

A molecular phylogeny of the subtribe Sporobolinae and a classification of the subfamily Chloridoideae (Poaceae)

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Abstract. The classification of the subtribe Sporobolinae containing the following six genera is poorly understood: *Calamovilfa* (five species endemic to North America), *Crypsis* (11 species endemic to Asia and Africa), *Psilolemma* (one species endemic to Africa), *Spartina* (17 species centered in North America), *Sporobolus* (186 species distributed worldwide), and *Thellungia* (one species from Africa and Asia). The goal of this study was to reconstruct the evolutionary history of the Sporobolinae using molecular data with increased species sampling. Most species in this subtribe have spikelets with a single floret, one-veined (occasionally three-veined) lemmas, a ciliate membrane or line of hairs for a ligule, and fruits with free pericarps (modified caryopses). A phylogenetic analysis was conducted on 161 species (250 samples), of which 134 species were in the Sporobolinae, using nuclear rITS (ribosomal internal transcribed spacer region) 1 and 2 sequences to infer evolutionary relationships. The maximum likelihood phylogram provides moderate support for a paraphyletic *Sporobolus* that includes *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*. The subtribe Zoysiinae (*Urochondra* and *Zoysia*) is sister to a highly supported Sporobolinae where the *Psilolemma jaegeri*–*Sporobolus somalensis* clade is sister to the remaining species of *Sporobolus* s.l. Within *Sporobolus* s.l. there are 15 major clades, of which 12 are strongly supported, two are moderately supported, and one is unsupported. A complete generic classification of the subfamily Chloridoideae is given.

Keywords: *Calamovilfa*, classification, *Crypsis*, ITS, phylogeny, *Psilolemma*, *Spartina*, *Sporobolus*, *Thellungia*

INTRODUCTION

In the most recent classification of the grass subfamily Chloridoideae, the tribe Zoysieae Benth. includes the *incertae sedis* genus *Urochondra* C.E. Hubb. and two subtribes, Zoysiinae Benth. and Sporobolinae Benth. (Peterson et al., 2007, 2010a). Zoysiinae includes a single genus, *Zoysia* Willd., with 11 species native to Australasia (Nightingale et al., 2005; Clayton et al., 2006). They are primarily mat-forming perennials with cylindrical racemes, spikelets that usually disarticulate below the glumes, lower glumes absent or much reduced, upper glumes laterally compressed and coriaceous, and one- to three-nerved hyaline lemmas with entire or mucronate apices. The subtribe Sporobolinae Benth. consists of four genera: *Calamovilfa* (A. Gray) Hack. ex Scribn. & Southw. (5 species endemic to North America); *Crypsis* Aiton

(11 species endemic to Asia and Africa); *Spartina* Schreb. (17 species centered in North America); and *Sporobolus* (186 species worldwide) (Mobberley, 1956; Lorch, 1962; Napper, 1963; Thieret, 1966, 2003; Tan, 1985; Peterson et al., 2003, 2004, 2007, 2010a; Nightingale et al., 2005; Clayton et al., 2006; Kern, 2012; Saarela, 2012). *Pogononeura* Napper, a monotypic, morphologically distinct genus with two- or three-flowered spikelets with short-awned lemmas (Clayton & Renvoize, 1986) has also previously been attributed to the Sporobolinae (Peterson et al., 2010a), but recent analyses place it in the Cynodonteae (Peterson et al., 2014a). The Sporobolinae share most of the same character trends as for the Zoysieae, such as, spikelets with a single floret, spiciform inflorescences of numerous deciduous racemes disposed along a central axis, lemmas usually rounded and rarely with apical awns, and glumes often modified and oddly

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shaped but differ by having modified caryopses with free pericarps (pericarps free, reluctantly so in *Spartina*), spikelets oriented abaxially along the axis (lemma is facing the rachis), lemmas that are similar in texture to the glumes, and paleas that are relatively long and about the same length as the lemma (Branderberg, 2003; Peterson et al., 2004, 2007). *Zoysia* have a true caryopsis (fused pericarps), spikelets oriented adaxially along the axis (lemma facing away from the rachis), lemmas less firm than the glumes, and paleas relatively short or very reduced when compared with the lemma (Peterson et al., 2007). *Urochondra* was shown to have similar characteristics as *Zoysia*, and additionally, has beaked caryopses formed from thickened style bases and caryopses with free pericarps (Clayton & Renvoize, 1986; Clayton et al., 2006; Peterson et al., 2010a).

Sporobolus is characterized by having single-flowered spikelets, one-nerved (rarely three-nerved) lemmas, fruits with free pericarps or modified caryopses, and ligules a ciliate membrane or line of hairs (Peterson et al., 1995, 1997). Species of *Sporobolus* generally inhabit dry or stony soils, to saline or alkaline sandy soils, to clay loam soils in prairies, savannahs, and along disturbed roadsides (Clayton & Renvoize, 1986; Peterson et al., 1997). Numerous infrageneric classifications of *Sporobolus* have been proposed over the last century, based primarily on morphology and anatomy. Stapf (1898) first divided the genus into two sections: *Chaetorhachia* Stapf and *Eusporobolus* Stapf. Pilger (1956) divided the latter section into six groups based on life form and characteristics of the glumes and panicles. Based on caryopsis morphology, Bor (1960) divided *Sporobolus* into five groups (Baaijens & Veldkamp, 1991) and Clayton (1965) treated the *Sporobolus indicus* (L.) R.Br. complex in the tropics and subtropics. Working on the Malesian species, Baaijens and Veldkamp (1991) divided *Sporobolus* into five sections based on a leaf anatomical survey and overall morphology. More recently, Weakley and Peterson (1998) recognized the *Sporobolus floridanus* complex to include five species in the southeastern United States and Shrestha et al. (2003) recognized seven clades within the genus, while Denham and Aliscioni (2010) recognized the *S. aeneus* (Trin.) Kunth complex to include five species. Recent major revisions of *Sporobolus* include Boechat and Wagner (1995) for Brazil, Simon and Jacobs (1999) and Simon (2005) for Australia, Peterson et al. (2003, 2009) for the United States and Canada, and Giraldo-Cañas and Peterson (2009) for Peru, Ecuador, and Colombia.

Molecular studies have provided new insights into the evolutionary history of *Sporobolus*, even

though the number of species sampled for molecular studies has been rather small. In the first molecular study of the genus, based on nuclear ribosomal DNA ITS sequences, Ortiz-Diaz and Culham (2000) presented 42 species of *Sporobolus*. Several DNA-based phylogenies present *Sporobolus* as paraphyletic with *Calamovilfa*, *Crypsis*, and *Spartina* embedded within (Ortiz-Diaz & Culham, 2000; Hilu & Alice, 2001; Columbus et al., 2007; Bouchenak-Khelladi et al., 2008; Peterson et al., 2010a). Peterson et al. (2010a) recommended future expansion of *Sporobolus* to include all of these genera, recognizing that only 42 *Sporobolus* species (ca. one fifth of the species in the genus) have been included in a single phylogenetic study (Ortiz-Diaz & Culham, 2000). Peterson et al. (2010a), in their study investigating 246 species of Chloridoideae using seven molecular markers, analyzed 15 species of Sporobolinae.

Here we present a new phylogenetic analysis of 58% of the species in *Sporobolus* based on analysis of the nuclear internal transcribed spacer regions (ITS1 and ITS2) and we discuss morphological and anatomical characters supporting relationships. We also include an updated classification of the Chloridoideae.

MATERIALS AND METHODS

TAXON SAMPLING

The taxon sampling consists of 250 samples representing 161 species of grasses, of which 157 species are included in subfamily Chloridoideae; these are represented in the following five tribes (Soreng et al., 2014): Centropodieae (one species), Triraphideae (two species), Eragrostideae (11 species), Cynodonteae (nine species), and Zoysieae (147 species). Our sampling was principally focused on genera that are morphologically similar to *Sporobolus*, including a large sample of 134 species within the subtribe Sporobolinae (Peterson et al., 2010a). The data set for *Sporobolus* includes 108 of the 186 species currently placed in the genus (Clayton et al., 2006). A complete list of taxa, voucher information, and GenBank numbers is given in the Appendix. Two species of Danthonioideae (*Danthonia compressa* Austin and *Rytidosperma penicellatum* (Labill.) Connor & Edgar), one species from Aristidoideae (*Aristida gypsophila* Beetle), and one species of Panicoideae (*Chasmanthium latifolium* (Michx.) H.O. Yates, phylogenetic root) were chosen as outgroups (Peterson et al., 2010a, 2011, 2012, 2014a, 2014b, 2014c; 2015, 2016).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

All procedures were performed in the Laboratory of Analytical Biology at the Smithsonian Institution. DNA isolation, amplification, and sequencing of ITS were accomplished following procedures outlined in Peterson et al. (2010a, 2010b, 2014c). The ITS region included 798 total characters (89.1 sequencing success) and includes complete sequences of internal transcribed spacer 1 (ITS1), the 5.8S ribosomal RNA gene, and internal transcribed spacer 2 (ITS2). Primers include ITS4 as reverse (5'-3':TCCTCCGCTTATTGATATGC) and ITS5a as forward (5'-3':CCTTATCATTAGAGGAAGGAG) (White et al., 1990; Stanford et al., 2000).

PHYLOGENETIC ANALYSES

We used Geneious 5.3.4 (Biomatters Limited, Auckland, New Zealand; Drummond et al., 2011) for contig assembly of bidirectional sequences, and we used Muscle (European Molecular Biology Laboratory, Heidelberg, Germany; Edgar, 2004) to align consensus sequences and adjust the final alignment. We conducted maximum likelihood (ML) and Bayesian analyses to infer overall phylogeny. We identified models of molecular evolution for the nrDNA region using jModeltest (SoftNews Net SRL, Bucharest, Romania; Posada, 2008). The Nucleotide substitution model selected by Akaike's Information Criterion, as implemented in jModelTest v.0.1.1, was GTR+I+G. The ML analysis was conducted with GARLI 0.951 (University of Texas, Austin, TX; Zwickl, 2006). The maximum likelihood bootstrap analysis was performed with 1000 replicates, with 10 random addition sequences per replicate. The output file containing the ML trees found for each bootstrap dataset was read into PAUP* 4.0b10 (Sinauer Associates, Sunderland, MA; Swofford, 2000), 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.

Bayesian posterior probabilities (PP) were estimated using the parallel version of MrBayes v3.1.2 (PubMed, NIH, Bethesda, MD; 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 se-

quences 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.

RESULTS

A total of 209 ITS sequences are newly reported in GenBank (see Appendix), and the proportion of invariable sites was 0.2174. Supplemental data from parsimony analysis indicates 448 parsimony informative characters.

The ML tree (Fig. 1) is well resolved with weak support for tribe Zoysiace (BS = 69%, PP = 0.95), strong support for subtribe Zoysiinae (BS = 100, PP = 100) and strong support for subtribe Sporobolinae (BS = 100, PP = 100). The Zoysiinae includes a monophyletic *Zoysia* (BS = 100, PP = 1.00) that is sister to *Urochondra setulosa* (Trin.) C.E. Hubb. The Sporobolinae includes a *Psilolemma jaegeri* (Pilg.) S.M. Phillips–*Sporobolus somalensis* Chiov. clade (BS = 65, PP = 0.90) that is sister to a moderately supported paraphyletic *Sporobolus* clade (BS = 71, PP = 100) that includes the remaining species of *Sporobolus*, as well as *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*.

Within *Sporobolus* s.l. there are 12 strongly supported clades (Fig. 1B–J, M–O; BS = 91–100, PP = 1.00), two moderately supported clades (Fig. 1A, K; BS = 82–87, PP = 1.00), and a single unsupported clade (Fig. 1L). Species in clades A–O are listed in Table 1. Within clade O there are three strongly supported subclades (BS = 96–100, PP = 1.00) that include: (1) *Spartina alterniflorus* Loisel., *S. anglica* C.E. Hubb., *S. foliosa* Trin., *S. maritima* (Curtis) Fernald, and *S. xtownsendii* H. Groves & J. Groves; (2) *S. bakeri* Merr., *S. xcaespitosa* A.A. Eaton, *S. ciliata* Brongn., *S. cynosuroides* (L.) Roth., *S. densiflora* Brongn., *S. gracilis* Trin., *S. montevidensis* Arechav., and *S. patens* (Aiton) Muhl.; and (3) *S. spartinae* (Trin) Merr. & Hitchc.

Species of *Sporobolus* not recovered in clades A–O (Fig. 1) include a poorly supported *Sporobolus acinifolius* Stapf–*S. albicans* Nees–*S. tenellus* (Spreng.) Kunth clade (BS < 50, PP = 0.95) that is sister to all remaining species in *Sporobolus* s.l.; *Sporobolus oxylepsis* Mez–*S. robustus* Kunth pair are sister to two accessions of *S. consimilis* Fresen. (BS = 98, PP = 1.00), and together these are sister to two accessions of *Thellungia advena* Stapf (BS = 100, PP = 1.00) in an unsupported clade; *Sporobolus tourneuxia* Coss. is sister to E–O clades; *Sporobolus phleoides* Hack. is sister to the H clade; three accessions

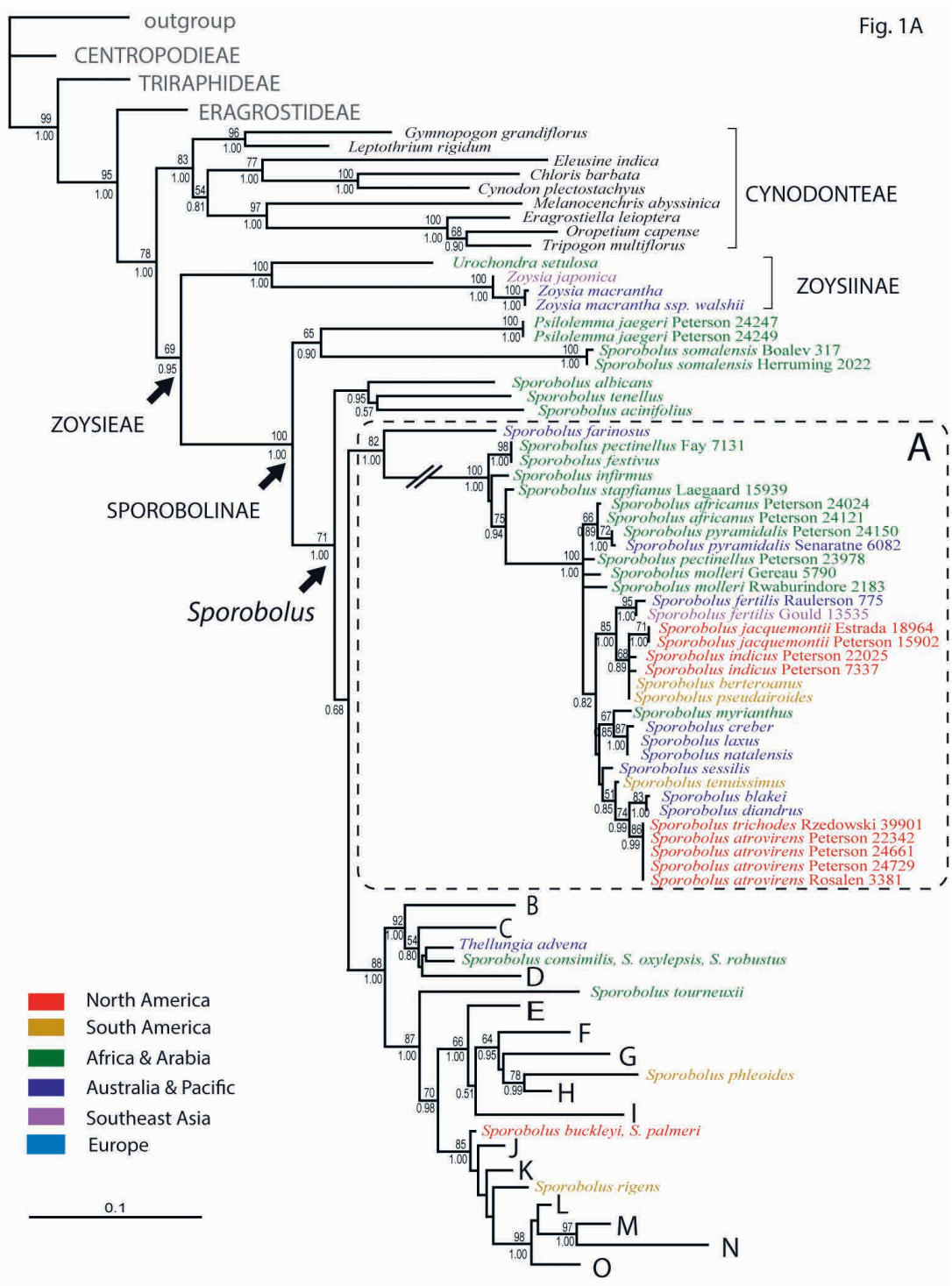


FIGURE 1A–D. Maximum likelihood tree inferred from nuclear ribosomal ITS sequence data. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities from Bayesian analysis; color indicates native distribution (see legend); clades outlined in dashed lines labeled A–O are discussed in the text; scale bar = 1% sequence divergence. (continued)

Fig. 1B

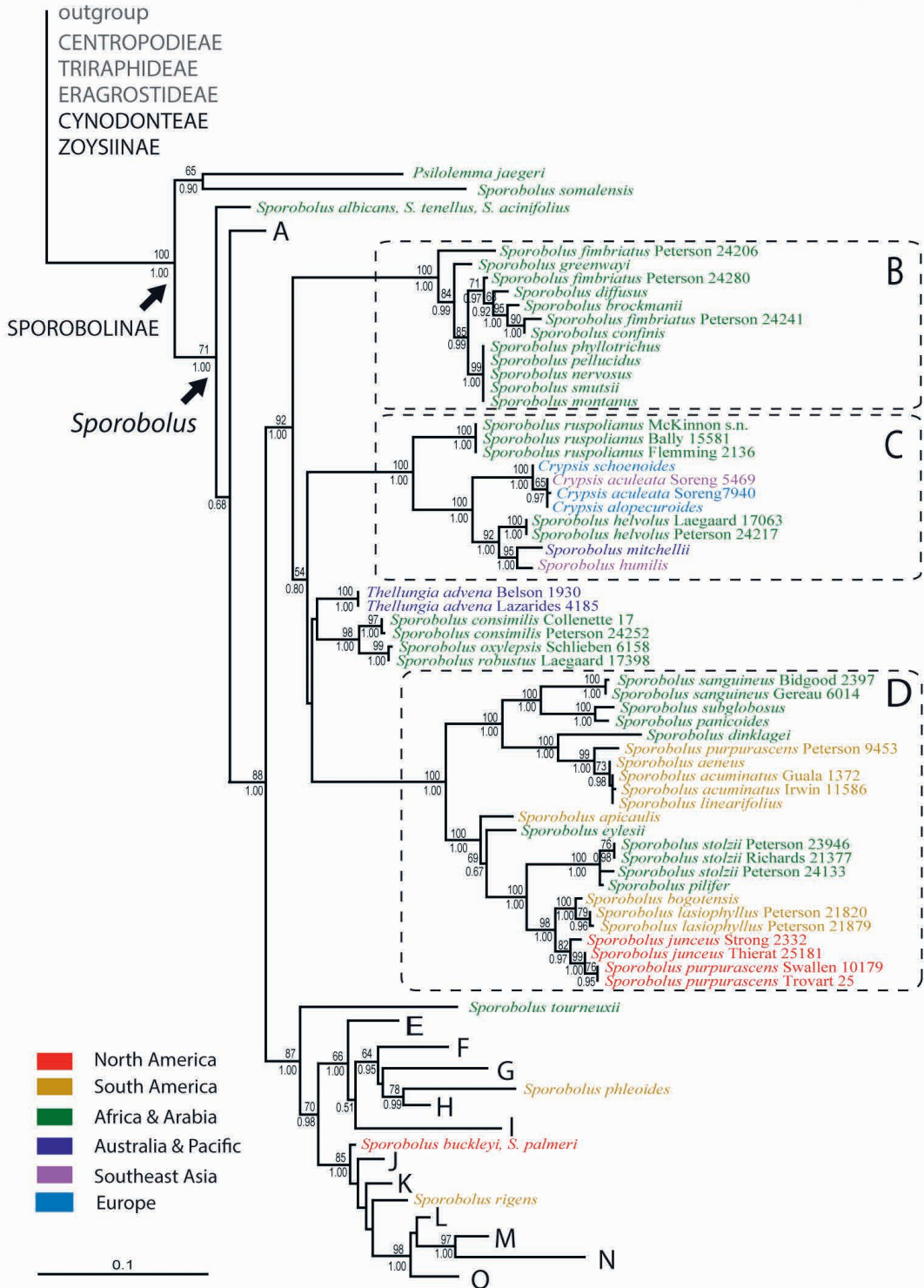


FIGURE 1B.

(continued)

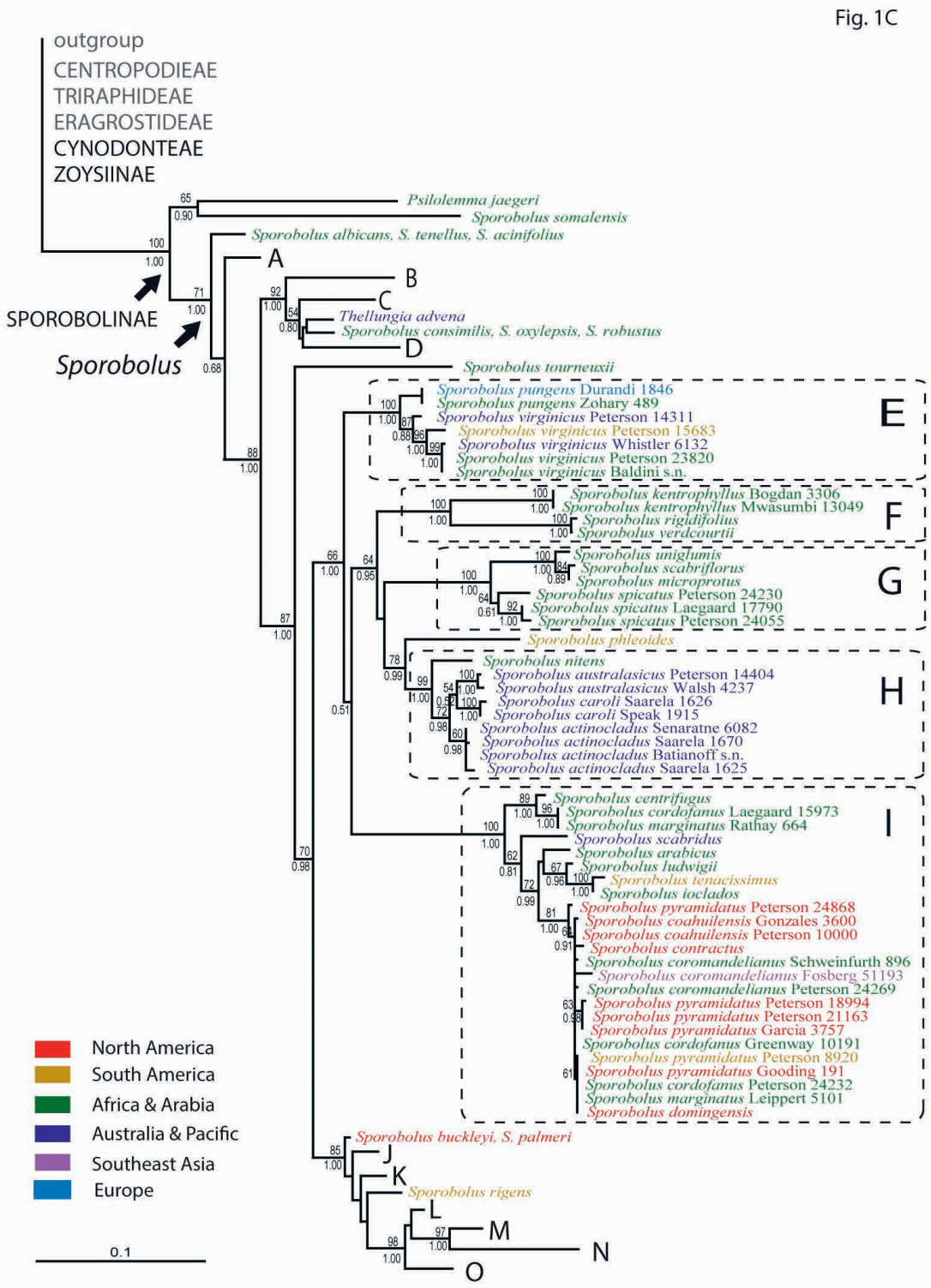


Fig. 1C

FIGURE 1C.

(continued)

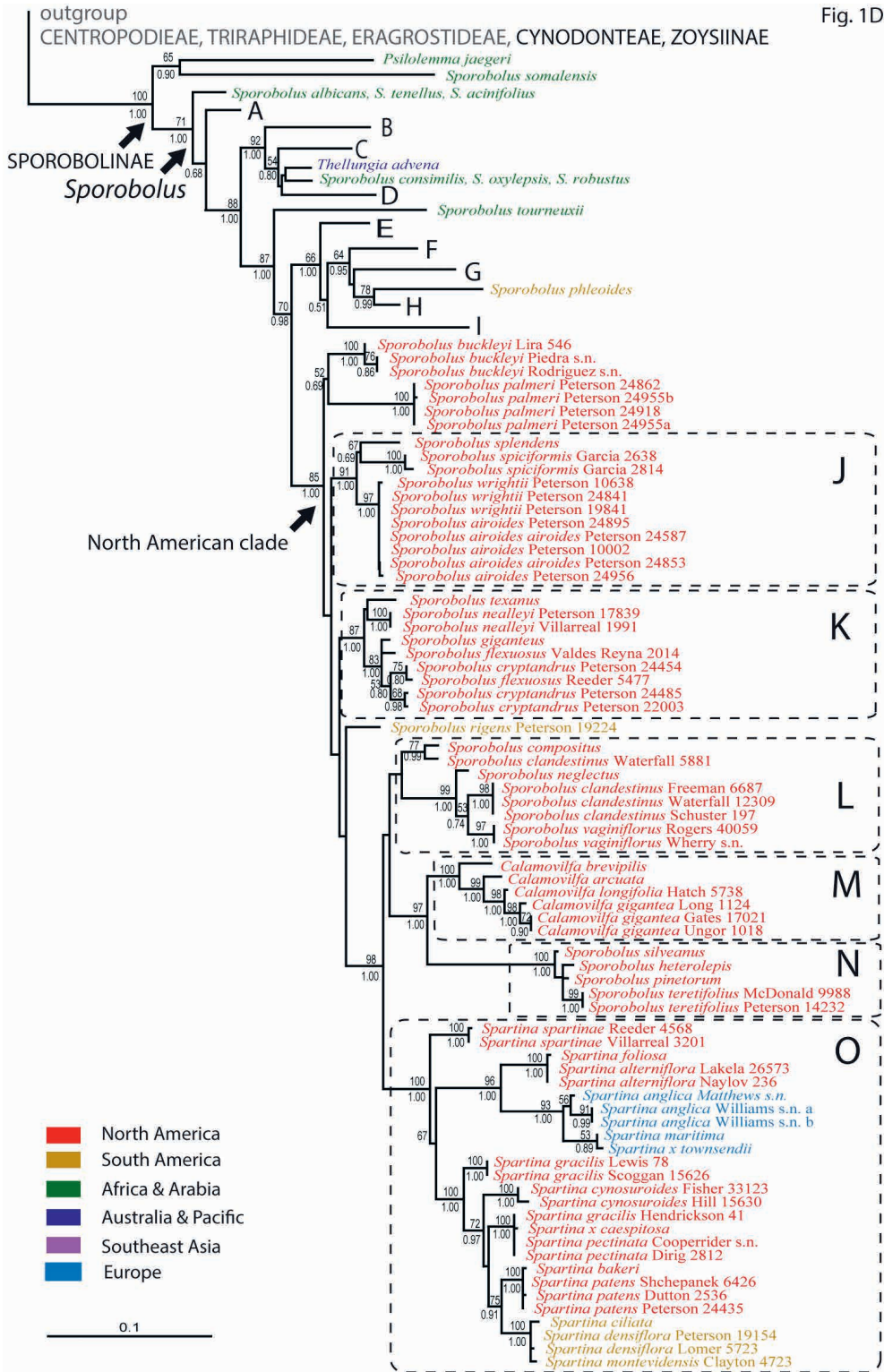


FIGURE 1D.

TABLE I. The major clades and *incertae sedis* within *Sporobolus* based on nuclear internal transcribed spacer DNA sequence analysis.^{1,2}

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- A:** *Sporobolus africanus* (Poir.) Robyns & Tournay, *S. atrovirens* (Kunth) Kunth, *S. berteruanus* (Trin.) Hitchc. & Chase, *S. blakei* De Nardi ex B.K. Simon, *S. creber* De Nardi, *S. diandrus* (Retz.) P. Beauv., *S. farinosus* Hosok., *S. fertilis* (Steud.) Clayton, *S. festivus* Hochst. ex A. Rich., *S. indicus* (L.) R.Br., *S. infirmus* Mez, *S. jacquemontii* Kunth, *S. laxus* B.K. Simon, *S. molleri* Hack., *S. natalensis* (Steud.) T. Durand & Schinz, *S. myrianthus* Benth., *S. pectinellus* Mez, *S. pseudairoides* Parodi, *S. pyramidalis* Beauv., *S. sessilis* B.K. Simon, *S. stapfianus* Gand., *S. tenuissimus* (Mart. ex Schrank) Kuntze, *S. trichodes* Hitchc.
- B:** *Sporobolus brockmanii* Stapf, *S. confinis* (Steud.) Chiov., *S. diffusus* Clayton, *S. fimbriatus*, *S. greenwayi* Napper, *S. montanus* (Hook. f.) Engl., *S. nervosus* Hochst., *S. pellucidus* Hochst., *S. phyllotrichus* Hochst., *S. smutzii* Stent
- C:** *Crypsis aculeatus* (L.) Aiton, *C. alopecuroides* (Piller & Mitterp.) Schrad., *C. schoenoides* (L.) Lam., *S. helvolus* (Trin.) T. Durand & Schinz, *S. humilis* J. Presl, *Sporobolus mitchellii* (Trin.) C.E. Hubb. ex S.T. Blake, *S. ruspolianus* Chiov.
- D:** *Sporobolus acuminatus* (Trin.) Hack., *S. aeneus* (Trin.) Kunth, *S. apiculatus* Boechat & Longhi-Wagner, *S. bogotensis* Swallen & García-Barr., *S. dinklagei* Mez, *S. eylesii* Stent & J.M. Rattray, *S. junceus* (P. Beauv.) Kunth, *S. lasiophyllus* Pilg., *S. linearifolius* Nicora, *S. panicoides* A. Rich., *S. pilifer* (Trin.) Kunth, *S. purpurascens* (Sw.) Ham., *S. sanguineus* Rendle, *S. stolzii* Mez, *S. subglobosus* Stapf ex C.E. Hubb.
- E:** *Sporobolus pungens* (Schreb.) Kunth, *S. virginicus* (L.) Kunth
- F:** *Sporobolus kentrophyllus* (K. Schum. ex Engl.) Clayton, *S. subulatus* Hack., *S. verdcourtii* Napper
- G:** *Sporobolus microprotus* Stapf, *S. scabriflorus* Stapf ex Massey, *S. spicatus* (Vahl) Kunth, *S. uniglumis* Stent & J.M. Rattray
- H:** *Sporobolus actinocladius* (F. Muell.) F. Muell., *S. australasicus* Domin, *S. caroli* Mez, *S. nitens* Stent
- I:** *Sporobolus arabicus* Boiss., *S. centrifugus* (Trin.) Nees, *S. coahuilensis* Valdés-Reyna, *S. contractus* Hitchc., *S. cordofanus* (Hochst. ex Steud.) Coss., *S. coromandelianus* (Retz.) Kunth, *S. domingensis* (Trin.) Kunth, *S. ioclados* (Nees ex Trin.) Nees, *S. ludwigii* Hochst., *S. marginatus* Hochst. ex A. Rich., *S. pyramidatus*, *S. scabridus* S.T. Blake, *S. tenacissimus* (L. f.) P. Beauv.
- J:** *Sporobolus airoides* (Torr.) Torr., *S. spiciformis* Swallen, *S. splendens* Swallen, *S. wrightii* Munro ex Scribn.
- K:** *Sporobolus cryptandrus* (Torr.) A. Gray, *S. flexuosus* (Thurb. ex Vasey) Rydb., *S. giganteus* Nash, *S. nealleyi* Vasey, *S. texanus* Vasey
- L:** *Sporobolus clandestinus* (Biehler) Hitchc., *S. compositus* (Poir.) Merr., *S. neglectus* Nash, *S. vaginiflorus* (Torr. ex A. Gray) Alph. Wood
- M:** *Calamovilfa arcuata* K.E. Rogers, *C. brevipilis* (Torr.) Scribn., *C. gigantea* (Nutt.) Scribn. & Merr., *C. longifolia* (Hook) Hack. ex Scribn.
- N:** *Sporobolus heterolepis* (A. Gray) A. Gray, *S. pinetorum* Weakley & P.M. Peterson, *S. silveanus* Swallen, *S. teretifolius* R.M. Harper
- O:** *Spartina alterniflora* Loisel., *S. anglica* C.E. Hubb., *S. bakeri* Merr., *S. caespitosa* A.A. Eaton, *S. ciliata* Brongn., *S. cynosuroides* (L.) Roth, *S. densiflora* Brongn., *S. foliosa* Trin., *S. gracilis* Trin., *S. martima* (Curtis) Fernald, *S. montevidensis* Arechav., *S. patens* (Aiton) Muhl., *S. pectinata* Link, *S. spartinae* (Trin.) Merr. ex Hitchc., *S. ×townsendii* H. Groves & J. Groves
- Incertae sedis:* *S. acinifolius* Stapf, *S. albicans* Nees, *S. buckleyi* Vasey, *S. consimilis* Fresen., *S. oxylepsis* Mez, *S. palmeri* Scribn., *S. phleoides* Hack., *S. rigens* (Trin.) Desv., *S. robustus* Kunth, *S. tenellus* (Spreng.) Kunth, *S. tourneuxii* Coss., *Thellungia advena* Stapf
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of *Sporobolus buckleyi* Vasey and four accessions of *S. palmeri* Scribn. (BS = 52, PP = 0.69) are sister to clades J–O and together form a moderately supported North American clade (BS = 85, PP = 1.00); and *Sporobolus rigens* (Trin.) E. Desv. is sister to a clade comprising the L–O clades (BS = 99, PP = 1.00).

DISCUSSION

SPOROBOLINAE AND *SPOROBOLUS*, INCERTAE SEDIS

We treat as incertae sedis those taxa that are not part of larger well-supported clades (i.e., with bootstrap support < 50 and Bayesian posterior probabilities < 0.70; see Table 1). Two species, *Psilolemma jaegeri* and *Sporobolus somalensis*, fall outside the main *Sporobolus* clade in the ITS tree. *Sporobolus somalensis* is an enigmatic species known only from Somalia and extending into the Ethiopian Ogaden (Phillips, 1995). *Psilolemma jaegeri* and *S. somalensis* are both mat-forming, stoloniferous perennials, although the latter species has open, subdichotomously branched panicles with numerous one-flowered spikelets, while *P. jaegeri* has narrow and spike-like panicles with 4- to 14-flowered spikelets (Phillips, 1974, 1995; Clayton et al., 2006). Additional study of *S. somalensis* along with *P. jaegeri* will be necessary to determine their relationship to other members of *Sporobolus* s.l. *Psilolemma jaegeri* is somewhat unique in that it has three-veined lemmas, but there are other species of *Sporobolus*—*S. acinifolius*, *S. albicans*, *S. fibrosus* Cope (not sampled), *S. palmeri*, *S. subtilis* Kunth (not sampled), and *S. tenellus* Kunth—that share this trait (Phillips, 1974; Cope, 1999). With the exception of *S. palmeri*, from Mexico, these are all African taxa. Three of these African taxa, which have not previously been sampled in molecular studies, form a poorly supported clade (*Sporobolus acinifolius*–*S. albicans*–*S. tenellus*), sister to the remaining species of *Sporobolus* (Fig. 1, BS < 50, PP = 0.95). These southern African species are mat-forming, rhizomatous perennials with cartilaginous to subcartilaginous leaf blade margins, subdichotomously branched panicles (narrow in *S. albicans*), and small spikelets (1–2.5 mm long) with three-veined lemmas (Gibbs Russell et al., 1991; Cope, 1999). *Sporobolus fibrosus*, *S. salsus* Mez, and *S. subtilis* are also morphologically similar to the three species in our study (Cope, 1999). Three-veined lemmas may be derived independently in *Psilolemma jaegeri*, the *S. acinifolius*–*S. albicans*–*S. tenellus* lineage, and in *S. palmeri* (which is nested deep in *Sporobolus*), or this may be a plesiomorphic character retained in these lineages.

The Australian genus, *Thellungia*, was initially described by Stapf to include a single species, *T. advena*. Phillips (1982) transferred this species into *Eragrostis* (*E. advena*), and more recently, based on plastid *rps16* and nuclear waxy sequences, Ingram and Doyle (2004, 2007) have shown it to be embedded within *Sporobolus*. *Thellungia* has unique features such as multiflowered (one to five), cleistogamous spikelets with long-curved rachillas (each floret readily disarticulates with a persistent rachilla joint), one-veined (rarely three-veined) lemmas, and caryopses with free pericarps (Lazarides, 1997; Palmer et al., 2005). All of these characteristics, with the exception of multiflowered spikelets, are common in species of *Sporobolus*. *Thellungia* is part of the *Sporobolus* lineage in our tree and is part of a strongly supported clade comprising clades B, C, and D plus a *Sporobolus consimilis*–*S. oxylepsis*–*S. robustus* clade.

Sporobolus buckleyi from the southwestern U.S.A. and Mexico and *S. palmeri*, a Mexican endemic known from Durango and San Luis Potosi, form a weakly supported clade on the ITS tree. Morphologically, *S. buckleyi* and *S. palmeri* share the densely caespitose, perennial habit and open, diffuse panicles with primary branches naked below on lower quarter to half (Espejo Serna et al., 2000; Peterson et al., 2004). *Sporobolus palmeri* differs from *S. buckleyi* in having shorter culms (13–50 versus 40–100 cm), longer spikelets (3.2–4.4 versus 1.2–2 mm), longer anthers (1.6–2.4 versus 0.2–0.4 mm), and longer caryopses (1.6–2.1 versus 0.6–1 mm).

Our study has provided new insights into the taxonomy of *S. palmeri*. There is much confusion between *S. palmeri* and *S. airoides* (Torr.) Torr., a morphologically similar but more widely distributed species occurring throughout the U.S.A. and Mexico and introduced in Arabia (Peterson et al., 2003, 2004; Clayton et al., 2006). *Sporobolus palmeri* was collected by the first two authors on a 2012 trip to northeastern Mexico, where it was found growing with *S. airoides*. In a subsequent survey of material in the US National Herbarium, we found that only the type collection of *S. palmeri* made in late 1890s and one other specimen made in the early 1900s were correctly determined, while the 10 other specimens included in the *S. palmeri* folder were misidentified. Superficially, *S. palmeri* resembles *S. airoides* but differs by having shorter culms [13–50 versus 35–120 (–150) cm], smaller leaf blades [(3–) 5–20 cm × 0.6–1.4 mm versus (3–) 10–45 (–60) cm × (1–) 2–5 (–6) mm], smaller panicles (7–20 × 5–20 versus 15–45 × 15–25 cm), longer pedicels (2.5–10 versus 0.5–2 mm), longer spikelets (3.2–4.4 versus 1.3–2.8 mm), longer lemmas (3.2–4.3 versus 1.2–2.5 mm) that are 3-veined

versus 1-veined, longer paleas (3.1–4.2 versus 1.1–2.4 mm), longer anthers (1.6–2.5 versus 1.1–1.8 mm), and longer modified caryopses (1.6–2.1 versus 1–1.4 mm) (Peterson et al., 2003, 2004). In addition to being confused taxonomically, *S. airoides* and *S. palmeri* have been considered to be closely related. Both species were recovered in the same strongly supported clade defined in a previous ITS analysis (Ortiz-Diaz & Culham, 2000), in contrast to the current study in which *S. palmeri* is excluded from the *S. airoides* clade (Fig. 1, clade J). The specimen in the earlier analysis may have been misidentified. Unfortunately voucher specimens are not listed in that study, and the sequences are not available in GenBank, thus it is not possible to check the original determination or to compare the earlier ITS sequence with our new ITS sequences for *S. airoides* and *S. palmeri*. Our analyses confirm that *S. palmeri* and *S. airoides* are not conspecific or even sister taxa, as they fall in different parts of our tree. Most likely these two species have originated from a single ITS haplotype and this is an example of rapid radiation, since a Bayesian strict consensus tree (not shown) would collapse at the base of the North American clade where clades J and K and *S. palmeri* and *S. buckleyi* reside. An illustration of *S. palmeri* is provided to familiarize the reader and other agrostologists with the general morphology of *Sporobolus* (Fig. 2).

Clade A.—We find strong support for a lineage corresponding with the *S. indicus* complex, as recognized by previous authors (Pilger, 1956; Baaijens & Veldkamp, 1991). The *Sporobolus indicus* complex, treated here as *S. sect. Sporobolus*, consists of at least 23 species, as confirmed in our phylogram (see Table 1). *Sporobolus farinosus* is sister to the remaining species in this lineage. In the next deepest split, *S. festivus*–*S. pectinellus*, *S. infirmus*, and *S. stapfianus* form a grade, with *S. stapfianus* sister to the remaining species. Several smaller clades of two to several species are present in this strongly supported clade. Clayton (1965) recognized *S. pellucidis* Hochst. as occurring in the *S. indicus* complex, but it clearly has affinities to *S. sect. Fimbriatae* Veldkamp (clade B). Morphological characteristics that support recognition of this clade include: long-lived annuals to perennials without stolons or cataphylls; conspicuously keeled and never pectinate leaf blades; densely to moderately contracted, occasionally rather open and diffuse, panicles; solitary branches along the lower culm nodes; very short lower glumes and longer upper glumes, the latter usually shorter than the lemma; ellipsoid to oblong (angular in cross-section)

caryopses; and phosphoenolpyruvate carboxykinase (PCK) leaf metabolism (Hattersley, 1987; Baaijens & Veldkamp, 1991). This lineage is widely distributed in North America, South America, Africa–Arabia, Australia–Pacific, and Southeast Asia (Fig. 1).

Clade B.—Our analyses identify a strongly supported clade including *S. fimbriatus* and allies. *Sporobolus fimbriatus* (Trin.) Nees was included in group 4B by Pilger (1956) and more recently in *S. sect. Fimbriatae* (Baaijens & Veldkamp, 1991), as treated here (Table 1). A *S. fimbriatus* lineage was also found by Ortiz-Diaz and Culham (2000), which also included *S. pyramidatus*. Ortiz-Diaz and Culham (2000) noted that the morphology of *S. pyramidatus* does not correspond to that of other taxa included in *S. sect. Fimbriatae*. Their result is likely an error, as the multiple samples of *S. pyramidatus* sampled here are clearly part of clade I in our tree. The *S. fimbriatus* clade is almost entirely African with a single species, *S. maderaspatanus* Bor, found in India and Ceylon (Lazarides, 1994). Baaijens and Veldkamp (1991) described this section as having intravaginal branched culms, upper glumes slightly shorter to as long as the spikelets, and PCK leaf metabolism. Baaijens and Veldkamp (1991) also included *S. agrostoides* Chiov., *S. brockmannii* Stapf, and *S. macranthelus* Chiov. as members of *S. sect. Fimbriatae*. Apparently, *Sporobolus diffusus* Clayton is the only annual member of the *S. fimbriatus* complex. Tetragonal to ellipsoid caryopses and short upper glumes one half to four fifths as long as the lemmas also characterize this lineage.

Clade C.—We have included three widespread species of *Crypsis* in our study and these form a strongly supported clade, and are part of a broader, well-supported clade. *Sporobolus helvolus* (Trin.) T. Durand & Schinz, *S. mitchellii* (Trin.) C.E. Hubb. ex S.T. Blake, and *S. humilis* J. Presl form a strongly supported clade that is sister to *Crypsis*, and together this lineage is sister to three accessions of *S. ruspolianus* Chiov. Ortiz-Diaz and Culham (2000) recovered a clade with 100% jackknife support that included *Crypsis alopecuroides* (Piller & Mitterp.) Schrad., *S. helvolus*, *S. mitchellii*, and *S. tremulus* (Willd.) Kunth. The later species is morphologically very similar to *S. virginicus* (L.) Kunth but differs by having shorter lower glumes (Lazarides, 1994). Characters that support this clade include: geniculate annuals or perennials with wiry culms, panicles short, < 12 cm long that are spike-like to subspiciform (ovate with stiffly spreading branches in *S. ruspolianus*), one-flowered spikelets with glumes that are usually shorter than the lemma, and one- to three-veined lemmas.



FIGURE 2. *Sporobolus palmeri* Scribn. [P.M. Peterson 24862 & K. Romaschenko (US)]. A. Habit. B. Sheath, ligule, and blade. C. Spikelet with stigmas. D. Lower glume. E. Upper glume. F. Spikelet with stamens. G. Lemma. H. Palea. I. Palea enclosing lodicules and pistil. J. Palea enclosing lodicules, pistil, and stamens. K. Lodicules. L. Caryopsis, dorsal view. M. Caryopsis, ventral view. N. Caryopsis, side view. O. Caryopsis, cross section. Drawn by Alice Tangerini.

Clade D.—Based on our phylogram we recognize the *S. junceus* (P. Beauv.) Kunth complex (*Sporobolus* sect. *Triachyrum*) to include 15 species. This lineage was previously identified in the ITS analysis of Ortiz-Diaz and Culham (2000), who sampled seven species, three of which are also sampled here (*S. purpurascens* (Sw.) Ham., *S. lasiophyllus* Pilg., *S. sanguineus* Rendle). Palisot de Beauvois (1812) first recognized the distinctive features of *Sporobolus junceus* by describing a new genus, *Heleochloa* P. Beauv. Later, *Triachyrum* Hochst. ex A. Braun was recognized to emphasize species that have panicles with five or more whorled primary branches and caryopses that are strongly compressed (Braun, 1841). Pilger (1956) included five species of the *S. junceus* complex in his group 3A. Baaijens and Veldkamp (1991) included in this group *S. pilifer* (Trin.) Kunth, a species we surveyed, along with *S. amaliae* Veldkamp, *S. harmandii* Henrard, *S. novoguineensis* Baaijens, and *S. sciadocladus* Ohwi. The characteristics that unite the *S. junceus* complex are: caespitose habit, either annual or perennial, leaf blades that are often heteromorphic (e.g., basal blades flat often with pectinate margins and cauline blades involute with margins usually smooth), panicles that have whorled primary branches, upper glumes that are as long or longer than the floret, and caryopses that are spherical or laterally flattened. Weakley and Peterson (1998) suggested that *S. junceus* and *S. purpurascens* may be sibling species. This hypothesis is supported in part by our tree, in which the North American samples of *S. purpurascens* and both samples of *S. junceus* are sister taxa. Clade D also includes a subclade we call the southern South American *S. aeneus* (Trin.) Kunth complex, a group of some 14 traditionally recognized species that were recently revised to include only five species (Denham & Aliscioni, 2010). We sampled three taxa that have been placed in this group, *S. aeneus*, *S. acuminatus* (Trin.) Hack. (= *S. aeneus* var. *aeneus* in Denham & Aliscioni, 2010), and *S. linearifolius* Nicora. These three species are sister to an accession of *S. purpurascens* collected in Ecuador, together forming a strongly supported clade (BS = 99, PP = 1.00). It is interesting that the accession of *S. purpurascens* from Ecuador does not align with the two other accessions of *S. purpurascens*, both collected in Texas. We see no major morphological differences between these three accessions of *S. purpurascens* other than that the North American plants are taller and have longer leaf blades.

Clade E.—This lineage is recovered with strong support (BS = 100, PP = 1.00) and corresponds to *Sporobolus* sect. *Virginicae* Veldkamp. Based on possessing stolons, contracted and densely spikeleted

panicles, fascicled to solitary branches, upper glumes as long as the spikelets, and C₄ NAD-ME (nicotinamide adenine dinucleotide cofactor malic enzyme) leaf metabolism, Baaijens and Veldkamp (1991) recognized the *Sporobolus virginicus* clade (*Sporobolus* sect. *Virginicae*) to include: *S. consimilis*, *S. humilis*, *S. pungens* (Schreb.) Kunth, and *S. virginicus*. Pilger (1956) recognized these same species in his group two, along with *S. compositus* (Poir.) Merr., *S. spicatus*, and *S. rigens*, which we find aligned in other lineages or incertae sedis based on their positions in our tree. Ortiz-Diaz and Culham (2000) identified *S. virginicus* as a distinct lineage, but they did not sample other members of the lineage. In our study *S. pungens* and *S. virginicus* exclusively form a clade.

Clade F.—This strongly supported clade (BS = 100, PP = 1.00), which has not previously been recovered in molecular studies, consists of two accessions of *S. kentrophyllus* (K. Schum. ex Engl.) Clayton that are sister to *S. subulatus* Hack.—*S. verdcourtii* Napper. Clayton (1974) placed *S. verdcourtii* as a synonym of *S. kentrophyllus*, but we retain this as a separate species since our sample forms a strongly supported clade (BS = 100, PP = 1.00) with *S. subulatus* and not with other accessions of *S. kentrophyllus*. These three African species are characterized in having the perennial habit with caespitose often tussocky culms, these often connected by stolons, culms 15–80 cm tall, whorled primary panicle branches that are bare on lower quarter to half; lower glumes one third to three quarters as long as the spikelet; upper glumes two thirds to as long as the spikelet; and ellipsoid caryopses 0.8–2 mm long.

Clade G.—This strongly supported clade (BS = 100, PP = 1.00), which has not previously been recovered in molecular studies, consists of four African species. Three accessions of the primarily mat-forming, tufted perennial with pungent leaf blades, *S. spicatus*, form a weakly supported clade (BS = 64, PP = 0.61) that is sister to a strongly supported *S. microprotus* Stapf—*S. scabriflorus* Stapf ex Massey—*S. uniglumis* Stent & J.M. Rattray clade (BS = 100, PP = 1.00) consisting of three small, caespitose annuals. Clayton (1974) placed *S. scabriflorus* as a synonym of *S. microprotus*, but our ITS sequences are not identical and there seem to be some morphological characters that separate these species. *Sporobolus scabriflorus* has scabrous to minutely pubescent lemmas and the caryopses are obovate whereas most individuals of *S. microprotus* have glabrous or smooth lemmas and spherical to subglobose caryopses (PMP, pers. observ.). Morphological characteristics that support recognition of clade G include caespitose annuals or perennials; leaf blades with pectinate-ciliate margins

near the base; panicles with whorled primary branches, especially on the lower nodes, the primary branches bare below; lower glumes that are tiny, ovate to oblong scales less than one third as long as the spikelet, the scales often suppressed or lacking; upper glumes two thirds to as long as the spikelet; and caryopses 0.7–1.1 mm long that are elliptic, obovate to spherical or subglobose, and usually laterally flattened.

Clade H.—Three endemic species from Australia—*S. australasicus* Domin, *S. caroli* Mez, and *S. scabridus* S.T. Blake—form a moderately supported clade (BS = 72, PP = 0.98) and are sister to the southern African *S. nitens* Stent. Together, these four species form a strongly supported (BS = 99, PP = 1.00) clade that has not been previously recovered in molecular studies. There are another four endemic Australian species, *S. contiguus* S.T. Blake, *S. lenticularis* S.T. Blake, *S. partimpatens* R. Mills ex B.K. Simon, and *S. pulchellus* R. Br., that probably belong in this group but were not included in our analysis (Simon & Jacobs, 1999; Simon, 2005). The following shared morphological features support recognition of Clade H: caespitose annuals, occasionally biennial or perennial, then with short rhizomes and stolons; leaf blade margins smooth or pectinate-ciliate; panicles with whorled primary branches, especially on the lower nodes, primary branches bare on lower quarter to half; lower glumes one to two thirds as long as the spikelet; upper glumes as long as the spikelet; and caryopses 0.6–1.5 mm long, elliptic to oblong, often subterete, sometimes quadrangular or trigonous.

Clade I.—We refer to this lineage as the *S. pyramidatus* (Lam.) Hitchc. complex only because this species is the most wide-ranging member in the Western Hemisphere. All species in this complex share the following morphological characteristics: caespitose annuals or rhizomatous perennials; leaf blade margins smooth or pectinate-ciliate, often cartilaginous, sometimes bearing stiff hairs; panicles with whorled primary branches, especially on the lower nodes, primary branches bare below; lower glumes one fifth to nearly as long as the spikelet; upper glumes about as long as the spikelet, rarely longer; caryopses ellipsoid to obovoid, 0.6–1 mm long. Species in this clade are widely distributed from Africa, North and South America, and Australia, although the deepest split, a strongly supported clade (BS = 89, PP = 1.00) containing *S. centrifugus* (Trin.) Nees, *S. cordofanus* (Hochst. ex Steud.) Coss., and *S. marginatus* Hochst. ex A. Rich., contains only indigenous African species probably indicating African origins for the *S. pyramidatus* complex. There is strikingly little morphological and genetic variation among the wide ranging *S. pyrami-*

datus and *S. coromandelianus* (Retz.) Kunth, and the narrowly distributed *S. coahuilensis* Valdés-Reyna and *S. contractus* Hitchc. Species delimitation among these four morphologically similar entities needs clarification, requiring a worldwide approach. Likewise, the two accessions of *S. cordofanus* and of *S. marginatus* are found in different, moderate to strongly supported subclades. This could be the result of multiple gene copies of ITS, multiple origins of these taxa, or there could have been a mishandling or misidentification of our samples in the laboratory. Baaijens and Veldkamp (1991) had tentatively included *S. coromandelianus* in their *S.* sect. *Triachyrum* (*S. junceus* complex) but noted that it differed by numerous anatomical characters from other members. Whorled primary panicle branches apparently have arisen independently at least two times within *Sporobolus* since this character state is also found in the *S. junceus* complex (clade D) and the F–G–H–I clade, the latter with poor support (BS < 50, PP = 0.51).

Clade J.—This clade was first recovered by Ortiz-Diaz and Culham (2000) and is found with strong support in our ITS tree. We refer to this as the *Sporobolus airoides* complex, which consists of four caespitose perennials (*S. airoides*, *S. spiciformis* Swallen, *S. splendens* Swallen, *S. wrightii* Munro ex Scribn.) with spiciform (*S. spiciformis* Swallen) to pyramidal panicles and ascending or spreading primary branches, short spikelets 1.3–2.8 mm long, and lower glumes about half as long as the lemmas. All four species occur in alkaline soils and quite often are conspicuous members of the plant community on xeric flats and playas. Polyploid races as high as $14x$ ($2n = 128$, $x = 9$) have been found in *Sporobolus airoides* (Stebbins, 1985; Peterson et al., 2003).

Clade K.—The *Sporobolus cryptandrus* (Torr.) A. Gray complex, a group of five species (*S. cryptandrus*, *S. flexuosus* (Thurb. ex Vasey) Rydb., *S. giganteus* Nash, *S. nealleyi* Vasey, *S. texanus* Vasey) is moderately supported as a clade (BS = 87, PP = 1.00). Ortiz-Diaz and Culham (2000) recovered this clade in their ITS analysis, which included four of the five species sampled here plus *S. contractus*. In our analysis, *S. contractus* is part of clade I. The five species in the *S. cryptandrus* complex are all located in the southwestern U.S.A./Mexico, and share the following morphological features: lower branches of the panicles are usually included in the uppermost culm sheath, lower glumes that are one third to one half as long as the lemma, upper glumes about as long or longer than the lemma, and ellipsoid to obovoid caryopses. Species in this complex tend to occur in salt-desert scrub and pinyon-juniper woodlands in slightly saline environments (Peterson et al., 2003).

Clade L.—Pilger (1956) delineated this as group five in his subgeneric treatment of *Sporobolus* and Riggins (1969, 1977) investigated most of the members of clade L in a study of the annual cleistogamous species and a biosystematic study of the *Sporobolus asper* (Michx.) Kunth [= *S. compositus*] complex. Our results support the derivation of *Sporobolus clandestinus* (Biehler) Hitchc., *S. compositus*, *S. neglectus* Nash, and *S. vaginiflorus* (Torr. ex A. Gray) Alph. Wood from a common ancestor. In our tree one individual of *S. clandestinus* (Waterfall 5881) does not align with three other samples of *S. clandestinus*; rather, this sample and *S. compositus* form a clade that is the unsupported sister of the rest of the *S. asper* complex in the ITS tree. This could indicate hybridization with a member of the highly variable *S. compositus* complex (Peterson et al., 2003, 2009), multiple origins of this taxon, or simply the occurrence of multiple copies of ITS since *S. asper* is a known hexaploid (Riggins, 1977). Important characters in this lineage include panicles included in the uppermost sheath with cleistogamous spikelets and laterally flattened caryopses. Ortiz-Diaz and Culham (2000) sampled only *S. asper* from this complex, which was placed in a clade with *Calamovilfa*, in contrast with our results.

Clade M.—This is the strongly supported *Calamovilfa* lineage, congruent with the multiple molecular studies that have found *Calamovilfa* to be nested within *Sporobolus* (Ortiz-Diaz & Culham, 2000; Hilu & Alice, 2001; Columbus et al., 2007; Peterson et al., 2010a). Based on caryopsis, embryo, lodicule, leaf epidermal, and anatomical characteristics, Reeder and Ellington (1960) pointed out the similarities of *Calamovilfa* with *Sporobolus*. Gray (1848) originally recognized *Calamovilfa* as a section of *Calamagrostis*, and later Hackel (1890) raised it to generic rank. Traditionally, agrostologists have emphasized the hairy callus to circumscribe the species of *Calamovilfa*. Reeder and Ellington (1960: 76) concluded, “while such hairs are lacking among species of *Sporobolus* [it] is apparently a matter of relatively minor taxonomic importance.” The occurrence of callus hairs one fourth to seven eighths as long as the lemma and the disarticulation of the entire spikelet with intact caryopses are two synapomorphic characters that support recognition of clade M [*C. arcuata* K.E. Rogers, *C. brevopilis* (Torr.) Hack. ex Scribn. & Southw., *C. gigantea* (Nutt.) Scribn. & Merr., and *C. longifolia* (Hook.) Hack. ex Scribn. & Southw.].

Thieret (1966, 2003) recognized two sections: sect. *Calamovilfa*, including *C. arcuata*, *C. curtissii* (Vasey) Scribn., and *C. brevopilis*, distinguished pri-

marily by short rhizomes and ligules to 0.7 mm long and sect. *Interior* Thieret, including *C. gigantea* and *C. longifolia*, distinguished by elongate rhizomes and longer ligules (0.7–2.5 mm). Our analysis does not support this sectional classification. In our tree, *C. brevopilis*, *C. arcuata*, and *C. longifolia* are successive sister groups (all strongly supported) of *C. gigantea* (*C. curtissii* was not sampled).

Clade N.—This clade consists of four species (*S. heterolepis* (A. Gray) A. Gray, *S. pinetorum* Weakley & P.M. Peterson, *S. silveanus* Swallen, and *S. teretifolius* R.M. Harper); three of these were previously studied and attributed to the *Sporobolus floridanus* complex, a group found in pine savannas and seeps of the coastal plain in southeastern U.S.A. (Weakley & Peterson, 1998). Clades M and N are depicted as strongly supported sister clades in our tree (BS = 97, PP = 1.00), consistent with earlier results (Hilu & Alice, 2001; Peterson et al., 2010a). It is not surprising that members of the *S. floridanus* complex are closely related to species of *Calamovilfa* since herbarium specimens of these two groups are often mistaken for one another (Weakley & Peterson, 1998). *Sporobolus heterolepis* (A. Gray) A. Gray, a species distributed in north-central U.S.A., has been considered to be a close relative of the complex (Pilger, 1956; Weakley & Peterson, 1998). Weakley and Peterson (1998) hypothesized a close relationship between *S. heterolepis* and *S. silveanus*, which is supported by our data. *Sporobolus interruptus* Vasey, an Arizonian endemic, has also been considered to be close to this lineage, and possibly a sister to *S. heterolepis* (Weakley & Peterson, 1998). Members of the *S. floridanus* complex share the following morphological features: the perennial caespitose habit, tall culms [(0.2–)0.25–2(–2.5) m], shiny and indurated basal sheaths or dull and fibrous sheaths, open to somewhat contracted panicles that are generally longer than wide with 1–2(–3) primary branches at the lower nodes, long purplish or plumbeous spikelets [3–7(–7.2)] mm long that are purplish or plumbeous, spikelets with a glabrous callus and paleas, and caryopses that fall free from the lemma and palea at maturity.

Clade O.—This is the strongly supported *Spartina* lineage. Hubbard (1947) and Clayton and Renvoize (1986: 245) suggested that *Spartina*, “lacks close relatives,” and based on panicles with spikes (multiple branches) that bear two rows on two sides of a somewhat flattened, triangular rachis (that superficially appears to be one-sided or pectinate) arrangement of the spikelets, included the genus in the Cynodonteae (Mobblerley, 1956). Molecular studies have since firmly placed *Spartina* within the Sporobolinae, nested within *Sporobolus* (Hilu & Alice, 2001; Co-

lumbus et al., 2007; Peterson et al., 2010a), as reflected in recent classifications (Peterson et al., 2004, 2007). These earlier analyses, which all had sparse sampling of *Spartina*, *Sporobolus* and relatives, variously placed *Spartina* in a strongly supported clade with *Calamovilfa* plus *S. heterolepis* (Hilu & Alice, 2001; matK), *Calamovilfa* (Columbus et al., 2007; combined ITS and *trnL-F*), and *Calamovilfa longifolia* plus *S. teretifolius-S. pinetorum* (Peterson et al., 2010a; combined ITS and plastid data). Our better-sampled tree is consistent with these earlier results. In our ITS tree, *Spartina* is part of a well-supported clade (BS = 98, PP = 1.00) that includes a clade of *Calamovilfa* (clade M) (plus a clade comprising *S. compositus* and one individual of *S. clandestinus*) and the *Sporobolus floridanus* complex (clade N) and the core *Sporobolus asper* complex (clade L). Our data suggests that *Spartina* and several of the other major North American lineages are derived from a common ancestor.

Within *Spartina*, our tree identifies three major lineages, one comprising mostly tetraploid ($2n = 40$) species *Spartina gracilis* Trin., *S. cynosuroides* (L.) Roth, *S. ×caespitosa* A.A. Eaton, *S. pectinata* Link, *S. bakeri* Merr., *S. patens* (Aiton) Muhl., *S. ciliata* Brongn., *S. densiflora* Brongn., and *S. montevidensis* Arechav.; one comprising the hexaploid ($2n = 60, 62$) species *S. alterniflora* Loisel., *S. foliosa* Trin., and *S. maritima* (Curtis) Fernald; and *S. spartinae* (Trin.) Merr. ex Hitchc. This topology is congruent with, and better resolved than, the trees recovered in earlier phylogenetic analyses based on ITS and the plastid *trnT-trnL* region (Baumel et al., 2002; Fortune et al., 2008), with the caveat that we did not sample *S. arundinacea* (Thouars) Carmich. Trees based on nuclear data differed from the present study only in the inferred interrelationships among *S. cynosuroides*, *S. pectinata*, and *S. gracilis*. These species formed a polytomy with the other lineages in the tetraploid clade, but are fully resolved here. This may reflect alignment differences and/or the different phylogenetic analyses conducted (parsimony in the earlier studies and ML and Bayesian here).

Baumel et al. (2002) sampled the nuclear *waxy* locus, which is incongruent with ITS. In the *waxy* trees the tetraploid species *S. argentinensis* (= *S. spartinae*) was sister to the hexaploid clade, and the heptaploid *S. densiflora* ($2n = 70$; Ayres et al., 2008; Fortune et al., 2008) was the sister group of the hexaploid plus *S. argentinensis* clade. Subsequent phylogenetic studies of *Spartina*, based on extensive cloning of the low copy nuclear gene *waxy*, focused on the hexaploid species (Fortune et al., 2007) and *S. densiflora* (Fortune et al., 2008). In the former study, two major lineages

were identified, neither of which was congruent with the clades identified in our ITS analysis. Multiple copies of *waxy* representing divergent lineages were found in *S. alterniflora* and *S. foliosa*, and the hexaploid lineage was not found to be monophyletic; these data support an allopolyploid origin for the hexaploid clade. Multiple divergent copies were also found in other *Spartina* species, and the phylogenetic tree based on these sequences was similarly discordant with the tree inferred from ITS data (Fortune et al., 2007). This study also sampled *waxy* in other Chloridoideae taxa, and found the sequences of *Thellungia advena*, *Sporobolus indica*, *Calamovilfa gigantea*, and *C. longifolia* to be part of the *Spartina* lineage. Fortune et al. (2007) hypothesized that the two major *waxy* clades represent paralogous copies of the gene that were inherited by *Spartina* (i.e., the paralogous copies were present prior to the origin of the genus) and also by other members of the Chloridoideae. The placement of *Sporobolus indicus* (in Clade A)—a taxon that shares a *waxy* paralogue with some *Spartina* species—near the base of the Sporobolinae subtree in our analyses suggests that the gene duplication may have occurred early during, or prior to, the evolution of the Sporobolinae lineage. In the seminal revisionary treatment of *Spartina*, Moberley (1956) recognized three complexes that, with the exception of *Spartina ciliata*, correspond with the three subclades in our phylogram. Moberley (1956) described complex 1 (*Spartina arundinacea* and *S. spartinae*) as having hard and slender culms, without rhizomes or with short (less than 1.5 cm) and thick rhizomes, panicles spike-like with closely imbricate spikes (multiple branches), spikelets lanceolate and closely imbricate, and upper glumes with hispid keels; complex 2 (*S. alterniflora*, *S. anglica*, *S. foliosa*, *S. longispica* Hauman & Parodi ex St.-Yves [now considered to be a hybrid of *S. alterniflora* and *S. densiflora* (Bortolus, 2006)], *S. maritima*, and *S. ×townsendii*) as having thick, fleshy, and succulent culms that become brownish in age with a distinctly disagreeable odor when fresh, smooth and glabrous leaf blades, and panicles with remote or moderately imbricate spikes, and upper glumes with glabrous, pilose, or rarely hispid keels; and complex 3 (*S. bakeri*, *S. ×caespitosa*, *S. ciliata*, *S. cynosuroides*, *S. densiflora*, *S. gracilis*, *S. patens*, *S. pectinata*, and *S. versicolor* Fabre) as having hard culms often tinged or streaked with purple, scabrous leaf blades, panicle spikes more or less spreading and often tinged or streaked with purple, closely imbricate spikelets, and upper glumes with hispid keels. Although *S. densiflora* has a complicated reticulate origin, we include it in complex three on the basis of its morphology.

CLASSIFICATION OF THE CHLORIDOIDEAE

Since Peterson et al. (2010a), the classification within the Chloridoideae has undergone considerable rearrangement (Kellogg, 2015; Peterson et al., 2011, 2012, 2014a, 2015, 2016; Soreng et al., 2015). We present an updated version of our classification (Table 2) to point out areas lacking critical data. Eight genera are listed as incertae sedis within the subfamily, and there are seven incertae sedis genera listed in the Cynodonteae. Most genera listed as incertae sedis have not yet been included in a molecular analysis simply because material is unavailable or, in a few cases, known only from a single collection. It is no longer possible to objectively evaluate relationships among taxa without baseline information from DNA sequence markers because there is no way to accurately polarize complex morphological traits (i.e., determine what is plesiomorphic or apomorphic) in the evolution of a lineage or ascertain the criteria of homology (i.e., the difference between an analogous or homologous character). An online version of this classification (continually updated) is available at

<http://tropicos.org/projectwebportal.aspx?pagename=ClassificationNWG&projectid=10> (Soreng et al., 2016).

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TABLE 2. A proposed tribal and subtribal classification of genera in subfamily Chloridoideae (Poaceae).

Subfamily Chloridoideae Kunth ex Beilschm.

Incertae sedis: *Indopoa* Bor, *Lepturopetium* Morat, *Myriostachya* (Benth.) Hook.f., *Pogonochloa* C. E.

Hubb., *Pseudozoyisia* Chiov., *Silentvalleya* V. J. Nair, *Viguiarella* A. Camus

Tribe Centropodieae P. M. Peterson, N. P. Barker & H. P. Linder: *Centropodia* Rchb., *Ellisochloa*

P. M. Peterson & N. P. Barker

Tribe Cynodonteae Dumort.

Incertae sedis: *Allolepis* Soderstr. & H. F. Decker, *Decaryella* A. Camus, *Jouvea* E. Fourn., *Kalinia* H. L.

Bell & Columbus, *Kampochloa* Clayton, *Lepturidium* Hitchc. & Ekman, *Oxychloris* Lazarides,

Sohnsia Airy Shaw, *Vietnamochloa* Veldkamp & Nowack

Subtribe Aeluropodinae P. M. Peterson: *Aeluropus* Trin., *Odyssea* Stapf

Subtribe Boutelouinae Stapf: *Bouteloua* Lag. (includes *Buchloe* Engelm., *Buchlomimus* Reeder, C. Reeder

& Rzed., *Cathesticum* J. Presl, *Chondrosium* Desv., *Cyclostachya* Reeder & C. Reeder, *Griffithsochloa*

G. J. Pierce, *Opizia* J. Presl, *Pentarraphis* Kunth, *Pringleochloa* Scribn., and *Soderstromia* C. V. Morton)

Subtribe Cteniinae P. M. Peterson, Romasch. & Y. Herrera: *Ctenium* Panz.

Subtribe Dactylocteniinae P. M. Peterson, Romasch. & Y. Herrera: *Acrachne* Wight & Arn. ex Chiov.,

Brachychloa S. M. Phillips, *Dactyloctenium* Willd., *Neobouteloua* Gould

Subtribe Eleusininae Dumort.: *Afrotrichloris* Chiov., *Apochiton* C. E. Hubb., *Astrebla* F. Muell., *Austro-*

chloris Lazarides, *Chloris* Sw. (includes *Ochthochloa* Edgew.), *Chrysochloa* Swallen, *Coelachyrum*

Hochst. & Nees (includes *Coelachyropsis* Bor), *Cynodon* Rich. [includes *Brachyachne* (Benth.) Stapf],

Daknopholis Clayton, *Dinebra* Jacq. (includes *Drake-Brockmania* Stapf, *Heterocarpha* Stapf &

C.E. Hubb., *Oxydenia* Nutt.), *Diplachne* P. Beauv., *Disakisperma* Steud. (includes *Cypholepis* Chiov.),

Eleusine Gaertn., *Enteropogon* Nees, *Eustachys* Desv., *Harpochloa* Kunth, *Leptochloa* P. Beauv.

(includes *Trichloris* E. Fourn. ex Benth.), *Lepturus* R. Br., *Lintonia* Stapf, *Micrachne* P. M. Peterson,

Romasch. & Y. Herrera, *Microchloa* R. Br. (includes *Rendlia* Chiov.), *Neostapfiella* A. Camus, *Oxychloris*

Lazarides, *Pommereulla* L.f., *Rheochloa* Filg., P. M. Peterson & Y. Herrera, *Schoenefeldia* Kunth,

Sclerodactylon Stapf, *Stapfochloa* H. Scholz, *Tetrapogon* Desf. (includes *Saugetia* Hitchc. & Chase)

(continued)

TABLE 2. (continued)

Subtribe Farragininae P. M. Peterson Romasch. & Y. Herrera: <i>Craspedorhachis</i> Benth., <i>Farrago</i> Clayton
Subtribe Gouiniinae P. M. Peterson & Columbus: <i>Gouinia</i> E. Fourn. ex Benth. & Hook, <i>Schenckochloa</i> J. J. Ortiz, <i>Tridentopsis</i> P. M. Peterson, <i>Triplasiella</i> P. M. Peterson & Romasch., <i>Triplasis</i> P. Beauv., <i>Vaseyochloa</i> Hitchc.
Subtribe Hilarinae P. M. Peterson & Columbus: <i>Hilaria</i> Kunth (includes <i>Pleuraphis</i> Torr.)
Subtribe Hubbardochloinae Auquier (syn. <i>Gymnopogoninae</i> P. M. Peterson Romasch. & Y. Herrera): <i>Bewsia</i> Goossens, <i>Dignathia</i> Stapf, <i>Gymnopogon</i> P. Beauv., <i>Hubbardochloa</i> Auquier, <i>Leptocarydion</i> Stapf, <i>Leptothrium</i> Kunth (includes <i>Latipes</i> Kunth), <i>Lophacme</i> Stapf
Subtribe Monanthochloinae Pilg. ex Potztl: <i>Distichlis</i> Raf. (includes <i>Monanthochloe</i> Engelm., <i>Reederochloa</i> Soderst. & H. F. Decker)
Subtribe Muhlenbergiinae Pilg.: <i>Muhlenbergia</i> Schreb. (includes <i>Aegopogon</i> Humb. & Bonpl. ex Willd., <i>Bealia</i> Scribn., <i>Blepharoneuron</i> Nash, <i>Chaboissaea</i> E. Fourn, <i>Lycurus</i> Kunth, <i>Pereilema</i> J. Presl, <i>Redfieldia</i> Vasey, <i>Schaffnerella</i> Nash, <i>Schedonnardus</i> Steud.)
Subtribe Orcuttiinae P. M. Peterson & Columbus: <i>Neostapfia</i> Burttt Davy, <i>Orcuttia</i> Vasey (includes <i>Tuctoria</i> Reeder)
Subtribe Orininae P. M. Peterson, Romasch. & Y. Herrera: <i>Cleistogenes</i> Keng, <i>Orinus</i> Hitchc.
Subtribe Pappophorinae Dumort. [syn. <i>Tridentinae</i> Keng & Keng f.]: <i>Neesiochloa</i> Pilg., <i>Pappophorum</i> Schreb., <i>Tridens</i> Roem. & Schult.
Subtribe Perotidinae P. M. Peterson, Romasch. & Y. Herrera: <i>Mosdenia</i> Stent, <i>Perotis</i> Aiton (includes <i>Lopholepis</i> Decne., <i>Toliara</i> Judz.), <i>Trigonochloa</i> P. M. Peterson & Snow
Subtribe Traginae P. M. Peterson & Columbus: <i>Monelytrum</i> Hack., <i>Orthacanthus</i> P. M. Peterson & Romasch., <i>Pogononeura</i> Napper, <i>Polevansia</i> De Winter, <i>Tragus</i> Haller, <i>Willkommia</i> Hack. (includes <i>Willbleibia</i> Herter)
Subtribe Trichoneurinae P. M. Peterson, Romasch. Y. Herrera: <i>Trichoneura</i> Andersson
Subtribe Triodiinae Benth.: <i>Triodia</i> R. Br. (includes <i>Monodia</i> S.W.L. Jacobs, <i>Plectrachne</i> Henrard, <i>Symplectrodia</i> Lazarides)
Subtribe Tripogoninae Stapf: <i>Desmostachya</i> (Stapf) Stapf, <i>Eragrostiella</i> Bor, <i>Halopyrum</i> Stapf, <i>Melanocenchris</i> Nees, <i>Oropetium</i> Trin., <i>Tripogon</i> Roem. & Schult., <i>Tripogonella</i> P. M. Peterson & Romasch.
Subtribe Scleropogoninae Pilg. (syn. <i>Munroinae</i> Parodi ex P. M. Peterson): <i>Blepharidachne</i> Hack., <i>Dasyochloa</i> Rydb., <i>Erioneuron</i> Nash, <i>Munroa</i> Torr., <i>Scleropogon</i> Phil., <i>Swallenia</i> Soderstr. & H. F. Decker
Subtribe Zaqiqahinae P. M. Peterson, Romasch. & Y. Herrera: <i>Zaqiqah</i> P. M. Peterson & Romasch.
Tribe Eragrostideae Stapf
Subtribe Cotteinae Reeder: <i>Cottea</i> Kunth, <i>Enneapogon</i> P. Beauv., <i>Kaokochloa</i> De Winter, <i>Schmidtia</i> Steud. ex J. A. Schmidt
Subtribe Eragrostidinae J. Presl: <i>Catalepis</i> Stapf, <i>Cladoraphis</i> Franch., <i>Eragrostis</i> Wolf [includes <i>Acamptocladus</i> Nash, <i>Diandrochloa</i> De Winter, <i>Ectrosia</i> R. Br., <i>Ectrosiopsis</i> (Ohwi) Ohwi ex Jansen see Nightingale and Weiller, 2005, <i>Harpachne</i> A. Rich., <i>Neeragrostis</i> Bush, <i>Planichloa</i> B. K. Simon, <i>Pogonarthria</i> Stapf, <i>Psammagrostis</i> C. A. Gardner & C. E. Hubb., <i>Stiburus</i> Stapf.], <i>Heterachne</i> Benth., <i>Richardsiella</i> Elffers & Kenn.-O'Byrne, <i>Steirachne</i> Ekman
Subtribe Uniolinae Clayton: <i>Entoplocamia</i> Stapf, <i>Fingerhuthia</i> Nees ex Lehm., <i>Tetrachaete</i> Chiov., <i>Tetrachne</i> Nees, <i>Uniola</i> L.
Tribe Triraphideae P. M. Peterson: <i>Habrochloa</i> C.E. Hubb., <i>Neyraudia</i> Hook. f., <i>Triraphis</i> R. Br.
Tribe Zoysieae Benth.
Subtribe Sporobolinae Benth: <i>Psilolemma</i> S. M. Phillips, <i>Sporobolus</i> R. Br. [includes <i>Calamovilfa</i> (A. Gray) Scribn., <i>Crypsis</i> Aiton, <i>Heleochoa</i> Host ex Roem., <i>Spartina</i> Schreb., <i>Thellungia</i> Stapf]
Subtribe Zoysiinae Benth.: <i>Urochondra</i> C. E. Hubb., <i>Zoysia</i> Willd.

¹ Letters in boldface correspond to the clades in Fig. 1.² The proposed assignments are based on plastid and nuclear DNA analyses and/or morphology.

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APPENDIX

LIST OF SPECIMENS SAMPLED TAXON (*ASTERISK INDICATES TYPE SPECIES FOR THE GENUS), VOUCHER (COLLECTOR, NUMBER, AND WHERE THE SPECIMEN IS HOUSED), COUNTRY OF ORIGIN, AND GENBANK ACCESSION FOR NUCLEAR DNA rITS REGION (ACCESSIONS IN BOLDFACE ARE NEW). HERBARIUM ACRONYMS FOLLOW THIERS (CONTINUOUSLY UPDATED).

- OUTGROUP:** *Aristida gypsophila* Beetle, *Peterson 15839 & Valdes-Reyna* (US), Mexico, GU359267; *Chasmanthium latifolium* (Michx.) H. O. Yates, *Peterson 22463* (US), U.S.A., GU359319; *Danthonia compressa* Austin, *Peterson 21986 & Levine* (US), U.S.A., GU359345; *Rytidosperma pallidum* (R. Br.) A. M. Humphreys & H. P. Linder, *Peterson 19685, Saarela & Sears* (US), U.S.A., GU359183; **CENTROPODIEAE:** **Ellisochloa rangei* (Pilg.) P. M. Peterson & N. P. Barker, *Barker 960* (BOL), Namibia, JQ345167; **TRIRAPHIDEAE:** *Neyraudia reynaudiana* (Kunth) Keng ex Hitchcock, *Soreng 5318 & Peterson* (US), China, GU359124; **Triraphis mollis* R. Br., *Peterson 14344, Soreng & Rosenberg* (US), Australia, GU359187; **ERAGROSTIDEAE:** **Cottea pappophoroides* Kunth, *Peterson 21463, Soreng, LaTorre & Rojas Fox* (US), Peru, GU359237; *Ectrosia scabrida* C. E. Hubb., *Lazarides 4772* (US), Australia, GU359317; *Enneapogon desvauxii* P. Beauv., *Peterson 21999 & Saarela* (US) Mexico, GU359339; *Entoplocamia aristulata* (Hack. & Rendle) Stapf, *Seydel 187* (US), South Africa, GU359342; *Eragrostis desertorum* Domin, *Peterson 14358, Soreng & Rosenberg* (US), Australia, GU359289; *Harpachne harpachnoides* (Hack.) B. S. Sun & S. Wang, *Soreng 5288, Peterson & Sun Hang* (US), China, GU359113; *Pogonarthria squarrosa* (Roem. & Schult.) Pilg., *Mawi 180, Majengo, Salum & Samwe* (MO), Tanzania, **KM010325**; **Psammagrostis wiseana* C. A. Gardner & C. E. Hubb., *Peterson 14345, Soreng & Rosenberg* (US), Australia, GU359137; *Schmidtia pappophoroides* Steud. ex J. A. Schmidt, *Smook 10558* (MO), South Africa, **KM010328**; *Tetrachne dregei* Nees, *Jarman 120* (US), South Africa, GU359218; *Uniola condensata* Hitchc., *Peterson 9342 & Judziewicz* (US), Ecuador, GU359191; **ZOYSIEAE:** *Calamovilfa arcuata* K.E. Rogers, *Rogers 42409, Sharp & Delgadillo* (US), U.S.A., **KM010315**; *Calamovilfa brevipilis* (Torr.) Hack. ex Scribn. & Southw., *Strong 848, Kell-off, Schuyler, Wurdack & Churchill* (US), U.S.A., **KM010316**; *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., *Gates 17021* (US), U.S.A., **KM010317**; *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., *Long 1124* (BRY), U.S.A., **KM010318**; *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., *Ungor 1018* (US), U.S.A., **KM010319**; *Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., *Hatch 5738 & Bearden* (US), U.S.A., GU359300; *Crypsis aculeata* (L.) Aiton, *Soreng 5469 & Peterson* (US), China, GU359238; **Crypsis aculeata* (L.) Aiton, *Soreng 7940* (US), Russia, JQ345163; *Crypsis alopecuroides* (Piller & Mitterp.) Schrad., *Soreng 7941, D. Johnson, P. Johnson, Dzubenko & Schilnikov* (US), Russia, **KM010320**; *Crypsis schoenoides* (L.) Lam., *Peterson 19814, Saarela & Sears* (US), U.S.A., GU359239; *Psilolemma jaegeri* (Pilg.) S. M. Phillips, *Peterson 24247, Soreng & Romaschenko* (US), Tanzania, **KM010326**; *Psilolemma jaegeri* (Pilg.) S. M. Phillips, *Peterson 24249, Soreng & Romaschenko* (US), Tanzania, **KM010327**; *Spartina townsendii* H. Groves & J. Groves, *Saarela 791 & Percy* (UBC), Canada, **KM010329**; *Spartina alterniflora* Loisel., *Lakela 26573* (US), U.S.A., **KM010330**; *Spartina alterniflora* Loisel., *Naylov 236* (US), U.S.A., **KM010331**; *Spartina anglica* C.E. Hubb., *Matthews s.n.* (CAN), United Kingdom, **KM010332**; *Spartina anglica* C. E. Hubb., *Williams 2004-1* (UBC), Canada, **KM010333**; *Spartina anglica* C. E. Hubb., *Williams*

2004-2 (UBC), Canada, **KM010334**; *Spartina bakeri* Merr., Killip 44361 (US), U.S.A., **KM010335**; *Spartina x caespitosa* A. A. Eaton, Eaton 587 (US), U.S.A., **KM010336**; *Spartina ciliata* Brongn., Rambo 56450 (US), Brazil, **KM010337**; *Spartina cynosuroides* (L.) Roth, Fisher 33123 (US), U.S.A., **KM010338**; *Spartina cynosuroides* (L.) Roth, Hill 15630 (US), U.S.A., **KM010339**; *Spartina densiflora* Brongn., Lomer 5723 (UBC), Canada, **KM010340**; *Spartina densiflora* Brongn., Peterson 19154, Soreng, Salariado & Panizza (US), Argentina, GU359206; *Spartina foliosa* Trin., Reeder 6652 & Reeder (US), Mexico, **KM010341**; *Spartina gracilis* Trin., Hendrickson 41 (USZ), U.S.A., **KM010342**; *Spartina gracilis* Trin., Lewis 78-1013 (CAN), Canada, **KM010343**; *Spartina gracilis* Trin., Scoggan 15626 (CAN), Canada, **KM010344**; *Spartina maritima* (Curtis) Fernald, Fernández Casas 5537, Castroviejo, Muñoz Garmendia & Susanna (US), Morocco, **KM010345**; *Spartina montevidensis* Arechav., Clayton 4723 & Eiten (US), Brazil, **KM010346**; *Spartina patens* (Aiton) Muhl., Dutton 2536 (CAN), U.S.A., **KM010347**; *Spartina patens* (Aiton) Muhl., Peterson 24435 & Romaschenko (US), U.S.A., **KM010348**; *Spartina patens* (Aiton) Muhl., Shchepanek 6426 & Dugal (CAN), Canada, **KM010349**; *Spartina pectinata* Link, Cooperrider s.n. (US), U.S.A., **KM010350**; *Spartina pectinata* Link, Dirig 2812 (US), U.S.A., **KM010351**; *Spartina spartinae* (Trin.) Merr. ex Hitchc., Reeder 4568 & C. Reeder (US), Mexico, **KM010352**; *Spartina spartinae* (Trin.) Merr. ex Hitchc., Villarreal 3201 (US), Mexico, **KM010353**; *Sporobolus acinifolius* Stapf, Smook 3530 (US), South Africa, **KM010354**; *Sporobolus actinocladius* (F.Muell.) F. Muell., Battanoff 04111164 (MEL), Australia, **KM010355**; *Sporobolus actinocladius* (F.Muell.) F. Muell., Saarela 1625 (US), Australia, **KM010356**; *Sporobolus actinocladius* (F. Muell.) F. Muell., Saarela 1670 (US), Australia, **KM010357**; *Sporobolus actinocladius* (F. Muell.) F. Muell., Senaratne E6082-5 (US), Australia, **KM010358**; *Sporobolus acuminatus* (Trin.) Hack., Guala 1372 & Filgueiras (US), Brazil, **KM010359**; *Sporobolus acuminatus* (Trin.) Hack., Irwin 11586, Souza & Reis dos Santos (US), Brazil, **KM010360**; *Sporobolus aeneus* (Trin.) Kunth, Irwin 25327, Onishi, da Fonseca, Souza, Reis dos Santos & Ramos (US), Brazil, **KM010361**; *Sporobolus africanus* (Poir.) Robyns & Tournay, Peterson 24024, Soreng & Romaschenko (US), Tanzania, **KM010362**; *Sporobolus africanus* (Poir.) Robyns & Tournay, Peterson 24121, Soreng & Romaschenko (US), Tanzania, **KM010363**; *Sporobolus airoides* (Torr.) Torr., Peterson 10002, Annable & Valdes-Reyna (US), Mexico, **KM010364**; *Sporobolus airoides* subsp. *airoides*, Peterson 24587 & Romaschenko (US), Mexico, **KM010365**; *Sporobolus airoides* subsp. *airoides*, Peterson 24853 & Romaschenko (US), Mexico, **KM010366**; *Sporobolus airoides* (Torr.) Torr., Peterson 24895 & Romaschenko (US), Mexico, **KM010367**; *Sporobolus airoides* (Torr.) Torr., Peterson 24956 & Romaschenko (US), Mexico, **KM010368**; *Sporobolus albicans* Nees, Smook 2459 & Russell (US), South Africa, **KM010369**; *Sporobolus apiculatus* Boechat & Longhi-Wagner, Irwin 8041, Souza & Reis des Santos (US), Brazil, **KM010370**; *Sporobolus arabicus* Boiss., Rawi 10781, Jalili & Armer (US), Kuwait, **KM010371**; *Sporobolus atrovirens* (Kunth) Kunth, Peterson 22342 & Saarela (US), Mexico, GU359207; *Sporobolus atrovirens* (Kunth) Kunth, Peterson 24661 & Romaschenko (US), Mexico, **KM010373**; *Sporobolus atrovirens* (Kunth) Kunth, Peterson 24729 & Romaschenko (US), Mexico, **KM010374**; *Sporobolus atrovirens* (Kunth) Kunth, Rosalen 3381 & Herrera (CIIDIR), Mexico, **KM010375**; *Sporobolus australasicus* Domin, Peterson 14404, Soreng & Rosenberg (US), Australia, **KM010376**; *Sporobolus australasicus* Domin, Walsh 4237 (MEL), Australia, **KM010377**; *Sporobolus berterioanus* (Trin.) Hitchc. & Chase, Peterson 8753, Annable & Poston (US), Ecuador, **KM010378**; *Sporobolus blakei* De Nardi ex B. K. Simon, Latz 10662 (MEL), Australia, **KM010379**; *Sporobolus bogotensis* Swallen & García-Barr., Peterson 14970 & Refulio Rodriguez (US), Peru, **KM010380**; *Sporobolus brockmanii* Stapf, Gillet 4016 (US), Somalia, **KM010381**; *Sporobolus buckleyi* Vasey, Lira 546, Martinez, Alvarez, Ramirez, Medrod & Gamboa (CIIDIR), Mexico, **KM010382**; *Sporobolus buckleyi* Vasey, Piedra s.n. (CIIDIR), Mexico, **KM010383**; *Sporobolus buckleyi* Vasey, Rodriguez 94 & Villareal (CIIDIR), Mexico, **KM010384**; *Sporobolus caroli* Mez, Saarela 1626, Peterson & Soreng (US), Australia, **KM010386**; *Sporobolus caroli* Mez, Speak 1915 (US), Australia, **KM010387**; *Sporobolus centrifugus* (Trin.) Nees, Hoener 2133 (US), South Africa, **KM010388**; *Sporobolus clandestinus* (Biehler) Hitchc., Freeman 6687 (US), U.S.A., **KM010389**; *Sporobolus clandestinus* (Biehler) Hitchc., Schuster 197 (US), U.S.A., **KM010390**; *Sporobolus clandestinus* (Biehler) Hitchc., Waterfall 5881 (US), U.S.A., **KM010385**; *Sporobolus clandestinus* (Biehler) Hitchc., Waterfall 12309 (US), U.S.A., **KM010391**; *Sporobolus coahuilensis* Valdés-Reyna, Gonzales 3600 (CIIDIR), Mexico, **KM010392**; *Sporobolus coahuilensis* Valdés-Reyna, Peterson 10000 & Annable (US), Mexico, **KM010393**; *Sporobolus compositus* (Poir.) Merr., Brodowich 1305 (US), U.S.A., **KM010372**; *Sporobolus confinis* (Steud.) Chiov., Pe-

- terson 24303, *Soreng & Romaschenko* (US), Tanzania, **KM010394**; *Sporobolus consimilis* Fresen., *Collenette 17* (US), Somalia, **KM010395**; *Sporobolus consimilis* Fresen., *Peterson 24252*, *Soreng & Romaschenko* (US), Tanzania, **KM010396**; *Sporobolus contractus* Hitchc., *Perez 196* (US), Mexico, **KM010397**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Greenway 10191* (US), Tanzania, **KM010398**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Laegaard 15973* (US), Zimbabwe, **KM010399**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Peterson 24232*, *Soreng & Romaschenko* (US), Tanzania, **KM010400**; *Sporobolus coromandelianus* (Retz.) Kunth, *Fosberg 51193*, *Mueller-Dombois*, *Wirawan*, *Cooray & Balakrishnan* (US), Sri Lanka, **KM010401**; *Sporobolus coromandelianus* (Retz.) Kunth, *Peterson 24269*, *Soreng & Romaschenko* (US), Tanzania, **KM010402**; *Sporobolus coromandelianus* (Retz.) Kunth, *Schweinfurth 896 & Nil* (US), Ethiopia, **KM010403**; *Sporobolus creber* De Nardi, *Brown 498* (MEL), Australia, **KM010403**; *Sporobolus cryptandrus* (Torr.) A. Gray, *Peterson 24454 & Romaschenko* (US), Mexico, **KM010405**; *Sporobolus cryptandrus* (Torr.) A. Gray, *Peterson 24485 & Romaschenko* (US), Mexico, **KM010406**; *Sporobolus diandrus* (Retz.) P. Beauv., *Peterson 14389*, *Soreng & Rosenberg* (US), Australia, **KM010407**; *Sporobolus diffusus* Clayton, *Lovett 2179*, *Handy & Bygott* (DSM), Tanzania, **KM010408**; *Sporobolus dinklagei* Mez, *Hale 11* (US), Liberia, **KM010409**; *Sporobolus domingensis* (Trin.) Kunth, *Swallen 10669* (US), U.S.A., **KM010410**; *Sporobolus eyesii* Stent & J.M. Rattray, *Wiche 717* (US), Malawi, **KM010411**; *Sporobolus farinosus* Hosok., *Wood 3275 & Perlman* (US), Guam, **KM010412**; *Sporobolus fertilis* (Steud.) Clayton, *Gould 13535* (US), Sri Lanka, **KM010413**; *Sporobolus fertilis* (Steud.) Clayton, *Raulerson 775* (US), Guam, **KM010414**; *Sporobolus festivus* Hochst. ex A. Rich., *Peterson 23853*, *Soreng & Romaschenko* (US), Tanzania, **KM010415**; *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24206*, *Soreng & Romaschenko* (US), Tanzania, **KM010416**; *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24241*, *Soreng & Romaschenko* (US), Tanzania, **KM010417**; *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24280*, *Soeng & Romaschenko* (US), Tanzania, **KM010418**; *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb., *Reeder 5477 & Reeder* (US), U.S.A., **KM010419**; *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb., *Valdes-Reyna 2014 & Peterson* (CIIDIR), Mexico, **KM010420**; *Sporobolus giganteus* Nash, *Page 2628* (US), U.S.A., **KM010422**; *Sporobolus greenwayi* Napper, *Greenway 12526* (US), Tanzania, **KM010423**; *Sporobolus helvolus* (Trin.) T. Durand & Schinz, *Laegaard 17063 & Traore* (US), Senegal, **KM010424**; *Sporobolus helvolus* (Trin.) T. Durand & Schinz, *Peterson 24217*, *Soreng & Romaschenko* (US), Tanzania, **KM010425**; *Sporobolus heterolepis* (A. Gray) A. Gray, *Davidse 19101* (US), U.S.A., **KM010426**; *Sporobolus humilis* subsp. *humilis* Veldkamp, *Clayton 5879* (US), Sri Lanka, **KM010427**; *Sporobolus indicus* (L.) R. Br., *Peterson 22025 & Saarela* (US), Mexico, GU359209; *Sporobolus indicus* (L.) R. Br., *Peterson 7337* (US), Panama, **KM010428**; *Sporobolus infirmus* Mez, *Haines 332* (US), Nigeria, **KM010429**; *Sporobolus ioclados* (Nees ex Trin.) Nees, *Smook 5920* (US), South Africa, **KM010430**; *Sporobolus jacquemontii* Kunth, *Estrada 18964* (CIIDIR), Mexico, **KM010431**; *Sporobolus jacquemontii* Kunth, *Peterson 15902 & Valdes-Reyna* (US), Mexico, **KM010432**; *Sporobolus junceus* (P. Beauv.) Kunth, *Strong 2332* (US), U.S.A., **KM010433**; *Sporobolus junceus* (P. Beauv.) Kunth, *Thieret 25181* (US), U.S.A., **KM010434**; *Sporobolus kentrophyllus* (K.Schum. ex Engl.) Clayton, *Bogdan 3306* (US), Kenya, **KM010435**; *Sporobolus kentrophyllus* (K.Schum. ex Engl.) Clayton, *Mwasumbi 13049* (DSM), Tanzania, **KM010436**; *Sporobolus lasiophyllus* Pilg., *Peterson 21820 & Soreng* (US), Peru, **KM010437**; *Sporobolus lasiophyllus* Pilg., *Peterson 21879*, *Soreng & Sanchez Vega* (US), Peru, GU359210; *Sporobolus laxus* B. K. Simon, *Simon 4166* (MEL), Australia, **KM010438**; *Sporobolus linearifolius* Nicora, *Reitz 5292* (US), Brazil, **KM010439**; *Sporobolus ludwigii* Hochst., *Smook 2857* (US), South Africa, **KM010440**; *Sporobolus marginatus* Hochst. ex A. Rich., *Leippert 5101* (US), Uganda, **KM010441**; *Sporobolus marginatus* Hochst. ex A. Rich., *Rattray 664* (US), Zimbabwe, **KM010442**; *Sporobolus microprotus* Stapf, *Laegaard 17894 & Traore* (US), Senegal, **KM010443**; *Sporobolus mitchellii* (Trin.) C. E. Hubb. ex S. T. Blake, *Forster 22301* (MEL), Australia, **KM010444**; *Sporobolus molleri* Hack., *Gereau 5790*, *Mbago & Kayombo* (DSM), Tanzania, **KM010445**; *Sporobolus molleri* Hack., *Rwaburindore 2183* (US), Uganda, **KM010446**; *Sporobolus montanus* (Hook. f.) Engl., *Dusen 420* (US), Cameroon, **KM010447**; *Sporobolus myrianthus* Benth., *Gereau 3491*, *Lovett & Kayombo* (DSM), Tanzania, **KM010448**; *Sporobolus natalensis* (Steud.) T. Durand & Schinz, *Eddie 1141* (MEL), Australia, **KM010449**; *Sporobolus nealleyi* Vasey, *Peterson 17839*, *Valdes-Reyna & Hinton* (US), Mexico, **KM010450**; *Sporobolus nealleyi* Vasey, *Villarreal 1991*, *Carranza & Valdez* (CIIDIR), Mexico, **KM010451**; *Sporobolus neglectus* Nash, *Theodore 5890 & Cochrane* (US), U.S.A., **KM010452**; *Sporobolus nervosus* Hochst., *Wood 2021* (US), Yemen,

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Hitchc., *Peterson 8920*, *Annable* & *Poston* (US), Ecuador, **KM010480**; *Sporobolus rigens* (Trin.) Desv., *Peterson 19224*, *Soreng*, *Salariado* & *Panizza* (US), Argentina, GU359213; *Sporobolus robustus* Kunth, *Laegaard 17398*, *Goudiaby*, *Madesn*, *Samba* & *Traore* (US), Senegal, **KM010481**; *Sporobolus ruspolianus* Chiov., *Bally 15581* & *Melville* (DSM), Somalia, **KM010482**; *Sporobolus ruspolianus* Chiov., *Flemming 2136* (US), Somalia, **KM010483**; *Sporobolus ruspolianus* Chiov., *McKinnon s.n.* (US), Somalia, **KM010421**; *Sporobolus sanguineus* Rendle, *Gereau 6014*, *Mbago*, *Kayonbo* & *Lyanga* (DSM), Tanzania, **KM010485**; *Sporobolus scabridus* S. T. Blake, *Forster 20462* (MEL), Australia, **KM010486**; *Sporobolus scabriflorus* Stapf ex Massey, *Troupin 1319* (US), Congo (Kinshasa) Dem. Rep., **KM010487**; *Sporobolus sessilis* B. K. Simon, *Senaratne E6095-1* (US), Australia, **KM010488**; *Sporobolus silveanus* Swallen, *Waller 3128* & *Bauml* (US), U.S.A., **KM010489**; *Sporobolus smutsii* Stent, *Oakes 1454* (US), South Africa, **KM010490**; *Sporobolus somalensis* Chiov., *Boalev 317* (US), Somalia, **KM010491**; *Sporobolus somalensis* Chiov., *Hemming 2022* (US), Somalia, **KM010492**; *Sporobolus spicatus* (Vahl) Kunth, *Baldini s.n.* (US), Oman, **KM010493**; *Sporobolus spicatus* (Vahl) Kunth, *Laegaard 17790* & *Traore* (US), Senegal, **KM010494**; *Sporobolus spicatus* (Vahl) Kunth, *Peterson 24055*, *Soreng* & *Romaschenko* (US), Tanzania, **KM010495**; *Sporobolus spicatus* (Vahl) Kunth, *Peterson 24230*, *Soreng* & *Romaschenko* (US), Tanzania, **KM010496**; *Sporobolus spiciformis* Swallen, *Garcia 2638* (CIIDIR), Mexico, **KM010497**; *Sporobolus spiciformis* Swallen, *Garcia 2814* (CIIDIR), Mexico, **KM010497**; *Sporobolus splendens* Swallen, *King 1687* (US), Mexico, **KM010499**; *Sporobolus stapfianus* Gand., *Laegaard 15939* (US), Zimbabwe, **KM010500**; *Sporobolus stolzii* Mez, *Peterson 23946*, *Soreng* & *Romaschenko* (US), Tanzania, **KM010501**; *Sporobolus stolzii* Mez, *Peterson 24133*, *Soreng* & *Romaschenko* (US), Tanzania, **KM010502**; *Sporobolus stolzii* Mez, *Richards 21377* (US), Zambia, **KM010503**; *Sporobolus subglobosus* Stapf ex C.E. 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