WEBBIA Journal of Plant Taxonomy and Geography

Firenze University Press
https://oaj.fupress.net/index.php/webbia

OPEN ACCESS

Citation: Peterson P.M., Romanschenko K., Arrieta Herrera Y. (2025). A phylogeny of the Cotteinae (Poaceae, Chloridoideae, Eragrostideae). *Webbia. Journal of Plant Taxonomy and Geography* 80(2) Suppl.: 197-205. doi: 10.36253/jopt-19153

Received: July 16, 2025

Accepted: September 23, 2025

Published: November 17, 2025

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Competing Interests: The Author(s) declare(s) no conflict of interest.

Editor: Robert J. Soreng

ORCID
PMP: 0000-0001-9405-5528
KR: 0000-0002-7248-4193
YHA: 0000-0003-3814-6518

A phylogeny of the Cotteinae (Poaceae, Chloridoideae, Eragrostideae)

Paul M. Peterson[1,*], Konstantin Romaschenko[1], Yolanda Herrera Arrieta[2]

[1] *Department of Botany MRC-166, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA*
[2] *Instituto Politécnico Nacional, CIIDIR Unidad-Durango-COFAA, Durango, C.P. 34220, México*
*Corresponding author. Email: peterson@si.edu

Abstract. To investigate the evolutionary relationships among 23 species in the Cotteinae we generated a DNA sequence-derived phylogeny utilizing three plastid (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) regions and the nuclear ribosomal internal transcribed spacer (ITS) region. The Bayesian tree provides strong support for the monophyly of the Cotteinae and its four genera, in order of divergence: *Cottea*, the *Kaokochloa* + *Schmidtia* clade, and the *Enneapogon* clade. Since the Eragrostideae clearly evolved from African ancestors and *Kaokochloa*, *Schmidtia,* and *Enneapogon* all share species from Africa, we hypothesize the ancestral area of Cotteinae to be Africa. Within *Enneapogon* we recovered four major clades, the first two splits with species primarily from Africa and the third split containing a basal species from Africa/Asia/Europe sister to all species from Australia. The ancestral area of *Enneapogon* is Africa and based on our current sample the 13 species from Australia appear to be derived from a single dispersal event from an ancestor shared with *E. persicus*.

Keywords: classification, *Cottea*, *Enneapogon*, *Kaokochloa*, molecular phylogenetics, *Schmidtia*.

INTRODUCTION

The entanglement of *Enneapogon* Desv. ex P.Beauv. with *Pappophorum* Schreb. has existed for a long time and a good summary clarifying the early formulation of concepts was given in Burbidge (1941). Desvaux in Palisot de Beauvois (1812) first transferred four species to *Enneapogon*, formally placed in *Pappophorum,* and added one additional species, *E. desvauxii* P. Beauv.

Kunth (1929) reduced *Enneapogon* to a subgenus of *Pappophroum* in the tribe Pappophoreae Kunth, and then Trinius (1830) placed *Enneapogon* as a section of *Pappophorum*. Up until 1965 most agrostologists followed Desvaux in recognizing *Enneapogon* as a distinct genus within the Pappophoreae.

The subtribe Cotteinae Reeder was erected to emphasize morphological features (principally glumes and lemmas with many veins with some

of the veins extending into awns, embryonic leaf having overlapping margins, dumbbell-shaped siliceous cells, and bicellular microhairs with a slender usually much elongated basal cell) to separate species of *Cottea* Kunth, *Enneapogon*, *Kaokochloa* DeWinter, and *Schmidtia* Steud. ex J.A.Schmidt from *Pappophorum* (Reeder 1965). Whereas *Pappophorum* (subtr. Pappophorinae) includes species with single-veined glumes and lemmas with veins extending into awns, embryonic leaf with margins that meet but do not overlap, saddle- or double axe-shaped siliceous cells, and short-stalked eragrostoid-type bicellular microhairs (Reeder 1965; Reeder 2003). Historically, most grass classifications included these genera in the Pappophoreae (Stebbins and Crampton 1961; Clayton 1970; Peterson et al. 2001; Weiller and Lazarides 2005; Roodt-Wilding and Spies 2006; Cope 2007), although Clayton and Renvoize (1986) placed the Cotteinae as a synonym of the Pappophoreae, and it was not until molecular DNA sequence studies emerged that our modern concept of the Pappophorinae was formed, consisting of *Neesiochloa* Pilg., *Pappophorum*, and *Tridens* Roem. & Schult. s.s. realigned in the tribe Cynodonteae Dumort. (Peterson et al. 2010a; Reutemann et al. 2011; Peterson et al. 2016; Soreng et al. 2015, 2017, 2022). The subtribes Cotteinae, Eragrostidinae J. Presl (*Eragrostis* Wolf), and Uniolinae Clayton (*Entoplocamia* Stapf, *Fingerhuthia* Nees ex Lehm., *Tetrachne* Nees, and *Uniola* L.) are all members of the tribe Eragrostideae Stapf (Peterson et al. 2010a; Soreng et al. 2022).

Within the Cotteinae, *Enneapogon* is the largest genus with at least 26 species, one cosmopolitan (*E. desvauxii*, although not found in Australia), 15 are endemic to Australia, six are found in southern Africa, and at least six extend into Asia (Phillips 1995; Weiller and Lazarides 2005; Cope 2007; Fish et al. 2015; Clayton et al. 2016; Plants of the World Online 2025). *Schmidtia* with two species is found in Africa and Pakistan, *Kaokochloa* with a single species occurs in southern Africa and northwestern Namibia, and *Cottea* with a single species is found in North and South America (Phillips 1995; Cope 2007; Fish et al. 2015). The genera of the Cotteinae can be differentiated by their lemma shape and the number of awns emanating from the apex. *Cottea* and *Schmidtia* have lobed lemmas (irregularly so in *Cottea*) with the former having 7–11 awns and the latter having only five awns, whereas *Enneapogon* and *Kaokochloa* have unlobed lemmas with the former having nine awns and the latter having two lateral awns with one or two additional central awns (never more than four awns total) [Renvoize 1988; Phillips 1995; Cope 2007; Fish et al. 2015; Clayton et al. 2016]. The spikelets of *Cottea* also disarticulate above the glumes and between the florets while all other members of the subtribe have spikelets that disarticulate above the glumes but not between the florets (Reeder 2003).

In a recent nuclear and plastid DNA-derived phylogeny of the entire grass family the Cotteinae is sister to remaining members of the Eragrostideae, and the Cotteinae has the following structure: (Cottea (*Kaokochloa* + *Schmidtia*) *Enneapogon*)) [Group Phylogeny Working Group (GPWG) 2024]. Another previous DNA-derived phylogeny indicated that *Schmidtia* was paraphyletic with species of *Enneapogon* forming a monophyletic clade nested within *Schmidtia* (based on ITS) or included in a polytomy (based on the plastid *trnL-F* marker) [Reutemann et al. 2011]. In our study we provide the latest estimate of the phylogeny within the Cotteinae by analyzing three markers from the plastid genome (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) and one from the nuclear genome (ITS). In comparison with the Reutemann et al. (2011) and GPWG (2024) studies we increase the sample size of *Enneapogon* from four (nuclear) and five samples (plastid) to 19 species.

MATERIAL AND METHODS

Taxon sampling

We sampled 64 individuals, representing 50 total species, and 19 (19/26 = 73%) species of *Enneapogon*, two (2/2 = 100%) species of *Schmidtia*, one species (1/1 = 100%) of *Cottea*, and one (1/1 = 100%) species of *Kaokochloa*. A complete list of taxa including authorities, voucher information, and GenBank numbers is presented in Appendix 1. A few of these DNA sequences were previously published in GenBank. We submitted 128 new sequences to GenBank, 102 of these representing *Enneapogon*, 16 in *Schmidtia*, eight in *Fingerhuthia,* and two in *Kaokochloa*.

We designed our study to characterize relationships among species of Cotteinae (*Cottea*, *Enneapogon*, *Kaokochloa,* and *Schmidtia*) and including outgroups from the Eragrostidinae J.Presl [*Eragrostis conrathii* (Hack.) S.M.Phillips, *E. dielsii* Pilg., *E. tincta* S.M.Phillips, and *E. xerophila* Domin]; Uniolinae [*Entoplocamia aristulata* (Hack. & Rendle) Stapf, *Fingerhuthia africana* Nees es Lehm., *F. sesleriiformis* Nees, *Tetrachne dregei* Nees, and *Uniola paniculata* L.]; Cynodonteae Dumort. [*Chloris barbata* Sw., *Cynodon plectostachyus* (K. Schum.) Pilg., *Eleusine indica* (L.) Gaertn., *Gymnopogon grandiflorus* Roseng., B.R.Arill. & Izag., *Halopyrum mucronatum* (L.) Stapf, *Leptothrium rigidum* Kunth, *Oropetium capense* Stapf, *Pappophorum bicolor* E.Fourn., *P. casepitosum* R.E.Fr., *P. pappiferum* (Lam.) Kuntze, *P. philippianum* Parodi, *P.*

vaginatum Buckley, and *Tripogon chinensis* Hack.]; and Zoysieae Benth. [*Sporobolus pyramidatus* (Lam.) Hitchc., *S. virginicus* (L.) Kunth, and *Zoysia macrantha* Desv.]; and Triraphideae P.M.Peterson (*Triraphis mollis* R.Br. and *T. ramosissima* Hack.) [Soreng et al. 2022].

Phylogenetic methods

All procedures related to the sequencing of the plastid and ITS regions were performed in the Laboratory of Analytical Biology at the Smithsonian Institution. Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2010a, 2010b, 2012, 2014, 2015a, 2015b, 2016). Geneious Prime v.2020.1.4 (Kearse et al. 2012) was utilized for contig assembly of bidirectional sequences of *rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer, and ITS regions; and Muscle (Edgar 2004) to align consensus sequences and adjust the final alignment. The Bayesian trees were constructed with MrBayes v3.2.7 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012).

The evolutionary model parameters for each region were estimated with GARLI 2.0 (Zwickl, 2006) (Table 1) and used as priors in Bayesian analysis. The combined data set was split into four partitions containing the ITS, *rpL32-trnL*, *rps16-trnK*, and *rps16* intron sequences. Bayesian analysis was initiated with random starting trees and was run for four million generations with every 1000th iteration being sampled. Upon completion of the search, the variance of split sequences was less than 0.01 and the potential scale reduction factor was close or equal to 1.0 indicating convergence of the chains (Huelsenbeck and Ronquist 2001). The search was monitored with Tracer v1.7.1 (Rambaut et al. 2018). The effective sample size (ESS) value was greater than 100, and 25% of the sampled values were discarded. All compatible branches were saved. Posterior probabilities (PP) of ≥0.95 indicated a credible interval of probability.

The parsimony bootstrap analysis (Felsenstein 1985) was performed using program IQ-Tree 3.0.1 implementing ultrafast bootstrap approximation (with 10000 bootstrap replicates) to assess branch supports (Minh et al. 2013; Hoang et al. 2018). Bootstrap values (BS) of ≥95% were interpreted as strong support.

RESULTS

Phylogenetic analyses

One hundred twenty-eight sequences (128/246 = 52%) in our study are newly reported in GenBank and 44% (108/246) are previously published sequences (Appendix 1)

Table 1. Characteristics of the four regions, *rps16-trnK, rps16* intron*, rpL32-trnL*, ITS, and parameters used in phylogenetic analysis, indicated by Akaike Information Criterion (AIC).

	rps16-trnK	*rps16 intron*	*rpL32-trnL*	Combined plastid data	*ITS*	Overall
Total aligned characters	1020	1019	1062	3101	745	3846
Number of sequences (success)	61	60	63	184	62	246
	(95.3%)	(93.8 %)	(98.4%)	(95.8%)	(96.9%)	(96.1%)
Number of new sequences (ratio)	32	31	33	96	32	128
	(52.5%)	(51.7%)	(52.4%)	(52.2%)	(51.6%)	(52.0%)
Likelihood score (-lnL)	3303.89	2907.35	3186.56		7719.76	
Number of substitution types	4	4	4	-	4	-
Model for among-sites rate variation	gamma	gamma	gamma	-	Invar+Gamma	-
Substitution rates	2.0469	1.0000	1.9637	-	0.9023	-
	4.1996	1.5457	2.6823		2.1809	
	1.0000	0.4216	1.0000		1.8644	
	2.0469	0.4216	1.9637		0.4373	
	4.1996	1.5457	2.6823		4.4558	
	1.0000	1.0000	1.0000		1.0000	
Character state frequencies	0.2893	0.3757	0.3438	-	0.2170	-
	0.1526	0.1334	0.1487		0.2948	
	0.1585	0.1855	0.1430		0.2867	
	0.3995	0.3054	0.3645		0.2016	
Proportion of invariable sites	0.7695	0.8365	0.6556	-	0.3163	-
Substitution model	TPM3u+F+G4	K3Pu+F+G4	TPM3u+F+G4	-	GTR+F+I+G4	-
Gamma shape parameter (α)	0.8768	0.4794	0.6840	-	1.3470	-

generated for earlier studies (Peterson et al. 2010a; 2015a; 2016), and two individuals: *Enneapogon desvauxii* and *E. oblongus* N.T.Burb. were available from GenBank. Four percent (10/256) of the sequences (ITS and plastid) in our dataset are missing. Total aligned characters for individual regions and other parameters are shown in Table 1.

Phylogeny

The Bayesian tree based on plastid (*rps16-trnK* spacer, *rps16* intron, *rpl32-trnL* spacer) and ITS regions is well resolved and a monophyletic Cotteinae including *Cottea, Enneapogon, Kaokochloa*, and *Schmidtia* is strongly supported (BS = 95-100; PP = 0.95-1.00) [Fig. 1]. The first split within the Cotteinae is *Cottea pappophoroides* Kunth and the second split includes *Kaokochloa nigrirostris* De Winter sister to three accessions of *Schmidtia pappophoroides* Steud. ex J.A.Schmidt + two accessions of *S. kalaharensis* Stent. The second split (*Kaokochloa nigrirostris* (*Schmidtia pappophoroides* + *S. kalaharensis*)) is then sister to a monophyletic clade containing 19 species of *Enneapogon*. The *Enneapogon* clade's first split is (*E. pretoriensis* Stent + *E. scaber* Lehm.) sister to remaining species in the genus. The second split in the *Enneapogon* clade contains two major clades: (*Enneapogon scoparius* Stapf + four accessions of *E. cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.) *E. desvauxii*); and *Enneapogon persicus* Boiss. (*E. nigricans* (R.Br.) P.Beauv. (*E. pallidus* (R.Br.) P.Beauv. (two accessions of *E. eremophilus* Kakudidi)) + *E. purpurascens* (R.Br.) P.Beauv. (*E. cylindricus* N.T.Burb. (two accessions of *E. avenaceus* (Lindl.) C.E.Hubb.)); sister to (two accessions of *E. polyphyllus* (Domin) N.T.Burb.+ two accessions of *E. intermedius* N.T.Burb.) + (*E. robustissimus* (Domin) N.T.Burb.+ *E. oblongus*) + (*E. lindleyanaus* (Domin) C.E.Hubb. (*E. caerulescens* (Gaudich.) N.T.Burb.+ *E. gracilis* (R.Br.) P.Beauv.)).

DISCUSSION

Phylogeny

The combined plastid/nuclear DNA-derived phylogeny supports three strongly supported monophyletic clades containing the Cotteinae, *Kaokochloa-Schmidtia*, and *Enneapogon*. *Schmidtia* was earlier found to be paraphyletic often aligning within the *Enneapogon* clade (Roodt-Wilding et al. 2006; Reutemann et al. 2011). We compared our ITS sequences (KM010328, PV954974, PV954975) of *Schmidtia papporphoroides* with the sequence used in Reutemann et al. (2011) and

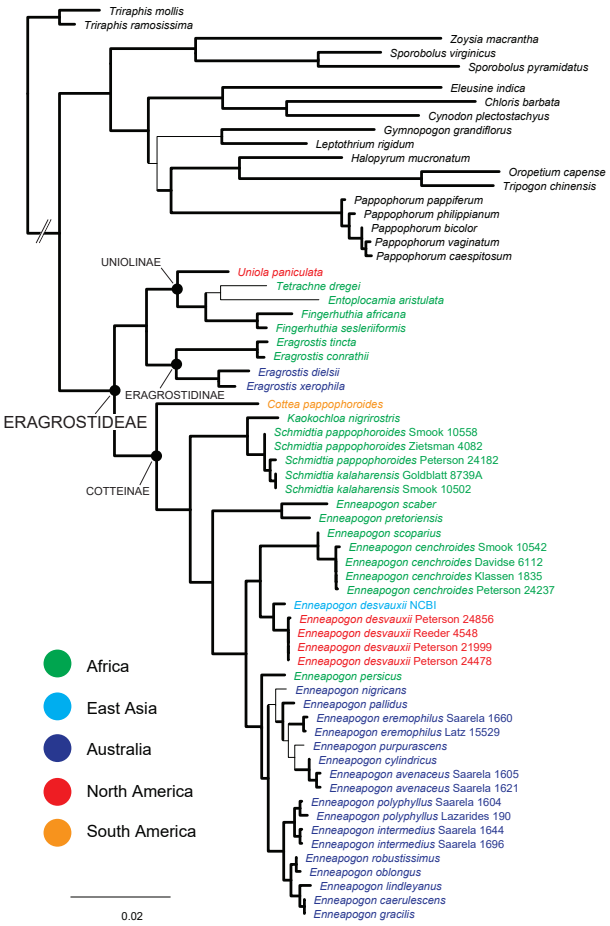

Figure 1. Bayesian tree inferred from combined plastid (*rps16-trnK, rps16, rpl32-trnL*) and nuclear (ITS) DNA sequences of the Cotteinae. Thick black branches in the phylogram indicate a bootstrap of 95-100 and/or posterior probability of 0.95-1.00. Scale bar = 2% substitutions per site.

Roodt-Wilding and Spies (2006) available in GenBank (DQ65584). The latter sequence was poorly edited with 57 possibly erroneous nucleotide substitutions. However, we did not use the plastid *trnL-F* marker in our analysis which also led to equivocal placement of *Schmidtia papporphoroides* in their analysis.

Burbidge (1941) indicated that the Australian species of *Enneapogon* separated into two groups, those with ribbed or prominently thickened nerves (veins) on the lemmas [*E. nigricans* = *E. flavescens* (Lindl.) N.T.Burb.], and those with a smooth lemmas, i.e., the veins not prominent (*E. avenaceus*). Our phylogeny (Fig. 1) does not support this hypothesis, at least in a phylogenetic context, since species with a smooth lemma are not always united in a subclade within the Australian *Enneapogon* clade. However, two accessions each of *Enneapo-*

gon intermedius and *E. polyphyllus* are sister in a subclade but *E. caerulescens, E. lindleyanus, E. oblongus,* and *E. robustissimus*, all treated by Burbidge (1941) as having prominently thickened veins are found in a clade with *E. gracilis* (treated as having smooth lemmas), whereas two accessions of *E. avenaceus* are sister to *E. cylindricus* (treated as having prominently thickened veins) in a different subclade. Burbidge does indicate that the ribbed lemma is probably a more primitive form found in species outside of Australia. Our Australian clade is sister to *E. persicus*, a species from the middle east, Asia, Africa, Spain, and India (Bor 1960, 1970; Chen and Phillips 2006; Cope 2007; Clayton et al. 2016; Aedo 2021; POWO 2025). *Enneapogon persicus* has ribbed lemmas and the first two splits within the genus are composed of primarily African species all with ribbed lemmas.

Biogeography

The tribe Eragrostideae clearly evolved from African ancestors since the stem (42.75 Ma) and crown (31.15 Ma) ages indicate the ancestral area to be Afrotropical 73% and 43%, respectively (Gallaher et al. 2022). The Cotteinae and Unioliinae each have a basal genus, *Cottea* and *Uniola,* that includes species with a western hemisphere distribution. Therefore, it is extremely hard to determine what the ancestral area for each of these subtribes might be. *Cottea pappophoroides* occurs in southwestern United States to central, eastern, and southern Mexico, and again in South America from Ecuador, Peru, Bolivia, and Argentina (Peterson et al. 2001; Sanchez-Ken 2018; Davila et al. 2019). Gallaher et al. (2022) determined the ancestral area for Cotteinae to be 10% cosmopolitan (from anywhere). However, based on our study the most plausible ancestral area for Cotteinae is African since *Kaokochloa* and *Schmidtia* are from Africa, and the first split of *Enneapogon* (*E. pretoriensis* and *E. scaber*), includes species distributed in Africa (Fish et al. 2015). We hypothesize that early in the evolutionary history of Cotteinae, individuals of proto-*Cottea* dispersed to the western hemisphere.

Within *Enneapogon* we recovered four major clades, the first two splits with species primarily from Africa and the third split containing a basal species from Africa/Asia/Europe (*E. persicus*) sister to all species from Australia (Bor 1960, 1970; Chen and Phillips 2006; Cope 2007; Clayton et al. 2016; Aedo 2021; POWO 2025). The ancestral area of *Enneapogon* is Africa since it shares a common ancestor with the *Kaokochloa-Schmidtia* clade and based on our current sample the 13 species from Australia appear to be derived from a single dispersal event from an ancestor shared with *E. persicus*.

ACKNOWLEDGEMENTS

We thank the Smithsonian Institution's Restricted Endowment Fund, the Scholarly Studies Program, Research Opportunities, Atherton Seidell Foundation, Biodiversity Surveys and Inventories Program, Small Grants, the National Geographic Society for Research and Exploration (Grant No. 8848-10, 8087-06); Robert J. Soreng for suggesting improvements to the manuscript; and Riccardo M. Baldini for editing the final manuscript.

REFERENCES

Aedo C. 2021. 121. *Enneapogon* Desv. ex P.Beauv. In: Romero Zarco C, Rico E, Crespo MB, Devesa JA, Buira A, Aedo C (Eds.), Flora Iberica Plantas vasculares de la Península Ibérica e Islas Baleares Vol. XIX(II) Gramineae (partim). Real Jardín Botánico, CSIC, Madrid, 1310-1312.

Bor NL. 1960. The grasses of Burma, Ceylon, India, and Pakistan (excluding Bambuseae). Pergamon Press, Oxford, 1-767.

Bor NL. 1970 Gramineae. In: Rechinger KH (Ed.), Flora Iranica 70/30. Akademische Druck und Verlagsanstalt, Graz, Austria, 1–573.

Burbidge NT. 1941. A revision of the Australian species of *Enneapogon* Desv. Proceedings of the Linnean Society of London. 153(1): 52-91.

Chen SL, Phillips SM. 2006. 21. Tribe Pappophoreae. In: Wu ZY, Raven PH, Hong DY (Eds.), Flora of China: Poaceae, volume 22. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, 456–457.

Clayton WD. 1970. Gramineae (Part 1). In: Milne-Redhead E, Polhill RM (Eds.), Flora of Tropical East Africa. Whitefriars Press, London, 1-176.

Clayton WD, Renvoize SA. 1986. Genera graminum: Grasses of the World. Kew Bulletin, Additional Series. 13: 1–389.

Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2016. GrassBase — The online World grass flora: The Board of Trustees, Royal Botanic Gardens. http://www.kew.org/data/grasses-db.html (accessed 29 July 2025).

Cope, TA. 2007. Poaceae (Gramineae) In: Knees SG, Miller AG (Eds.), Flora of the Arabian Peninsula and Socotra, vol. 5 part 1. Edinburgh University Press and Royal Botanic Gardens, Kew. Edinburgh, 1-387.

Dávila P, Mejia-Saulés MT, Soriano-Martínez AM, Herrera-Arrieta Y. 2018. Conocimiento taxonómico de la Poaceae en México. Botanical Sciences. 96(3): 462–514. https://doi.org/10.17129/botsci.1894

Edgar R. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research. 32: 1792–1797.

Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution. 39: 783–791.

Fish L, Mashau AC, Moeaha MJ, Nembudani MT. 2015. Identification guide to Southern African grasses, an identification manual with keys, descriptions and distributions. Strelitzia. 36(ix): 1–798.

Gallaher TJ, Peterson PM, Soreng RJ, Zuloaga FO, Li DZ, Clark LG, Tyrrell CD, Welker CAD, Kellogg EA, Teisher JK. 2022. Grasses through space and time: An overview of the biogeographical and macroevolutionary history of the Poaceae. Journal of Systematics and Evolution. 60(3): 522–569. https://doi.org/10.1111/jse.12857

Grass Phylogeny Working Group (GPWG) III Arthan W +72 additional authors, 2024. A nuclear phylogenomic tree of grasses (Poaceae) recovers current classification despite gene tree incongruence. New Phytologist. 245(2) 818–834. https://doi.org/10.1111/nph.20263

Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018. UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution. 35(2): 518–522. https://doi.org/10.1093/molbev/msx281

Huelsenbeck JP, Ronquist FR. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics (Oxford, England). 17(8): 754–755.

Kunth KS. 1929. Révision des Graminées, Vol. 1. Dessins de Madame Eulalia Delile, Paris.

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics. 28: 1647–1649. https://pmc.ncbi.nlm.nih.gov/articles/PMC3371832/

Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution. 305: 1188–1195. https://doi.org/10.1093/molbev/mst024

Palisot de Beauvois AMFJ. 1812. Essai d'une nouvelle agrostographie; ou nouveaux genres des Graminées; avec figures représentant les caractères de tous les genres. Fain, Paris, France, 1–82.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015a). A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae). Taxon. 64(3): 445–467. https://doi.org/10.12705/643.5

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015b. Phylogeny and subgeneric classification of *Bouteloua* with a new species, *B. herrera-arrietae* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae). Journal of Systematics and Evolution. 53(4): 351–366. https://doi.org/10.1111/jse.12159

Peterson PM, Romaschenko K, Herrera Arrieta Y. 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 Zaqiqahinae; and a subgeneric classification of *Distichlis*. Taxon. 65(6): 1263–1287. https://doi.org/10.12705/656.4

Peterson PM, Romaschenko K, Johnson G. 2010a. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Molecular Phylogenetics and Evolution. 55: 580–598. https://doi.org/10.1016/j.ympev.2010.01.018

Peterson PM, Romaschenko K, Johnson G. 2010b. A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. American Journal of Botany. 97: 1532–1554. https://doi.org/10.3732/ajb.0900359

Peterson PM, Romaschenko K, Soreng RJ. 2014. A laboratory guide for generating DNA barcodes in grasses: A case study of *Leptochloa* s.l. (Poaceae: Chloridoideae). Webbia. 69(1): 1–12. https://doi.org/10.1080/00837792.2014.927555

Peterson PM, Soreng RJ, Davidse G, Filgueiras TS, Zuloaga FO, Judziewicz EJ. 2001. Catalogue of New World grasses (Poaceae): II. subfamily Chloridoideae. Contributions from the United States National Herbarium 41: 1–255. https://www.biodiversitylibrary.org/item/13801#page/1/mode/1up

Phillips SM. 1995. Poaceae (Gramineae). In: Hedberg I, Edwards S (Eds.), Flora of Ethiopia and Eritrea. The National Herbarium, Addis Abada University, Addis Abada, Ethiopia and Department of Systematic Botany, Uppsala Sweden, 1–420.

Plants of the World Online (POWO). 2025. Facilitated by the Royal Botanic Gardens, Kew http://www.plantsoftheworldonline.org (accessed 29 July 2025).

Reeder JR. 1965. The tribe Orcuttieae and the subtribes of the Pappophoreae (Gramineae). Madroño. 18(1): 18–28. https://www.jstor.org/stable/41423175

Reeder JR. 2003. 18. Pappophoreae Kunth In: Barkworth ME, Capels KM, Long S, Piep MB (Eds.), Flora of North America North of Mexico, Vol. 25 Magno-

liophyta: Commelinidae (in part): Poaceae, part 2. Oxford University Press, New York, 285–289.

Rambaut A, Drummond A, Xie D, Baele G, Suchard M. 2018. Posterior summarization in Bayesian phylogenetics using tracer 1.7. Systematic Biology. 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Renvoize SA. 1968. The Afro-Asian species of *Enneapogon* P. Beauv. (Gramineae). Kew Bulletin. 22: 393–401.

Reutemann AG, Tivano JC, Lucero LE, Vegetti AC, Giussani LM. 2011. Phylogenetic relationships within Pappophoreae s.l. (Poaceae: Chloridoideae): Additional evidence based on ITS and *trnL-F* sequence data. South African Journal of Botany. 77: 693–702. https://doi.org/10.1016/j.sajb.2011.03.010

Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A. 2012. Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. Taxon. 61(1): 18–44. https://doi.org/10.1002/tax.611002

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. Systematic Biology. 61: 539–542. https://academic.oup.com/sysbio/article/61/3/539/1674894

Roodt-Wilding R, Spies JJ. 2006. Phylogenetic relationships in southern African chloridoid grasses (Poaceae) based on nuclear and chloroplast sequence data. Systematic and Biodiversity. 4(4): 401–415. https://doi.org/10.1017/S1477200006002131

Sanchez-Ken JG. 2018. Riqueza de especies, clasificación y listado de las gramíneas (Poaceae) de México. Acta Botánica Mexicana. 126(126): 1–115. https://doi.org/10.21829/abm126.2019.1379

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O. 2015. A worldwide phylogenetic classification of the Poaceae (Gramineae). Journal of Systematics and Evolution. 53(2): 117–137. https://onlinelibrary.wiley.com/doi/10.1111/jse.12150/epdf

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Teisher JK, Clark LG, Barberá B, Gillespie LJ, Zuloaga FO. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. Journal of Systematics and Evolution. 55(4): 259–290. https://doi.org/10.1111/jse.12262

Soreng RJ, Peterson PM, Zuloaga FO, Romaschenko K, Clark LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA, De-Zhu L, Davidse G. 2022. A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. Journal of Systematics and Evolution. 60(3): 476–521. https://doi.org/10.1111/jse.12847

Stebbins GL, Crampton B. 1961. A suggested revision of the grass genera of temperate North America. Recent Advances in Botany: 133–145. University of Toronto Press.

Trinius CB. 1830.Graminum Genera quadam speciesque complures definitionibus novis ilustravit. Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1(1): 54–93.

Weiller CM, Lazarides M. 2005. *Enneapogon*. In: Mallett K (Ed.), Flora of Australia Volume 44B Poaceae 3. CSIRO Publishing, Melbourne, 1–486.

Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. University 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,* and ITS regions; **bold** indicates new accession; a dash (–) indicates missing data; an asterisk (*) indicates type for the genus.

	Taxa	Voucher	Country	*rps16-trnK*	*rps16 intron*	*rpl32-trnL*	ITS
1	*Chloris barbata* Sw.	Peterson 22255 & Saarela (US)	Mexico, Sinaloa	GU360514	GU360435	GU359873	GU359320
2	**Cottea pappophoroides* Kunth	Peterson 21463, Soreng, LaTorre & Rojas Fox (US)	Peru, Ancash	GU360600	GU360456	GU359842	GU359237
3	*Cynodon plectostachyus* (K.Schum.) Pilg.	Troupin 11610 (US)	Rwanda	GU360592	GU360449	GU359890	GU359247
4	*Eleusine indica* (L.) Gaertn.	Peterson 21362, Saarela & Flores Villegas (US)	Mexico, Mexico	GU360496	GU360472	GU359797	GU359338
5	*Enneapogon avenaceus* (Lindl.) C.E.Hubb.	Saarela 1605, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982154**	**PV982186**	**PV959292**	**PV954944**
6	*Enneapogon avenaceus* (Lindl.) C.E.Hubb.	Saarela 1621, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982155**	**PV982187**	**PV959293**	**PV954945**
7	*Enneapogon caerulescens* (Lindl.) C.E.Hubb.	Trudgen 15129 (MEL)	Australia, Western Australia	**PV982156**	**PV982188**	**PV959294**	**PV954946**
8	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Davidse 6112 & Loxton (MO)	South Africa, Northern Cape	**PV982157**	**PV982189**	**PV959295**	**PV954947**
9	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Klaassen 1835, Rugheimer, Mannheimer, Hochobes & Hasheela (US)	Namibia, Karas	**PV982158**	**PV982190**	**PV959296**	**PV954948**
10	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Peterson 24237, Soreng, Romaschenko & Mbago (US)	Tanzania, Tanga	**PV982159**	**PV982191**	**PV959297**	**PV954949**
11	*Enneapogon cenchroides* (Licht. ex Roem. & Schult.) C.E.Hubb.	Smook 10542 (MO)	South Africa, Northern Cape	**PV982160**	**PV982192**	**PV959298**	**PV954950**
12	*Enneapogon cylindricus* N.T.Burb.	Latz 14219 (MEL)	Australia, Northern Territory	**PV982161**	**PV982193**	**PV959299**	**PV954951**
13	**Enneapogon desvauxii* P.Beauv.	GenBank (NCBI)	China	OM307675	OM307675	OM307675	MF029719
14	**Enneapogon desvauxii* P.Beauv.	Peterson 21999 & Saarela (US)	Mexico, Chihuahua	GU360495	GU360486	GU359796	GU359339
15	**Enneapogon desvauxii* P.Beauv.	Peterson 24478 & Romaschenko (US)	Mexico, Coahuila	**PV982162**	**PV982194**	**PV959300**	**PV954952**
16	**Enneapogon desvauxii* P.Beauv.	Peterson 24856 & Romaschenko (US)	Mexico, San Luis Potosí	**PV982163**	**PV982195**	**PV959301**	**PV954953**
17	**Enneapogon desvauxii* P.Beauv.	Reeder 4548 & Reeder (US)	USA, Texas	**PV982164**	**PV982196**	**PV959302**	**PV954954**
18	*Enneapogon eremophilus* Kakudidi	Saarela 1660, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982165**	**PV982197**	**PV959303**	**PV954955**
19	*Enneapogon eremophilus* Kakudidi	Latz 15529 (MEL)	Australia, Northern Territory	**PV982166**	**PV982198**	**PV959304**	**PV954956**
20	*Enneapogon gracilis* P.Beauv.	Walsh, Stewart & O'Brien 6957 (MEL)	Australia, Victoria	**PV982167**	**PV982199**	**PV959305**	**PV954957**
21	*Enneapogon intermedius* N.T.Burb.	Saarela 1644, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982168**	**PV982200**	**PV959306**	**PV954958**
22	*Enneapogon intermedius* N.T.Burb.	Saarela 1696, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982169**	**PV982201**	**PV959307**	**PV954959**
23	*Enneapogon lindleyanus* (Domin) C.E.Hubb.	Jobson 1106 (MEL)	Australia, Queensland	**PV982170**	**PV982202**	**PV959308**	**PV954960**
24	*Enneapogon nigricans* (R.Br.) P.Beauv.	Hosking 2490 (MEL)	Australia, New South Wales	**PV982171**	**PV982203**	**PV959309**	**PV954961**
25	*Enneapogon oblongus* N.T.Burb.	USDA PI238297	Australia	NC036682	NC036682	NC036682	–
26	*Enneapogon pallidus* P.Beauv.	Dixon 1300 (MO)	Australia, Northern Territory	**PV982172**	**PV982204**	**PV959310**	**PV954962**
27	*Enneapogon persicus* Boiss.	Peterson 24265, Soreng, Romaschenko & Mbago (US)	Tanzania, Shinyanga	**PV982173**	**PV982205**	**PV959311**	**PV954963**
28	*Enneapogon polyphyllus* (Domin) N.T.Burb.	Lazarides 190 & Palmer (MO)	Australia, Northern Territory	**PV982174**	**PV982206**	**PV959312**	**PV954964**
29	*Enneapogon polyphyllus* (Domin) N.T.Burb.	Saarela 1604, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	**PV982175**	**PV982207**	**PV959313**	**PV954965**
30	*Enneapogon pretoriensis* Stent	Balkwill 6765, Balkwill & Cron (MO)	South Africa, Transvaal	**PV982176**	–	**PV959314**	–
31	*Enneapogon purpurascens* P.Beauv.	Latz 13064 (MO)	Australia, Northern Territory	**PV982177**	**PV982208**	**PV959315**	**PV954966**
32	*Enneapogon robustissimus* (Domin) N.T.Burb.	Latz 12379 (US)	Australia, Northern Territory	**PV982178**	**PV982209**	**PV959316**	**PV954967**
33	*Enneapogon scaber* Lehm.	Sachse 008 (MO)	South Africa, Western Cape	JQ345237	JQ345279	JQ345322	JQ345168
34	*Enneapogon scoparius* Stapf	Smook 9055 (MO)	Namibia	**PV982179**	**PV982210**	**PV959317**	**PV954968**

(Continued)

Appendix 1. (Continued).

	Taxa	Voucher	Country	*rps16-trnK*	*rps16 intron*	*rpl32-trnL*	ITS
35	*Entoplocamia aristulata* (Hack. & Rendle) Stapf	Seydel 187 (US)	Namibia	GU360492	GU360468	GU359793	GU359342
36	*Eragrostis conrathii* (Hack.) S.M.Phillips	Schweickerdt 1652 (US)	South Africa, Pretoria	–	–	MK872569	MK863244
37	*Eragrostis dielsii* Pilg.	Peterson 14399, Soreng & Rosenberg (US)	Australia, Western Australia	GU360537	GU360400	GU359779	GU359297
38	*Eragrostis tincta* S.M.Phillips	Kemp 1290 (MO)	Swaziland	MK872800	MK872655	MK872567	MK863242
39	*Eragrostis xerophila* Domin	Saarela 1624, Peterson, Soreng & Judziewicz (US)	Australia, Northern Territory	MK872798	MK872653	MK872565	MK863240
40	**Fingerhuthia africana* Nees ex Lehm.	Bester 7070 (MO)	South Africa, Northern Cape	**PV982180**	**PV982211**	**PV959318**	**PV954969**
41	*Fingerhuthia sesleriiformis* Nees	Phillipson 608 (MO)	South Africa, Eastern Cape	**PV982181**	**PV982212**	**PV959319**	**PV954970**
42	*Gymnopogon grandiflorus* Roseng., B.R.Arill. & Izag.	Peterson 16642 & Refulio-Rodriguez (US)	Peru, Apurimac	GU360581	GU360383	GU359816	GU359200
43	**Halopyrum mucronatum* (L.) Stapf	Peterson 23837, Soreng, Romaschenko & Abeid (US)	Tanzania, Lindi	KX582970	KX582903	KX582650	KX582374
44	**Kaokochloa nigrirostris* De Winter	Smook 7779 (MO)	Namibia, Kaokoveld	–	–	**PV959320**	**PV954971**
45	**Leptothrium rigidum* Kunth	Davidse 3281 (MO)	Jamaica, Kingston Parish	KF827794	KF827727	KF827662	KF827541
46	*Oropetium capense* Stapf	Venter 9939 & Venter (MO)	South Africa, Free State	KM011120	KM010917	KM010692	KM010324
47	*Pappophorum bicolor* E.Fourn.	Pohl 12464 (MO)	Mexico, Luis Potosí	KX582985	KX582914	KX582671	KX582397
48	*Pappophorum caespitosum* R.E.Fr.	Tivano 801 et al. (SF)	Argentina	–	–	–	JN175281
49	**Pappophorum pappiferum* (Lam.) Kuntze	Peterson 21689, Soreng, La Torre & Rojas Fox (US)	Peru, Ancash	GU360700	GU360276	GU359996	GU359128
50	*Pappophorum philippianum* Parodi	Renvoize 4225, Cope & Beck (MO)	Bolivia, La Paz	KX582986	KX582915	KJ768980	KJ768885
51	*Pappophorum vaginatum* Buckley	Wagner 3930 & Brown (MO)	Mexico, Durango	KX582987	KX582916	KX582676	KX582399
52	*Schmidtia kalihariensis* Stent	Goldblatt 8739A& Manning (MO)	Namibia, Keetmanshoop	**PV982182**	**PV982213**	**PV959321**	**PV954972**
53	*Schmidtia kalihariensis* Stent	Smook 10502 (MO)	South Africa, Northern Cape	**PV982183**	**PV982214**	**PV959322**	**PV954973**
54	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Peterson 24182, Soreng, Romaschenko & Abeid (US)	Tanzania, Dodoma	**PV982184**	**PV982215**	**PV959323**	**PV954974**
55	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Smook 10558 (MO)	South Africa, Northern Cape.	KM011124	KM010921	KM010697	KM010328
56	**Schmidtia pappophoroides* Steud. ex J.A.Schmidt	Zietsman 4082, Peyper, Seutloali & Tadi (MO)	South Africa, Orange Free State	**PV982185**	**PV982216**	**PV959324**	**PV954975**
57	*Sporobolus pyramidatus* (Lam.) Hitchc.	Peterson 21163, Saarela, Rosen & Reid (US)	Mexico, Durango	GU360628	GU360359	GU359910	GU359228
58	*Sporobolus virginicus* (L.) Kunth	Peterson 15683 & Soreng (US)	Chile, Region I	GU360610	GU360362	GU359892	GU359215
59	**Tetrachne dregei* Nees	Jarman 120 (US)	South Africa, Free State	GU360622	GU360365	GU359904	GU359218
60	*Tripogon chinensis* Hack.	Boufford 29012, Bartholomew, Chen, Donoghue, Ree, Sun Hang & Wu Su-Gong (MO)	China, Sichuan	KX583020	KX582946	KX582731	KX582451
61	**Triraphis mollis* R.Br.	Peterson 14344, Soreng & Rosenberg (US)	Australia, Western Australia	GU360669	GU360336	GU359933	GU359187
62	*Triraphis ramosissima* Hack.	Seydel 4278 (US)	Namibia	GU360651	GU360338	GU359931	GU359188
63	**Uniola paniculata* L.	Peterson 11160, Annable & Valdes-Reyna (US)	USA, Texas	GU360648	GU360341	GU359926	GU359192
64	*Zoysia macrantha* Desv.	Soreng 5913 & Peterson (US)	Australia, New South Wales	GU360641	GU360346	GU360017	GU359142