -, EF561671*, -, -, EF196897*; *Distichlis acerosa*

Appendix 1. Continued.

(Griseb.) H.L.Bell & Columbus, *Bell 392* (RSA), Argentina, Catamarca, –, –, –, EF561672*, –, –, EF196898*; *Distichlis australis* (Griseb.) H.L.Bell & Columbus, *Bell 330* (RSA), Argentina, Rio Negro, –, –, –, EF561650*, –, –, EF196875*; *Distichlis australis* (Speg.) Villamil, *Bell 357* (RSA), Argentina, Santa Cruz, –, –, –, EF561651*, –, –, EF196876*; *Distichlis bajaensis* H.L.Bell, *Stephenson 68-304a* (MSC), Mexico, Baja California, –, –, –, GU562866*, –, –, GU562864*; *Distichlis distichophylla* (Labill.) Fassett, *Cochrane 1198* (MEL), Australia, Victoria, –, –, –, EF561652*, –, –, EF196877*; *Distichlis distichophylla* (Labill.) Fassett, *Walsh 6160* (MEL), Australia, South Australia, **KX582964**, **KX582896**, –, –, **KX582621**, **KX582521**, **KX582469**, –, –, **KX582344**; *Distichlis eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Bell 250* (RSA), Mexico, San Luis Potosí, –, –, –, JN681724*, –, –, EF153077*; *Distichlis eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Peterson 24864 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, KP873561, **KX582522**, –, –, KP873345; *Distichlis eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Peterson 24959 & Romaschenko* (US), Mexico, Mexico, –, –, –, **KX582622**, **KX582523**, –, –, **KX582345**; *Distichlis eludens* (Soderstr. & H.F.Decker) H.L.Bell & Columbus, *Reeder 6430 & Reeder* (US), Mexico, San Luis Potosí, GU360701, GU360290, –, –, JQ345320, **KX582524**, –, –, GU359139; *Distichlis humilis* Phil, *Bell 405* (RSA), Argentina, Jujuy, –, –, –, EF561654*, –, –, EF196879*; *Distichlis humilis* Phil, *Peterson 12833*, *Annable, Lægaard, Soreng & Rojas-Ponce* (US), Bolivia, Potosí, –, –, –, **KX582525**, –, –, **KX582346**; *Distichlis humilis* Phil, *Peterson 19362*, *Soreng, Salariato & Panizza* (US), Argentina, Catamarca, GU360502, GU360478, **KX582774**, GU359835, GU359693, GU359430, JQ345078, GU359333; *Distichlis laxiflora* Hack, *Bell 367* (RSA), Argentina, Buenos Aires, –, –, –, EF561656*, –, –, EF196881*; *Distichlis laxiflora* Hack, *Bell 381* (RSA), Argentina, Córdoba, –, –, –, EF561657*, –, –, EF196882*; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Bell 236* (RSA), –, –, –, JN681725*, –, –, EF153065*; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Bell 244* (RSA), U.S.A., Texas, –, –, –, EF196899*; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Bell 260* (RSA), U.S.A., California, –, –, –, EF561674*, –, –, EF196900*; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Blakley 4729* (US), U.S.A., California, –, –, –, **KX582623**, **KX582526**, –, –, **KX582347**; *Distichlis littoralis* (Engelm.) H.L.Bell & Columbus, *Moran 10570* (US), Mexico, Baja California, GU360699, GU360422, **KX582775**, GU359970, GU359748, GU359460, JQ345079, GU359157; *Distichlis palmeri* (Vasey) Fassett, *Columbus 3586* (RSA), Mexico, Sonora, –, –, –, EF561658*, –, –, EF196883*; *Distichlis palmeri* (Vasey) Fassett, *Felger 91-39* (RSA), Mexico, Sonora, –, –, –, EF561659*, –, –, EF196884*; *Distichlis scoparia* (Nees ex Kunth) Arechav, *Bell 328* (RSA), Mexico, Rio Negro, –, –, –, EF196885*; *Distichlis scoparia* (Nees ex Kunth) Arechav, *Peterson 17475*, *Soreng & Refulio-Rodriguez* (US), Argentina, Neuquen, GU360501, GU360477, **KX582776**, GU359803, GU359694, GU359480, **KX582265**, GU359334; *Distichlis spicata* (L.) Greene, *Banks 2224 & Kinney* (US), U.S.A., California, –, –, –, **KX582624**, **KX582527**, –, –, **KX582347**; *Distichlis spicata* var. *stricta* (Torr.) Scribn, *Beatley 3317* (US), U.S.A., Nevada, –, –, –, **KX582625**, –, –, **KX582348**; *Distichlis spicata* (Griseb.) H.L.Bell & Columbus, *Bell 231* (RSA), U.S.A., California, –, –, –, EF561662*, –, –, EF153040*; *Distichlis spicata* (L.) Greene, *Bell 237* (RSA), U.S.A., Texas, –, –, –, EF561663*, –, –, EF196887*; *Distichlis spicata* (L.) Greene, *Bell 245* (RSA), Mexico, Coahuila, –, –, –, EF561664*, –, –, EF196888*; *Distichlis spicata* (L.) Greene, *Bell 258* (RSA), U.S.A., California, –, –, –, EF196889*; *Distichlis spicata* (L.) Greene, *Bell 259* (RSA), U.S.A., California, –, –, –, EF561665*, –, –, EF196890*; *Distichlis spicata* (L.) Greene, *Bell 277* (RSA), Canada, British Columbia, –, –, –, EF561666*, –, –, EF196891*; *Distichlis spicata* (L.) Greene, *Bell 290* (RSA), U.S.A., Virginia, –, –, –, EF561667*, –, –, EF196892*; *Distichlis spicata* (L.) Greene, *Bell 340* (RSA), Argentina, Chubut, –, –, –, EF561668*, –, –, EF196893*; *Distichlis spicata* (L.) Greene, *Bell 375* (RSA), Chile, Valparaiso, –, –, –, EF561669*, –, –, EF196895*; *Distichlis spicata* (L.) Greene, *Columbus 3432* (RSA), Peru, –, –, –, EF561670*, –, –, EF196896*; *Distichlis spicata* (L.) Greene, *Peterson 17484*, *Soreng & Refulio-Rodriguez* (US), Argentina, Neuquen, GU360500, GU360476, **KX582777**, GU359802, GU359706, GU359479, **KX582266**, GU359335; *Distichlis spicata* (L.) Greene, *Peterson 19309*, *Soreng, Salariato & Panizza* (US), Argentina, San Juan, GU360499, GU360475, XX000000, GU359801, GU359695, GU359478, **KX582267**, GU359346; *Distichlis spicata* (L.) Greene, *Peterson 24436*, *Romaschenko & Knapp* (US), U.S.A., Maryland, –, –, –, **KX582626**, –, –, –, *Distichlis spicata* (L.) Greene, *Peterson 24867 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582627**, –, –, **KX582349**; *Distichlis spicata* (L.) Greene, *Peterson 24958 & Romaschenko* (US), Mexico, Durango, –, –, –, **KX582628**, –, –, –, **KX582350**; *Distichlis spicata* (L.) Greene, *Reeder 5286 & Reeder* (US), U.S.A., Nevada, –, –, –, **KX582528**, –, –, **KX582351**; *Elyusine multiflora* Hochst. ex A.Rich, *Peterson 24272*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Shinyanga, KP873763, KP874044, **KX582779**, KP873576, **KX582529**, KP873919, **KX582268**, KP873360; *Enteropogon sechellensis* (Baker) T.Durand & Schinz, *Peterson 23815*, *Soreng & Romaschenko* (US), Tanzania, Dar Es Salaam, KP873787, KP874064, **KX582783**, KP873602, **KX582531**, KP873934, –, –, KP873386; *Eragrostiella bifaria* (Vahl) Bor, *Clayton 5950* (US), Sri Lanka, –, –, –, GU359828, –, –, –, *Eragrostiella bifaria* (Vahl) Bor, *Peterson 23852*, *Soreng, Romaschenko & Abeid* (US), Tanzania, Lindi Region, **KX582965**, **KX582897**, –, –, **KX582629**, –, –, **KX582470**, –, –, **KX582352**; *Eragrostiella bifaria* (Vahl) Bor, *Peterson 24189*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Kilimanjaro, **KX582966**, **KX582898**, –, –, **KX582630**, –, –, **KX582471**, –, –, **KX582353**; *Eragrostiella brachyphylla* (Stapf) Bor, *Davidse 7323* (MO), Sri Lanka, North Central, –, –, **KX582899**, **KX582785**, –, –, –, **KX582354**; *Eragrostiella leioptera* (Stapf) Bor, *Chand 7961* (US), India, GU360529, JQ345280, **KX582786**, GU359827, GU359769, GU359486, JQ345086, GU359305; *Erioneuron avenaceum* (Kunth) Tateoka, *Barkley 147865* (US), U.S.A., Texas, –, –, –, **KX582631**, –, –, –, *Erioneuron avenaceum* (Kunth) Tateoka, *Peterson 19329*, *Soreng, Salariato & Panizza* (US), Argentina, La Rioja, GU360525, GU360403, **KX582790**, GU359822, GU359773, GU359441, **KX582270**, GU359310; *Erioneuron avenaceum* (Kunth) Tateoka, *Peterson 24455*, *Romaschenko & Valdés-Reyna* (US), Mexico, Nuevo León, –, –, –, **KX582632**, –, –, –, **KX582355**; *Erioneuron avenaceum* (Kunth) Tateoka, *Peterson 24650 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582633**, –, –, –, **KX582356**; *Erioneuron avenaceum* (Kunth) Tateoka, *Peterson 24747*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582634**, –, –, –, **KX582357**; *Erioneuron avenaceum* (Kunth) Tateoka, *Peterson 24902 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582635**, –, –, –, **KX582358**; *Erioneuron avenaceum* var. *avenaceum* (Kunth) Tateoka, *Reeder 5936 & Reeder* (US), U.S.A., New Mexico, –, –, –, **KX582636**, –, –, –, **KX582359**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 19866 & Lara Contreras* (US), Mexico, Coahuila, –, –, –, **KX582637**, –, –, –, **KX582360**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 24477 & Romaschenko* (US), Mexico, Coahuila, –, –, –, **KX582638**, –, –, –, **KX582361**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 24483 & Romaschenko* (US), Mexico, Coahuila, –, –, –, **KX582639**, –, –, –, **KX582362**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 24615 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582640**, –, –, –, **KX582363**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 24667 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582641**, –, –, –, **KX582364**; *Erioneuron nealleyi* (Vasey) Tateoka, *Peterson 24774*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582642**, –, –, –, **KX582365**; *Erioneuron pilosum* var. *pilosum* (Buckley) Nash, *Correll 15874*, Rollins & Chambers (US), U.S.A., Texas, –, –, –, **KX582643**, –, –, –, **KX582366**; *Erioneuron pilosum* (Buckley) Nash, *Hinckley 4676* (US), U.S.A., Texas, **KX582967**, **KX582900**, –, –, –, **KX582367**; *Erioneuron pilosum* (Buckley) Nash, *Peterson 19964 & Lara Contreras* (US), Mexico, Coahuila, GU360524, GU360388, **KX582791**, GU359821, GU359774, –, –, **KX582271**, GU359311; *Erioneuron pilosum* (Buckley) Nash, *Peterson 24594 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582644**, –, –, –, *Erioneuron pilosum* (Buckley) Nash, *Peterson 24619 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582645**, –, –, –, **KX582368**; *Erioneuron pilosum* (Buckley) Nash, *Peterson 24738*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582646**, –, –, –, **KX582369**; *Erioneuron pilosum* (Buckley) Nash, *Peterson 24759*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582647**, –, –, –, **KX582370**; *Erioneuron pilosum* (Buckley) Nash, *Peterson 24877 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582648**, –, –, –, **KX582371**; *Erioneuron pilosum* var. *pilosum* (Buckley) Nash, *Reeder 5445 & Reeder* (US), U.S.A., Arizona, –, –, –, **KX582649**, –, –, –, **KX582372**; *Erioneuron pilosum* (Buckley) Nash, *Wallis 4814* (US), U.S.A., Texas, **KX582968**, **KX582901**, –, –, –, **KX582373**; *Eustachys calvescens* (Hack.) Caro & E.A.Sánchez, *Chase 10971* (US), Brazil, Mato Grosso State, KP873789, KP874066, –, –, KP873604, –, –, KP873936, **KX582272**, KP873388; *Farrago racemosa* Clayton, *Peterson 23851*, *Soreng, Romaschenko & Abeid* (US), Tanzania, Lindi reg, KF827772, KF827706, –, –, KF827634, –, –, KF827582, –, –, KF827516; *Gouinia brasiliensis* (S.Moore) Swallen, *Nee 36355* (US), Bolivia, Sta. Cruz Dep., –, –, –, KF827707, –, –, KF827635, –, –, KF827517; *Gouinia gracilis* Ekman ex Swallen, *Ekman s.n.* (US), Cuba, Oricute Prov, KF827773, KF827708, –, –, KF827636, –, –, KF827518; *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J.Ortiz, *Beetle 918* (US), Mexico, Yucatan, **KX582969**, **KX582902**, –, –, KF827637, **KX582533**, **KX582472**, **KX582273**, KF827519; *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J.Ortiz, Martínez S. 29764, Alvarez & Ramirez (MO), Mexico, Campeche, KF827774, KF827709, **KX582792**, KF827638, **KX582534**, KF827583, **KX582274**, KF827520; *Gouinia paraguayensis* (Kuntze) Parodi, *Peterson 11526 & Annable* (US), Argentina, San Juan, GU360504, GU360384, **KX582793**, GU359817, GU359732, GU359437, JQ345091,

Appendix 1. Continued.

GU359314; *Gouinia virgata* var. *robusta* J.J.Ortiz, *Reeder 4714 & Reeder* (US), Mexico, Zacatecas, KF827775, KF827710, –, KF827639, –, KF827584, –, KF827521; *Gouinia virgata* var. *virgata* (J.Presl) Scribn, *Rzedowski 14670* (US), Mexico, Jalisco, –, KF827711, –, KF827640, –, –, KF827522; *Gouinia virgata* (J.Presl) Scribn, *Swallen 2818* (US), Mexico, Yucatan Peninsula, –, KF827712, –, –, –, –, KF827523; *Gouinia virgata* var. *virgata* (J.Presl) Scribn, *Villarreal-Quintanilla 8105*, *Carranza, Rodriguez & Villarreal* (MO), Mexico, Nuevo León, KF827713, **KX582794**, KF827641, **KX582535**, –, **KX582275**, KF827524; *Gymnopogon grandiflorus* Roseng, B.R.Arill. & Izag, *Peterson 16642 & Refulio-Rodriguez* (US), Peru, Apurimac, GU360581, GU360383, **KX582795**, GU359816, GU359733, GU359436, JQ345092, GU359200; *Halopyrum mucronatum* (L.) Stapf, *Peterson 23837*, *Soreng, Romaschenko & Abeid* (US), Tanzania, Lindi Region, **KX582970**, **KX582903**, –, **KX582650**, –, **KX582473**, –, **KX582374**; *Harpochloa falx* (L.f.) Kuntze, *Zietsman 4015*, *Peyper, Avenant & van der Walt* (MO), South Africa, Mpumalanga, KP873799, KP874072, **KX582797**, KP873613, **KX582536**, –, **KX582276**, KP873400; *Hilaria belangeri* (Steud.) Nash, *Martinez 2446 & Borja Luyando* (US), Mexico, Tamaulipas, –, –, –, **KX582651**, –, –, –, **KX582375**; *Hilaria cenchroides* Kunth, *Columbus 3758* (RSA), –, –, –, –, –, EF153055*; *Hilaria cenchroides* Kunth, *Peterson 21296*, *Saarela & Flores Villegas* (US), Mexico, Zacatecas, –, –, –, **KX582652**, –, –, –, **KX582376**; *Hilaria cenchroides* Kunth, *Peterson 21326*, *Saarela & Flores Villegas* (US), Mexico, Mexico, GU360698, GU360381, –, GU359814, GU359735, –, **KX582277**, GU359230; *Hilaria cenchroides* Kunth, *Peterson 22339 & Saarela* (US), Mexico, Oaxaca, GU360697, GU360380, **KX582798**, GU359813, GU359736, GU359424, JQ345094, GU359143; *Hilaria cenchroides* Kunth, *Peterson 24658 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582653**, –, –, –, **KX582377**; *Hilaria cenchroides* Kunth, *Peterson 24713*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582654**, –, –, –, **KX582378**; *Hilaria ciliata* (Scribn.) Nash, *Devender 1140*, *Reina, Hansen, Ruiz, Guido, van der Heiden, Mejia & Plascencia* (US), Mexico, Sinaloa, **KX582971**, **KX582904**, **KX582799**, **KX582655**, **KX582537**, **KX582474**, **KX582278**, –, **Hubbardochloa gracilis** Auquier, *Troupin s.n.* (MO), Rwanda, –, –, –, –, –, –, **KX582379**; *Jouvea pilosa* (J.Presl) Scribn, *Peterson 11017 & Annable* (US), Mexico, Colima, GU360696, GU360379, **KX582800**, GU359812, GU359737, GU359433, JQ345095, GU359144; *Jouvea pilosa* (J.Presl) Scribn, *Reina G. 2007-1095*, *Devender, Chamberland & Bertelsen* (US), Mexico, Sonora, **KX582972**, **KX582905**, **KX582801**, KJ768979, **KX582538**, **KX582475**, **KX582279**, KJ768884; *Kalinia obtusiflora* (E.Fourn.) H.L.Bell & Columbus, *Koch 7456* (US), Mexico, Lago de Texcoco, **KX582973**, **KX582906**, –, **KX582656**, **KX582539**, –, –, **KX582380**; *Kalinia obtusiflora* (E.Fourn.) H.L.Bell & Columbus, *Reeder 3489*, *Reeder & Soderstrom* (US), Mexico, Chihuahua, **KX582974**, **KX582907**, –, **KX582657**, **KX582540**, –, –, **KX582381**; *Kalinia obtusiflora* (E.Fourn.) H.L.Bell & Columbus, *Reeder 5530 & Reeder* (US), U.S.A., Arizona, **KX582975**, **KX582908**, –, **KX582658**, **KX582541**, –, –, **KX582382**; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Mboya 565* (MO), Tanzania, Manyara, KF827790, KF827723, **KX582802**, KF827658, **KX582542**, KF827593, **KX582280**, KF827537; *Leptochloa virgata* (L.) P.Beauv, *Seidel 2710* (US), Bolivia, La Paz, JQ345264, JQ345306, **KX582803**, JQ345351, **KX582543**, JQ345226, JQ345121, JQ345121, **KX582807**, JQ345355, **KX582547**, JQ345228, JQ345128, JQ345198; *Melanocenchris jacquemontii* Jaub. & Spach, *Wisner 24* (US), India, –, –, –, **KX582808**, GU359973, –, –, **KX582283**, GU359169; *Melanocenchris rothiana* Nees, *Clayton 5634* (US), Sri Lanka, GU360686, –, **KX582809**, GU359974, –, –, –, *Micrachne fulva* (Stapf) P.M.Peterson, *Robson 1122* (US), Mozambique, GU360585, GU360444, **KX582810**, GU359884, –, GU359348, JQ345056, GU359253; *Microchloa altera* (Rendle) Stapf, *Robinson 6362* (US), Zambia, Central Prov, KP873807, KP874079, **KX582811**, KP873621, **KX582548**, KP873947, **KX582284**, KP873408; *Monelytrum luederitzianum* Hack, *Smook 10031* (US), South Africa, GU360682, GU360421, **KX582812**, GU359969, GU359749, GU359459, JQ345130, GU359158; *Mosdenia leptostachys* (Fialho & Hiern) Clayton, *Schweickerdt 1542* (US), South Africa, GU360681, GU360420, **KX582813**, GU359967, GU359750, GU359458, JQ345131, GU359159; *Muhlenbergia japonica* Steud, *Soreng 5301*, *Peterson & Sun Hang* (US), China, HM143668, HM143572, **KX582814**, HM143184, HM143476, HM143389, JQ345132, HM143082; *Muhlenbergia phleoides* (Kunth) Columbus, *Peterson 24938*, *Romaschenko & González-Elizondo* (US), Mexico, Durango, –, –, **KX582815**, **KX582659**, –, –, –, **KX582383**; *Muhlenbergia schreberi* J.F.Gmel, *Peterson 19443*, *Soreng, Salariato & Panizza* (US), Argentina, Tucuman, GU360679, GU360404, –, GU359950, GU359765, GU359456, JQ345133, GU359161; *Munroa andina* Phil, *Amarilla 17 & Moreno* (CORD), Argentina, Jujuy, KT273287*, –, –, KT273310*, KT273293*, KT273299*, –, KT273305*; *Munroa andina* var. *andina* Phil, *Peterson 19552*, *Soreng, Salariato & Panizza* (US), Argentina, Jujuy, GU360722, –, **KX582816**, GU359965, GU359934, **KX582285**, GU359120; *Munroa argentina* Griseb, *Amarilla 11* (CORD), Argentina, San Miguel del Tucumán, KT273288*, –, –, KT273311*, KT273295*, KT273300*, –, KT273306*; *Munroa argentina* Griseb, *Peterson 15505*, *Soreng & Judziewicz* (US), Chile, Region II (Antofagasta), GU360723, –, **KX582817**, GU360006, GU359633, GU359385, **KX582286**, GU359121; *Munroa decumbens* Phil, *Chiappella 2576b & Amarilla* (CORD), Argentina, La Rioja, KT273291*, –, –, KT273314*, KT273297*, KT273303*, –, KT273309*; *Munroa mendocina* Phil, *Chiappella 2618 & Amarilla* (CORD), Argentina, Catamarca, KT273290*, –, –, KT273313*, KT273296*, KT273302*, –, KT273308*; *Munroa squarrosa* (Nutt.) Torr, *Angulo 392 & Amarilla* (XAL), Mexico, Chihuahua, KT273289*, –, –, KT273312*, KT273292*, KT273301*, –, KT273307*; *Munroa squarrosa* (Nutt.) Torr, *Columbus 3894* (RSA), U.S.A., New Mexico, –, –, –, JN681750*, –, –, EF153069*; *Neesiochloa barbata* (Nees) Pilg, *Swallen 4491* (US), Brazil, GU360724, GU360279, **KX582818**, GU360005, GU359634, –, –, GU359122; *Neobouteloua lophostachya* (Griseb.) Gould, *Peterson 11515 & Annable* (US), Argentina, San Juan, GU360725, GU360273, **KX582819**, GU360004, GU359635, GU359396, JQ345134, GU359123; *Neobouteloua lophostachya* (Griseb.) Gould, *Porter 11974 & Columbus* (MO), Argentina, La Rioja, **KX582976**, –, –, **KX582660**, **KX582549**, –, –, **KX582384**; *Neobouteloua pauciracemosa* M.G.López & Biurrun, *Porter 11968 & Columbus* (US), Argentina, La Rioja Prov, KP873812, –, –, KP873627, –, –, KP873413; *Neostapfia colusana* (Burt) Davy, *Burt Davy, Reeder 6198 & Reeder* (RSA), U.S.A., California, –, –, –, JN681752*, –, –, EF153071*; *Odysea mucronata* (Forssk.) Stapf, *Drake-Brockmann 667* (US), Somalia, Bulhar, –, –, –, **KX582661**, –, –, –, **KX582385**; *Odysea mucronata* (Forssk.) Stapf, *McKinnon 206* (US), Somalia, –, –, –, **KX582662**, –, –, –, **KX582386**; *Odysea mucronata* (Forssk.) Stapf, *Spellenberg 7470* (MO), Yemen, Hodeidah Governate, **KX582977**, **KX582909**, **KX582821**, **KX582663**, **KX582550**, **KX582476**, **KX582287**, **KX582387**; *Odysea paucineris* (Nees) Stapf, *Peterson 24312*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Arusha, **KX582978**, **KX582910**, –, **KX582664**, **KX582551**, **KX582477**, –, **KX582388**; *Odysea paucineris* (Nees) Stapf, *Smook 8026* (MO), South Africa, Cape Prov, **KX582979**, **KX582911**, **KX582822**, **KX582665**, **KX582552**, **KX582478**, **KX582288**, **KX582389**; *Odysea paucineris* (Nees) Stapf, *Snow 6826 & Chatukuta* (MO), Botswana, Central, –, –, –, JN681753*, –, –, –, **Orcuttia californica** Vasey, *Columbus 2687* (RSA), –, –, –, JN681754*, –, –, –, EF153072*; *Orcuttia inaequalis* Hoover, *Boykin 32 & Hall* (UNM), U.S.A., California, –, –, –, –, –, AY354366-AY354328*; *Orcuttia inaequalis* Hoover, *Hoover 1256* (US), U.S.A., California, GU360726, –, –, GU360002, GU359605, –, –, **KX582390**; *Orcuttia pilosa* Hoover, *Boykin 41 & Hall* (UNM), U.S.A., California, –, –, –, –, –, AY354357-AY354319*; *Orcuttia pilosa* Hoover, *Reeder 6213 & Reeder* (RSA), U.S.A., California, –, –, –, –, –, AY354384-AY354346*; *Orcuttia tenuis* Hitchc, *Boykin 12 & Hall* (UNM), U.S.A., California, –, –, –, –, –, AY354372-AY354334*; *Orcuttia tenuis* Hitchc, *Boykin 62 & Hall* (UNM), U.S.A., California, –, –, –, –, –, AY354373-AY354335*; *Orcuttia tenuis* Hitchc, *Stone 771* (US), U.S.A., California, GU360727, GU360271, –, GU360001, –, GU359398, JQ345136, JQ345199; *Orcuttia viscida* (Hoover) Reeder, *Reeder 6234 & Reeder* (US), U.S.A., California, –, –, –, GU360000, –, –, –, **KX582391**; *Orinus kokonorica* (K. S.Hao) Keng ex X. L.Yang, *Soreng 5447*, *Peterson & Sun Hang* (US), China, Qinghai, GU360728, GU360270, **KX582823**, GU359999, GU359628, GU359399, JQ345137, GU359140; *Orinus thordii* (Stapf ex Hemsely) Bor, *Soreng 5515*, *Peterson & Sun Hang* (US), China, Xizang (Tibet), GU360721, GU360269, **KX582824**, GU359998, GU359626, GU359400, **KX582289**, GU359126; *Orinus thordii* (Stapf ex Hemsely) Bor, *Soreng 5529*, *Peterson & Sun Hang* (US), China, Xizang (Tibet), GU360714, GU360268, **KX582825**, GU359997, GU359595, GU359401, **KX582290**, GU359112; *Oropetium aristatum* (Stapf) Pilg, *Fay 5932* (MO), Central African Republic, Bamingui-Bangoran, **KX582980**, **KX582912**, **KX582826**, **KX582666**, **KX582553**, **KX582479**, **KX582291**, **KX582392**; *Oropetium capense* Stapf, *Smook 6739* (TCD), –, –, –, HE575782*, –, –, –, **Oropetium capense Stapf, *Venter 9939 & Venter* (MO), South Africa, Free State, Ladybrand, KM011120, KM010917, **KX582827**, KM010692, **KX582554**, KM010533, **KX582292**, KM010324; *Oropetium minimum* (Hochst.) Pilg, *Friis 3317*, *Tadesse & Vollesen* (MO), Ethiopia, Sidamo, **KX582981**, –, **KX582828**, **KX582667**, **KX582555**, –, **KX582293**, –, **Oropetium minimum** (Hochst.) Pilg, *Gillet 4163* (FT), Somalia, Boundary Pilar 93, –, –, –, –, –, **KX582393**; *Oropetium minimum* (Hochst.) Pilg, *Vorontsova 43724* (K), Kenya,**

Appendix 1. Continued.

KX582982, –, –, KX582668, –, –, KX582394; *Oropetium thomaeum* (L. f.) Trin, *Kimeu 136* (K), KX582983, –, –, KX582669, –, –, KX582395; *Oropetium thomaeum* (L. f.) Trin, *Peterson 24193*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Kilimanjaro, KX582984, KX582913, –, –, KX582670, –, –, KX582396; *Oxychloris scariosa* (F. Muell.) Lazarides, *Forster 20737 & Holland* (MEL), Australia, Queensland, KP873813, KP874086, –, –, KP873631, KX582556, KP873952, –, –, KP873414; *Pappophorum bicolor* E. Fourn, *Pohl 12464* (MO), Mexico, Luis Potosí, KX582985, KX582914, –, –, KX582671, KX582557, KX582480, –, –, KX582397; *Pappophorum caespitosum* R.E. Fr., *Tivano 801 et al.* (SF), Argentina, –, –, –, –, –, JN175281*; *Pappophorum pappiferum* (Lam.) Kuntze, *Peterson 21689*, *Soreng, La Torre & Rojas Fox* (US), Peru, Ancash, GU360700, GU360276, KX582829, GU359996, GU359596, GU359402, JQ345138, GU359128; *Pappophorum pappiferum* (Lam.) Kuntze, *Peterson 24583 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, KX582672, –, –, –, KX582398; *Pappophorum philippianum* Parodi, *Renvoize 4225*, *Cope & Beck* (MO), Bolivia, La Paz, KX582986, KX582915, KX582830, KJ768980, KX582558, KX582481, –, –, KJ768885; *Pappophorum vaginatum* Buckley, *Gould 2912* (US), U.S.A., Arizona, –, –, –, KX582673, KX582559, –, –, –, *Pappophorum vaginatum* Buckley, *Hinckley 4002* (US), U.S.A., Texas, –, –, –, KX582674, –, –, –, *Pappophorum vaginatum* Buckley, *Swallen 10089* (US), U.S.A., Texas, –, –, –, KX582675, KX582560, –, –, –, *Pappophorum vaginatum* Buckley, *Wagner 3930 & Brown* (MO), Mexico, Durango, KX582987, KX582916, –, –, –, KX582676, KX582561, –, –, –, KX582399; *Perotis arenacea* (Judz.) P.M. Peterson, *Phillipson 4117 & Raharilala* (MO), Madagascar, Toliara, JQ345272, JQ345313, KX582831, JQ345358, –, –, –, JQ345150, JQ345202; *Perotis hordeiformis* Nees, *Soreng 5717*, *Peterson & Sun Hang* (US), China, Sichuan, GU360708, GU360283, KX582832, GU359991, GU359600, GU359520, JQ345139, GU359132; *Pleuraphis jamesii* Torr, *Beetle 2061* (US), U.S.A., Colorado, –, –, –, KX582677, –, –, –, KX582400; *Pleuraphis jamesii* Torr, *Columbus 3221* (RSA), U.S.A., Wyoming, –, –, –, JN681737*, –, –, –, EF153056*; *Pleuraphis jamesii* Torr, *Reeder 5480 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582678, –, –, –, KX582401; *Pleuraphis mutica* Buckley, *Reeder 5229 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582679, –, –, –, KX582402; *Pleuraphis mutica* Buckley, *Reeder 5452 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582680, –, –, –, KX582403; *Pleuraphis rigida* Thurber, *Beatley 6979* (US), U.S.A., Nevada, –, –, –, KX582681, –, –, –, KX582404; *Pleuraphis rigida* Thurber, *Boyd 11566* (BRY), U.S.A., JQ345269, JQ345311, –, –, –, JQ345356, KX582562, JQ345229, –, –, –, JQ345200; *Pleuraphis rigida* Thurber, *Reeder 8010 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582682, –, –, –, KX582405; *Pogononeura biflora* Napper, *Greenway 10091* (US), Tanzania, Serengeti National Park, –, –, –, KM010694, –, –, –, *Polevansia rigida* De Winter, *Smook 6000* (US), South Africa, –, –, –, GU360287, KX582834, –, –, –, GU359602, GU359523, KX582295, GU359136; *Polevansia rigida* De Winter, *Spies 7621*, –, –, –, –, –, –, –, DQ655811*; *Schenckochloa barbata* (Hack.) J.J. Ortiz, *Swallen 4690* (US), Brazil, Natal, KP827806, –, –, –, KP827674, –, –, –, KP827552; *Schoenefeldia transiens* (Pilg.) Chiov, *Peterson 24216*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Tanga, KP873815, KP874088, KX582837, KP873632, KX582565, KP873954, –, –, –, KP873415; *Sclerodactylum macrostachyum* (Benth.) A. Camus, *Koopman 383 & Raveloarison* (US), Madagascar, Cape Ste. Marie, –, –, –, KX582683, –, –, –, *Scleropogon brevifolius* Phil, *Peterson 19280*, *Soreng, Salariado & Panizza* (US), Argentina, San Juan, GU360635, –, –, –, KX582838, GU359919, GU359611, GU359530, JQ345144, GU359203; *Scleropogon brevifolius* Phil, *Peterson 24849 & Romaschenko* (US), Mexico, Zacatecas/San Luis Potosí, –, –, –, KX582684, KX582566, –, –, –, KX582406; *Scleropogon brevifolius* Phil, *Peterson 24855 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, KX582685, KX582567, –, –, –, KX582407; *Scleropogon brevifolius* Phil, *Peterson 24904 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, KX582686, KX582568, –, –, –, KX582408; *Scleropogon brevifolius* Phil, *Reeder 5474 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582687, KX582569, –, –, –, *Scleropogon brevifolius* Phil, *Reeder 5534 & Reeder* (US), U.S.A., Arizona, –, –, –, KX582688, KX582570, –, –, –, *Sohnsia filifolia* (E. Fourn.) Airy Shaw, *Peterson 11129 & Annable* (US), Mexico, San Luis Potosí, GU360634, GU360350, KX582839, GU359918, GU359612, GU359531, JQ345145, GU359204; *Stapfochloa canterae* (Arechav.) P.M. Peterson, *Pedersen 9597* (US), Paraguay, Misiones Dep, KP873661, KP873978, –, –, –, KP873444, –, –, –, KP873839, –, –, –, KP873230; *Swallenia alexandreae* (Swallen) Soderstr. & H.F. Decker, *Carter 2784* (US), U.S.A., GU360639, GU360364, KX582845, GU359920, GU359669, GU359512, JQ345148, GU359217; *Tetrapogon brandegeei* (Vasey) P.M. Peterson, *Carter 2897 & Kellog* (US), Mexico, Baja California, KP873767, KP874048, –, –, –, KP873581, –, –, –, KP873922, –, –, –, KP873365; *Tetrapogon fasciculatus* (Hitchc. & Chase) P.M. Peterson, *Ekman s.n.* (US), Dominican Republic, GU360638, GU360317, KX582846, GU359982, GU359608, GU359528, JQ345142, GU359156; *Tragus andicola* Zapater & Sulekic, *Jorgensen 1711* (US), Argentina, Catamarca Prov, KX582988, –, –, –, KX582689, –, –, –, *Tragus australianus* S.T. Blake, *Symon 13792* (US), Australia, GU360618, GU360368, KX582847, GU359900, GU359673, GU359515, KX582299, GU359222; *Tragus berteronianus* Schult, *FLSP 457* (US), Peru, GU360616, GU360370, KX582848, GU359898, GU359675, GU359503, JQ345151, GU359224; *Tragus berteronianus* Schult, *Peterson 21615*, *Soreng, La Torre & Rojas Fox* (US), Peru, Ancash, GU360617, GU360369, KX582849, GU359899, GU359662, GU359535, KX582300, GU359223; *Tragus berteronianus* Schult, *Peterson 24190*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Kilimanjaro, KX582989, KX582917, –, –, –, KX582690, KX582572, KX582482, –, –, –, KX582409; *Tragus berteronianus* Schult, *Peterson 24210*, *Soreng, Romaschenko & Mbago* (US), Tanzania, Tanga, KX582990, KX582918, –, –, –, KX582691, KX582573, KX582483, –, –, –, KX582410; *Tragus berteronianus* Schult, *Peterson 24875 & Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, KX582692, KX582574, –, –, –, KX582411; *Tragus heptaneuron* W.D. Clayton, *Gillett 13019* (US), Kenya, GU360615, GU360371, KX582850, GU359897, GU359676, GU359526, KX582301, GU359225; *Tragus koelerioides* Asch, *Smook 6844* (US), South Africa, GU360614, GU360372, KX582851, GU359896, GU359677, GU359551, KX582302, GU359226; *Tragus mongolorum* Ohwi, *Clayton 5229* (US), Sri Lanka, GU360612, –, –, –, KX582852, GU359894, –, –, –, *Tragus pedunculatus* Pilg, *Schweickerdt 2297* (US), South Africa, GU360613, GU360373, KX582853, GU359895, GU359678, GU359552, KX582303, GU359185; *Tragus racemosus* (L.) All, *Hochobes 1334* (US), Namibia, Hardap, KX582991, –, –, –, KX582693, –, –, –, KX582412; *Tragus racemosus* (L.) All, *Klaassen 1278* (US), Namibia, Okavango, KX582992, KX582919, –, –, –, KX582694, –, –, –, KX582413; *Tragus racemosus* (L.) All, *Klaassen 1292 & al.* (US), Namibia, Okavango, KX582993, –, –, –, KX582695, –, –, –, KX582414; *Tragus racemosus* (L.) All, *Smook 4590* (US), South Africa, Cape Reg, KX582994, –, –, –, KX582696, –, –, –, KX582415; *Trichoneura eleusinooides* (Rendle) Ekman, *Seydel 448* (US), South Africa, GU360705, GU360277, KX582854, GU359988, GU359601, GU359522, JQ345154, GU359135; *Tridens × oklahomensis* (Feath.) Feath, *Barrell 138-73* (US), U.S.A., Kansas, –, –, –, KX582697, –, –, –, KX582416; *Tridens albescens* (Vasey) Wootton & Standl, *Reeder 4586 & Reeder* (US), Mexico, Chihuahua, KX582995, KX582920, –, –, –, –, –, –, –, KX582417; *Tridens albescens* (Vasey) Wootton & Standl, *Swallen 10249* (US), U.S.A., Texas, –, –, –, KX582921, –, –, –, –, –, –, –, *Tridens ambiguus* (Elliott) Schult, *Grelen 195* (US), U.S.A., Louisiana, KX582996, KX582922, –, –, –, KX582698, –, –, –, KX582484, –, –, –, KX582418; *Tridens brasiliensis* (Nees ex Steud.) Parodi, *Milgura de Romero 2397*, *Belgrano, Denham & Romero* (MO), Argentina, Misiones, –, –, –, –, –, –, –, KX582419; *Tridens brasiliensis* (Nees ex Steud.) Parodi, *Quarin 3794 & Norrmann* (US), Argentina, Corrientes Prov, –, –, –, KX582699, –, –, –, KX582420; *Tridens brasiliensis* (Nees ex Steud.) Parodi, *Renvoize 3642* (US), Argentina, Corrientes, –, –, –, KX582700, –, –, –, *Tridens buckleyanus* (Vasey ex L.H. Dewey) Nash, *Palmer 10961* (MO), U.S.A., Texas, KX582997, KX582923, –, –, –, KX582701, –, –, –, KX582485, –, –, –, KX582421; *Tridens carolinianus* (Steud.) Henrard, *Boyce 1567*, *Wells & Shunk* (US), U.S.A., North Carolina, KX582998, KX582924, –, –, –, KX582702, –, –, –, KX582486, –, –, –, KX582422; *Tridens congestus* (L.H. Dewey) Nash, *Trouart 35* (US), U.S.A., Texas, KX582999, KX582925, –, –, –, KX582703, –, –, –, KX582423; *Tridens flaccidus* (Döll) Parodi, *Davidse 3002* (US), Venezuela, Guárico, –, –, –, KX582704, –, –, –, KX582424; *Tridens flaccidus* (Döll) Parodi, *Goodland 611* (US), Guyana, Rupununi, –, –, –, KX582705, –, –, –, *Tridens flavus* (L.) Hitchc, *Cronquist 4709* (US), U.S.A., Georgia, KX583000, KX582926, –, –, –, KX582706, –, –, –, KX582487, –, –, –, KX582425; *Tridens flavus* (L.) Hitchc, *Davidse 38002* (MO), U.S.A., Missouri, KF827816, KF827750, KX582855, KF827688, KX582575, KF827614, –, –, –, KF827567; *Tridens flavus* (L.) Hitchc, *Fernald 2758 & Griscom* (US), U.S.A., Virginia, –, –, –, KX582927, –, –, –, KX582707, –, –, –, KX582426; *Tridens flavus* var. *chapmanii* (Small) Shinnars, *McCauley 438* (MO), U.S.A., Missouri, KF827817, KF827751, KX582856, KF827689, KX582576, KF827615, KX582304, KF827568; *Tridens flavus* var. *chapmanii* (Small) Shinnars, *Peterson 24412*, *Romaschenko, Knapp & Frye* (US), U.S.A., Maryland, KX583001, KX582928, –, –, –, KX582708, –, –, –, KX582427; *Tridens flavus* var. *chapmanii* (Small) Shinnars, *Wilbur 2772 & Webster* (US), U.S.A., Georgia, KX583004, –, –, –, KX582579, –, –, –, KX582430; *Tridens flavus* var. *flavus* (L.) Hitchc, *Peterson 24414*, *Romaschenko, Knapp & Frye* (US), U.S.A., Maryland, KX583002, KX582929, –, –, –, KX582709, KX582577, –, –, –, KX582428; *Tridens flavus* var. *flavus* (L.) Hitchc, *Peterson 24421*, *Romaschenko, Knapp & Frye* (US), U.S.A., Maryland, KX583003, KX582930, –, –, –, KX582710, KX582578, –, –, –, KX582429; *Tridens hackelii* (Arechav.) Parodi, *Rosengurt 4544* (US), Uruguay, Artigas Dep, –, –, –, KX582711, –, –, –, KX582431; *Tridens langosii* (Nash) Nash, *Woods 4065* (US), U.S.A., Texas, –, –, –, KX582712, –, –, –, KX582432; *Tridens muticus* var. *elongatus* (Buckley) Shinnars, *Correll 17162* (US), –, –, –, KX582931, –, –, –, KX582713, –, –, –, *Tridens muticus* var. *elongatus* (Buckley) Shinnars, *Hitchcock 5495* (US), –, –, –, KX582932, –, –, –, –, –, –, –, *Tridens muticus* var. *elongatus* (Buckley) Shinnars, *Steyermark 78202* (US), U.S.A., Missouri, KX583005, KX582933, –, –, –, –

Appendix 1. Continued.

KX582714, –, –, –, **KX582433**; *Tridens nicorae* Anton, *Anderson 2428* (US), Argentina, San Luis Dept, **KX583006**, –, –, –, **KX582715**, –, –, –, **KX582434**; *Tridens strictus* (Nutt.) Nash, *Robinson 2787* (US), U.S.A., Arkansas, **KX583007**, –, –, –, –, –, **KX582435**; *Tridens strictus* (Nutt.) Nash, *Summers 9414* & *Hudson* (MO), U.S.A., Missouri, **KX583008**, **KX582934**, **KX582857**, **KX582716**, **KX582580**, **KX582488**, –, **KX582436**; *Tridens texanus* (S.Watson) Nash, *Correll 15960*, *Rollins & Chambers* (US), U.S.A., Texas, –, **KX582935**, –, **KX582717**, –, –, –, –, **Tridens texanus** (S.Watson) Nash, *Fleetwood 3074* (US), U.S.A., Texas, –, –, –, –, –, –, **KX582437**; *Tridens texanus* (S.Watson) Nash, *Peterson 24618* & *Romaschenko* (US), Mexico, San Luis Potosí, –, –, –, **KX582718**, –, –, –, **KX582438**; *Tridens texanus* (S.Watson) Nash, *Reeder 4564* & *Reeder* (US), Mexico, Coahuila, **KX583009**, **KX582936**, –, **KX582719**, –, **KX582489**, –, **KX582439**; *Tridens texanus* (S.Watson) Nash, *Valdes-Reyna 1497* & *Carranza* (US), Mexico, Nuevo Leon, **KX583010**, **KX582937**, –, **KX582720**, –, **KX582490**, –, **KX582440**; *Tridentopsis eragrostoides* (Vasey & Scribn.) P.M.Peterson, *Ekman 16606* (US), Cuba, Pinar del Río, **KX583011**, **KX582938**, –, **KX582721**, –, –, –, **KX582491**, –, **KX582441**; *Tridentopsis eragrostoides* (Vasey & Scribn.) P.M.Peterson, *Gould 11468* (US), U.S.A., Texas, **KX583012**, –, –, –, **KX582722**, –, –, –, **KX582442**; *Tridentopsis eragrostoides* (Vasey & Scribn.) P.M.Peterson, *Sohns 1250* (US), Mexico, San Luis Potosí, **KX583013**, **KX582939**, –, **KX582723**, –, **KX582492**, –, **KX582443**; *Tridentopsis mutica* (Torr.) P.M.Peterson, *Gould 9978* (US), U.S.A., New Mexico, KF827815, KF827749, –, KF827687, **KX582581**, KF827613, –, KF827566; *Tridentopsis mutica* (Torr.) P.M.Peterson, *Peterson 10498* & *Annable* (US), U.S.A., Texas, **KX583014**, **KX582940**, –, **KX582724**, **KX582582**, –, –, –, **KX582444**; *Tridentopsis mutica* (Torr.) P.M.Peterson, *Peterson 21997* & *Saarela* (US), Mexico, Chihuahua, GU360667, GU360321, **KX582858**, GU359947, GU359682, GU359557, **KX582305**, GU359173; *Tridentopsis mutica* (Torr.) P.M.Peterson, *Peterson P24474* & *Romaschenko* (US), Mexico, Coahuila, –, –, –, **KX582725**, **KX582583**, –, –, **KX582445**; *Trigonochloa uniflora* (Hochst. ex A.Rich.) P. M.Peterson & N.Snow, *Greenway 14075* (MO), Tanzania, JQ345261, –, –, JQ345347, –, –, –, –, *Trigonochloa uniflora* (Hochst. ex A.Rich.) P. M.Peterson & N.Snow, *Snow 6978*, *Burgoyne & Gumbi* (MO), South Africa, KwaZulu Natal, –, –, –, JQ345348, –, –, –, JQ345192; *Triodia basedowii* Pritz, *Latz 20217* (MEL), Australia, Northern Territory, –, –, –, JX051513*, –, –, –, JX051459*; *Triodia basedowii* Pritz, *Peterson 14437*, *Soreng & Rosenberg* (US), Australia, Western Australia, GU360666, GU360322, **KX582859**, GU359946, GU359683, GU359550, **KX582306**, GU359174; *Triodia basedowii* Pritz, *Saarela 1632*, *Peterson, Soreng & Judziewicz* (US), Australia, Northern Territory, **KX583015**, **KX582941**, –, **KX582726**, **KX582584**, **KX582493**, –, **KX582446**; *Triodia bitextura* Lazarides, *Forbes 2556* (MEL), Australia, Western Australia, –, –, –, –, –, JX051451*; *Triodia brizoides* N.T.Burb, *Peterson 14432*, *Soreng & Rosenberg* (US), Australia, Western Australia, GU360665, GU360323, **KX582860**, GU359945, GU359651, GU359559, **KX582307**, GU359175; *Triodia bromioides* (F.Muell.) Lazarides, *Crisp s.n.* (CANB), Australia, Western Australia, –, –, –, JX051510*, –, –, –, JX051461*; *Triodia bynoei* (C.E.Hubb.) Lazarides, *Peterson 14424*, *Soreng & Rosenberg* (US), Australia, Western Australia, GU360664, GU360324, **KX582861**, GU359944, GU359649, GU359560, **KX582308**, GU359176; *Triodia compacta* (N.T.Burb.) S.W.L.Jacobs, *Thorne 19420* & *Eichler* (MEL), Australia, South Australia, –, –, –, JX051504*, –, –, –, JX051467*; *Triodia danthonioides* (F.Muell.) Lazarides, *Donaldson 1451* & *Flowers* (CANB), Australia, Western Australia, –, –, –, –, –, JX051483*; *Triodia desertorum* (C.E.Hubb.) Lazarides, *Lepschi 4499* & *Craven* (US), Australia, GU360663, GU360325, **KX582862**, GU359943, GU359672, GU359561, **KX582309**, GU359177; *Triodia fitzgeraldii* N.T.Burb, *Lazarides 3169* (US), Australia, GU360662, GU360326, **KX582863**, GU359942, GU359641, GU359562, **KX582310**, GU359178; *Triodia intermedia* Cheell, *Peterson 14384*, *Soreng & Rosenberg* (US), Australia, Western Australia, GU360661, GU360327, **KX582864**, GU359941, GU359642, GU359563, JQ345155, GU359179; *Triodia irritans* var. *laxispicata* N.T.Burb, *Hind 5731*, *D'Aubert & Jones* (US), Australia, GU360660, GU360328, **KX582865**, GU359940, GU359643, GU359564, **KX582311**, GU359180; *Triodia irritans* R.Br. *Latz 16048* & *Albrecht* (MEL), Australia, Northern Territory, –, –, –, JX051515*, –, –, –, JX051468*; *Triodia lanigera* Domin, *Walsh 6589*, *Halford & Mallinson* (MEL), Australia, Western Australia, –, –, –, –, –, JX051460*; *Triodia longiceps* J.M.Black, *Latz 14521* (MEL), Australia, Northern Territory, –, –, –, JX051508*, –, –, –, JX051458*; *Triodia melvillei* (C.E.Hubb.) Lazarides, *Peterson 14383*, *Soreng & Rosenberg* (US), Australia, Western Australia, GU360659, GU360329, **KX582866**, GU359939, GU359644, GU359542, **KX582312**, GU359181; *Triodia pungens* R.Br. *Thompson BUC800* & *Simon* (US), Australia, GU360658, GU360330, **KX582867**, GU359938, GU359645, GU359540, **KX582313**, GU359182; *Triodia rigidissima* (Pilg.) Lazarides, *Spjut 7263*, *White, Phillips & Lacy* (US), Australia, GU360657, GU360331, **KX582868**, GU359937, GU359646, GU359556, **KX582314**, GU359198; *Triodia scariosa* N.T.Burb, *Burbridge 2675* (CANB), Australia, Western Australia, –, –, –, JX051485*, –, –, –, JX051465*; *Triodia scariosa* N.T.Burb, *Hurry 52F*, *Murphy & Walsh* (MEL), Australia, Victoria, –, –, –, JX051484*, –, –, –, JX051476*; *Triodia scariosa* N.T.Burb, *Mant 25* (ANUC), Australia, Southern Australia, –, –, –, –, –, JX051449*; *Triodia schinzii* (Henrad) Lazarides, *Beauglehole 60370* (MEL), Australia, Western Australia, –, –, –, JX051488*, –, –, –, JX051452*; *Triodia schinzii* (Henrad) Lazarides, *Saarela 1683*, *Peterson, Soreng & Judziewicz* (US), Australia, Northern Territory, **KX583016**, **KX582942**, –, **KX582727**, –, **KX582494**, –, **KX582447**; *Triodia stenostachya* Domin, *Batianoff 940377A* (MEL), Australia, Queensland, –, –, –, JX051486*, –, –, –, JX051450*; *Triodia tomentosa* S.W.L.Jacobs, *Craven 8869*, *Zich & Lyne* (MEL), Australia, Western Australia, –, –, –, JX051503*, –, –, –, JX051462*; *Triodia tomentosa* S.W.L.Jacobs, *Flowers 107* & *Donaldson* (CANB), Australia, Western Australia, –, –, –, –, –, JX051482*; *Triodia triticoides* C.A.Gardner, *Peterson 14406*, *Soreng & Rosenberg* (US), Australia, Western Australia, –, –, –, JX051506*, –, –, –, JX051457*; *Triplasis americana* P.Beauv. *Kral 12065* (MO), U.S.A., Georgia, KF827818, KF827752, **KX582869**, KF827690, **KX582585**, KF827616, **KX582315**, KJ768887; *Triplasis purpurea* (Walter) Chapm. *Peterson 14238*, *Weakley & LeBlond* (US), U.S.A., North Carolina, GU360656, GU360347, **KX582870**, GU359921, GU359647, GU359536, JQ345156, GU359184; *Triplasis purpurea* (Walter) Chapm. *Peterson 24420*, *Romaschenko*, *Knapp & Frye* (US), U.S.A., Maryland, KF827819, KF827753, **KX582871**, KF827691, **KX582586**, **KX582496**, **KX582316**, KF827569; *Tripogon bromioides* Roth, *Clayton 5460* (US), Sri Lanka, Uva Prov, **KX583018**, **KX582944**, –, **KX582729**, –, **KX582497**, –, **KX582449**; *Tripogon bromioides* Roth, *Clayton 6160* & *Jayorekera* (US), Sri Lanka, Kmukle, **KX583019**, **KX582945**, –, **KX582730**, –, **KX582498**, –, **KX582450**; *Tripogon chinensis* Hack, *Boufford 29012*, *Bartholomew, Chen, Donoghue, Ree, Sun Hang & Wu Su-Gong* (MO), China, Sichuan, **KX583020**, **KX582946**, **KX582872**, **KX582731**, **KX582587**, **KX582499**, **KX582317**, **KX582451**; *Tripogon loliiformis* (F.Muell.) C.E.Hubb. *Saarela 1677*, *Peterson, Soreng & Judziewicz* (US), Australia, Northern Territory, **KX583021**, **KX582947**, –, **KX582732**, –, **KX582500**, –, **KX582452**; *Tripogon loliiformis* (F.Muell.) C.E.Hubb. *Stajsis 720* (MEL), Australia, Victoria, –, –, –, **KX582733**, –, –, –, **KX582453**; *Tripogon minimus* Hochst. ex Steud. *Laegaard 15919* (MO), Zimbabwe, Lake Kyle, **KX583022**, –, –, –, **KX582588**, –, –, –, *Tripogon multiflorus* Miré & H.Gillet, *Spellenberg 7441* (MO), Yemen, Ibb Governate, JQ345274, JQ345315, **KX582873**, JQ345360, **KX582589**, JQ345232, JQ345157, JQ345204; *Tripogon nanus* Keng f. *Boufford 28865*, *Bartholomew, Chen, Donoghue, Ree, Sun Hang & Wu Su-Gong* (MO), China, Sichuan, **KX583023**, **KX582948**, **KX582874**, **KX582734**, **KX582590**, –, **KX582318**, **KX582454**; *Tripogon purpurascens* Duthie, *Spellenberg 7438* (MO), Yemen, **KX583024**, **KX582949**, **KX582875**, **KX582735**, **KX582591**, **KX582501**, **KX582319**, **KX582455**; *Tripogon spicatus* (Nees) Ekman, *Peterson 21784* & *Soreng* (US), Peru, Ancash, GU360640, GU360333, **KX582876**, GU359935, GU359648, GU359537, **KX582320**, GU359170; *Tripogon spicatus* (Nees) Ekman, *Peterson 24722*, *Romaschenko & Zamudio Ruiz* (US), Mexico, Querétaro, –, –, –, **KX582736**, **KX582592**, –, –, **KX582456**; *Tripogon trifidus* Munro ex Hook.f. *Laegaard 21668* & *Norsangri* (MO), Thailand, Chiang Mai Prov, KP873822, KP874094, **KX582877**, KP873641, **KX582593**, KP873957, **KX582321**, KP873422; *Tripogon yunnanensis* J.L.Yang ex S.M.Phillips & S.L.Chen, *Soreng 5564*, *Peterson & Sun Hang* (US), China, Xizang (Tibet), –, GU360487, **KX582878**, –, –, GU359538, **KX582322**, GU359186; *Tuctoria fragilis* (Swallen) Reeder, *Reeder 7131* (RSA), Mexico, Baja California Sur, –, –, –, –, –, AY354354*; *Tuctoria fragilis* (Swallen) Reeder, *Reeder 7255* & *Reeder* (US), Mexico, –, –, –, GU359929, –, –, –, GU359189; *Tuctoria greenii* (Vasey) Reeder, *Reeder 6235* & *Reeder* (US), U.S.A., California, –, –, –, **KX582737**, –, –, –, **KX582457**; *Tuctoria greenii* (Vasey) Reeder, *Reeder 6656* & *Reeder* (US), U.S.A., California, –, –, –, GU359928, –, –, JQ345159, GU359190; *Tuctoria mucronata* (Crampton) Reeder, *Columbus 4682.5* (RSA), U.S.A., California, –, –, –, JN681766*, –, –, EF153095*; *Vaseyochloa multinervosa* (Vasey) Hitchc. *Swallen 10041* (US), U.S.A., Texas, GU360646, GU360342, **KX582882**, GU359925, GU359656, GU359544, –, GU359193; *Vaseyochloa multinervosa* (Vasey) Hitchc. *Swallen 10124* (US), U.S.A., Texas, –, –, –, **KX582738**, **KX582594**, –, **KX582458**; *Willkommia sarmantosa* Hack, *Schweickerdt 2181* (US), South Africa, GU360645, GU360343, **KX582883**, GU359924, GU359657, GU359545, JQ345161, GU359194; *Willkommia texana* var. *texana* Hitchc. *Gould 12525* (US), U.S.A., Texas, GU360644, GU360344, **KX582884**, –, **KX582595**, GU359546, **KX582325**, GU359195.

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**A molecular phylogeny and classification of the
Cynodonteae (Poaceae: Chloridoideae) with four
new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*,
and *Zaqiqah*; three new subtribes: Dactylocteniinae,
Orininae, and Zaqiqahinae; and a subgeneric
classification of *Distichlis***

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

Taxon 65: 1263–1287

Fig. S1 (next page). Maximum-likelihood tree inferred from ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; color indicates native distribution (see legend).



Fig. S2 (next page). Maximum-likelihood tree inferred from combined plastid (*rps16-trnK*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; color indicates native distribution (see legend).



- NA
- SA
- Africa
- Australia + Pacific
- Eurasia