

A molecular phylogeny and classification of the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae (Poaceae: Chloridoideae: Cynodonteae)

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Abstract The classification of twenty Cynodonteae genera (*Bewsia*, *Craspedorhachis*, *Ctenium*, *Dignathia*, *Farrago*, *Gouinia*, *Gymnopogon*, *Latipes*, *Leptocarydion*, *Leptothrium*, *Lophacme*, *Lopholepis*, *Mosdenia*, *Perotis*, *Schenckochloa*, *Toliara*, *Trichoneura*, *Trigonochloa*, *Triplasis*, *Vaseyochloa*) has been poorly understood. The goals of this study were to reconstruct the evolutionary history of the tribe Cynodonteae, emphasizing these twenty genera using molecular data with increased species sampling. A phylogenetic analysis was conducted on 159 samples, of which 94 species (140 individuals) were in the Cynodonteae, using four plastid (*rpl32-trnL* spacer, *ndhA* intron, *rps16-trnK* spacer, *rps16* intron) and nuclear ITS 1&2 (ribosomal internal transcribed spacer regions) sequences to infer evolutionary relationships and revise the classification. Strong support was found for six lineages. *Craspedorhachis*, *Ctenium*, *Dignathia*, *Gymnopogon*, *Trichoneura*, and *Triplasis* appear monophyletic; *Leptothrium* is paraphyletic with *Latipes inermis* embedded within; *Perotis* is paraphyletic with *Lopholepis* and *Toliara* embedded within; and *Gouinia* is monophyletic with the resurrection of *Schenckochloa*. The molecular results support the recognition of six subtribes; five (Cteniinae, Farragininae, Gymnopogoninae, Perotidinae, Trichoneurinae) are newly described. A new genus, *Tridentopsis*, is described; five new combinations, *Leptothrium inerme*, *Perotis arenacea*, *Perotis ornithocephala*, *Tridentopsis eragrostoides*, and *Tridentopsis mutica* are made; and *Holboellia ornithocephala* is lectotypified.

Keywords classification; ITS; phylogeny; plastid DNA sequences; *Tridentopsis*

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

■ INTRODUCTION

The species in subfamily Chloridoideae Kunth ex Beil-schm. and tribe Cynodonteae Dumort. share two structural traits: all exhibit Kranz or C₄ leaf anatomy (except two species of *Ellisochloa* P.M.Peterson & N.P.Barker from southern Africa; Peterson & al., 2011) and most have chloridoid bicellular microhairs (broad, short terminal cell the same thickness as the basal cell) present on leaf surfaces (Peterson & al., 2007, 2010a). Based on leaf anatomical structure, two main subtypes of C₄ photosynthesis—classical NAD-ME and PCK—have been observed (Hattersley & Watson, 1992). The Cynodonteae currently consists of at least 78 genera and there appear to be no definitive morphological features that differentiate Cynodonteae from Chloridoideae since most of the structural variation in the entire subfamily is exhibited in the tribe. However, Cynodonteae receive moderate to high support as a monophyletic lineage in molecular analyses (Hilu & Alice, 2001; Columbus & al., 2007; Peterson & al., 2010a).

Reveal (2004) pointed out that Martinov (1820) used Chlorideae as a tribal name. However, Martinov's "Chlorideae" was

not validly published as it corresponds to the fifth order in Kunth's (1815) system, as one of 10 sections, an order or section within a family being an example of a misplaced rank-denoting term (Art. 5.1 & 37.6 of the *ICN*, McNeill & al., 2012). Therefore, we revert back to next oldest name, Cynodonteae Dumort.

Recent molecular DNA studies within the subfamily Chloridoideae, specifically in the tribe Cynodonteae, have not been exhaustive, and they lack an adequate sample of species to assess phylogenetic relationships and determine monophyly of the genera (Hilu & Alice, 2001; Columbus & al., 2007; Bouchenak-Khelladi & al., 2008; Peterson & al., 2010a). The most comprehensive estimates of the phylogeny of the Chloridoideae to date have been presented in Peterson & al. (2010a) where 246 species included in 95 genera were sampled for seven markers (*ndhA* intron, *ndhF*, *rps16-trnK*, *rps16* intron, *rps3*, *rpl32-trnL*, ITS). The resulting classification from this work recognized 13 subtribes within the Cynodonteae. *Gouinia* E.Fourn. ex Benth. & Hook.f., *Schenckochloa* J.J.Ortiz (included in *Gouinia*), *Triplasis* P.Beauv., and *Vaseyochloa* Hitchc. were placed in subtribe Tridentinae

Keng & Keng f. In that same classification, *Farrago* Clayton, *Latipes* Kunth (included in *Leptothrium* Kunth), *Leptocarydion* Hochst. ex Stapf, *Leptothrium*, and *Lophacme* Stapf (sometimes erroneously spelled *Lophachme*) were placed in Chloridoideae–incertae sedis (not yet placed in a tribe); and *Bewsia* Goossens, *Craspedorhachis* Benth., *Ctenium* Panz., *Dignathia* Stapf, *Gymnopogon* P.Beauv., *Lopholepis* Decne., *Mosdenia* Stent, *Perotis* Aiton, and *Trichoneura* Andersson were placed in the Cynodonteae–incertae sedis (not yet placed in a subtribe). *Toliara* Judz. and *Trigonochloa* P.M.Peterson & N.Snow are newly described genera and have been shown to have affinities to *Perotis* (Judziewicz, 2009; Peterson & al., 2012; Snow & Peterson, 2012).

The aim of our paper is to discern the evolutionary relationships and present a new classification of 20 target genera. These 20 genera of uncertain affinities include: *Bewsia* (monotypic, Africa), *Craspedorhachis* (3 species, Africa), *Ctenium* (20 species, Africa, South America, North America, Asia), *Dignathia* (5 species, Africa, Asia), *Farrago* (monotypic, endemic to Tanzania), *Gouinia* (10 species, South and North America; including *Schenckochloa*), *Gymnopogon* (14 species, South and North America, Asia), *Leptocarydion* (monotypic, Africa and Asia), *Leptothrium* (3 species, Asia, Africa, and South America; including *Latipes*), *Lophacme* (2 species, Africa), *Lopholepis* (monotypic, Asia), *Mosdenia* (monotypic, Africa), *Perotis* (14 species, Africa, Asia, Australasia), *Toliara* (monotypic, endemic to Madagascar), *Trichoneura* (8 species, Africa, South and North America, Asia), *Trigonochloa* (2 species, Africa and Asia), *Triplasis* (2 species, North and South America), and *Vaseyochloa* (monotypic, endemic to Texas, U.S.A.) (Smith, 1971; Clayton & al., 1974, 2006; Gibbs Russell & al., 1991; Phillips, 1995; Cope, 1999; Raimondo, 2001). In addition to these 20 target genera, we sample 37 species that represent 12 subtribes known to be included in the Cynodonteae (Peterson & al., 2010a, 2011, 2012).

Using plastid (*rpl32-trnL*, *ndhA*, *rps16-trnK*, *rps16*) and nuclear ITS DNA sequence markers, we present a new phylogenetic analysis of Cynodonteae that includes these 20 genera that were previously assigned to either the Cynodonteae or Chloridoideae. The number of species sampled within many of these 20 genera is expanded and for the first time we are including species of *Craspedorhachis*, *Farrago*, *Latipes*, *Leptocarydion*, *Leptothrium*, and *Schenckochloa* (Peterson & al., 2010a, 2012). In addition, we discuss morphological and anatomical characters supporting relationships and propose changes to the classification.

■ MATERIALS AND METHODS

Taxon sampling. — The taxon sampling consists of 159 samples, representing 113 species of grasses, of which 110 species are included in subfamily Chloridoideae; these are partitioned to represent the following five tribes and subtribes: Centropodieae with a single species, Triraphideae with two species, Eragrostideae with eight species, Zoysieae with five species, Cynodonteae: Tripogoninae with two species,

Pappophorinae with three species, Tragineae with two species, Aeluropodinae with three species, Hilariinae with two species, Muhlenbergiinae with two species, Scleropogoninae with a single species, Boutelouinae with a single species, Monanthochloinae with a single species, Triodiinae with a single species, Eleusininae with thirteen species, and Orcuttiinae with five species (see Electr. Suppl.: Appendix S1). We removed the following genera from our study because they did not align within or among clades containing the 20 target genera: *Allolepis* Soderst. & H.F.Decker, *Brachychloa* S.M.Phillips, *Cleistogenes* Keng, *Dactyloctenium* Willd., *Jouvea* E.Fourn., *Lepturidium* Hitchc. & Ekman, *Neobouteloua* Gould, *Orinus* Hitchc., *Pogononeura* Napper, and *Sohnsia* Airy Shaw; and we lack leaf material for two species placed in the Cynodonteae–incertae sedis: *Hubbardochloa* Auquier and *Kampochloa* Clayton, and *Oxychloris* Lazarides which lies within the Eleusininae (Peterson & al., in prep.; Soreng & al., 2013, see suprageneric classification). Our sampling was primarily focused on 20 genera (*Bewsia*, *Craspedorhachis*, *Ctenium*, *Dignathia*, *Farrago*, *Gouinia*, *Gymnopogon*, *Latipes*, *Leptocarydion*, *Leptothrium*, *Lophacme*, *Lopholepis*, *Mosdenia*, *Perotis*, *Schenckochloa*, *Toliara*, *Trichoneura*, *Trigonochloa*, *Triplasis*, *Vaseyochloa*) that are morphologically similar, and most of these genera have been previously aligned near one another (Peterson & al., 2010a). The dataset for these 20 genera includes sixty-five percent (58/89) of the species currently placed in these genera by Clayton & al. (2006). A complete list of taxa, voucher information, and GenBank numbers can be found in Appendix S1 (Electr. Suppl.). Outside of the Chloridoideae, one species of Danthonioidae (*Danthonia compressa* Austin), one species from Aristidoideae (*Aristida gypsophila* Beetle), and one species of Panicoideae (*Chasmanthium latifolium* (Michx.) H.O.Yates, phylogenetic root) were chosen as the outgroup. All collections gathered by PMP after 1998 were collected in silica but the majority of samples used in this study were selected 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), and ITS was accomplished following procedures outlined in Peterson & al. (2010a, b). We specifically targeted four of the plastid regions which proved to be most informative in our previous studies on chloridoid grasses (Peterson & al., 2010a, b, 2011, 2012).

Phylogenetic analyses. — We used Geneious v.5.3.4 (Drummond & al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *ndhA* intron, *rps16* intron, *rps16-trnK*, and ITS regions, and we used Muscle (Edgar, 2004) to align consensus sequences and adjust the final alignment (Supplementary Data includes sequence alignments). We identified models of molecular evolution for the cpDNA and nrDNA regions using jModelTest v.0.1.1 (Posada, 2008). We applied maximum-likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined datasets were partitioned in accordance with the number of the markers used. Nucleotide

substitution models selected by Akaike's information criterion, as implemented in jModelTest, were specified for each partition (Table 1). The ML analysis was conducted with GARLI v.0.951 (Zwickl, 2006). We used the standard option in PAUP* v.4.0b10 (Swofford, 2000) to generate the number of the parsimony informative characters for the five DNA regions (Table 1). The ML bootstrap analysis was performed with 1000 replicates, with 10 random addition sequences per replicate. The output file containing trees of ML found for each bootstrap dataset was then read into PAUP where the majority-rule consensus tree was constructed. Bootstrap (BS) values of 90%–100% were interpreted as strong support, 70%–89% as moderate, and 50%–69% as weak. We also calculated the uncorrected *p*-value in PAUP to demonstrate the sequence divergence among members of *Leptothrium* and *Latipes*.

Bayesian posterior probabilities (PP) were estimated using parallel version of the 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 four million generations, sampling once per 100 generations. The analysis was run until the value of 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 (PP) of 0.95–1.00 were considered as strong support.

In the phylograms the native distribution of each species is indicated as follows: North America (red), South America (tan), Central Africa (Tanzania, Kenya; dark green), Southern Africa (light green), and Southeast Asia (purple).

RESULTS

Phylogenetic analyses. — Forty-eight percent (320/660) of the sequences used in our study are newly reported here and in GenBank, and only 16.7% (132/792) are missing (Electr. Suppl.: Appendix S1). Total aligned characters for individual regions are noted in Table 1. Plastid *rpl32-trnL* had the highest sequencing success of 94.3% of taxa recovered across the entire dataset. Recovery of other regions ranged from 66% to 90%.

Analysis of combined plastid and ITS sequences. — There was hard incongruence within the Gymnopogoninae clade between the plastid (combined) and ITS tree. The plastid tree depicts a monophyletic *Gymnopogon* (BS = 100, PP = 1.00), whereas the ITS tree renders *Gymnopogon* paraphyletic and includes *Bewsia* and *Lophacme* embedded within *Gymnopogon*. Therefore, in our combined plastid–ITS analysis we removed

Table 1. Summary of the four plastid regions and nrDNA ITS used in maximum-likelihood and Bayesian searches indicated by Akaike's information criterion.

Characteristic	<i>rpl32-trnL</i>	<i>ndhA</i> intron	<i>rps16</i> intron	<i>rps16-trnK</i>	Combined plastid data	ITS	Overall combined dataset
Total aligned characters	991	1124	989	954	4158	822	4980
Sequencing success (%)	94.3	66	80	85	82	90	83
Number of new sequences	78 (52%)	49 (47%)	65 (52%)	68 (51%)	260 (51%)	78 (55%)	338 (52%)
Likelihood score (–lnL)	7224.00	7181.83	5282.39	6408.54		17040.45	
Number of substitution types	6	6	6	6	–	6	
Model for among-site rate variation	gamma	gamma	gamma	gamma	–	gamma	
Substitution rates	1.2412 2.0479 0.4612 1.6880 1.7126 1.0000	1.2742 2.6666 0.5249 1.6465 2.525 1.0000	1.0553 1.3476 0.2844 1.2456 1.7866 1.0000	1.0989 2.7853 0.4664 1.4675 2.3991 1.0000	–	1.2515 2.9776 1.7603 0.8442 5.0446 1.0000	
Character state frequencies	0.3599 0.1355 0.1315 0.3730	0.3665 0.1373 0.1484 0.3476	0.3914 0.1097 0.1646 0.3341	0.3006 0.1383 0.1421 0.4188	–	0.2450 0.2053 0.2457 0.3039	
Proportion of invariable sites	0.1858	0.2778	0.2883	0.0378	–	0.2547	
Substitution model	GTR+I+G	TVM+G	TIM3+I+G	TIM3+G	–	GTR+I+G	
Gamma shape parameter (α)	1.2015	1.3218	1.6015	1.2233	–	1.0682	
Number of parsimony-informative characters ^a	251	259	184	259	953	328	1281

^aSupplementary data from parsimony analysis.



Fig. 1. Phylogram of maximum-likelihood tree from analysis of combined plastid and ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; clades outlined in dashed lines are discussed in text; scale bar = 3% sequence divergence; color indicates native distribution (see legend).

ITS sequences of *Bewsia* and *Lophacme*. There were no other examples of conflict between the two datasets.

The ML tree from the combined plastid (*rpl32-trnL*, *ndhA*, *rps16-trnK*, *rps16*) and ITS regions (Fig. 1) is well resolved with strong support for the six major clades labeled as: Cteniinae, Farragininae, Gymnopogoninae, Perotidinae, and Trichoneurinae (all at BS = 100, PP = 1.00) and Gouiniinae (BS = 95, PP = 1.00). The Farragininae-Perotidinae clade (BS = 65, PP = 0.84) is sister to the Gymnopogoninae clade (BS = 100, PP = 1.00); these are sister (BS = 68, PP = 0.98) to the Cteniinae-Trichoneurinae clade (BS = 58, PP = 0.98); and all five subtribes are sister with strong support (BS = 100, PP = 1.00) to the Gouiniinae. The Orcuttiinae is sister to these six major clades that form a monophyletic lineage (BS = 0.95, PP = 1.00).

The Gouiniinae clade consists of a monophyletic *Gouinia* (BS = 97, PP = 1.00) sister to *Vaseyochloa multinervosa*; these are sister (BS = 55, PP = 0.54) to *Tridens muticus* (BS = 100, PP = 1.00). *Tridens flavus* L., the type for the genus, is sister to *Pappophorum pappiferum* (Lam.) Kuntze and is clearly aligned with the Pappophorinae. *Schenckochloa barbata* is sister to the *Gouinia-Vaseyochloa-Tridens* clade (BS = 100, PP = 1.00), and all are sister (BS = 0.68, PP = 0.94) to a monophyletic *Triplasis* (BS = 97, PP = 1.00). Within *Gouinia*: the *G. brasiliensis*-*G. paraguayensis* (BS = 79, PP = 1.00) pair is sister to *G. latifolia*-*G. virgata* (BS = 57, PP = 0.94).

The Cteniinae clade consists of a monophyletic *Ctenium* with two distinct subclades: *C. newtonii*-*C. elegans*-*C. somalense* (BS = 100, PP = 1.00) sister to *C. aromaticum*-*C. cirrhosum*-*C. brevispicatum* (BS = 99, PP = 1.00).

The Trichoneurinae clade consists of a monophyletic *Trichoneura* with three distinct subclades with four accessions of *T. eleusinoidea* (BS = 86, PP = 0.99) sister to the *T. grandiglumis*-*T. mollis* (BS = 90, PP = 1.00) and *T. weberbaueri*-*T. lindleyana*-*T. elegans* (BS = 60, PP = 1.00) clade.

The Farragininae clade includes *Farrago racemosa* Clayton sister to a monophyletic *Craspedorhachis* (BS = 97, PP = 1.00). To test the repeatability of our work we included four samples of the *Craspedorhachis rhodesiana* Rendle that were collected all by *Strohbach 5699* but placed on different herbarium sheets. All sequences were identical.

The Perotidinae clade includes a paraphyletic *Perotis* (BS = 84, PP = 1.00) sister to *Mosdenia leptostachys* (Ficalho & Hiern) Clayton. Embedded within *Perotis* are *Lopholepis ornithocephala* (Hook.) Steud. and *Toliara arenacea* Judz. Within the *Perotis* clade four different accessions of *Perotis patens* Gand. (BS = 81, PP = 0.99) are sister to *Toliara*; and all of these are sister to *P. leptopus*-*P. vaginata* (BS = 98, PP = 1.00). *Perotis rara* R. Br. forms an unsupported clade with *Lopholepis ornithocephala*; and this is sister to the *P. somalensis*-*P. hildebrandtii* clade (BS = 94, PP = 0.99).

Within the Gymnopogoninae clade a monophyletic *Dignathia* (BS = 100, PP = 1.00) with three species is sister to a paraphyletic *Leptothrium* (BS = 100, PP = 1.00) that includes *Latipes inermis*. *Latipes inermis* forms a clade with *Leptothrium rigidum* (BS = 67, PP = 1.00). *Gymnopogon* appears monophyletic with strong support (BS = 100, PP = 1.00) and is sister to *Lophacme-Bewsia* (BS = 90, PP = 0.97). Four

accessions of *Leptocarydion vulpiastrum* (De Not.) Stapf are sister to the *Bewsia-Lophacme-Gymnopogon* clade (BS = 100, PP = 1.00); and all of these (BS = 100, PP = 1.00) are sister to the *Dignathia-Leptothrium* clade (BS = 0.92, PP = 1.00).

Analysis of ITS sequences. — The ML tree based on data from the nrITS region is remarkably well resolved and very similar to the combined plastid-ITS tree (Fig. 2). There is strong support (BS = 100, PP = 1.00) for four of the major clades (Cteniinae, Farragininae, Perotidinae, Trichoneurinae) and moderate support for the Gouiniinae (BS = 87, PP = 1.00) and Gymnopogoninae (BS = 78, PP = 1.00). All six subtribes form a monophyletic clade (BS = 73, PP = 0.94). Within the Gouiniinae clade, *Tridens muticus* is sister to *Gouinia*; and within the Gymnopogoninae clade, *Lophacme* and *Bewsia biflora* render *Gymnopogon* paraphyletic.

Analysis of plastid sequences. — The ML tree based on combined plastid sequences (Fig. 3) depicts the Cteniinae, Farragininae, Perotidinae, and Trichoneurinae clades with strong support (BS = 98–100, PP = 1.00), the Gymnopogoninae with moderate support (BS = 84, PP = 1.00), and the Gouiniinae with weak support (BS = 61, PP = 0.64). All six subtribes form a monophyletic clade (BS = 88, PP = 1.00). Resolution and support for clades within the Perotidinae are lacking and within *Perotis* there is only a single strongly supported clade with two accessions of *P. indica* whereas within the combined plastid-ITS tree there are five strongly supported clades within *Perotis* and six highly supported clades within the ITS tree. The plastid tree resolves a strongly supported (BS = 100, PP = 1.00), monophyletic *Gymnopogon*.

■ DISCUSSION

Within these 20 genera of Cynodonteae we found strong support for six lineages we treat as subtribes: the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae. *Craspedorhachis*, *Ctenium*, *Dignathia*, *Gymnopogon*, *Trichoneura*, and *Triplasis* all appear monophyletic; *Leptothrium* is paraphyletic with *Latipes inermis* Chiov. embedded within; *Perotis* is paraphyletic with *Lopholepis* and *Toliara* embedded within; and *Gouinia* is monophyletic with the resurrection of *Schenckochloa*.

Gouiniinae. — With a limited sample of species per genus, *Gouinia*, *Tridens*, *Triplasis*, and *Vaseyochloa* were included in a clade (Columbus & al., 2007) and later formally treated in the subtribe Tridentinae (Peterson & al., 2010a). However, the type for *Tridens* (*T. flavus* (L.) Hitchc.) was not included. In our study *Tridens flavus* is clearly sister to *Pappophorum* (Fig. 1), a member of the Pappophorinae. *Tridens muticus* is separated from *T. flavus* in Valdes-Reyna's (2003) key by containing narrow panicles with appressed, ascending branches. The palea nerves of *T. flavus* are glabrous and not long hairy as in *T. muticus* and both species of *Triplasis*, also a member of the *Gouinia* clade. Based on a trigonous caryopsis, glumes shorter than the florets, a triangular rachilla, and anatomical differences, Ortíz (1991) erected *Schenckochloa* to include a single species native to western Brazil, *S. barbata* (Hack.) J.J.Ortíz. Therefore, we

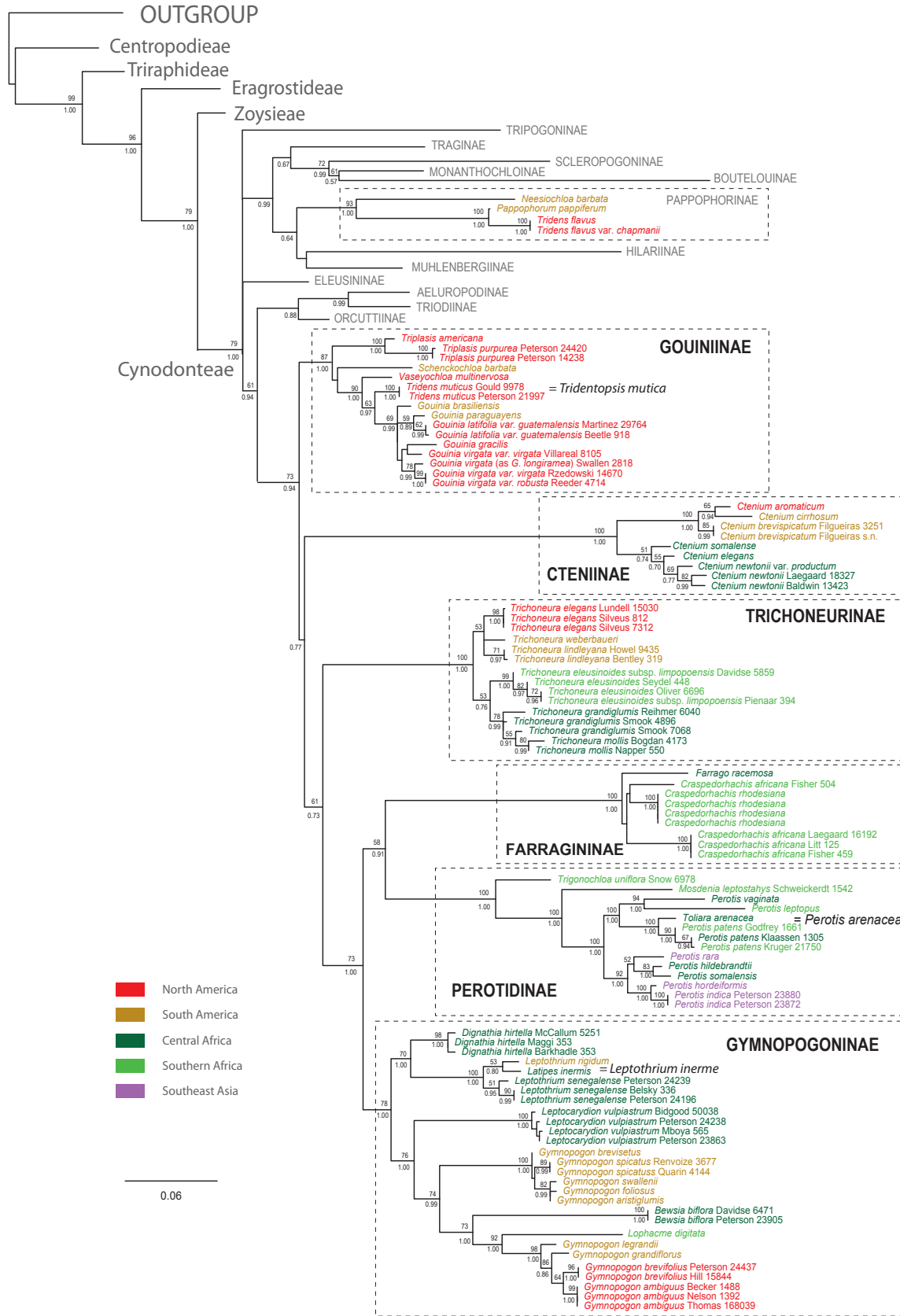


Fig. 2. Phylogram of maximum-likelihood tree from analysis of ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; clades outlined in dashed lines are discussed in text; scale bar = 6% sequence divergence; color indicates native distribution (see legend).



Fig. 3. Phylogram of maximum-likelihood tree from analysis of combined plastid sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; clades outlined in dashed lines are discussed in text; scale bar = 1% sequence divergence; color indicates native distribution (see legend).

resurrect subtribe Gouiniinae to now include *Gouinia*, *Tridens muticus*, *Triplasis*, *Schenckochloa*, and *Vaseyochloa*, all from the New World (Peterson & al., 2007). Since *Vaseyochloa* is sister to *Gouinia* s.str. (BS = 97, PP = 1.00, Fig. 1) and is morphologically distinct with caryopses that have two distinct horn-like style bases, we are inclined to be conservative and retain its use. The subtribal circumscription in Peterson & al. (2007) is still tenable since it was prepared to include *Gouinia* (including *Schenckochloa*) and *Vaseyochloa*. However, after reviewing the morphologies of the species in the *Gouinia* clade the following trends seem worth mentioning: palea keels are strongly winged to somewhat winged, or at least expanded near the base, and spikelets terminate in a rachilla extension (Swallen, 1935; Ortíz-Díaz, 1993). Based on having paleas that are not widened or bowed-out below and caryopses that are dorsally flattened, deeply concave to folded on the dorsal or hilar surface, and thickened towards the margins below, we place *Tridens muticus* in a new genus, *Tridentopsis*. We have preliminary data for 12 of the 17 species currently placed in *Tridens* (Peterson & Romaschenko, in prep.) and have included in the generic description of *Tridentopsis* below the morphological features of *Tridens muticus* and *Tridens eragrostoides* (Vasey & Scribn.) Nash, the only other species we are aware of that aligns within the new genus.

Cteniinae. — Within the Cynodonteae, *Ctenium* is morphologically and genetically distinct. The genus is characterized by having inflorescences of a single or sometimes 2–6 curved pectinate racemes; spikelets with two basal sterile florets, one fertile floret, and 1–3 rudimentary florets above the fertile; upper glumes that are 2 or 3-veined with a dorsal, subapical awn. The *Ctenium* clade contains two strongly supported, geographically separated subclades (New World and Africa), each with three species. However, this result might be erroneous since we are lacking data for 14 *Ctenium* species. It is also possible that *Kampochloa brachyphylla* Clayton lies within the Cteniinae, since it is readily mistaken for *Ctenium* but the spikelets lack two lower sterile florets (Clayton, 1967a). In the future we hope to obtain material of *Kampochloa* Clayton, known only from Angola.

Trichoneurinae. — The *Trichoneura* clade, like *Ctenium*, is genetically distinct and has a geographical signal. A central African clade (*T. grandiglumis*–*T. mollis*) is sister to a New World clade (*T. weberbaueri*–*T. lindleyana*–*T. elegans*) and these together are sister to a southern African clade (*T. eleusinoides*; see Fig. 1). We have sampled seven of the eight known species of *Trichoneura*, so this seems plausible. Napper (1963) indicated that *Pogononeura biflora* Napper was probably related to *Trichoneura* or *Leptochloa*. However, *Pogononeura* has recently been reanalyzed and apparently aligns near the Pappophorinae or Tragiinae and not in the Sporobolinae as previously reported (Peterson & al., 2010a; Peterson & al., in prep.). Unique morphological characteristics for the Trichoneurinae include: inflorescences with numerous unilateral racemes borne along a central axis; cuneate, and laterally compressed spikelets with glumes longer than the florets; and dorsally compressed caryopses that are plano- or concavo-convex.

Farragininae. — *Farrago racemosa*, as described by Clayton (1967b), is an interesting Tanzanian endemic that was thought to be a close relative of *Dignathia*, both placed in the Zoysiinae by Clayton & Renvoize (1986). The senior authors (PMP & KR) traveled to Namatumuzi, Tanzania (type locality) in 2012 to gather material of this enigmatic grass characterized in having dorsally compressed fertile spikelets with long-awned somewhat coriaceous glumes and delicate, hyaline lemmas that are dorsally hairy. Our DNA analyses clearly place *Farrago* as sister to *Craspedorhachis*. The latter African genus also has dorsally compressed spikelets with delicate, hyaline lemmas less firm than the glumes but differs from *Farrago* in having a perennial habit and conspicuously winged lower glumes and 3-veined lemmas (unveined in *Farrago*) (Watson & Dallwitz, 1992). *Craspedorhachis* was thought to have affinities with *Willkommia* Hack. and *Microchloa* R.Br. (Clayton & Renvoize, 1986), both recently realigned in the Tragiinae and Eleusiniinae, respectively (Peterson & al., 2010a). Based on only *rps3*, Peterson & al. (2010a) reported that *Craspedorhachis africana* was embedded within *Perotis* but they attributed this result to a lack of variation within the marker.

Perotidinae. — Peterson & al. (2010a) reported that *Perotis* was polyphyletic by containing *Lopholepis ornithocephala*, and these were sister to *Mosdenia*. Even though the laterally compressed spikelet of *Lopholepis* has undergone profound morphological change and resembles a bird's head in outline, other characters are consistent with those found in *Perotis* since it has leaf blades that are broad and clasping at the base with antrorse-ciliate margins, a single narrow raceme, and glumes exceeding the length of the florets. Clayton (1972) mentions *Lopholepis ornithocephala* as being the “third member” of an alliance with *Leptothrium senegalense* and *L. rigidum* Kunth (see discussion under Gymnopogoninae). *Toliara arenacea* was also found to be sister to *Perotis* in Peterson & al. (2012), and when initially described by Judziewicz (2009) was thought to be most closely related and morphologically similar to *Perotis*. However, when compared to *Perotis*, *Toliara* lacks awned glumes, has only two stamens, and has a pubescent ovary (Judziewicz, 2009). *Perotis* is clearly paraphyletic and we make the necessary combinations by transferring these two species to *Perotis* below. *Mosdenia* and *Trigonochloa* both align as strongly supported successive sisters to *Perotis* in our analyses (Peterson & al., 2010a, 2012; Snow & Peterson, 2012). *Mosdenia leptostachys* differs from species of *Perotis* in having stolons and unawned glumes and *Trigonochloa* differs from *Perotis* in having trigonous caryopses that have a narrow but deep sulcus on the hilar side (Gibbs Russell & al., 1991; Snow & Peterson, 2012). Character trends within the African and southeast Asian Perotidinae include: lanceolate to lanceolate-ovate leaf blades that are broad and clasping at the base with antrorse-ciliate margins; racemose inflorescence of one to several branches, if one, then usually narrow; and glumes that exceed the single fertile floret.

Gymnopogoninae. — Relationships among members of the Gymnopogoninae clade were previously elucidated, in part, when the *Bewsia-Gymnopogon* clade was depicted as sister to *Dignathia* (BS = 83, PP = 1.00; see fig. 3 in Peterson & al., 2010a). We expand this here to include *Dignathia-Leptothrium*

sister to a clade where *Leptocarydion* is sister to *Bewsia-Lophacme* and the *Gymnopogon* clades (see Fig. 1). *Dignathia* differs from *Leptothrium* in having spikelets sub-orbicular below with a long apical beak and *Leptocarydion vulpiastrum* differs from the latter two genera in having apically awned lemmas with conspicuously ciliate lateral veins (Clayton & al., 1974). *Bewsia* differs from *Lophacme* in having 2–4-flowered spikelets (1- or 2-flowered in *Lophacme*) with dorsally-awned lemmas, the awn typically arising 1/5 to 1/2 below the apex (lemmas apically awned in *Lophacme*) (Clayton & al., 2006). Species of *Gymnopogon*, like *Bewsia*, have subapically awned lemmas but the spikelets are usually 1-flowered (rarely 2-flowered), and *Bewsia biflora* is known only from Africa whereas the 14 species of *Gymnopogon* are principally distributed in the New World (a single species is known from Asia) (Smith, 1971; Clayton & al., 1974, 2006). Character trends in the Gymnopogoninae include: inflorescences with many racemes scattered along a central axis or sub-digitately arranged, laterally compressed spikelets with glumes usually longer than the florets, and lemmas that are usually awned or mucronate.

While in Italy in 2012, PMP gathered a small leaf sample annotated as *Latipes inermis* Chiov. housed in the University of Florence (Universita' di Firenze) Tropical Herbarium (FT) collected by C.F. Hemming 3416 in Somalia. The specimen was found in a folder labeled *Leptothrium senegalense*. We included this sample in our analysis and PMP noted on the small collection envelope, “but not that,” in reference to the folder label. *Latipes*, a genus described by Kunth (1829) to include a single species, *Latipes senegalensis* Kunth, was placed in synonymy of *Leptothrium* by Clayton (1972), where he made a new combination, *Leptothrium senegalense* (Kunth) Clayton. Kunth (1829) had based the genus *Leptothrium* on *L. rigidum* Kunth, a species known from the Caribbean and northwestern South America. Later, Clayton (1974) in his treatment of *Leptothrium* for the *Flora of Tropical East Africa* placed *Latipes inermis* as a synonym of *Leptothrium senegalense*. Morphologically, the type of *Latipes inermis* (Puccioni & Stefanini 354, seen digitally) is morphologically similar to the C.F. Hemming 3416 specimen in having glumes that are long and dorsally flattened (also a character of *Leptothrium rigidum*). We have looked at many specimens of *Leptothrium rigidum* and morphologically the only difference between it and *Latipes inermis* is a few tubercles or underdeveloped microhairs at the base of the glumes and the surface of the glumes usually appear dull or minutely roughened. In contrast, *Latipes inermis* has glumes that lack tubercles and the surfaces are shiny. Our sample of *Latipes inermis* forms a clade with *Leptothrium rigidum* (see Fig. 1; BS = 67, PP = 1.00), and the pair is sister to four accessions of *Leptothrium senegalense*. The average sequence divergence among the four accessions of *Leptothrium senegalense* is $p = 0.001585$, and the two recent Tanzanian collections from Kilimanjaro and Tanga/Kilimanjaro Regions (Peterson, Soreng & Romaschenko 24196 & 24239) are the most disparate (p range 0.00034–0.00238). There is 2.4 times more sequence divergence between the *Latipes inermis* and *Leptothrium rigidum* samples (average $p = 0.00376$) than among the four accessions of *Leptothrium senegalense*. The coastal sand dune and low-elevation desert habitats where these

two taxa reside in Africa and the Caribbean/northwestern South America (Colombia, Guyana, Peru, Venezuela) are very similar but apparently populations of these two species have diverged genetically. Therefore, it seems best to recognize *Latipes inermis* and *Leptothrium rigidum* as sister species and we make the new combination of the former in *Leptothrium*, rather than just a synonym of *Leptothrium rigidum* or *L. senegalense*. The biogeographical pattern (Caribbean–South American/African) of the three species of *Leptothrium* is perhaps uncommon in angiosperms or at least rarely documented. Three closely related species of *Jacquemontia* Choisy (Convolvulaceae) have a similar distribution with *J. obcordata* (Mills.) House found in eastern Mexico and the Antilles, *J. ovalifolia* (Choisy) Hallier f. from eastern and western Africa, and *J. sandwicensis* A.Gray endemic to Hawaii (Namoff & al., 2010).

■ TAXONOMY

Based on our results we propose a new classification for these 20 genera in the tribe Cynodonteae, describe a new genus, and make five new combinations.

Cteniinae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.**

– Type: *Ctenium* Panz., Ideen Revis. Gräs.: 38, 61. 1813.

The subtribe is characterized in having a densely caespitose annual or perennial habit; leaves often aromatic, ligules membranous; inflorescence usually a single (sometimes 2–6), unilateral, usually curved pectinate raceme(s); spikelets 3–12 mm long, laterally compressed with two glumes and two basal sterile florets, one fertile floret usually with 1–3 rudimentary sterile florets above; upper glume 2- or 3-veined, dorsally awned usually from the middle; lemmas 3-veined, membranous, subapically awned.

Included genus: *Ctenium*.

Farragininae P.M. Peterson, Romasch. & Y.Herrera, **subtr. nov.**

– Type: *Farrago* Clayton in Kew Bull. 21: 125. 1967.

The subtribe is characterized by containing an annual or perennial habit, culms often wiry, sometimes stoloniferous; inflorescence of one to several racemes scattered along a central axis, sometimes digitately inserted; fertile spikelets 2.4–4.4 mm long, dorsally compressed with two glumes, one floret; upper glumes 2–3 times longer than lemma, 1-veined, coriaceous to membranous, sometimes awned; lemmas 1–2.2 mm long, 3-veined, hyaline, glabrous or hairy, apex obtuse or truncate; caryopsis ellipsoid, dorsally compressed.

Included genera: *Craspedorhachis* and *Farrago*.

Gymnopogoninae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.**

– Type: *Gymnopogon* P.Beauv., Ess. Agrostogr.: 41, 164. 1812.

The subtribe is characterized by containing a perennial or annual habit, 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 1.6–11 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*, *Lepotocarydion*, *Leptothrium*, and *Lophacme*.

Leptothrium inerme (Chiov.) P.M.Peterson, **comb. nov.** ≡ *Latipes inermis* Chiov., Pl. Nov. Aethiop.: 22. 1928 – Holotype: SOMALIA. Sultanato di Obbia, duna di Obbia, 16 Apr. 1924, *Puccioni & Stefanini 354* [406] (FT barcode 000187 [image!]).

Perotidinae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.** – Type: *Perotis* Aiton, Hort. Kew. 1: 85. 1789.

The subtribe is characterized by containing an annual or perennial habit, culms erect or geniculate and decumbent; leaf blades usually lanceolate to lanceolate-ovate, broad and clasping at the base, margins often atrorsely ciliate; ligules membranous; inflorescence of one to several multilateral, rarely unilateral racemes scattered along a central axis with pedicelled or sessile spikelets; fertile spikelets 1.2–4.5(–11) mm long, one floret, rarely two; glumes exceeding apex of floret, usually 1.5–2.4 times longer than lemma, 1-veined; apex usually awned, sometimes acuminate or acute; lemmas usually 0–1(–3)-veined, hyaline, sometimes membranous, apex usually obtuse or sometimes acute.

Included genera: *Mosdenia*, *Perotis*, and *Trigonochloa*.

Perotis arenacea (Judz.) P.M.Peterson, **comb. nov.** ≡ *Toliara arenacea* Judz. in Adansonia, sér. 3, 31(2): 274–276, fig. 1. 2009 – Holotype: MADAGASCAR. Toliara Prov., 35 km N of Toliara on road to Morombe and 5 km E by road, 23°05'05" S 043°38'45" E, 50 m, 21 Feb. 1993, *P.B. Phillipson & J.R. Raharilala 4117* (P; isotypes: GRA, MO!, TAN).

Perotis ornithocephala (Hook.) P.M.Peterson, **comb. nov.** ≡ *Holboellia ornithocephala* Hook., Bot. Misc. 2: 144. 1831 ≡ *Lopholepis ornithocephala* (Hook.) Steud., Syn. Pl. Glumac. 1: 112. 1854 – **Lectotype (designated here):** INDIA. Peninsula Ind. orientalis, Maduræ, *herb. Wight 1741* (K barcode 000245202 [image!]; isolectotype: US No. 1063439!).

Trichoneurinae P.M.Peterson, Romasch. & Y.Herrera, **subtr. nov.** – Type: *Trichoneura* Andersson in Kongl. Vetensk. Acad. Handl. 1853: 148. 1855.

The subtribe is characterized by containing an annual or perennial habit, culms erect or geniculate and decumbent; ligules membranous; inflorescence of numerous unilateral racemes borne along a central axis; spikelets 4–14 mm long with 4–9 fertile florets, laterally compressed; upper glumes 1.2–2.3 times longer than lowest floret, 1-veined, usually muticus or awned; lemmas 3-veined, usually awned; caryopsis dorsally compressed, shallowly plano- or concavo-convex.

Included genus: *Trichoneura*.

Gouiniinae P.M.Peterson & Columbus in Aliso 23: 592. 2007 – Type: *Gouinia* E.Fourn. ex Benth. & Hook.f., Gen. Pl. 3: 1178. 1883.

Included genera: *Gouinia*, *Schenckochloa*, *Tridentopsis*, *Triplasis*, and *Vaseyochloa*.

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

Diagnosis. – *Tridentopsis* differs from *Tridens* Roem. & Schult. in having paleas that are not widened or bowed-out below; caryopses that are dorsally flattened and deeply concave to folded on the dorsal or hilar surface and thickened towards the margin below, surface reticulate, reddish-brown.

Description. – Plants caespitose perennials with knotty, short rhizomatous bases. Culms 20–100 cm tall, nodes often bearded, the hairs up to 2 mm long, soft. Leaf sheaths glabrous, scabrous, often pilose; ligules 0.5–3 mm long; blades up to 15 cm long, 1–5 mm wide, flat to involute. Panicles 7–30 cm long, to 20 cm wide, narrow or widely spreading; branches up to 12 cm long, erect to widely spreading and reflexed. Spikelets 3–13 mm long, 5–15-flowered, laterally compressed; disarticulation above the glumes; glumes 2–10 mm long, 1–7-veined, glabrous; lemmas 2–7 mm long, 3-veined, usually purple-tinted, midveins sometimes excurrent, puberulent to pilose along the veins; paleas 1.5–5 mm long, shorter than the lemmas, margins not widened or bowed out below, glabrous or hairy. Caryopsis 1–2.4 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. $2n = 40$.

Distribution and habitat. – The two species are distributed in the southwestern United States, northern Mexico, and the Caribbean. Plants occur on clay to sandy and rocky soils in arid environments from 0–2000 m.

Tridentopsis mutica (Torr.) P.M.Peterson, **comb. nov.** ≡ *Tricuspis mutica* Torr. in Pacif. Railr. Rep. 4(5): 156. 1857 ≡ *Triodia mutica* (Torr.) Scribn. in Bull. Torrey Bot. Club 10(1): 30. 1883 ≡ *Sieglingia mutica* (Torr.) Kuntze, Revis. Gen. Pl. 2: 789. 1891 ≡ *Tridens muticus* (Torr.) Nash, Fl. S.E. U.S.: 143. 1903 – Holotype: U.S.A. New Mexico, San Miguel Co., Fort Smith to the Rio Grande, Laguna Colorado, 22 Sep. 1853, *J.M. Bigelow s.n.* (NY barcode 00431678 [image!]; isotypes: MO No. 3056475 [image!], NY barcode 431679 [image!], US No. 3376126! fragm. ex NY).

Tridentopsis eragrostoides (Vasey & Scribn.) P.M. Peterson, **comb. nov.** ≡ *Triodia eragrostoides* Vasey & Scribn. in Contr. U.S. Natl. Herb. 1(2): 58. 1890 ≡ *Sieglingia eragrostoides* (Vasey & Scribn.) L.H.Dewey in Contr. U.S. Natl. Herb. 2(3): 539. 1894 ≡ *Tridens eragrostoides* (Vasey & Scribn.) Nash in Small, Fl. S.E. U.S.: 142. 1903 – Lectotype (designated by Hitchcock in Contr. U.S. Natl. Herb. 17: 357. 1913): U.S.A. Texas, San Diego, 1889, *G.C. Nealley s.n.* (US No. 81811!).

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TAXON

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Electronic Supplement to

**A molecular phylogeny and classification
of the Cteniinae, Farragininae, Gouiniinae,
Gymnopogoninae, Perotidinae, and Trichoneurinae
(Poaceae: Chloridoideae: Cynodonteae)**

Paul M. Peterson, Konstantin Romaschenko & Yolanda Herrera Arrieta

Taxon 63: 275–286

Appendix S1. List of specimens sampled: taxon (*asterisk indicates type for the genus), voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rpl32-trnL*, *ndhA*, *rps16*, *rps16-trnK* and ITS regions (**bold** indicates new accession); an n-dash (–) indicates missing data.

OUTGROUP: *Aristida gypsophila* Beetle, *Peterson 15839 & Valdes-Reyna* (US), Mexico, GU359977, GU359386, GU360286, GU360570, GU359267; *Chasmanthium latifolium* (Michx.) H.O.Yates, *Peterson 22463* (US), U.S.A., GU359891, GU359379, GU360438, GU360517, GU359319; *Danthonia compressa* Austin, *Peterson 21986 & Levine* (US), U.S.A., GU359865, GU359370, GU360483, GU360521, GU359345; **CENTROPODIEAE:** **Ellisochloa rangei* (Pilg.) P.M.Peterson & N.P.Barker, *Barker 960* (BOL), Namibia, –, JF729166, JF729184, JF729079, JQ345167; **TRIRAPHIDAE:** *Neyraudia reynaudiana* (Kunth) Keng ex Hitchcock, *Soreng 5318 & Peterson* (US), China, GU360003, GU359397, GU360272, –, GU359124; **Triraphis mollis* R.Br., *Peterson 14344*, *Soreng & Rosenberg* (US), Australia, GU359933, GU359539, GU360336, GU360669, GU359187; **ERAGROSTIDAE:** **Cottea pappophoroides* Kunth, *Peterson 21463*, *Soreng, LaTorre & Rojas Fox* (US), Peru, GU359842, GU359363, GU360456, GU360600, GU359237; *Ectrosia scabrida* C.E.Hubb., *Lazarides 4772* (US), Australia, GU359799, GU359476, GU360459, GU360497, GU359317; *Enneapogon scaber* Lehm., *Sachse 008* (MO), South Africa, JQ345322, JQ345208, JQ345279, JQ345237, JQ345168; *Enteropogon macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., *Laegaard 15902* (US), Zimbabwe, GU359795, GU359472, GU360470, GU360494, GU359340; *Eragrostis kennedyae* F.Turner, *Latz 13486* (MO), Australia, JQ345323, JQ345209, JQ345281, JQ345238, JQ345169; *Harpachne harpachnoides* (Hack.) B.S.Sun & S.Wang, *Soreng 5288, Peterson & Sun Hang* (US), China, GU359815, GU359435, GU360382, GU360611, GU359113; **Psammagrostis wiseana* C.A.Gardner & C.E.Hubb., *Peterson 14345*, *Soreng & Rosenberg* (US), Australia, GU359986, GU359533, GU360288, GU360703, GU359137; *Uniola condensata* Hitchc., *Peterson 9342 & Judziewicz* (US), Ecuador, GU359927, GU359534, GU360340, GU360649, GU359191; **ZOYSIEAE:** *Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., *Hatch 5738 & Bearden* (US), U.S.A., GU359880, GU359357, GU360441, GU360548, GU359300; **Crypsis aculeata* (L.) Aiton, *Soreng 7940* (US), Russia, JQ345316, JQ345205, JQ345275, JQ345233, JQ345163; *Spartina densiflora* Brongn., *Peterson 19154*, *Soreng, Salariato & Panizza* (US), Argentina, GU359916, GU359510, GU360352, JQ345271, GU359206; *Sporobolus virginicus* (L.) Kunth, *Peterson 15683 & Soreng* (US), Chile, GU359892, GU359502, GU360362, GU360610, GU359215; *Zoysia macrantha* subsp. *walshii* M.E.Nightingale, *Loch 435* (US), Australia, GU359922, GU359548, GU360345, GU360642, GU359197; **CYNODONTEAE: Tripogoninae:** *Tripogon multiflorus* Miré & H.Gillet, *Spellenberg 7441* (MO), Yemen, JQ345360, JQ345232, JQ345315, JQ345274, JQ345204; *Eragrostiella leioptera* (Stapf) Bor, *Chand 7961* (US), India, GU359827, GU359486, JQ345280, GU360529, GU359305; **CYNODONTEAE: Pappophorinae:** **Neesiochloa barbata* (Nees) Pilg., *Swallen 4491* (US), Brasil, GU360005, –, GU360279, GU360724, GU359122; **Pappophorum pappiferum* (Lam.) Kuntze, *Peterson 21689*, *Soreng, La Torre & Rojas Fox* (US), Peru, GU359996, GU359402, GU360276, GU360700, GU359128; *Tridens flavus* var. *chapmanii* (Small) Shinners, *McCanley 438* (MO), U.S.A., **KF827689, KF827615, KF827751, KF827817, KF827568;** **Tridens flavus* (L.) Hitchc., *Davidse 38002* (MO), U.S.A., **KF827688, KF827614, KF827750, KF827816, KF827567;** **CYNODONTEAE: Tragineae:** *Monelytrum luederitzianum* Hack., *Smook 10031* (US), South Africa, GU359969, GU359459, GU360421, GU360682, GU359158; *Tragus berteronianus* Schult., *FLSP 457* (US), Peru, GU359898, GU359503, GU360370, GU360616, GU359224; **CYNODONTEAE: Scleropogoninae:** **Scleropogon brevifolius* Phil., *Peterson 19280*, *Soreng, Salariato & Panizza* (US), Argentina, GU359919, GU359530, –, GU360635, GU359203; **CYNODONTEAE: Hilariinae:** **Hilaria cenchroides* Kunth, *Peterson 22339 & Saarela* (US), Mexico, GU359813, GU359424, GU360380, GU360697, GU359143; *Pleuraphis rigida* Thurber, *Boyd 11566* (BRY), U.S.A., JQ345356, JQ345229, JQ345311, JQ345269, JQ345200; **CYNODONTEAE: Monanthochloinae:** *Distichlis humilis* Phil., *Peterson 19362*, *Soreng, Salariato & Panizza* (US), Argentina, GU359835, GU359430, GU360478, GU360502, GU359333; **CYNODONTEAE: Boutelouinae:** *Bouteloua simplex* Lag., *Peterson 21289*, *Saarela & Flores Villegas* (US), Mexico, GU359834, GU359406, GU360297, GU360607, GU359231; **CYNODONTEAE: Muhlenberginae:** *Muhlenbergia japonica* Steud., *Soreng 5301*, *Peterson & Sun Hang* (US), China, HM143184, HM143389, HM143572, HM143668, HM143082; **Muhlenbergia schreberi* J.F.Gmel., *Peterson 19443*, *Soreng, Salariato & Panizza* (US), Argentina, GU359950, GU359456, GU360404, GU360679, GU359161; **CYNODONTEAE: Aeluropodinae:** **Aeluropus lagopoides* (L.) Trin. ex Thwaites, *Weinert s.n. & Mosawi*, Iraq, GU360013, GU359391, GU360284, GU360576, GU359261; *Aeluropus littoralis* (Gouan) Parl., *Ferguson 634*, *Greese, GU360018*, *GU359390*, *GU360308*, *GU360575*, *GU359262*; *Aeluropus pungens* (M.Bieb.) K.Koch, *Yunatov s.n.*, *Li Shyin & Yuan Yfen*, China, GU360014, GU359389, GU360319, GU360574, GU359263; **CYNODONTEAE: Triodiinae:** *Triodia intermedia* Cheel, *Peterson 14384*, *Soreng, & Rosenberg* (US), Australia, GU359941, GU359563, GU360327, GU360661, GU359179; **CYNODONTEAE: Eleusininae:** *Astrebla pectinata* (Lindl.) F.Muell. ex Benth., *Chalmers 5* (US), Australia, GU359861, GU359421, GU360311, GU360567, GU359286; *Austrochloris dichanthioides* (Everist) Lazarides, *Anson s.n.* (US), Australia, GU359860, GU359420, GU360310, GU360566, GU359272; *Chloris barbata* Sw., *Peterson 22255 & Saarela* (US), Mexico, GU359873, GU359377, GU360435, GU360514, GU359320; *Cynodon maritimus* Kunth, Howard 10214 & Howard (US), Bahamas, GU359889, GU359365, GU360448, GU360591, GU359248; *Coelachyrum poiflorum* Chiov., *Burger 2915* (US), Ethiopia, GU359843, –, GU360457, GU360601, GU359236; *Eleusine indica* (L.) Gaetrn., *Peterson 21362*, *Saarela & Flores Villegas* (US), Mexico, GU359797, GU359473, GU360472, GU360496, GU359338; *Eustachys petraea* (Sw.) Desv., *Strong 3124* (US), U.S.A., GU359833, GU359438, GU360385, GU360637, GU359313; **Dinebra retroflexa* (Vahl) Panz., *Ndegwa 610* (US), Kenya, GU359778, GU359355, GU360479, GU360503, GU359332; *Dinebra chinensis* (Nees) P.M.Peterson & N.Snow, Snow 6909 (MO), Botswana, JQ345325, –, –, JQ345240, JQ345171; *Leptochloa digitata* (R.Br.) Domin., *Risler 476* (MO), Australia, JQ345331, JQ345213, JQ345289, JQ345246, JQ345178; **Disakisperma dubium* (Kunth) P.M.Peterson & N.Snow, *Peterson 22334 & Saarela* (US), Mexico, GU359811, GU359442, GU360416, GU360695, GU359145; *Lintonia nutans* Stapf, *Mwasumbi 14374* (US), Tanzania, GU359980, GU359426, GU360427, GU360690, GU359151; *Sclerodactylon macrostachyum* (Benth.) A.Camus, *Stoddart 741* (US), Seychelles, GU359963, –, –, –, **CYNODONTEAE: Orcuttinae:** *Orcuttia inaequalis* Hoover, *Hoover 1256* (US), U.S.A., GU360002, –, –, GU360726, –, *Orcuttia tenuis* Hitchc., *Stone 771* (US), U.S.A., GU360001, GU359398, GU360271, GU360727, JQ345199; *Orcuttia viscidula* (Hoover) Reeder, *Reeder 6234 & Reeder* (US), U.S.A., GU360000, –, –, –, *Tuctoria fragilis* (Swallen) Reeder, *Reeder 7255* (US), Mexico, GU359929, –, –, GU359189; *Tuctoria greenii* (Vasey) Reeder, *Reeder 6656 & Reeder* (US), U.S.A., GU359928, –, –, GU359190; **CYNODONTEAE: Gouiniinae:** *Gouinia brasiliensis* (S.Moore) Swallen, *Nee 36355* (US), Bolivia, **KF827635, –, KF827707, –, KF827517;** *Gouinia gracilis* Ekman ex Swallen, *Ekman s.n.* (US type), Cuba, **KF827636, –, KF827708, KF827773, KF827518;** *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J.Ortiz, *Martinez 29764*, *Alvarez & Ramirez* (MO), Mexico, **KF827638, KF827583, KF827709, KF827774, KF827520;** *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J.Ortiz, *Beetle 918, KF827637, –, –, KF827519; **Gouinia virgata* (J.Presl) Scribn. var. *virgata*, *Swallen 2818* (US), Mexico, –, –, **KF827712, –, KF827523;** *Gouinia paraguayensis* (Kuntze) Parodi, *Peterson 11526 & Annable* (US), Argentina, GU359817, GU359437, GU360384, GU360504, GU359314; *Gouinia virgata* var. *robusta* J.J.Ortiz, *Reeder 4714* (US) Mexico, **KF827639, KF827584, KF827710, KF827775, KF827521;** **Gouinia virgata* (J.Presl) Scribn. var. *virgata*, *Rzedowski 14670* (US), Mexico, **KF827640, –, KF827711, –, KF827522;** **Gouinia virgata* (J.Presl) Scribn. var. *virgata*, *Villareal 8105*, Carranza, Rodriguez & Villareal (MO), Mexico, **KF827641, –, KF827713, KF827776, KF827524;** **Schenckochloa barbata* (Hack.) J.J.Ortiz, *Swallen 4690* (US), Brazil, **KF827674, –, –, KF827806, KF827552;** **Triplasis americana* P.Beauv., *Kral 12065* (MO), U.S.A., **KF827690, KF827616, KF827752, KF827818, –;** *Triplasis purpurea* (Walter) Chapm., *Peterson 14238*, *Weakley & LeBlond* (US), U.S.A., GU359921, GU359536, GU360347, GU360656, GU359184; *Triplasis purpurea* (Walter) Chapm., *Peterson 24420*, *Romaschenko, Knapp & Frye* (US), **KF827691, –, KF827753, KF827819, KF827569;** **Tridenopsis mutica* (Torr.) P.M.Peterson, *Gould 9978* (US), U.S.A., **KF827687, KF827613, KF827749, KF827815, KF827566;** **Tridenopsis mutica* (Torr.) P.M.Peterson, *Peterson 21997 & Saarela* (US), Mexico, GU359947, GU359557, GU360321, GU360667, GU359173; **Vaseyochloa multinervis* (Vasey) Hitchc., *Swallen 10041* (US), U.S.A., GU359925, GU359544, GU360342, GU360646, GU359193; **CYNODONTEAE: Cteniniinae:** **Ctenium aromaticum* (Walter) Alph. Wood, *Peterson 14235*, *Weakley & LeBlond* (US), U.S.A., GU359839, –, –, GU359240; *Ctenium brevispicatum* J.G.Sm., *Filgueiras 3251 & Oliveira* (US), Brazil, **KF827627, KF827578, KF827700, KF827764, KF827508;** *Ctenium brevispicatum* J.G.Sm., *Filgueiras & Oliveira s.n.* (MO), Brazil, JQ345317, JQ345206, JQ345276, JQ345234, JQ345164; *Ctenium cirrhosum* (Nees) Kunth, *Grola 1452* (US), Brazil, GU359838, –, GU360353, GU360597, GU359241; *Ctenium elegans* Kunth, *Laegaard 18359*, *Mipro & Sobere* (US), Burkina Faso, –, –, **KF827701, KF827765, KF827509;** *Ctenium newtonii* Hack., *Baldwin 13423* (US), Ghana, –, –, **KF827766, KF827510;** *Ctenium newtonii* Hack., *Laegaard 18327*, *Mipro & Sobere* (US), Burkina Faso, **KF827628, KF827579, KF827702, KF827767, KF827511;** *Ctenium newtonii* var. *productum* Pilg., *White 842* (MO), Gabon, **KF827629, –, KF827703, KF827768, KF827512;** *Ctenium somalense* (Chiov.) Chiov.,*

Appendix S1. Continued.

Magogo 279 & Glover (FT), Kenya, **KF827630, KF827580, KF827704, KF827769, KF827513**; CYNODONTEAE: *Trichoneurinae*: *Trichoneura mollis* (Kunth) Ekman, *Napper 550* (US), Kenya, **KF827686, -, KF827748, -, KF827565**; *Trichoneura mollis* (Kunth) Ekman, *Bogdan 4173* (US), Kenya, **KF827685, -, -, KF827564**; *Trichoneura elegans* Swallen, *Lundell 15030* (US), U.S.A., **KF827675, KF827604, KF827740, KF827807, KF827553**; *Trichoneura elegans* Swallen, *Silveus 812* (US), U.S.A., **KF827676, KF827606, KF827741, KF827808, KF827555**; *Trichoneura elegans* Swallen, *Silveus 7312* (US), U.S.A., -, **KF827605, -, -, KF827554**; *Trichoneura eleusinoides* (Rendle) Ekman, *Oliver 6696*, Muller & Steenkamp (US), South Africa, **KF827678, KF827608, -, -, KF827557**; *Trichoneura eleusinoides* (Rendle) Ekman, *Seydel 448* (US), South Africa, GU359988, GU359522, GU360277, GU360705, GU359135; *Trichoneura eleusinoides* subsp. *limpopoensis* L.Fish, *Davidse 5859* (US), South Africa, **KF827677, KF827607, -, KF827809, KF827556**; *Trichoneura eleusinoides* subsp. *limpopoensis* L.Fish, *Pienaar 394* (MO), South Africa, **KF827679, -, KF827742, KF827810, KF827558**; *Trichoneura grandiglumis* (Nees) Ekman, *Reihmer 6040* (US), Namibia, **KF827680, KF827609, KF827743, KF827743, KF827811, KF827559**; *Trichoneura grandiglumis* (Nees) Ekman, *Smook 7068* (US), South Africa, **KF827682, KF827610, KF827745, KF827812, KF827561**; *Trichoneura grandiglumis* (Nees) Ekman, *Smook 4896* (MO), South Africa, **KF827681, -, KF827744, -, KF827560**; *Trichoneura lindleyana* (Kunth) Ekman, *Bentley 319* (US), Galapagos Islands, **KF827683, KF827611, KF827746, KF827813, KF827562**; *Trichoneura lindleyana* (Kunth) Ekman, *Howel 9435* (US), Galapagos Islands, **KF827684, KF827612, KF827747, KF827814, KF827563**; *Trichoneura weberbaueri* Pilg., *Peterson 15686 & Soreng* (US), Chile, GU359948, GU359565, GU360361, GU360668, GU359172; CYNODONTEAE: *Farragininae*: *Farrago racemosa* Clayton, *Peterson 23851*, *Soreng & Romaschenko* (US), Tanzania, **KF827634, KF827582, KF827706, KF827772, KF827516**; *Craspedorhachis africana* Benth., *Fisher 459 & Schweickerdt* (US), Zimbabwe, **KF827618, -, -, KF827755, KF827499**; *Craspedorhachis africana* Benth., *Fisher 504 & Schweickerdt* (US), Zimbabwe, **KF827619, -, -, KF827756, KF827500**; *Craspedorhachis africana* Benth., *Laegaard 16192* (US), Zimbabwe, **KF827620, KF827571, KF827693, KF827757, KF827757, KF827501**; *Craspedorhachis africana* Benth., *Litt 125* (US), Zimbabwe, **KF827621, KF827572, KF827694, KF827758, KF827502**; *Craspedorhachis africana* Benth., *Schweickerdt 484* (US), Zimbabwe, **KF827622, KF827573, KF827695, KF827759, KF827503**; *Craspedorhachis rhodesiana* Rendle, *Strohbach 5699* (US), Namibia, **KF827623, KF827574, KF827696, KF827760, KF827504**; *Craspedorhachis rhodesiana* Rendle, *Strohbach 5699-2* (US), Namibia, **KF827624, KF827575, KF827697, KF827761, KF827505**; *Craspedorhachis rhodesiana* Rendle, *Strohbach-3* (US), Namibia, **KF827625, KF827576, KF827698, KF827762, KF827506**; *Craspedorhachis rhodesiana* Rendle, *Strohbach 5699-9* (US), Namibia, **KF827626, KF827577, KF827699, KF827763, KF827507**; CYNODONTEAE: *Perotidinae*: *Perotis ornithocephala* (Hook.) P.M.Peterson, *Clayton 5582* (US), Sri Lanka, GU359878, -, -, GU360689, -, *Mosdenia leptostachys* (Ficalho & Hiern) Clayton, *Smook 1145* (US), South Africa, GU359968, -, -, -, *Mosdenia leptostachys* (Ficalho & Hiern) Clayton, *Schweickerdt 1542* (US), South Africa, GU359967, GU359458, GU360420, GU360681, GU359159; *Perotis hildebrandtii* Mez, *Peterson 23814*, *Soreng & Romaschenko* (US), Tanzania, **KF827667, KF827602, KF827732, KF827799, -, Perotis hildebrandtii Mez, *Renvoize 1784 & Abdallah* (US), Tanzania, GU360008, -, -, GU360709, -, *Perotis hordeiformis* Nees, *Soreng 5717*, *Peterson & Sun Hang* (US), China, GU359991, GU359520, GU360283, GU360708, GU359132; *Perotis indica* (L.) Kuntze, *Peterson 23872*, *Soreng & Romaschenko* (US), Tanzania, **KF827668, -, KF827733, KF827800, KF827545**; *Perotis indica* (L.) Kuntze, *Peterson 23880*, *Soreng & Romaschenko* (US), Tanzania, **KF827601, KF827734, KF827801, KF827546**; *Perotis leptopus* Pilg., *Sheuyanga 2008 & Lijo* (US), Namibia, **KF827670, KF827602, KF827735, KF827802, KF827547**; *Perotis patens* Gand., *Kruger 21750* (US), South Africa, -, -, **KF827737, KF827804, KF827549**; *Perotis patens* Gand., *Moss 11760* (US), South Africa, **KF827672, -, KF827738, -, -, Perotis patens Gand., *Godfrey 1661* (US), South Africa, GU359990, GU359521, GU360293, GU360707, GU359133; *Perotis patens* Gand., *Klaassen 1305* (US), Namibia, **KF827671, KF827603, KF827736, KF827803, KF827548**; *Perotis rara* R.Br., *Roc 1900* (US), Australia, GU359989, -, GU360285, GU360706, GU359134; *Perotis somalensis* Chiov., *Clemmi 305* (FT), Somalia, **KF827673, -, -, KF827550**; *Perotis vaginata* Hack., *Reekmans 10368* (US), Burundi, -, -, **KF827739, KF827805, KF827551**; *Perotis arenacea* (Judz.) P.M.Peterson, *Phillipson 4117* (MO), Madagascar, JQ345358, JQ345313, JQ345272, JQ345202; *Trigonochloa uniflora* (Hochst. ex A.Rich.) P.M.Peterson & N.Snow, *Greenway 14075* (MO), Tanzania, JQ345347, -, -, JQ345261, -, *Trigonochloa uniflora* (Hochst. ex A.Rich.) P.M.Peterson & N.Snow, *Snow 6978*, *Burgoyne & Gumbi* (MO), South Africa, JQ345348, -, -, JQ345192; CYNODONTEAE: *Gymnopogoninae*: *Bewisia biflora* (Hack.) Gooss., *Davidse 6471*, *Simon, Drummond & Bennett* (US), Rhodesia (Zimbabwe), GU359858, -, GU360294, GU360564, GU359274; *Bewisia biflora* (Hack.) Gooss., *Peterson 23905*, *Soreng & Romaschenko* (US), Tanzania, **KF827617, KF827570, KF827692, KF827754, KF827498**; *Dignathia gracilis* Stapf, *Greenway 10449* (US), Kenya, **KF827631, -, -, Dignathia hirtella Stapf, *Barkhadle 353* (FT), Somalia, **KF827632, KF827581, KF827705, KF827770, KF827514**; *Dignathia hirtella* Stapf, *McCallum Webster 5251* (US), Kenya, -, GU359368, GU360481, GU360490, GU359316; *Dignathia hirtella* Stapf, *Maggi 353*, *Tardelli & Bavazzano* (FT), Somalia, **KF827633, -, -, KF827771, KF827515**; *Dignathia villosa* C.E.Hubb., *Ellis 204* (US), Ethiopia, GU359820, GU359367, GU360480, GU360519, -, *Gymnopogon ambiguus* (Michx.) Britton, *Sterns & Poggenb., Becker 1488* (MO), U.S.A., **KF827642, KF827585, KF827714, KF827777, KF827525**; *Gymnopogon ambiguus* (Michx.) Britton, *Sterns & Poggenb., Nelson 1392* (US), U.S.A., **KF827643, KF827586, KF827715, KF827778, KF827526**; *Gymnopogon ambiguus* (Michx.) Britton, *Sterns & Poggenb., Thomas 168039* (BRY), U.S.A., **KF827587, KF827716, KF827779, KF827527**; *Gymnopogon aristiglumis* Hitchc., *Calderon 949* (US), El Salvador, **KF827645, -, -, KF827780, KF827528**; *Gymnopogon spicatus* (Spreng.) Kuntze, *Quarin 4144*, *Urbani, Martinez & Kraemer* (US), Argentina, **KF827654, KF827590, KF827720, KF827786, KF827533**; *Gymnopogon brevifolius* Trin., *Hill 15844* (US), U.S.A., **KF827646, KF827588, KF827717, KF827781, KF827529**; *Gymnopogon brevifolius* Trin., *Peterson 24437*, *Romaschenko & Knapp* (US), Mexico, **KF827647, KF827589, KF827718, KF827782, KF827530**; *Gymnopogon burchellii* (Munro ex Döll) Ekman, *Swallen 8524* (US), Brazil, **KF827649, -, -, -, Gymnopogon chapmanianus Hitchc., *Anderson 19657*, U.S.A., *Gymnopogon chapmanianus*, *Anderson 19657* (US), U.S.A., **KF827650, -, -, KF827784, -, Gymnopogon floridanus Swallen, *Kral 51634* (US), U.S.A., **KF827651, -, -, -, Gymnopogon foliosus (Willd.) Nees, *Guillesspie 752*, *Tiwari & Lall*, Guyana, **KF827652, -, -, -, Gymnopogon brevisetus (Hack.) J.P.Sm., *Nee 37732* (MO), Bolivia, **KF827648, -, KF827719, KF827783, KF827531**; *Gymnopogon grandiflorus* Roseng., B.R.Arrill. & Izag., *Peterson 16642 & Refulio-Rodriguez* (US), Peru, GU359816, GU359436, GU360383, GU360581, GU359200; *Gymnopogon legrandii* Roseng., B.R.Arrill. & Izag., *Carrasco 6293* (US), Uruguay, **KF827653, -, -, KF827785, KF827532**; *Gymnopogon spicatus* (Spreng.) Kuntze, *Renvoize 3677* (US), Argentina, **KF827655, -, -, KF827787, KF827534**; *Gymnopogon swallenii* (syn *G.legrandii*) J.P.Sm., *Irwin 8507*, *Jouga & Reis des Santos* (US), Brazil, **KF827656, KF827591, KF827721, KF827788, KF827535**; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Bidgood 50038*, *Darbyshive, Hoensklaar, Leliyo, Sanchez-Ken & Vollesen* (MO), Tanzania, **KF827657, KF827592, KF827722, KF827789, KF827536**; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Mboya 565* (MO), Tanzania, **KF827658, KF827593, KF827723, KF827790, KF827537**; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Peterson 23863*, *Soreng & Romaschenko* (US), Tanzania, **KF827659, KF827594, KF827724, KF827791, KF827538**; *Leptocarydion vulpiastrum* (De Not.) Stapf, *Peterson 24238*, *Soreng & Romaschenko* (US), Tanzania, **KF827660, KF827595, KF827725, KF827792, KF827539**; *Leptothrium rigidum* Kunth, *Davidse 3281* (MO), Jamaica, **KF827662, KF827596, KF827727, KF827794, KF827541**; *Leptothrium inermis* (Chiov.) P.M.Peterson, *Hemming 3416* (FT), Somalia, **KF827661, -, KF827726, KF827793, KF827540**; *Leptothrium senegalense* (Kunth) Clayton, *Belsky 336* (MO), Kenya, **KF827663, KF827597, KF827728, KF827795, KF827542**; *Leptothrium senegalense* (Kunth) Clayton, *Laegaard 17937 & Traore* (US), Senegal, **KF827664, -, KF827729, KF827796, -, Leptothrium senegalense (Kunth) Clayton, *Peterson 24196*, *Soreng & Romaschenko* (US), Tanzania, **KF827665, KF827598, KF827730, KF827797, KF827543**; *Leptothrium senegalense* (Kunth) Clayton, *Peterson 24239*, *Soreng & Romaschenko* (US), Tanzania, **KF827666, KF827599, KF827731, KF827798, KF827544**; *Lophacme digitata* Stapf, *Smook 1453* (MO), South Africa, JQ345354, -, JQ345309, JQ345267, JQ345197.****************