

A PHYLOGENY OF THE HUBBARDODCHLOINAE INCLUDING TETRACHAETE (CYNODONTEAE: CHLORIDOIDEAE: POACEAE)

PAUL M. PETERSON AND KONSTANTIN ROMASCHENKO

Department of Botany
National Museum of Natural History
Smithsonian Institution
Washington, D.C. 20013-7012
peterson@si.edu; romashchenkok@si.edu

YOLANDA HERRERA ARRIETA

Instituto Politécnico Nacional
CIIDIR Unidad Durango-COFAA
Durango, C.P. 34220, México
yherrera@ipn.mx

ABSTRACT

The phylogeny of subtribe Hubbardochloinae is revisited, here with the inclusion of the monotypic genus *Tetrachaete*, based on a molecular DNA analysis using *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS markers. *Tetrachaete elionurooides* is aligned within the Hubbardochloinae and is sister to *Dignathia*. The biogeography of the Hubbardochloinae is discussed, its origin likely in Africa or temperate Asia.

In a previous molecular DNA phylogeny (Peterson et al. 2016), the subtribe Hubbardochloinae [Auquier [*Bewsia* Gooss., *Dignathia* Stapf, *Gymnopogon* P. Beauv., *Hubbardochloa* Auquier, *Leptocarydion* Hochst. ex Stapf, *Leptothrium* Kunth, and *Lophacme* Stapf] was found in a clade with moderate support (BS = 75, PP = 1.00) sister to the Farragininae P.M. Peterson et al. In the present study, *Tetrachaete elionurooides* Chiov. is included in a phylogenetic analysis (using *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS DNA markers) in order to test its relationships within the Cynodonteae with heavy sampling of species in the supersubtribe Gouiniiodinae P.M. Peterson & Romasch.

Chiovenda (1903) described *Tetrachaete* Chiov. with a single species, *T. elionurooides* Chiov. He characterized it as being a dwarf, delicate, xerophilous annual with short leaf blades and greatly amplified (inflated) sheaths partially enclosing short inflorescences, and resembling slender forms of *Elionurus royleanus* Nees ex A. Rich. In addition to the above characters, *Tetrachaete* has narrow, spiciform inflorescences with short racemose branches bearing two sessile, contiguous 1-flowered spikelets, each with two bristle-like glumes, and a coriaceous, gibbous, 3-veined, and short-awned lemma (Clayton et al. 2006). Initially, *Tetrachaete* was placed in the Zoysieae Benth. but was thought not to resemble any current members (Chiovenda 1903).

MATERIALS AND METHODS

Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2010, 2014a, b, 2015a, b, 2016). We used Geneious Prime 2020 (Kearse et al. 2012) for contig assembly of bidirectional sequences of *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS regions, and Muscle (Edgar 2004) to align consensus sequences and adjust the final alignment. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModeltest (Posada 2008) and applied maximum-likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined data sets were partitioned in accordance with the number of markers used. Nucleotide substitution models selected by Akaike's Information Criterion, as

implemented in jModelTest v.0.1.1, were specified for each partition. The ML analysis was conducted with GARLI 0.951 (Zwickl 2006). The ML bootstrap analysis used 1000 replicates with 10 random addition sequences per replicate. The tree file from the ML result was read into PAUP where the majority-rule consensus tree was constructed. Bayesian posterior probabilities (PP) were estimated using a parallel version of the MrBayes v3.2.7 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis was initiated with random starting trees and was initially run for four million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences 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.

RESULTS AND DISCUSSION

Three new sequences from two species are reported in GenBank, along with all other species included in this study (Appendix 1). Total aligned characters for individual regions and other parameters are noted in Table 1. The resulting plastid and ITS topologies were inspected for conflicting nodes, and given that none were found, the plastid and ITS sequences were combined.

The ML tree from the combined plastid and ITS regions (Fig. 1) is well resolved (posterior probabilities identified in the Bayesian analysis are included on the ML tree, and most clades include a PP = 1), with strong support (BS = 100) for the following clades: the **Cteniinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus, **Farragininae** P.M. Peterson, Romasch. & Y. Herrera with two genera, **Gouiniinae** P.M. Peterson & Columbus with five genera, **Hubbardochloinae** Auquier with eight genera, **Perotidinae** P.M. Peterson, Romasch. & Y. Herrera with three genera, **Trichoneurinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus, and the **Zaqiqahinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus. These seven subtribes form the Gouiniodinae (PP = 1, BS = 89) previously delimited in Peterson et al. (2014a; 2016).

Tetrachaete elionurooides is clearly aligned within the Hubbardochloinae and is sister to three species of *Dignathia* (PP = 0.96, BS = 73). *Tetrachaete* and *Dignathia* share a cylindrical, spiciform inflorescence with each branch bearing 1 or 2 spikelets, glumes longer than the floret, coriaceous and gibbous 3-veined lemmas that bare an awn or mucro (Clayton & Renvoize 1986; Clayton et al. 2006). *Tetrachaete elionurooides* has recently been classified in the subtribe Unioliinae, tribe Eragrostideae (Soreng et al. 2015, 2017) — the present study is the first to include it within a molecular DNA study. Even though Clayton (1973) previously included *Tetrachaete* within the Zoysieae or Zoysiinae Benth. (Clayton & Renvoize 1986), inclusion within the Unioliinae by Soreng et al. (2015, 2017) probably was a result of confusion with molecular reports for *Tetrachne* Nees, a genus with a strikingly similar orthography. The circumscription of the Zoysieae in the 20th century has changed considerably since Columbus et al. (2007) interpreted it to include the Sporobolinae Benth. and the Zoysiinae sensu stricto with only *Urochondra* C.E. Hubb. and *Zoysia* Willd.

In our new cladogram (Fig. 1) the *Tetrachaete–Dignathia* clade is sister to *Leptothrium*, and together they are sister to remaining taxa in the Hubbardochloinae consisting of *Leptocarydion* (basal) sister to the *Bewsia* (*Hubbardochloa*–*Lophacme*) + *Gymnopogon*. This topology is similar to those of earlier studies, and again, *Hubbardochloa* is a weakly supported (PP = 0.95, BS = 69) sister to *Lophacme* (Peterson et al. 2016). This is perhaps a consequence of our data set since we have only ITS sequences for *Hubbardochloa*, but we have additional evidence from At103 sequences (Peterson & Romaschenko, unpublished) that support their union.

Table 1. Characteristics of the five DNA regions, *rps16-trnK*, *rps16* intron, *rpl32-trnL*, *ndhA* intron, and ITS, and parameters used in Bayesian analyses indicated by Akaike Information Criterion.

Characteristic	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	Combined plastid data	ITS	Overall
Total aligned characters	954	989	998	1224	4165	822	4987
Number of sequences	77	75	86	63	301	83	386
Likelihood score (-lnL)	4747.48	4160.57	5081.98	5192.84		13353.53	
Number of substitution types	6	6	6	6		6	
Model for among-sites rate variation	gamma	gamma	gamma	gamma		gamma	
Substitution rates	1.08484	1.05191	0.95937	1.41777		0.93969	
	2.63283	1.18636	1.84326	2.65062		2.86085	
	0.38677	0.28231	0.33665	0.50658		1.70535	
	1.69488	1.35625	1.64568	2.00718		0.65184	
	2.53685	1.50278	1.35965	2.76826		4.95421	
	1.00000	1.00000	1.00000	1.00000		1.00000	
Character state frequencies	0.31138	0.39017	0.36487	0.36803		0.25255	
	0.13354	0.11028	0.13373	0.13454		0.21184	
	0.13695	0.16498	0.12286	0.14589		0.24684	
	0.39348	0.33271	0.36497	0.35436		0.30716	
Proportion of invariable sites	0.12125	0.28284	0.19469	0.29151		0.26061	
Gamma shape parameter (α)	1.50178	1.12559	1.04856	0.97096		1.02378	

Like *Tetrachaete elionurooides*, the Hubbardochloinae probably originated in Africa, since most species of *Dignathia* and *Leptothrium* (sister to the *Dignathia-Tetrachaete* clade in Fig. 1) are distributed in Africa or temperate Asia (Clayton & Renvoize 1986; Clayton et al. 2006). The Gouiniodinae also probably originated in Africa or Asia, since *Zaqiqah* P.M. Peterson & Romasch. (basal and sister to all other genera in the supersubtribe, see Fig. 1) occurs in Ethiopia, Saudi Arabia, Somalia, Socotra, and Yemen (Peterson et al. 2016). Only *Gymnopogon* with 14 species is composed entirely of western hemisphere species from North and South America, whereas the other seven Hubbardochloinae genera include some species with an African distribution (Peterson et al. 2016; Soreng et al. 2017).

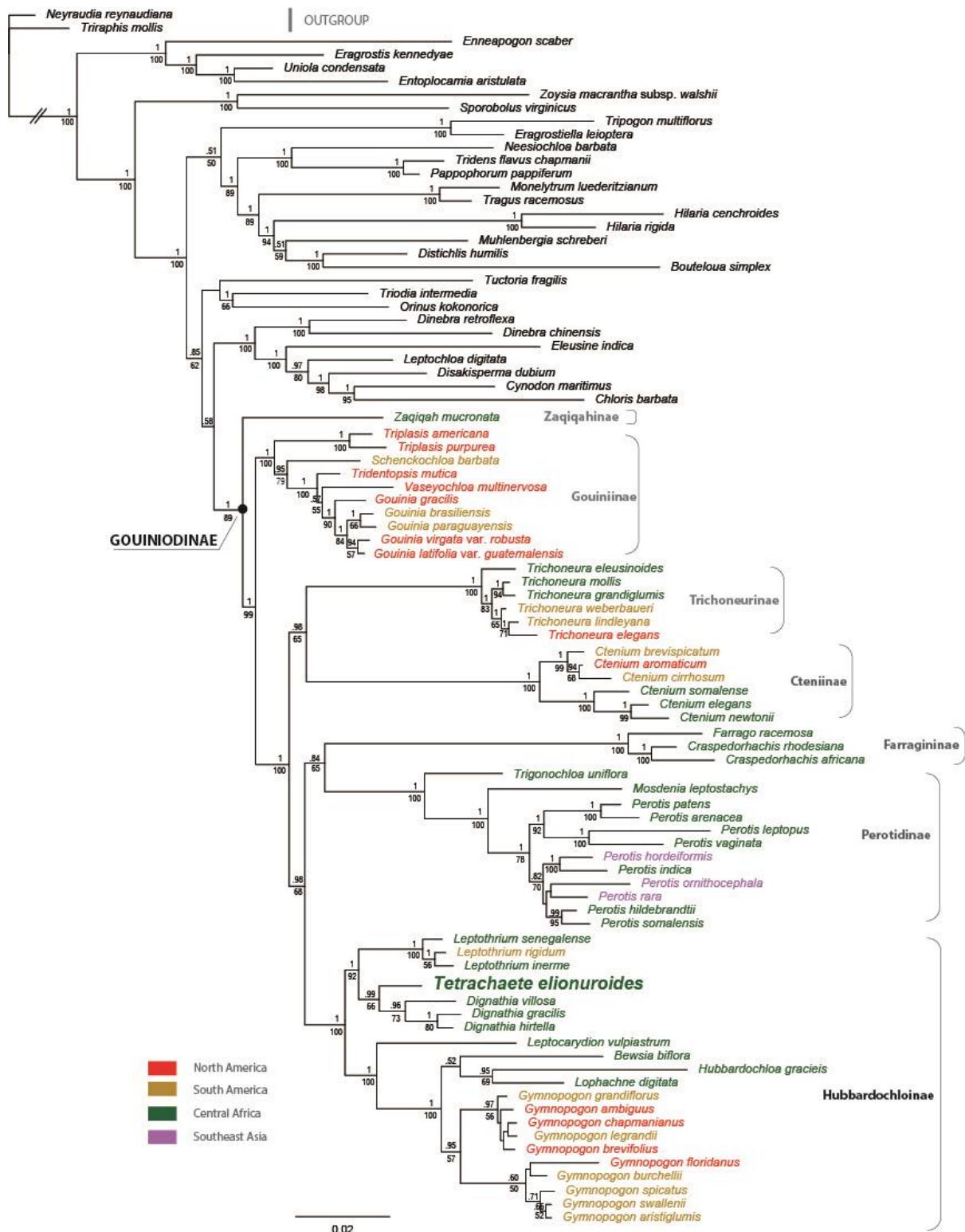


Figure 1. Maximum-likelihood tree inferred from combined plastid (*ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK* and ITS sequences. Numbers above branches are posterior probabilities; numbers below branches are bootstrap values; scale bar = 2%.

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LITERATURE CITED

- Chiovenda, E. 1903. Fam. Graminaceae (2). In R. Pirotta (ed.). Flora della Colonia Eritrea. Annuario Reale Ist. Bot. Roma 8(1): 21–70.
- Clayton, W.D. 1973. The tribe Zoysieae Miq. Studies in the Gramineae: XXXII. Kew Bull. 28: 37–48.
- Clayton, W.D. and S.A. Renvoize. 1986. Genera Graminum: Grasses of the World. Kew Bull. Add.. Ser. 13: 1–389.
- Clayton, W.D., M.S. Vorontsova, K.T. Harman, and H. Williamson. 2006 onwards. GrassBase – The Online World Grass Flora. <<http://www.kew.org/data/grasses-db.html>> Accessed 14 Aug 2020.
- Columbus, J., R. Cerros-Tlatilpa, M. Kinney, M. Siqueiros-Delgado, H.L. Bell, M. Griffith, and N. Refulio Rodríguez. 2007. Phylogenetics of Chloridoideae (Gramineae): A preliminary study based on the nuclear ribosomal internal transcribed spacer and chloroplast *trnL-F* sequences. Aliso 23: 565–579.
- Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32: 1792–1797.
- Huelsenbeck, J.P. and F.R. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17: 754–755.
- Kearse, M., R. Moi, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Mentjies, and A. Drummond. 2012. GeneiousBasic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649.
- Peterson, P.M., K. Romaschenko and Y. Herrera Arrieta. 2014a. A molecular phylogeny and classification of the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae (Poaceae: Chloridoideae: Cynodonteae). Taxon 63: 275–286.
- Peterson, P.M., K. Romaschenko, and Y. Herrera Arrieta. 2015a. A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae). Taxon 64: 445–467.
- Peterson, P.M., K. Romaschenko, and Y. Herrera Arrieta. 2015b. Phylogeny and subgeneric classification of *Bouteloua* with a new species, *B. herrera-arrietae* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae). J. Syst. Evol. 53: 351–366.
- Peterson, P.M., K. Romaschenko and Y. Herrera Arrieta. 2016. 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 Zaqqahinae; and a subgeneric classification of *Distichlis*. Taxon 65: 1263–1287.
- Peterson, P.M., K. Romaschenko, and G. Johnson. 2010. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Molec. Phylogen. Evol. 55: 580–598.
- Peterson, P.M., K. Romaschenko, and R.J. Soreng. 2014b. A laboratory guide for generating DNA barcodes in grasses: A case study of *Leptochloa* s.l. (Poaceae: Chloridoideae). Webbia 69: 1–12.
- Posada, D. 2008. jModelTest model averaging. Molec. Biol. Evol. 25: 1253–1256.
- Romaschenko, K., P.M. Peterson, R.J. Soreng, N. Garcia-Jacas, O. Futorna, and A. Susanna. 2012. Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. Taxon 61: 18–44.

- Ronquist, F.R. and J.P. Huelsenbeck. 2003. Mr Bayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1575–1574.
- Soreng, R.J., P.M. Peterson, K. Romaschenko, G. Davidse, J.K. Teisher, L.G. Clark, P. Barberá, L.J. Gillespie, and F.O. Zuloaga. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. *J. Syst. Evol.* 55: 259–290.
- Soreng, R.J., P.M. Peterson, K. Romaschenko, F.O. Zuloaga, E.J. Judziewicz, T.S. Filgueiras, J.I. Davis, and O. Morrone. 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). *J. Syst. Evol.* 53: 117–137.
- Zwickl, D.J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Univ. of Texas, Austin.

Appendix 1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16-trnK*, *rps16 intron*, *rpl32-trnL*, *ndhA intron*, and ITS regions (**bold** indicates new accession); a dash (–) indicates missing data.

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16 intron</i>	<i>rpl32-trnL</i>	<i>ndhA intron</i>	ITS
<i>Bewsia biflora</i> (Hack.) Gooss.	Peterson 23905, Soreng, Romaschenko & Abeid (US)	Tanzania, Ruvuma	KF827754	KF827692	KF827617	KF827570	KF827498
<i>Bouteloua simplex</i> Lag.	Peterson 21289, Saarela & Flores Villegas (US)	Mexico, Zacatecas	GU360607	GU360297	GU359834	GU359406	GU359231
<i>Chloris barbata</i> Sw.	Peterson 22255& Saarela (US)	Mexico, Sinaloa	GU360514	GU360435	GU359873	GU359377	GU359320
<i>Craspedorhachis africana</i> Benth.	Laegaard 16192 (US)	Zimbabwe	KF827757	KF827693	KF827620	KF827571	KF827501
<i>Craspedorhachis rhodesiana</i> Rendle	Strohbach 5699 (US)	Namibia	KF827760	KF827696	KF827623	KF827574	KF827504
<i>Ctenium aromaticum</i> (Walter) Alph. Wood	Peterson 14235, Weakley & LeBlond (US)	USA, North Carolina	–	–	GU359839	–	GU359240
<i>Ctenium brevispicatum</i> J.G.Sm.	Filgueiras 3251 & Oliviera (US)	Brazil, Goiás	KF827764	KF827700	KF827627	KF827578	KF827508
<i>Ctenium cirrhosum</i> (Nees) Kunth	Grola 1452 & Filgueiras (US)	Brazil	GU360597	GU360353	GU359838	–	GU359241
<i>Ctenium elegans</i> Kunth	Laegaard 18359, Mipro & Sobere (US)	Burkina Faso	KF827765	KF827701	–	–	KF827509
<i>Ctenium newtonii</i> Hack.	Laegaard 18327, Mipro & Sobere (US)	Burkina Faso, Nazinga Park	KF827767	KF827702	KF827628	KF827579	KF827511
<i>Ctenium somalense</i> (Chiov.) Chiov.	Magogo 279 & Glover (FT)	Kenya, Kwale	KF827769	KF827704	KF827630	KF827580	KF827513
<i>Cynodon maritimus</i> Kunth	Howard 10214 & Howard (US)	Bahamas, Bimini	GU360591	GU360448	GU359889	GU359365	GU359248
<i>Dignathia gracilis</i> Stapf	Greenway 10449 (US)	Kenya	–	–	KF827631	–	–

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Dignathia hirtella</i> Stapf	Barkhadle 353 (FT)	Somalia	KF827770	KF827705	KF827632	KF827581	KF827514
<i>Dignathia villosa</i> C.E. Hubb.	Ellis 204 (US)	Ethiopia	GU360519	GU360480	GU359820	GU359367	—
<i>Dinebra chinensis</i> (L.) P. M. Peterson & N. Snow	Snow 6909 (MO)	Botswana	JQ345240	—	JQ345325	—	JQ345171
<i>Dinebra retroflexa</i> (Vahl) Panz.	Ndegwa 610 (US)	Kenya	GU360503	GU360479	GU359778	GU359355	GU359332
<i>Disakisperma dubium</i> (Kunth) P. M. Peterson & N. Snow	Peterson 22334 & Saarela (US)	Mexico, Oaxaca	GU360695	GU360416	GU359811	GU359442	GU359145
<i>Distichlis humilis</i> Phil.	Peterson 19362, Soreng, Salariato & Panizza (US)	Argentina, Catamarca	GU360502	GU360478	GU359835	GU359430	GU359333
<i>Eleusine indica</i> (L.) Gaetn.	Peterson 21362, Saarela & Flores Villegas (US)	Mexico, Mexico	GU360496	GU360472	GU359797	GU359473	GU359338
<i>Enneapogon scaber</i> Lehm.	Sachse 8 (MO)	South Africa, Western Cape	JQ345237	JQ345279	JQ345322	JQ345208	JQ345168
<i>Entoplocamia aristulata</i> (Hack. & Rendle) Stapf	Seydel 187 (US)	South Africa	GU360492	GU360468	GU359793	GU359469	GU359342
<i>Eragrostiella leioptera</i> (Stapf) Bor	Chand 7961 (US)	India	GU360529	JQ345280	GU359827	GU359486	GU359305
<i>Eragrostis kennedyae</i> F.Turner	Latz 13486 (MO)	Australia	JQ345238	JQ345281	JQ345323	JQ345209	JQ345169
<i>Farrago racemosa</i> Clayton	Peterson 23851, Soreng, Romaschenko & Abeid (US)	Tanzania, Lindi	KF827772	KF827706	KF827634	KF827582	KF827516
<i>Gouinia brasiliensis</i> (S. Moore) Swallen	Nee 36355 (US)	Bolivia, Sta. Cruz	—	KF827707	KF827635	—	KF827517
<i>Gouinia gracilis</i> Ekman ex Swallen	Ekman s.n. (US)	Cuba, Oricute	KF827773	KF827708	KF827636	—	KF827518

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Gouinia latifolia</i> var. <i>guatemalensis</i> (Hack.) J.J. Ortíz	Beetle 918 (US)	Mexico, Yucatan	KX582969	KX582902	KF827637	KX582472	KF827519
<i>Gouinia paraguayensis</i> (Kuntze) Parodi	Peterson 11526 & Annable (US)	Argentina, San Juan	GU360504	GU360384	GU359817	GU359437	GU359314
<i>Gouinia virgata</i> var. <i>robusta</i> J.J. Ortíz	Reeder 4714 & Reeder (US)	Mexico, Zacatecas	KF827775	KF827710	KF827639	KF827584	KF827521
<i>Gymnopogon ambiguus</i> (Michx.) Britton, Sterns & Pogggenb.	Thomas 168039 (BRY)	USA	KF827779	KF827716	KF827644	KF827587	KF827527
<i>Gymnopogon aristiglumis</i> Hitchc.	Calderon 949 (US)	El Salvador	KF827780	–	KF827645	–	KF827528
<i>Gymnopogon brevifolius</i> Trin.	Hill 15844 (US)	USA	KF827781	KF827717	KF827646	KF827588	KF827529
<i>Gymnopogon burchellii</i> (Munro ex Döll) Ekman	Swallen 8524 (US)	Brazil	–	–	KF827649	–	–
<i>Gymnopogon chapmanianus</i> Hitchc.	Anderson 19657 (US)	USA	KF827784	–	KF827650	–	–
<i>Gymnopogon floridanus</i> Swallen	Kral 51634 (US)	USA	–	–	KF827651	–	–
<i>Gymnopogon grandiflorus</i> Roseng., B.R. Arill. & Izag.	Peterson 16642 & Refulio-Rodriguez (US)	Peru, Apurimac	GU360581	GU360383	GU359816	GU359436	GU359200
<i>Gymnopogon legrandii</i> Roseng., B.R. Arill. & Izag.	Carrasco 6293 (US)	Uruguay	KF827785	–	KF827653	–	KF827532
<i>Gymnopogon spicatus</i> (Spreng.) Kuntze	Quarin 4144, Urbani, Martinez & Kraemer (US)	Argentina	KF827786	KF827720	KF827654	KF827590	KF827533

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Gymnopogon swallenii</i> J.P. Sm.	Irwin 8507 (US)	Brazil	KF827788	KF827721	KF827656	KF827591	KF827535
<i>Hilaria cenchroides</i> Kunth	Peterson 22339 & Saarela (US)	Mexico, Oaxaca	GU360697	GU360380	GU359813	GU359424	GU359143
<i>Hilaria rigida</i> (Thurb.) Benth. ex Scribn.	Boyd 11566 (BRY)	USA	JQ345269	JQ345311	JQ345356	JQ345229	JQ345200
<i>Hubbardochloa gracilis</i> Auquier	Troupin s.n. (MO)	Rwanda	–	–	–	–	KX582379
<i>Leptocarydion vulpiastrum</i> (De Not.) Stapf	Peterson 24238, Soreng & Romaschenko (US)	Tanzania	KF827792	KF827725	KF827660	KF827595	KF827539
<i>Leptochloa digitata</i> (R.Br.) Domin	Risler 476 & Kerrigan (MO)	Australia, Northern Territory	JQ345246	JQ345289	JQ345331	JQ345213	JQ345178
<i>Leptothrium inermis</i> (Chiov.) P.M. Peterson	Hemming 3416 (FT)	Somalia	KF827793	KF827726	KF827661	–	KF827540
<i>Leptothrium rigidum</i> Kunth	Davidse 3281 (MO)	Jamaica, Parish.	KF827794	KF827727	KF827662	KF827596	KF827541
<i>Leptothrium senegalense</i> (Kunth) Clayton	Peterson 24239, Soreng & Romaschenko (US)	Tanzania	KF827798	KF827731	KF827666	KF827599	KF827544
<i>Lophacme digitata</i> Stapf	Smook 1453 (MO)	South Africa, Transvaal	JQ345267	JQ345309	JQ345354	–	JQ345197
<i>Monelytrum luederitzianum</i> Hack.	Smook 10031 (US)	South Africa	GU360682	GU360421	GU359969	GU359459	GU359158
<i>Mosdenia leptostachys</i> (Ficalho & Hiern) Clayton	Schweickerdt 1542 (US)	South Africa	GU360681	GU360420	GU359967	GU359458	GU359159
<i>Muhlenbergia schreberi</i> J.F. Gmel.	Peterson 19443, Soreng, Salariato & Panizza (US)	Argentina, Tucuman	GU360679	GU360404	GU359950	GU359456	GU359161

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Neesiochloa barbata</i> (Nees) Pilg.	Swallen 4491 (US)	Brazil	GU360724	GU360279	GU360005	–	GU359122
<i>Neyraudia reynaudiana</i> (Kunth) Keng ex Hitchcock	Soreng 5318, Peterson & Sun Hang (US)	China, Yunnan	–	GU360272	GU360003	GU359397	GU359124
<i>Orinus kokonorica</i> (K. S. Hao) Keng ex X. L. Yang	Soreng 5447, Peterson & Sun Hang (US)	China, Qinghai	GU360728	GU360270	GU359999	GU359399	GU359140
<i>Pappophorum pappiferum</i> (Lam.) Kuntze	Peterson 21689, Soreng, La Torre & Rojas Fox (US)	Peru, Ancash	GU360700	GU360276	GU359996	GU359402	GU359128
<i>Perotis arenacea</i> (Judz.) P.M. Peterson	Phillipson 4117 & Raharilala (MO)	Madagascar, Toliara	JQ345272	JQ345313	JQ345358	–	JQ345202
<i>Perotis hildebrandtii</i> Mez	Peterson 23814, Soreng & Romaschenko (US)	Tanzania	KF827799	KF827732	KF827667	KF827600	MW241083
<i>Perotis hordeiformis</i> Nees	Soreng 5717, Peterson & Sun Hang (US)	China, Sichuan	GU360708	GU360283	GU359991	GU359520	GU359132
<i>Perotis indica</i> (L.) Kuntze	Peterson 23880, Soreng & Romaschenko (US)	Tanzania	KF827801	KF827734	KF827669	KF827601	KF827546
<i>Perotis leptopus</i> Pilg.	Sheuyange & Lifo (US)	Namibia	KF827802	KF827735	KF827670	KF827602	KF827547
<i>Perotis ornithocephala</i> (Hook.) P.M. Peterson	Clayton 5582 (US)	Sri Lanka	GU360689	–	GU359878	–	–
<i>Perotis patens</i> Gand.	Godfrey 1661 (US)	South Africa	GU360707	GU360293	GU359990	GU359521	GU359133
<i>Perotis rara</i> R. Br.	Roc 1900 (US)	Australia	GU360706	GU360285	GU359989	–	GU359134
<i>Perotis somalensis</i> Chiov.	Clemmi 305 (FT)	Somalia, J. Hoose	–	–	KF827673	–	KF827550
<i>Perotis vaginata</i> Hack.	Reekmans 10368 (US)	Burundi	KF827805	KF827739	–	–	KF827551

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Schenckochloa barbata</i> (Hack.) J.J. Ortíz	Swallen 4690 (US)	Brazil, Natal	KF827806	–	KF827674	–	KF827552
<i>Sporobolus virginicus</i> (L.) Kunth	Peterson 15683 & Soreng (US)	Chile, Region I	GU360610	GU360362	GU359892	GU359502	GU359215
<i>Tetrachaete elionurooides</i> Chiov.	Tardelli 254 (FT)	Somalia, Ghedo	–	–	MW240441	–	MW241084
<i>Tragus berteronianus</i> Schult.	FLSP 457 (US)	Peru	GU360616	GU360370	GU359898	GU359503	GU359224
<i>Trichoneura elegans</i> Swallen	Lundell 15030 (US)	USA, Texas	KF827807	KF827740	KF827675	KF827604	KF827553
<i>Trichoneura eleusinoides</i> (Rendle) Ekman	Seydel 448 (US)	South Africa	GU360705	GU360277	GU359988	GU359522	GU359135
<i>Trichoneura grandiglumis</i> (Nees) Ekman	Smook 7068 (US)	South Africa	KF827812	KF827745	KF827682	KF827610	KF827561
<i>Trichoneura lindleyana</i> (Kunth) Ekman	Bentley 319 (US)	Ecuador, Galapagos Islands	KF827813	KF827746	KF827683	KF827611	KF827562
<i>Trichoneura mollis</i> (Kunth) Ekman	Napper 550 (US)	Kenya, Lukenya	–	KF827748	KF827686	–	KF827565
<i>Trichoneura weberbaueri</i> Pilg.	Peterson 15686 & Soreng (US)	Chile	GU360668	GU360361	GU359948	GU359565	GU359172
<i>Tridens flavus</i> var. <i>chapmanii</i> (Small) Shinners	McCauley 438 (MO)	USA, Missouri	KF827817	KF827751	KF827689	KF827615	KF827568
<i>Tridentopsis mutica</i> (Torr.) P.M. Peterson	Peterson 21997& Saarela (US)	Mexico, Chihuahua	GU360667	GU360321	GU359947	GU359557	GU359173
<i>Trigonochloa uniflora</i> (Hochst. ex A. Rich.) P.M.P. & N.Snow	Snow 6978, Burgoyne & Gumbi (MO)	South Africa, Kwazulu Natal	–	–	JQ345348	–	JQ345192
<i>Triodia intermedia</i> Cheel	Peterson 14384, Soreng & Rosenberg (US)	Australia, Western Australia	GU360661	GU360327	GU359941	GU359563	GU359179

Taxon	Voucher	Country	<i>rps16-trnK</i>	<i>rps16</i> intron	<i>rpl32-trnL</i>	<i>ndhA</i> intron	ITS
<i>Triplasis americana</i> P. Beauv.	Kral 12065 (MO)	USA, Georgia	KF827818	KF827752	KF827690	KF827616	KJ768887
<i>Triplasis purpurea</i> (Walter) Chapm.	Peterson 14238, Weakley & LeBlond (US)	USA, North Carolina	GU360656	GU360347	GU359921	GU359536	GU359184
<i>Tripogon multiflorus</i> Miré & H.Gillet	Spellenberg 7441 (MO)	Yemen, Ibb Governorate	JQ345274	JQ345315	JQ345360	JQ345232	JQ345204
<i>Triraphis mollis</i> R. Br.	Peterson 14344, Soreng & Rosenberg (US)	Australia, Western Australia	GU360669	GU360336	GU359933	GU359539	GU359187
<i>Tuctoria fragilis</i> (Swallen) Reeder	Reeder 7255 & Reeder (US)	Mexico	–	–	GU359929	–	GU359189
<i>Uniola condensata</i> Hitchc.	Peterson 9342 & Judziewicz (US)	Ecuador, Chimborazo	GU360649	GU360340	GU359927	GU359534	GU359191
<i>Vaseyochloa multinervosa</i> (Vasey) Hitchc.	Swallen 10041 (US)	USA, Texas	GU360646	GU360342	GU359925	GU359544	GU359193
<i>Zaqiqah mucronata</i> (Forssk.) P.M. Peterson & Romasch.	Spellenberg 7470 (MO)	Yemen, Hodeidah Governorate	KX582977	KX582909	KX582663	KX582476	KX582387
<i>Zoysia macrantha</i> subsp. <i>walshii</i> M.E. Nightingale	Loch 435 (US)	Australia	GU360642	GU360345	GU359922	GU359548	GU359197