

# A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae)

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**Abstract** The grass subtribe Sporobolinae contains six genera: *Calamovilfa* (5 spp. endemic to North America), *Crypsis* (10 spp. endemic to Asia and Africa), *Psilolemma* (1 sp. endemic to Africa), *Spartina* (17 spp. centered in North America), *Sporobolus* (186 spp. distributed worldwide), and *Thellungia* (1 sp. endemic to Australia). Most species in this subtribe have spikelets with a single floret, 1-veined (occasionally 3 or more) lemmas, a ciliate membrane or line of hairs for a ligule, and fruits with free pericarps (modified caryopses). Phylogenetic analyses were conducted on 177 species (281 samples), of which 145 species were in the Sporobolinae, using sequence data from four plastid regions (*rpl32-trnL* spacer, *ndhA* intron, *rps16-trnK* spacer, *rps16* intron) and the nuclear ribosomal internal transcribed spacer regions (ITS) to infer evolutionary relationships and provide an evolutionary framework on which to revise the classification. The phylogenetic analysis provides weak to moderate support for a paraphyletic *Sporobolus* that includes *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*. In the combined plastid tree, *Psilolemma jaegeri* is sister to a trichotomy that includes an unsupported *Urochondra-Zoysia* clade (subtr. Zoysiinae), a strongly supported *Sporobolus somalensis* lineage, and a weakly supported *Sporobolus* s.l. lineage. In the ITS tree the Zoysiinae is sister to a highly supported Sporobolinae in which a *Psilolemma jaegeri*–*Sporobolus somalensis* clade is sister to the remaining species of *Sporobolus* s.l. Within *Sporobolus* s.l. the nuclear and plastid analyses identify the same 16 major clades of which 11 are strongly supported in the ITS tree and 12 are strongly supported in the combined plastid tree. The positions of three of these clades representing proposed sections *Crypsis*, *Fimbriatae*, and *Triachyrum* are discordant in the nuclear and plastid trees, indicating their origins may involve hybridization. Seven species fall outside the major clades in both trees, and the placement of ten species of *Sporobolus* are discordant in the nuclear and plastid trees. We propose incorporating *Calamovilfa*, *Crypsis*, *Spartina*, *Thellungia*, and *Eragrostis megalosperma* within *Sporobolus*, and make the requisite 35 new combinations or new names. The molecular results support the recognition of 11 sections and 11 subsections within *Sporobolus* s.l.; four sections are new: *Airoides*, *Clandestini*, *Cryptandri*, and *Pyramidati*; three sections are new combinations: *Calamovilfa*, *Crypsis*, and *Spartina*; four subsections are new combinations: *Calamovilfa*, *Crypsis*, *Ponceletia*, and *Spartina*; seven subsections are new: *Actinocladi*, *Alterniflori*, *Floridani*, *Helvoli*, *Pyramidati*, *Spicati*, and *Subulati*; 30 new combinations in *Sporobolus*: *S. aculeatus*, *S. advenus*, *S. alopecuroides*, *S. alterniflorus*, *S. angelicus*, *S. arcuatus*, *S. bakeri*, *S. borszczowii* subsp. *acuminatus*, *S. borszczowii* subsp. *ambiguus*, *S. brevipilis*, *S. coarctatus*, *S. cynosuroides*, *S. densiflorus*, *S. factorovskyi*, *S. foliosus*, *S. hadjikyriakou*, *S. ×longispinus*, *S. maritimus*, *S. megalospermus*, *S. michauxianus*, *S. minuartioides*, *S. niliacus*, *S. pumilus*, *S. rigidus*, *S. rigidus* var. *magnus*, *S. spartinus*, *S. schoenoides*, *S. ×townsendii*, *S. turkestanicus*, and *S. vericolor*; and five new names in *Sporobolus*: *S. arenicola*, *S. ×eatonianus*, *S. hookerianus*, *S. mobberleyanus*, and *S. vaseyi* are made. Lectotypes are designated for *Crypsis factorovskyi*, *Heleochoa ambigua*, and *Torgesia minuartioides*.

**Keywords** *Calamovilfa*; classification; *Crypsis*; ITS; phylogeny; plastid DNA sequences; *Pogononeura*; *Psilolemma*; *Spartina*; *Sporobolus*; *Thellungia*; Zoysiaceae

**Supplementary Material** The alignments are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

## ■ INTRODUCTION

In the most recent classification of the grass subfamily Chloridoideae Kunth ex Beilschm., the tribe Zoysiaceae Benth. includes the incertae sedis genus *Urochondra* C.E.Hubb. and

two subtribes, Zoysiinae Benth. and Sporobolinae Benth. (Peterson & al., 2007, 2010a; Soreng & al., 2013). Zoysiinae includes a single genus, *Zoysia* Willd., with 11 species native to Australasia (Nightingale & al., 2005; Clayton & 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 1–3-nerved hyaline lemmas with entire or mucronate apices. The subtribe Sporobolinae consists of: *Calamovilfa* (A.Gray) Hack. ex Scribn. & Southw. (5 spp. endemic to North America), *Crypsis* Aiton (11 spp. endemic to Asia and Africa), *Pogononeura* Napper (monotypic, endemic to East Africa), *Spartina* Schreb. (17 spp. centered in North America), and *Sporobolus* R.Br. (186 spp. worldwide) (Moberley, 1956; Lorch, 1962; Napper, 1963; Thieret, 1966, 2003; Tan, 1985; Peterson & al., 2003, 2004, 2007, 2010a; Nightingale & al., 2005; Clayton & al., 2006; Kern, 2012; Saarela, 2012). The Sporobolinae share most of the same character trends as for the Zoysieae, i.e., spikelets with a single floret, spiciform inflorescences of numerous deciduous racemelets disposed along a central axis, lemmas usually rounded and rarely with apical awns, and glumes often modified and oddly shaped, but differ by having modified caryopses (pericarps free, reluctantly so in *Spartina*; a free pericarp that separates completely from the seed has been referred to as the “cistoid type” whereas the “follicoid type” has a free pericarp adjoining the seed; we do not know which subtype applies to *Spartina*, see Sendulsky & al., 1986; Yang & al., 2008), 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 (Peterson & al., 2004, 2007). *Zoysia* species have a true caryopsis with 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 & al., 2007). *Urochondra* was shown to have similar characteristics as *Zoysia*, and additionally, has beaked caryopses formed from thickened style bases (Clayton & Renvoize, 1986; Clayton & al., 2006; Peterson & al., 2010a). Based on sharing caryopses with free pericarps, 1-veined lemmas, and ciliate ligules (= a line of hairs), Hubbard (1947) suggested *Crypsis*, *Urochondra*, and *Sporobolus* be placed in the tribe Sporoboleae Stapf.

*Sporobolus* is characterized in having single-flowered spikelets, 1-nerved (rarely 3-nerved) lemmas, fruits with free pericarps (cistoid type), or “modified caryopses” as proposed by Brandenburg (2003), and ligules a ciliate membrane or line of hairs (Peterson & al., 1995, 1997). Species of *Sporobolus* generally inhabit dry or stony soils to saline or alkaline sandy to clay loam soils in prairies, savannahs, and along disturbed roadsides (Clayton & Renvoize, 1986; Peterson & 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, which he elevated to *Sporobolus* subg. *Sporobolus* (Stapf) Pilg., into six groups based on life form and characteristics of the glumes and panicles. Based on caryopsis morphology, Bor (1960) divided *Sporobolus* into five unnatural 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 & Veldkamp (1991) divided *Sporobolus* into five sections based on a leaf anatomical survey and overall morphology. More recently, Weakley & Peterson (1998) recognized the *Sporobolus floridanus* Chapm. complex to include five species in the southeastern United States, Shrestha & al. (2003) recognized seven clades within the genus, and Denham & Aliscioni (2010) recognized the *S. aeneus* complex to include five species. Recent major revisions of *Sporobolus* include Boechat & Longii-Wagner (1995) for Brazil, Simon & Jacobs (1999) for Australia, Peterson & al. (2003, 2009) for the United States and Canada, and Giraldo-Cañas & Peterson (2009) for Peru, Ecuador, and Colombia.

Two subtypes of C<sub>4</sub> photosynthesis based on nicotinamide adenine dinucleotide cofactor malic enzyme (NAD-ME) and phosphoenolpyruvate carboxykinase (PCK) have been found in the Zoysieae with some verified by biochemical assay (Gutierrez & al., 1974; Brown, 1977; Hattersley & Watson, 1992). Species with NAD-ME and PCK subtypes based on anatomical and biochemical determination have been found in *Sporobolus*. Based on anatomical descriptions, *Calamovilfa*, *Crypsis*, *Pogononeura*, *Psilolemma* S.M.Phillips, and *Urochondra* are NAD-ME or PCK. *Spartina* and *Zoysia* are PCK based on anatomical and biochemical determinations (Hattersley & Watson, 1992; Sage & al., 1999).

The ecological and economic importance among members of the Sporobolinae is high since some species are dominant components of xeric grasslands (*Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., *Spartina pectinata* Link., *Sporobolus airoides* (Torr.) Torr., *S. consimilis* Fresen., *S. heterolepis* (A.Gray) A.Gray, *S. juncea* (P.Beauv.) Kunth, *S. spicatus* (Vahl) Kunth, and *S. wrightii* Munro ex Scribn.), coastal habitats (e.g., *Sporobolus virginicus* (L.) Kunth), such as intertidal mud flats, estuaries, coastal salt marshes (e.g., *Spartina alterniflora* Loisel. and *S. maritima* (Curtis) Fernald), and many are invasive (e.g., *Crypsis alopecuroides* (Piller & Mitterp.) Schrad., *Spartina alterniflora*, *S. anglica* C.E.Hubb., *S. densiflora* Brongn., *Sporobolus africanus* (Poir.) Robyns & Tournay, *S. fertilis* (Steud.) Clayton, *S. indicus*, and *S. pyramidalis* P.Beauv.) (Wood & Gaff, 1989; Watson & Dallwitz, 1992; Ainouche & al., 2009; Chelaifa & al., 2010).

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 an earlier molecular study of *Sporobolus*, Ortiz-Diaz & Culham (2000) analyzed 42 species using the nuclear ribosomal DNA (ITS) region. They found strong support in their strict consensus tree for the monophyly of *Sporobolus* with the inclusion of *Calamovilfa* and *Crypsis*. Several other DNA-based phylogenies present *Sporobolus* as paraphyletic with *Calamovilfa*, *Crypsis*, *Pogononeura*, and *Spartina* embedded within (Hilu & Alice, 2001; Columbus & al., 2007; Bouchenak-Khelladi & al., 2008; Peterson & al., 2010a). Peterson & al. (2010a) recommended future expansion of *Sporobolus* to include all of these genera.

Understanding the evolutionary history of the Sporobolinae is part of our long-range plan to elucidate the phylogeny and classification of the subfamily Chloridoideae. To accomplish

the immediate goal of understanding the evolutionary history of the Sporobolinae we are using a large dataset of 170 species of Chloridoideae to test the monophyly of *Sporobolus* and identify intrageneric taxonomic units. Here, we present a new phylogenetic analysis for 118 of the 186 species that belong to *Sporobolus* based on analysis of ITS and four plastid regions (*rpl32-trnL*, *ndhA*, *rps16*, *rps16-trnK*). We discuss morphological and anatomical characters supporting relationships and propose changes to the classification. The main objectives of our work are to discriminate among the major groups within *Sporobolus* and hypothesize basic evolutionary trends. In addition, we include a brief review of the chromosome numbers reported within the Zoysieae.

## ■ MATERIALS AND METHODS

**Taxon sampling.** — The taxon sampling consists of 281 samples, representing 175 species of grasses, of which 170 species are included in subfamily Chloridoideae; these are partitioned to represent the following five tribes (Soreng & al., 2013): Centropodieae with a single species, Triraphideae with two species, Eragrostideae with 12 species, Cynodonteae with 10 species, and Zoysieae with 148 species. Our sampling is principally focused on genera that are morphologically similar and phylogenetically related to *Sporobolus*, including a large sample of 144 species within the subtribe Sporobolinae (Peterson & al., 2010a). The dataset for *Sporobolus* includes 118 of the 186 species (63%) currently placed in the genus (Clayton & al., 2006). We tried to sample from all continents as many species of *Sporobolus* as possible and many of these specimens were obtained from existing collections housed in the United States National Herbarium. All groups and clades of *Sporobolus* species represented in previous molecular studies are more heavily sampled here. A complete list of taxa, voucher information, and GenBank numbers can be found in Appendix 1. Outside of the Chloridoideae, three species of Danthoioideae (*Capeochloa cincta* spp. *sericea* (N.P.Barker) N.P.Barker & H.P.Linder, *Danthonia compressa* Austin, *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 & al., 2010a, 2011, 2012, 2014a). In the phylograms the native distribution of each species is indicated as follows: North America (red), South America (tan), Africa and Arabia (green), Australia and Pacific Islands (dark purple), Southeast Asia (light purple), and Europe (blue).

**DNA extraction, amplification, and sequencing.** — All procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA isolation, amplification, and sequencing of the *rpl32-trnL* spacer and the *ndhA* intron (small single-copy region), the *rps16-trnK* spacer and the *rps16* intron (large single-copy region), and ITS were accomplished following procedures outlined in Peterson & al. (2010a, b). We specifically targeted these four plastid regions, which were most informative in our previous studies on chloroid grasses (Peterson & al., 2010a, b, 2011, 2012, 2014a, b).

**Phylogenetic analyses.** — We used Geneious v.5.3.4 (Drummond & al., 2011) for contig assembly of bidirectional sequences, and we used Muscle (Edgar, 2004) to align consensus sequences and adjust the final alignment. We conducted maximum likelihood (ML) and Bayesian analyses to infer overall phylogeny. The combined datasets were partitioned by region (i.e., there were five partitions). Nucleotide substitution models selected by Akaike's information criterion, as implemented in jModelTest v.0.1.1 (Posada, 2008), were specified for each partition (Table 1). The ML analysis was conducted with GARLI v.0.951 (Zwickl, 2006). The maximum likelihood bootstrap analysis was performed with 1000 replicates, with 10 random addition sequences per replicate. The output file containing trees of ML found for each bootstrap dataset was read into PAUP\* v.4.0b10 (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 parallel version of the MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis was initiated with random starting trees and was initially run for four million generations, sampling once per 100 generations. The analysis was run until the value of standard deviation of split sequences dropped below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn-in was set at 0.25. Posterior probabilities of 0.95–1.00 were considered as strong support.

## ■ RESULTS

**Phylogenetic analyses.** — Eighty-three percent (994/1199) of the sequences used in our study are newly reported here and in GenBank, and only 14.7% (206/1405) of the sequences are missing in the combined matrix (Appendix 1). The following species are only in the combined plastid tree: *Calamovilfa curtissii* (Vasey) Scribn., *Sporobolus aldabrensis* Renvoize, *S. conrathii* (Conrath & Hack.) Chiov., *S. elongatus* R.Br., *S. floridanus*, *S. maderaspatanus* Bor, *S. micranthus* (Steud.) T.Durand & Schinz, *S. mildbraedii* Pilg., *S. olivaceus* Napper, and *Zoysia pacifica* (Goudswaard) M.Hotta & Kuroki; and *S. smutsii* Napper and *S. tenacissimus* (L.f.) P.Beauv. are only in the ITS tree. Total alignment characters for individual regions are noted in Table 1. Plastid *rpl32-trnL* had the highest sequencing success; this region was recovered from 95.8% of taxa recovered in the dataset. Recovery of other regions ranged from 70.1% to 89.1%.

There was hard incongruence between the combined plastid and ITS datasets (discussed below); therefore, we did not combine them and the two datasets were analyzed separately. We chose to emphasize 16 primarily homogeneous clades that exist in the ITS and combined plastid phylograms (Figs. 1, 2).

**Analysis of ITS sequences.** — The phylogenetic tree derived from ITS sequences (Fig. 1) is well resolved with



moderate support (BS = 71, PP = 1.00) for tribe Zoysieae (BS = 69%, PP = 0.95), strong support for subtribe Zoysiinae (BS = 100, PP = 1.00) and strong support for subtribe Sporobolinae (BS = 100, PP = 1.00). The Zoysiinae includes a monophyletic *Zoysia* (BS = 100, PP = 1.00) that is sister to *Urochondra setulosa*. *Sporobolus* is paraphyletic, as the Sporobolinae includes a weakly supported *Psilolemma jaegeri* (Pilg.) S.M. Phillips–*Sporobolus somalensis* clade (BS = 65, PP = 0.90) that is sister to a moderately supported clade (BP = 71, PP = 1.00) comprising the remaining species of *Sporobolus* as well as *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*.

Within *Sporobolus* s.l. there are 11 strongly supported clades (B–G, I, J, M–O; BS = 91–100, PP = 1.00), three moderately supported clades (A, H, K; BS = 78–87, PP = 0.99–1.00), one clade supported only by Bayesian inference (X, BS < 50, PP = 0.95), and one unsupported clade (L). Species in clades A–O, X are listed in Table 2). The J–O clade is moderately supported (Fig. 1B, BS = 85, PP = 1.00) and contains species predominantly from North America. Within clade O there are three strongly supported subclades (BS = 96–100, PP = 1.00) that include: (1) *Spartina alterniflora* Loisel., *S. anglica*, *S. foliosa* Trin., *S. maritima*, and *S. ×townsendii* H.Groves & J.Groves; (2) *S. bakeri* Merr., *S. ×caespitosa* A.A.Eaton, *S. ciliata* Brongn., *S. cynosuroides* (L.) Roth., *S. densiflora*, *S. gracilis*, *S. montevidensis* Arechav., *S. patens* (Aiton) Muhl., and *S. pectinata*; and (3) *S. spartinae* (Trin) Merr. & Hitchc.

Species of *Sporobolus* not in clades A–O include: the *Sporobolus acinifolius* Stapf–*S. albicans* Nees–*S. tenellus*

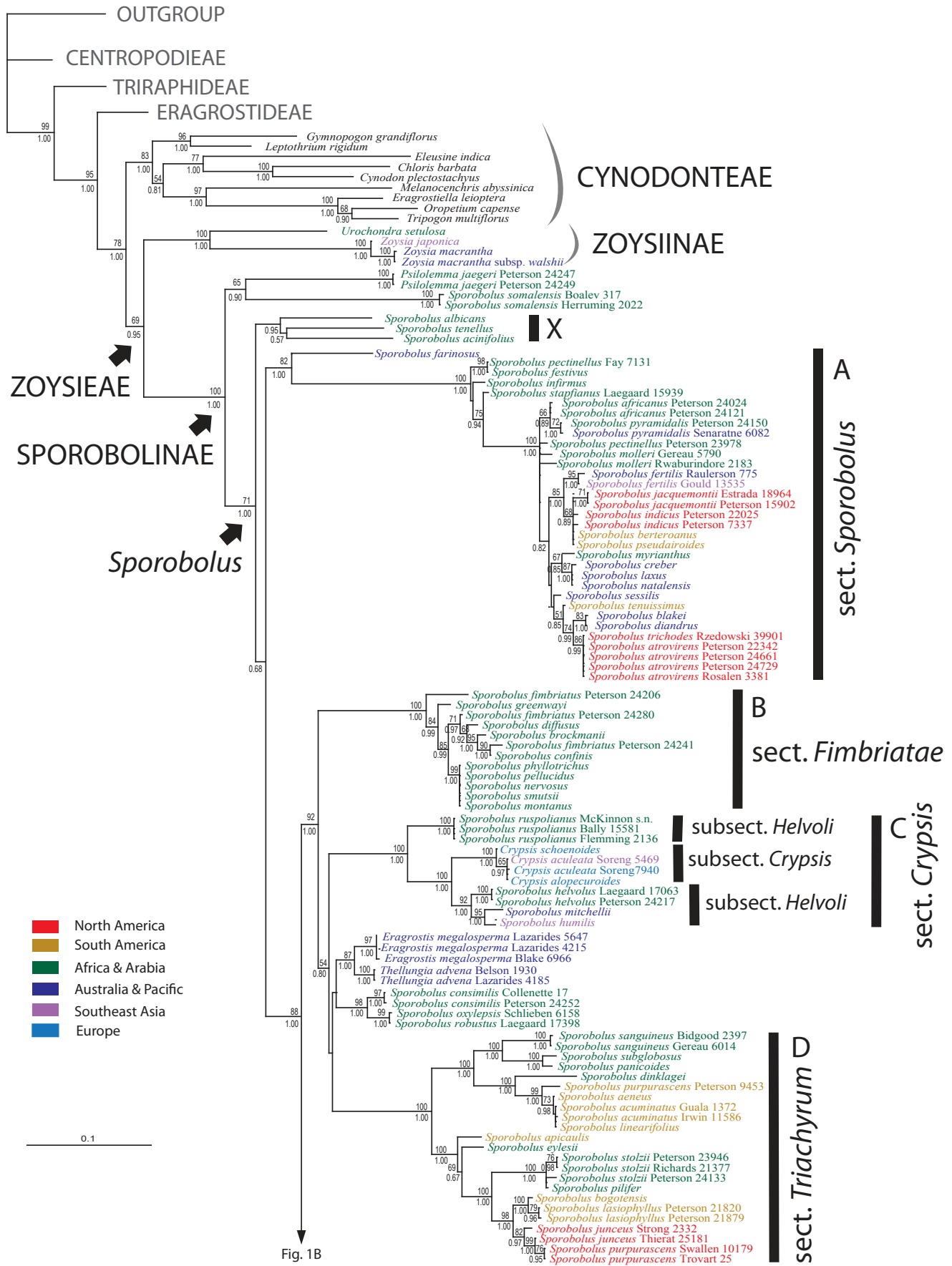
(Spreng.) Kunth clade supported only by Bayesian inference (Fig. 1 clade X, BS < 50, PP = 0.95) that is sister to all remaining species in *Sporobolus* s.l. (PP = 0.68); *Sporobolus oxylepsis* Mez–*S. robustus* Kunth pair are sister to two accessions of *S. consimilis* (BS = 98, PP = 1.00), and together these are sister to the *Thellungia advena*–*Eragrostis megalosperma* pair (BS = 87, PP = 1.00); *Sporobolus tourneuxii* is sister to E–O clades; three accessions of *Sporobolus buckleyi* and four accessions of *S. palmeri* (BS = 52, PP = 0.69) are sister to clades J–O, and 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 = 98, PP = 1.00).

**Analysis of combined plastid sequences.** — The phylogenetic tree based on combined plastid sequences (Fig. 2) is well resolved with weak support (BS = 51, PP = 0.71) for a paraphyletic *Sporobolus* that includes *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*. *Pogononeura biflora* Napper is aligned within the Cynodonteae. The Zoysieae clade is moderately supported (BS = 88, PP = 1.00) and *Psilolemma* is sister to a clade supported only by Bayesian posterior probabilities (BS < 50, PP = 0.96) containing a trichotomy with an unsupported *Urochondra*–*Zoysia* clade, a strongly supported (BS = 95, PP = 1.00) *Sporobolus somalensis*, and a weakly supported (BS = 51, PP = 0.71) *Sporobolus* s.l.

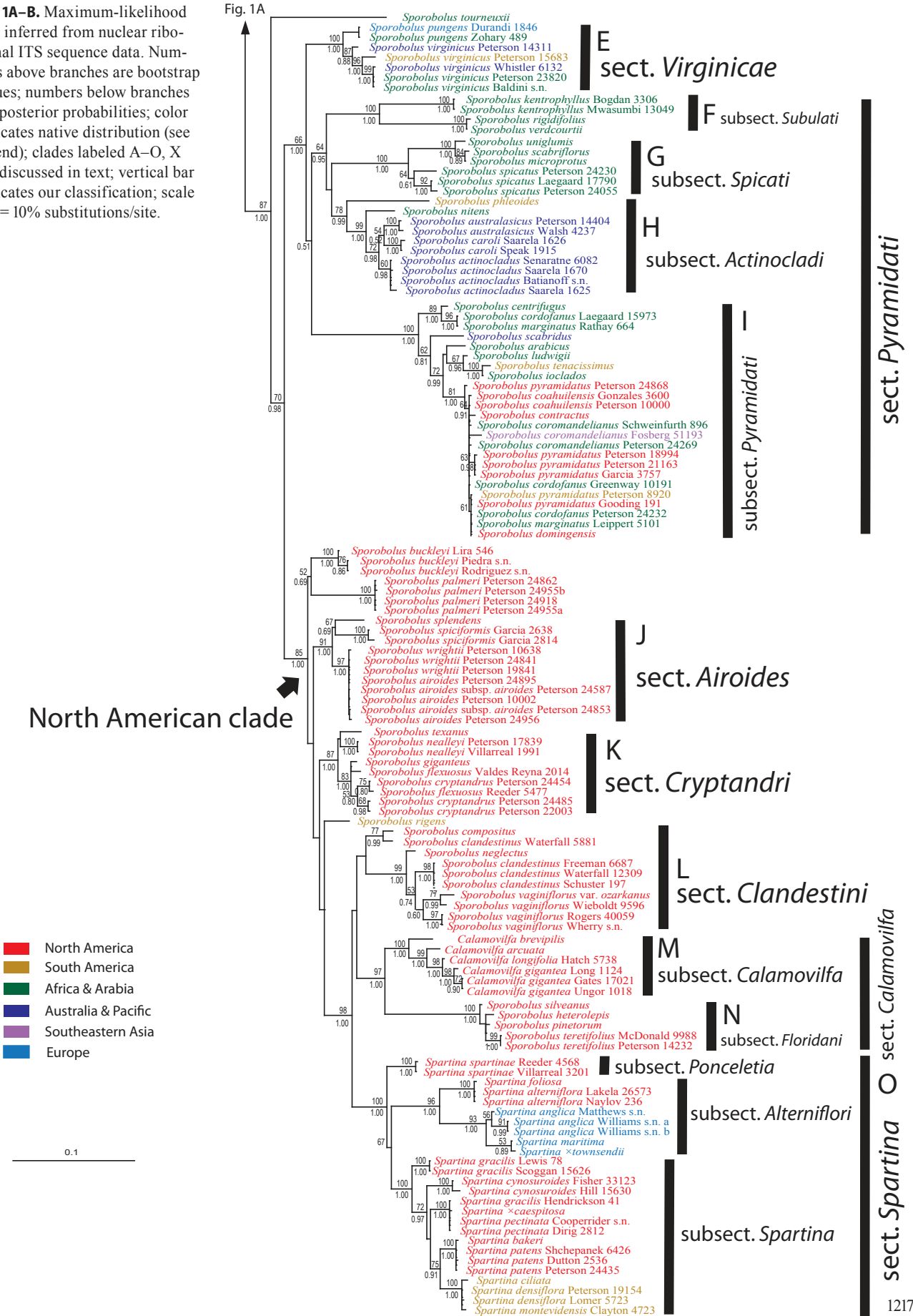
A *Sporobolus acinifolius*–*S. albicans*–*S. tenellus* clade (Fig. 2 clade X, BS = 51, PP = 0.95) is sister to a lineage of the remaining species that includes 12 strongly supported clades

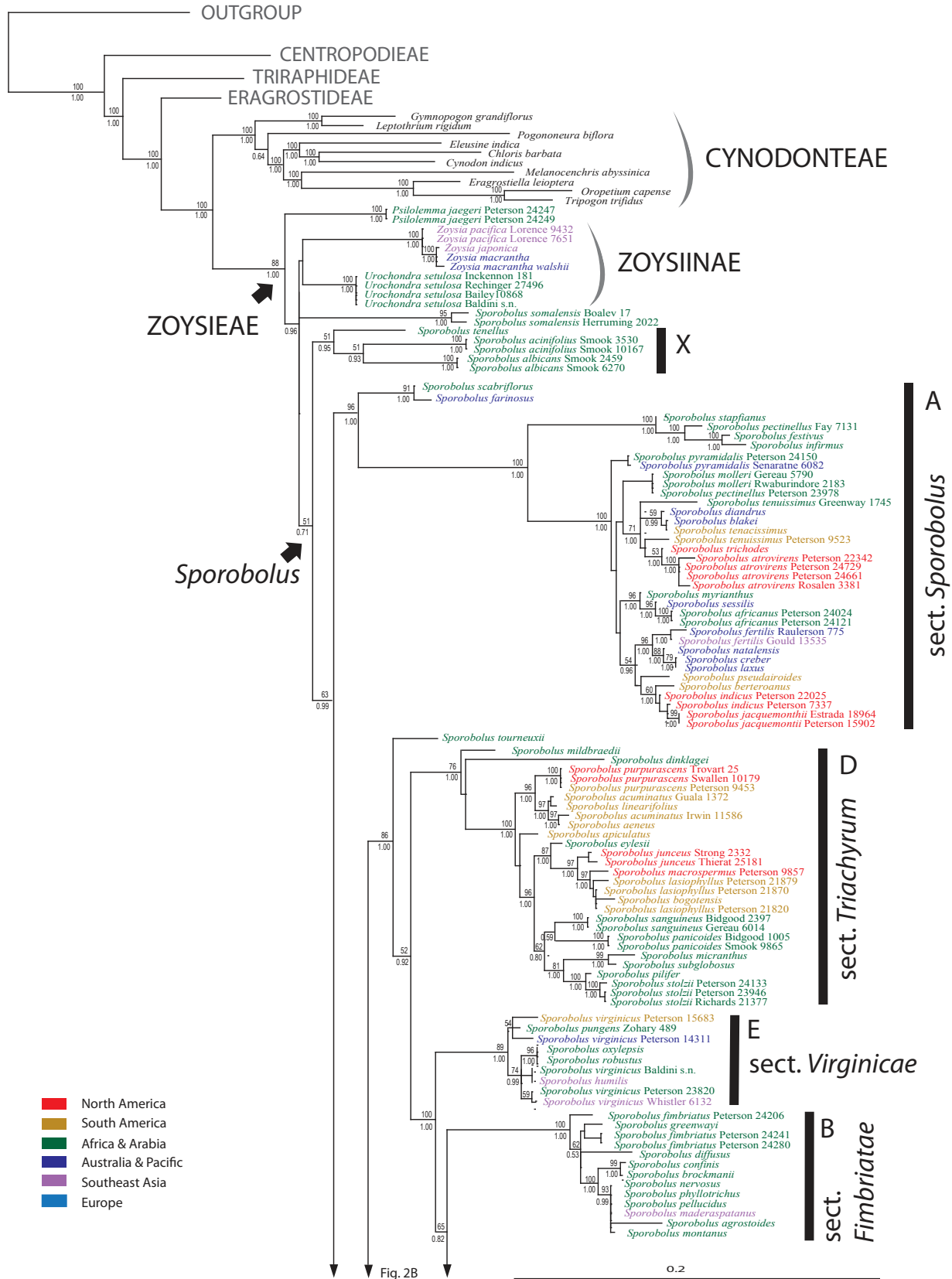
**Table 1.** Characteristics of the five regions, *rpl32-trnL*, *ndhA* intron, *rps16* intron, *rps16-trnK* and ITS, and parameters used in maximum likelihood and Bayesian analyses indicated by Akaike information criterion (AIC).

	<i>rpl32-trnL</i>	<i>ndhA</i> intron	<i>rps16</i> intron	<i>rps16-trnK</i>	Combined plastid data	ITS
Total aligned characters	937	1236	964	954	4091	798
Sequencing success (%)	95.8	70.1	84.9	84.5	83.8	89.1
Number of new sequences	229 (85%)	155 (79%)	198 (83%)	199 (83%)	781 (82%)	213 (84%)
Likelihood score (–lnL)	6,954.03	7,917.23	5,082.78	6,057.03		19,070.08
Number of substitution types	6	6	6	6	–	6
Model for among-site rate variation	gamma	gamma	gamma	gamma	–	gamma
Substitution rates	1.5591 2.3107 0.5085 1.3749 1.9527 1.0000	1.3196 2.1199 0.5392 1.6311 2.8176 1.0000	0.9545 1.1785 0.1955 0.9182 1.7342 1.0000	1.3190 2.7049 0.5019 1.1862 2.2382 1.0000	–	1.3286 3.0338 1.2604 0.9521 5.0943 1.0000
Character state frequencies	0.3598 0.1288 0.1242 0.3871	0.3778 0.1301 0.1524 0.3394	0.4061 0.1076 0.1521 0.3339	0.2975 0.1454 0.1506 0.4063	–	0.2670 0.1914 0.2346 0.3069
Proportion of invariable sites	0.1814	0.2938	0.3078	0.2131	–	0.2174
Substitution model	GTR+I+G	TVM+G	TIM3+I+G	TIM3+G	–	GTR+I+G
Gamma shape parameter ( $\alpha$ )	1.0674	1.2902	1.1756	1.5083	–	1.1222



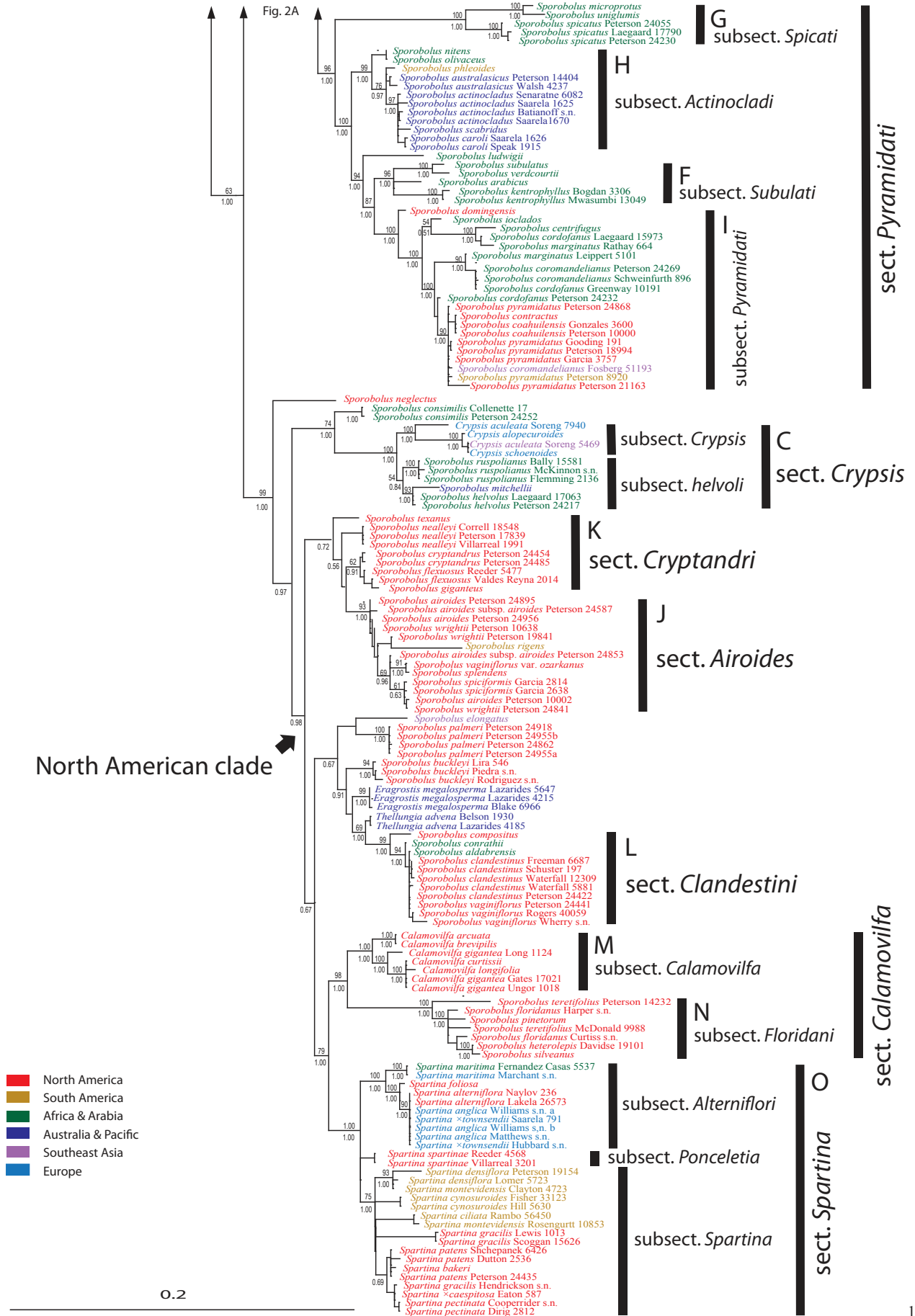
**Fig. 1A–B.** Maximum-likelihood tree inferred from nuclear ribosomal ITS sequence data. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; color indicates native distribution (see legend); clades labeled A–O, X are discussed in text; vertical bar indicates our classification; scale bar = 10% substitutions/site.





**Fig. 2A–B.** Maximum-likelihood tree inferred from combined plastid (*rpl32-trnL*, *ndhA*, *rps16*, and *rps16-trnK*) sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; color indicates native distribution (see legend); clades labeled A–O, X are discussed in text; vertical bar indicates our classification; scale bar = 20% substitutions/site.







(Fig. 2 clades A–C, F–J, L–O; BS = 93–100, PP = 1.00), two moderately supported clades (Fig. 2 clade D, BS = 76, PP = 1.00; Fig. 2 clade E, BS = 89, PP = 1.00), and one unsupported grade (Fig. 2K). The North American clade (J–O) received only Bayesian support (Fig. 2B, BS < 50, PP = 0.98). Within clade O there are two moderately to strongly supported subclades that include: (1) *Spartina alterniflora*, *S. anglica*, *S. foliosa*, *S. maritima*, and *S. ×townsendii* (BS = 100, PP = 1.00) and (2) *S. bakeri*, *S. ×caespitosa*, *S. ciliata*, *S. cynosuroides*, *S. densiflora*, *S. gracilis*, *S. montevidensis*, *S. patens*, and *S. pectinata* (BS = 75, PP = 1.00).

The species composition of each clade in the combined plastid phylogram is nearly identical to the species composition given in the ITS-derived phylogram (Table 2). Species not in clades A–O include: *Sporobolus tourneuxii* sister to B, D, E–I clades; *Sporobolus ludwigii* sister to F and I clades; *Sporobolus neglectus* Nash sister to C, J–O clades; *Sporobolus consimilis* sister to clade C; *Sporobolus elongatus* R.Br. sister

to *S. palmeri*; and *Sporobolus buckleyi*, *Eragrostis megalosperma*, and *Thellungia advena* form a grade, all of these sister to clade L.

**Incongruences between the ITS and combined plastid phylograms.** — The ITS/plastid incongruence scheme is shown in Fig. 3. There are three types of incongruences among the species within our trees which we define as follows: (1) those taxa that fall in different major clades in the nuclear and combined plastid trees, (2) those species that are outside the major clades in one of the two trees, and (3) those taxa that do not align in a major clade in either tree. The following species fall into category 1 (ITS clade listed first, then plastid): *Sporobolus arabicus* Boiss. (I, F), *S. humilis* J.Presl (C, E), *S. scabridus* S.T.Blake (I, H), *S. scabriflorus* Stapf ex Massey (G, A), *S. vaginiflorus* var. *ozarkanus* (Fernald) Shinnery (L, J); category 2: *S. conrathii* (Conrath & Hack.) Chiov. (–, L), *S. oxylepsis* (–, E), *S. neglectus* (L, –), *S. rigens* (–, J), *S. robustus* (–, E); and category 3: *Eragrostis megalosperma*, *S. buckleyi*, *S. con-*

**Table 2.** A proposed classification of the Sporobolinae and subgeneric classification of *Sporobolus* based on combined plastid and nuclear ITS DNA analysis. Letters in **bold** correspond to the clades (A–O, X) in Figs. 1–3; \* indicates species not examined in this study; chromosome numbers are given in brackets [ ].

Sporobolinae Benth.

Incertae sedis: *Sporobolus somalensis* Chiov.

*Psilolemma* S.M.Phillips, Type: *P. jaegeri* (Pilg.) S.M.Phillips: *P. jaegeri*

*Sporobolus* R.Br., Type: *S. indicus* (L.) R.Br.

Incertae sedis: *S. acinifolius* Stapf, *S. advenus* (Stapf) P.M.Peterson, (*Thellungia*), *S. albicans* Nees [2n = 54], *S. buckleyi* Vasey [2n = 40], *S. conrathii* (Conrath & Hack.) Chiov., *S. consimilis* Fresen., *S. elongatus* R.Br. [2n = 36], *S. megalospermus* (F.Muell. ex Benth.) P.M.Peterson, *S. oxylepsis* Mez, *S. palmeri* Scribn., *S. rigens* (Trin.) Desv., *S. tenellus* (Spreng.) Kunth, *S. tourneuxii* Coss.

*S.* sect. *Airoides* (Torr.) P.M.Peterson, Type: *S. airoides* (Torr.) Torr. (**J**): *S. airoides* [2n = 80, 90, 108, 126], *S. spiciformis* Swallen [2n = 40], *S. splendens* Swallen, *S. wrightii* Munro ex Scribn. [2n = 36]

*S.* sect. *Calamovilfa* (A.Gray) P.M.Peterson, Type: *S. brevipilis* (Torr.) P.M.Peterson (**M, N**)

subsect. *Calamovilfa* (A.Gray) P.M.Peterson (**M**): *S. arcuatus* (K.E.Rogers) P.M.Peterson, *S. arenicola* P.M.Peterson (*Calamovilfa gigantea*) [2n = 60], *S. brevipilis*, *S. curtissianus* (Vasey) P.M.Peterson, *S. rigidus* (Buckley) P.M.Peterson (*Calamovilfa longifolia*) [2n = 40, 60]

subsect. *Floridani* P.M.Peterson, Type: *S. floridanus* Chapm. (**N**): \**S. curtissii* Small ex Kearney, *S. floridanus*, *S. heterolepis* (A.Gray) A.Gray [2n = 72], \**S. interruptus* Vasey [2n = 30], *S. pinetorum* Weakley & P.M.Peterson, *S. silveanus* Swallen, *S. teretifolius* R.M.Harper

*S.* sect. *Clandestini* P.M.Peterson, Type: *S. clandestinus* (Biehler) Hitchc. (**L**): *S. aldabrensis* Renvoize, *S. compositus* (Poir.) Merr. [2n = 54, 88, 108], *S. clandestinus*, *S. neglectus* Nash [2n = 36], *S. vaginiflorus* (Torr. ex A.Gray) Alph.Wood [2n = 54]

*S.* sect. *Crypsis* (Aiton) P.M.Peterson, Type: *S. aculeatus* (L.) P.M.Peterson (**C**):

subsect. *Crypsis* (Aiton) P.M.Peterson (**C**, in part): *S. aculeatus*, *S. alopecuroides* (Pillar & Mitterp.) P.M.Peterson [2n = 16, 18], \**S. borszczowii* Regel, \**S. factorovskii* (Eig) P.M.Peterson, \**S. hadjikyriakou* (Raus & H.Scholz) P.M.Peterson, \**S. minuartioides* (Bornm.) P.M.Peterson, \**S. niliacus* (Fig. & De Not.) P.M.Peterson (*Crypsis vaginiflora*) [2n = 48], *S. schoenoides* (L.) P.M.Peterson [2n = 32], \**S. turkestanicus* (Eig) P.M.Peterson

subsect. *Helvoli* P.M.Peterson, Type: *S. helvolus* (Trin.) T.Durand & Schinz (**C**, in part): *S. helvolus* [2n = 36], *S. mitchellii* (Trin.) C.E.Hubb., *S. ruspolianus* Chiov.

*S.* sect. *Cryptandri* P.M.Peterson, Type: *S. cryptandrus* (Torr.) A.Gray (**K**): *S. cryptandrus* [2n = 36, 38, 72], *S. flexuosus* (Thurb. ex Vasey) Rydb. [2n = 36, 38], *S. giganteus* Nash [2n = 36], *S. nealleyi* Vasey [2n = 40], *S. texanus* Vasey

*S.* sect. *Fimbriatae* Veldkamp, Type: *S. fimbriatus* (Trin.) Nees (**B**): *S. agrostoides* Chiov., *S. brockmanii* Stapf, *S. confinis* (Steud.) Chiov., *S. diffusus* Clayton, *S. fimbriatus* [2n = 54], *S. greenwayi* Napper, \**S. macranthus* (Steud.) T.Durand & Schinz, *S. maderaspatanus* Bor [2n = 12], *S. montanus* (Hook.f.) Engl. [2n = 18], *S. nervosus* Hochst. [2n = 36], *S. pellucidus* Hochst., *S. phyllotrichus* Hochst., *S. smutzii* Stent

*S.* sect. *Pyramidati* (P.M.Peterson) P.M.Peterson, Type: *S. pyramidatus* (Lam.) Hitchc. (**F, G, H, I**):

subsect. *Pyramidati* P.M.Peterson (**I**): *S. centrifugus* (Trin.) Nees, *S. coahuilensis* Valdés-Reyna, *S. contractus* Hitchc. [2n = 36], *S. cordofanus* (Hochst. ex Steud.) Coss., *S. coromandelianus* (Retz.) Kunth [2n = 36], *S. domingensis* (Trin.) Kunth, *S. ioclados* (Nees ex Trin.) Nees [2n = 18], *S. ludwigii* Hochst., *S. marginatus* Hochst. ex A.Rich [2n = 18, 36], *S. pyramidatus* [2n = 24, 36, 54], *S. scabridus* S.T.Blake, *S. tenacissimus* (L.f.) P.Beauv.

*similis*, *S. elongatus*, *S. palmeri*, *S. somalensis*, *S. tourneuxii*, and *Thellungia advena*. There are topological differences in the placement of eight major clades (clades B–I) between the ITS and combined plastid tree.

## ■ DISCUSSION

Our phylogenetic trees provide weak to moderate support for a paraphyletic *Sporobolus* that includes *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia*. Within the Sporobolinae, the *Psilolemma jaegeri* and *Sporobolus somalensis* lineages align outside the remaining species of *Sporobolus*. Within *Sporobolus* we identify 16 major clades of which 12 are strongly supported in the combined plastid tree and 11 are strongly supported in the ITS tree. The species included in these 16 major clades are given in Table 2 along with our proposed classification of the Sporobolinae. In *Sporobolus* we identified a North American

clade (J–O) that is composed primarily of species indigenous to North America. The early diverging (deeply nested) subclades in our J–O clade are almost entirely composed of North American species (see Figs. 1B, 2B, North American clade) while derived clades include species with European, South American, African or Australian origins. Based on our results we propose incorporating *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia* within *Sporobolus*, and make the requisite nomenclatural changes in the taxonomy section.

In our discussion below we first address species that align outside the Sporobolinae in tribe Cynodontae, then discuss species that do not align (incertae sedis) within one of the 16 major clades within *Sporobolus*. Next, we discuss each of the major clades within *Sporobolus* beginning with clade X and continuing with clades A through O. Finally, we include a summary of the chromosome base numbers for the Zoysieae and address incongruences between the ITS and combined plastid phylogenies.

**Table 2.** Continued.

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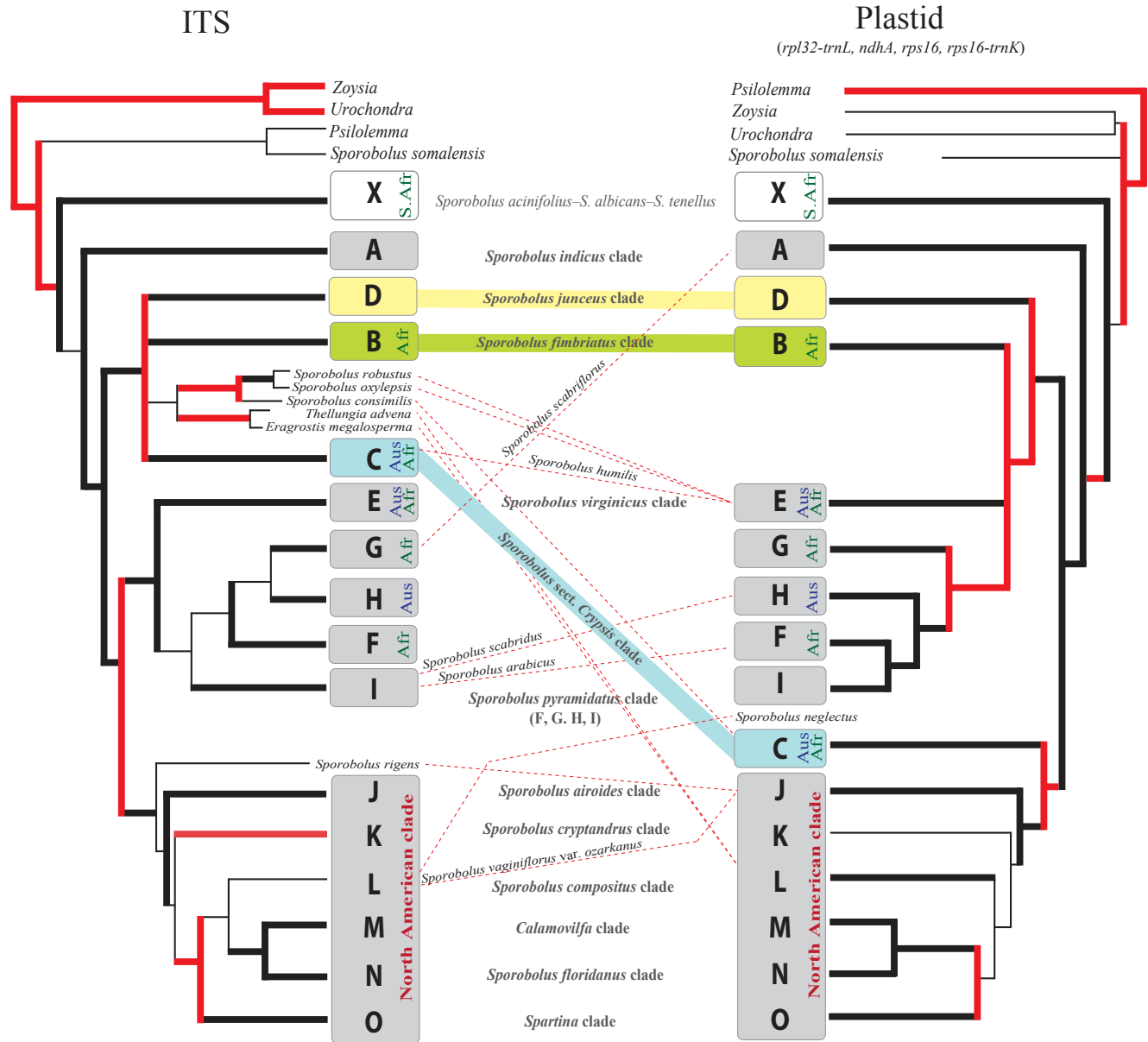
subsect. <i>Actinocladi</i> P.M.Peterson, Type: <i>S. actinocladus</i> (F.Muell.) Muell. ( <b>H</b> ): <i>S. actinocladus</i> , <i>S. australasicus</i> Domin, <i>S. caroli</i> Mez, * <i>S. contiguus</i> S.T.Blake, * <i>S. lenticularis</i> S.T.Blake, <i>S. olivaceus</i> Napper, <i>S. nitens</i> Stent, * <i>S. partimpatens</i> R.Mills ex B.K.Simon, <i>S. phleoides</i> Hack., * <i>S. pulchellus</i> R.Br.
subsect. <i>Spicati</i> P.M.Peterson, Type: <i>S. spicatus</i> (Vahl) Kunth ( <b>G</b> ): <i>S. microprotus</i> Stapf, <i>S. scabriflorus</i> Stapf ex Massey, <i>S. spicatus</i> , <i>S. uniglumis</i> Stent & J.M.Ratray
subsect. <i>Subulati</i> P.M.Peterson, Type: <i>S. subulatus</i> Hack. ( <b>F</b> ): <i>S. arabicus</i> Boiss. [ $2n = 36$ ], <i>S. kentrophyllus</i> (K.Schum. ex Engl.) Clayton [ $2n = 36$ ], <i>S. subulatus</i> , <i>S. verdcourtii</i> Napper
<i>S. sect. Spartina</i> (Schreb.) P.M.Peterson & Saarela, Type: <i>S. cynosuroides</i> (L.) P.M.Peterson & Saarela ( <b>O</b> ):
subsect. <i>Alterniflori</i> P.M.Peterson & Saarela, Type: <i>S. alterniflorus</i> (Loisel.) P.M.Peterson & Saarela: <i>S. alterniflorus</i> [ $2n = 62$ ], <i>S. anglicus</i> (C.E.Hubb.) P.M.Peterson & Saarela [ $2n = 120, 122, 124, 127$ ], <i>S. foliosus</i> , (Trin.) P.M.Peterson & Saarela [ $2n = 60, 62$ ], * <i>S. ×longispicus</i> (Hauman & Parodi ex St.-Yves) P.M.Peterson & Saarela, <i>S. martimus</i> (Curtis) P.M.Peterson & Saarela [ $2n = 60$ ], <i>S. ×townsendii</i> (H.Groves & J.Groves) P.M.Peterson & Saarela [ $2n = 62$ ]
subsect. <i>Ponceletia</i> (Thouars) P.M.Peterson & Saarela, Type: <i>S. mobberleyanus</i> P.M.Peterson & Saarela ( <i>Spartina arundinacea</i> ): * <i>S. mobberleyanus</i> [ $2n = 40$ ], <i>S. spartinus</i> (Trin.) P.M.Peterson & Saarela [ $2n = 40$ ]
subsect. <i>Spartina</i> (Schreb.) P.M.Peterson & Saarela: <i>S. bakeri</i> (Merr.) P.M.Peterson & Saarela [ $2n = 40$ ], <i>S. coarctatus</i> (Trin.) P.M.Peterson & Saarela ( <i>Spartina ciliata</i> ), <i>S. cynosuroides</i> (L.) P.M.Peterson & Saarela [ $2n = 40$ ], <i>S. densiflorus</i> (Brongn.) P.M.Peterson & Saarela (= <i>S. montevidensis</i> ), <i>S. ×eatonianus</i> P.M.Peterson & Saarela ( <i>Spartina ×caespitosa</i> ) [ $2n = 40$ ], <i>S. hookeriana</i> P.M.Peterson & Saarela ( <i>Spartina gracilis</i> ) [ $2n = 40$ ], <i>S. michauxianus</i> (Hitche.) P.M.Peterson & Saarela ( <i>Spartina pectinata</i> ) [ $2n = 40$ ], <i>S. pumilus</i> (Roth) P.M.Peterson & Saarela ( <i>Spartina patens</i> ) [ $2n = 40$ ], * <i>S. versicolor</i> (Fabre) P.M.Peterson & Saarela
<i>S. sect. Sporobolus</i> (Gruppe 1, Pilger, 1956; part of <i>Truncatae</i> , Bor, 1960; part of <i>S. sect. Agrosticula</i> (Raddi) Veldkamp, Baaijens & Veldkamp, 1991), Type: <i>S. indicus</i> ( <b>A</b> ): <i>S. africanus</i> (Poir.) Robyns & Tournay [ $2n = 18, 36$ ], <i>S. atrovirens</i> (Kunth) Kunth [ $2n = 24$ ], <i>S. berterooanus</i> (Trin.) Hitche. & Chase, <i>S. blakei</i> De Nardi ex B.K.Simon, <i>S. creber</i> De Nardi, <i>S. diandrus</i> (Retz.) P.Beauv. [ $2n = 24$ ], <i>S. farinosus</i> Hosok., <i>S. fertilis</i> (Steud.) Calyton [ $2n = 36$ ], <i>S. festivus</i> Hochst. ex A.Rich. [ $2n = 20, 24, 36$ ], * <i>S. fourcadii</i> Stent, <i>S. indicus</i> [ $2n = 18, 24, 36$ ], <i>S. infirmus</i> Mez, <i>S. jacquemontii</i> Kunth [ $2n = 24$ ], <i>S. laxus</i> B.K.Simon, * <i>S. minor</i> Trin. ex Kunth, <i>S. molleri</i> Hack. [ $2n = 12$ ], <i>S. natalensis</i> (Steud.) T.Durand & Schinz, <i>S. myrianthus</i> Benth., <i>S. pectinellus</i> Mez, <i>S. pseudairioides</i> Parodi, <i>S. pyramidalis</i> P.Beauv. [ $2n = 24, 30$ ], * <i>S. quadratus</i> Clayton, <i>S. sessilis</i> B.K.Simon, <i>S. stapfianus</i> Gand., <i>S. tenuissimus</i> (Mart. ex Schrank) Kuntze [ $2n = 12$ ], <i>S. trichodes</i> Hitche.
<i>S. sect. Triachyrum</i> (Hochst. ex A.Braun) Veldkamp, Type: <i>S. discosporus</i> Nees ( <b>D</b> ): <i>S. acuminatus</i> (Trin.) Hack., * <i>S. adustus</i> (Trin.) Roseng., B.R.Arrill. & Izag., <i>S. aeneus</i> (Trin.) Kunth, * <i>S. amaliae</i> Veldkamp, <i>S. apiculatus</i> Boechat & Longhi-Wagner, <i>S. bogotensis</i> Swallen & García-Barr., * <i>S. camporum</i> Swallen, * <i>S. cubensis</i> Hitche., <i>S. dinklagei</i> Mez, * <i>S. discosporus</i> , * <i>S. eximius</i> (Nees ex Trin.) Ekman, <i>S. eylesii</i> Stent & J.M.Ratray, * <i>S. harmandii</i> Henrard, <i>S. junceus</i> (P.Beauv.) Kunth, <i>S. lasiophyllus</i> Pilg., <i>S. linearifolius</i> Nicora, <i>S. macropernum</i> Scribn. ex Beal, <i>S. micranthus</i> (Steud.) T.Durand & Schinz, <i>S. mildbraedii</i> Pilg., * <i>S. multinodis</i> Hack., * <i>S. novoguineensis</i> Baaijens, * <i>S. nudiramus</i> Boechat & Longhi-Wagner, <i>S. panicoides</i> A.Rich., * <i>S. paniculatus</i> (Trin.) T.Durand & Schinz, * <i>S. paucifolius</i> Boechat & Longhi-Wagner, <i>S. pilifer</i> (Trin.) Kunth [ $2n = 20, 40, 54$ ], <i>S. purpurascens</i> (Sw.) Ham. [ $2n = 60$ ], * <i>S. recurvatus</i> Boechat & Longhi-Wagner, * <i>S. reflexus</i> Boechat & Longhi-Wagner, <i>S. sanguineus</i> Rendle [ $2n = 20$ ], * <i>S. sciadocladus</i> Ohwi, <i>S. stolzii</i> Mez, <i>S. subglobosus</i> Stapf ex C.E.Hubb.
<i>S. sect. Virginicae</i> Veldkamp, Type: <i>S. virginicus</i> (L.) Kunth ( <b>E</b> ): <i>S. humilis</i> J.Presl [ $2n = 20$ ], <i>S. pungens</i> (Schreb.) Kunth, <i>S. robustus</i> Kunth, <i>S. virginicus</i> [ $2n = 20, 30, 40, 50, 60$ ].

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**Cynodonteae.** — *Pogononeura biflora*, a morphologically distinct genus with 2- or 3-flowered spikelets and short-awned lemmas (Clayton & Renvoize, 1986), was previously found embedded within the *Sporobolus* clade (Peterson & al., 2010a), whereas in our combined plastid phylogram it is placed in the Cynodonteae. The isotype consists of three culms, two of which are genuine *P. biflora*, and a third culm with an attached marking tag (*P.J. Greenway 10091*) that is *Sporobolus cordofanus* (Hochst. ex Steud.) Coss. Our original sample used in Peterson & al. (2010a) was taken from another mixed collection

of *P. biflora* and *S. cordofanus*, and we apparently removed a leaf from the culm of the latter species (*P.J. Greenway 10620, Turner & Watson, US*), this being the basis for the earlier erroneous report. After resampling a leaf blade from the isotype specimen of *P. biflora* (*Greenway 10091, US-2589348*) and sequencing the *rpl32-trnL* plastid region, we found *P. biflora* to align within the Cynodonteae (Fig. 2A, see Cynodonteae).

**Sporobolinae and *Sporobolus*, incertae sedis.** — We treat as incertae sedis those taxa that are not exclusively part of the 15 major clades in the ITS and combined plastid phylograms



**Fig. 3.** A comparison of the ITS and combined plastid phylograms. Bold letters in rectangular boxes indicate clades of *Sporobolus* species discussed in text and most clades include the predominant geographic distribution of its members abbreviated as: Afr (African), Aus (Australian), S.Afr (South African), and North American; unlabeled clades are of the mixed geographic origin; thick branches represent statistically supported relationships (high bootstrap of 89–100 and/or posterior probability of 0.95–1.00); thin branches indicate unsupported relationships; red branches indicate support not found in alternate phylogeny; dashed red lines show the transition of species between clades or at least sister to a clade; thick colored lines trace the transition of clades among major phylogenetic groups.



(Figs. 1 and 2 clades A–O; see Table 2). Two species, *Psilolemma jaegeri* and *Sporobolus somalensis*, fall outside the main *Sporobolus* clade in the ITS and plastid trees. *Sporobolus somalensis* is an enigmatic species known only from Somalia and extending into the Ethiopian Ogaden (Phillips, 1995). *Sporobolus somalensis* forms an unsupported polytomy with the *Zoysiinae* and the *Sporobolus* clade in the combined plastid phylogram and is weakly supported as sister to *Psilolemma jaegeri* in the ITS phylogram (Fig. 1A, BS = 65, PP = 0.90), forming a clade that is sister to the remainder of the *Sporobolus* clade. *Sporobolus somalensis* may deserve recognition at the generic level but we hesitate to provide a new name based on its differing affinities in the nuclear and plastid trees, and because there are few morphological characteristics delineating this from other species of *Sporobolus*. Based on subround lower glumes and upper glumes as long as the spikelet, Clayton (1971) described *S. compactus* Clayton, a presumed sister species to *S. somalensis*; *S. compactus* was not sampled here. *Psilolemma jaegeri* and *S. somalensis* are both mat-forming, stoloniferous perennials, although the latter species has open panicles with numerous 1-flowered spikelets while *P. jaegeri* has narrow and spike-like panicles with 4–14-flowered spikelets (Phillips, 1974, 1995; Clayton & 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. Another option would be to include *Psilolemma* in *Sporobolus*, and, if so, then *Zoysia* and *Urochondra* would also have to be included in *Sporobolus* since in the plastid tree *Psilolemma* is sister to all members of the *Zoysieae*. *Psilolemma jaegeri* is somewhat unusual in that it has 3-veined lemmas, but there are other species of *Sporobolus*, i.e., *S. acinifolius*, *S. albicans*, *S. fibrosus* Cope (not sampled), *S. palmeri*, and *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.

The Australian genus *Thellungia* was initially described by Stapf to include a single species, *T. advena* Stapf. Phillips (1982) transferred this species into *Eragrostis* (*E. advena* (Stapf) S.M. Phillips), and more recently, based on plastid *rps16* and nuclear *waxy* sequences, Ingram & Doyle (2004, 2007) have shown it to be embedded within *Sporobolus* and in our ITS tree it is sister to *Eragrostis megalosperma* (BS = 87, PP = 1.00). *Thellungia* has unique features such as multi-flowered (1–5), cleistogamous spikelets with long-curved rachillas (each floret readily disarticulates with a persistent rachilla joint), 1-veined (rarely 3) lemmas, and caryopses with free pericarps (Lazarides, 1997; Palmer & al., 2005). All of these characteristics, with the exception of multi-flowered spikelets, are common in species of *Sporobolus*. *Thellungia* is part of the *Sporobolus* lineage in our trees, but its placement is strongly discordant in our nuclear and plastid analyses. In the ITS tree it is part of a strongly supported clade comprising clades B, C and D plus a *Sporobolus consimilis*–*S. oxylepsis*–*S. robustus* clade, collectively a lineage of primarily African taxa whereas in the plastid tree it is part of a large North American lineage that includes clades J–O plus *S. palmeri*, *S. buckleyi*, *S. elongatus*, and clade C plus *S. consimilis*. Within the plastid North American clade

*Thellungia* is sister (weakly supported, BS = 69, PP = 1.00) to the *S. clandestinus* clade (L). Given its discordant position in the nuclear and plastid trees, *Thellungia advena* likely had a hybrid origin, involving ancestors of different major clades. Although its origins are unclear, *Thellungia advena* is clearly a member of the *Sporobolus* clade and we make the necessary combination below to include the species in *Sporobolus*.

*Eragrostis megalosperma*, an Australian endemic species, has several unusual morphological features and was reported by Lazarides (1997) and Palmer & al. (2005) to have no obvious relationships with other members of *Eragrostis*. However, *E. megalosperma* and *Thellungia* (*Eragrostis*) *advena* share ciliate ligules, spiciform panicles, multi-flowered spikelets that are often cleistogamous with a zig-zag rachilla, 1 or 3-veined lemmas, green stamens, and strongly compressed caryopses with free pericarps. *Eragrostis megalosperma* can be separated from *Thellungia* in having leaf sheaths that are longer than the internodes, 5–27-flowered spikelets (versus 1–5), and lemmas 1.8–2.5 mm long (versus 2.8–3 mm). Like *Thellungia*, *E. megalosperma* is also a member of the *Sporobolus* clade and we make the new combination below.

*Sporobolus buckleyi* from the southwestern U.S.A. and Mexico and *S. palmeri*, a Mexican endemic known from Durango and San Luis Potosí, form a weakly supported clade in the ITS tree. However, in the plastid tree *S. buckleyi* is sister to *Eragrostis megalosperma*, *Thellungia* plus the *S. clandestinus* complex (clade L). Morphologically, *S. buckleyi* and *S. palmeri* share the densely caespitose, perennial habit and open, diffuse panicles with primary branches without additional branches (naked) below on lower 1/4–1/2 of the axis (Espejo Serna, 2000; Peterson & 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* (see Fig. 4). There is much confusion in the herbarium between *S. palmeri* and *S. airoides* (Torr.) Torr., a morphologically similar species but more widely distributed occurring throughout the U.S.A., Mexico, and introduced in Arabia (Peterson & al., 2003, 2004; Clayton & 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 US, we found that only the type collection of *S. palmeri* made in the late 1890s and one other 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 mm versus 0.5–2 mm), longer spikelets (3.2–4.4 mm versus 1.3–2.8 mm), longer lemmas (3.2–4.3 mm versus 1.2–2.5 mm) that are 3- versus 1-veined, longer paleas (3.1–4.2 mm versus 1.1–2.4 mm), longer anthers (1.6–2.5 mm versus 1.1–1.8 mm), and longer modified caryopses (1.6–2.1 versus 1–1.4 mm; Peterson & al., 2003, 2004). In addition to being





**Fig. 4.** *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.

confused taxonomically, *S. airoides* and *S. palmeri* have been considered to be closely related. Both species were placed in the same strongly supported clade in a previous ITS analysis (Ortiz-Diaz & Culham, 2000), in contrast to our ITS tree 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 were 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 the ITS and plastid trees (*S. airoides* in clade J, *S. palmeri* as noted above). An illustration of *S. palmeri* is given to familiarize the reader and other agrostologists with the general morphology of *Sporobolus* (Fig. 4).

**Clade X.** — Three African taxa (*Sporobolus acinifolius*, *S. albicans*, *S. tenellus*), which have not previously been sampled in molecular studies, form a clade supported by Bayesian posterior probabilities in both ITS and combined plastid trees (Fig. 1A, PP = 0.95; Fig. 2A, BS = 51, PP = 0.95), and this clade is sister to the remaining species of *Sporobolus*. 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 3-veined lemmas (Gibbs Russell & 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). The latter species also has a prolonged rachilla above the floret nearly as long as the floret (Stapf, 1898). We have preliminary results suggesting *S. subtilis* is embedded within the tribe Eragrostideae (Peterson & al., unpub.). Therefore, we hesitate to use *S. sect. Chaetorhachia* (type = *S. subtilis*) to delineate the species in clade X but will address this question in future studies. Three-veined lemmas may be derived independently in *Eragrostis megalosperma*, *Psilolemma jaegeri*, the *S. acinifolius*–*S. albicans*–*S. tenellus* lineage, *S. palmeri* (which is nested deep in *Sporobolus*), and *Thellungia advena*, or this may be a plesiomorphic character retained in these lineages.

We consider the X clade to be an ancestral lineage of unclear origin that requires further investigation. Therefore, in order to assess the monophyly of *Sporobolus* further we removed the members of the X clade (*Sporobolus acinifolius*, *S. albicans*, *S. tenellus*) from the ITS and combined plastid analyses since this lineage has some unique morphological features and is genetically isolated. We then reanalyzed each dataset. In both cases we obtained stronger support for the *Sporobolus* crown node (BS = 76 for ITS, 52 for combined plastid; PP = 1.00 for both). These results lend support for retaining *Sporobolus* as taxonomic unit.

**Clade A.** — We find strong support for a lineage corresponding to the *S. indicus* complex, as recognized by previous authors (Pilger, 1956; Baijens & Veldkamp, 1991). The *Sporobolus indicus* complex, treated here as *S. sect. Sporobolus*, consists of at least 23 species, as confirmed in our phylograms

(see Table 2). Within this lineage, *S. farinosus* Hosok. is strongly supported as the sister species of the remainder of the lineage in both trees. In the plastid tree, *S. scabriflorus* is sister to *S. farinosus*, whereas in the ITS tree *S. scabriflorus* is part of the distantly related clade G, suggesting this taxon may be of hybrid origin. In the next deepest split in this clade, four species (*S. festivus* Hochst. ex A. Rich., *S. infirmus* Mez, *S. pectinellus* Mez, *S. stapfianus* Gand.) comprise a clade that is sister to a strongly supported clade of the rest of the sampled species in the plastid tree, whereas in the ITS tree these four species comprise a poorly supported grade that is sister to a strongly supported clade of the remaining species in this section. Several smaller clades of two to several species (the same species in both trees) are present in the ITS and plastid trees; e.g., the clade with *S. tenuissimus* (Mart. ex Schrank) Kuntze, *S. blakei* De Nardi ex B.K. Simon, *S. diandrus* (Retz.) P. Beauv., *S. trichodes* Hitchc., and *S. atrovirens* (Kunth) Kunth received stronger support (BS = 71, PP = 1.00) in the plastid tree. Relationships of other taxa in the clade vary slightly. For example, in the ITS tree five taxa (*S. fertilis*, *S. jacquemontii* Kunth, *S. indicus*, *S. berterioanus* (Trin.) Hitchc. & Chase, *S. pseudairoides* Parodi) and four taxa (*S. myrianthus* Benth., *S. creber* De Nardi, *S. laxus* B.K. Simon, *S. natalensis* (Steud.) T. Durand & Schinz) each form separate weakly to moderately supported clades, whereas in the plastid tree *S. fertilis* is part of the lineage that includes *S. creber*, *S. laxus*, and *S. natalensis*. Some of these taxa may be of hybrid origin. In addition to the 23 sampled species, we include three additional species (*S. fourcadii* Stent, *S. minor* Trin. ex Kunth, *S. quadratus* Clayton) in this section based on their morphology, as described in Clayton (1965). Clayton (1965) also recognized *S. pellucidus* Hochst., *S. olivaceus* Napper, and *S. elongatus* as occurring in the *S. indicus* complex. These taxa are not part of this lineage, and we treat them here in *S. sect. Fimbriatae* Veldkamp (clade B), *S. sect. Triachyrum* (Hochst. ex A. Braun) Veldkamp (clade D), and *incertae sedis*, respectively. *Sporobolus elongatus* probably belongs in the *S. indicus* complex as placed by Pilger (1956), Jovet & Guédes (1968), Baijens & Veldkamp (1991), Mandret (1992), Ortiz-Diaz & Culham (2000), and Shrestha & al. (2003). However, for *S. elongatus* we have data for a single plastid marker (*rpl32-trnL*) and in our plastid phylogram the affinities of this species are not conclusive. 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 PCK leaf metabolism (Hattersley, 1987; Baijens & Veldkamp, 1991). This lineage is widely distributed in North America, South America, Africa & Arabia, Australia & Pacific, and Southeast Asia (Figs. 1A, 2A).

**Clade B.** — Our analyses identify a strongly supported clade including *S. fimbriatus* and allies. *Sporobolus fimbriatus* was included in group 4B by Pilger (1956) and more recently in *S. sect. Fimbriatae* (Baijens & Veldkamp, 1991), as

treated here (Table 2). A *S. fimbriatus* lineage was also found by Ortiz-Diaz & Culham (2000) who included *S. pyramidatus*. Ortiz-Diaz & 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 nuclear and plastid trees. The *S. fimbriatus* clade is almost entirely African with a single species, *S. maderaspatanus* Bor, found in India and Ceylon (Lazarides, 1994). Baaijens & 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 & Veldkamp (1991) also included *S. agrostoides* Chiov, *S. brockmannii* Stapf, and *S. macranthelus* Chiov. as members of *S. sect. Fimbriatae*. Apparently, *S. diffusus* Clayton is the only annual member of the *S. fimbriatus* complex. Tetragonal to ellipsoid caryopses and short upper glumes 1/2–4/5 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 (Figs. 1A, 2B; BS = 100, PP = 1.00) in the combined plastid and ITS phylograms; this *Crypsis* lineage is part of a broader, well-supported clade. In the ITS phylogram *Sporobolus helvolus* (Trin.) T.Durand & Schinz, *S. mitchellii* (Trin.) C.E.Hubb. ex S.T.Blake, and *S. humilis* form a strongly supported clade that is sister to *Crypsis*, and together this lineage is the sister to three accessions of *S. ruspolianus* Chiov. Ortiz-Diaz & Culham (2000) recovered a clade with 100% jackknife support that included *Crypsis alopecuroides*, *S. helvolus*, *S. mitchellii*, and *S. tremulus* (Willd.) Kunth. The latter species is morphologically very similar to *S. virginicus* but differs by having shorter lower glumes (Lazarides, 1994). Therefore, we recognize *S. sect. Crypsis* to include the four species of *Sporobolus* that are part of clade C in the ITS and plastid trees, along with nine species currently placed in *Crypsis* (Cope, 1999; Raus & Scholz, 2004; Clayton & al., 2006). Characters that support recognition of *S. sect. Crypsis* include: plants that are 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*), 1-flowered spikelets with glumes that are shorter than the lemma, and 1–3-veined lemmas. Within *S. sect. Crypsis* we recognize two subsections, *Crypsis* and *Helvoli*. Subsection *Crypsis* includes nine species, all formerly treated at the generic rank (see description in Taxonomy section) and subsection *Helvoli* includes three species all having the perennial habit with culms that are decumbent, prostrate or erect, either rhizomatous or stoloniferous; panicles that are contracted, spiciform or open, 0.4–2 cm wide; and subterete spikelets 1.4–2 mm long. The discordant placement of *S. humilis* J.Presl found in clade C in the ITS tree and found in clade E in the plastid tree is discussed under clade E.

**Clade D.** — Based on our phylograms we recognize the *S. junceus* clade (*Sporobolus* sect. *Triachyrum*) to include 33 species (see Table 2), 18 of which were surveyed in our DNA analysis. This lineage was previously identified in the ITS analysis of Ortiz-Diaz & Culham (2000), who sampled seven species, four of which were also sampled here (*S. lasiophyllus*

Pilg., *S. macrospermus* Scribn. ex Beal, *S. purpurascens* (Sw.) Ham., *S. sanguineus* Rendle). Palisot de Beavois (1812) first recognized the distinctive features of *Sporobolus junceus* by describing a new genus, *Heleochoa* 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: 712). Pilger (1956) included five species of the *S. junceus* complex in his group 3A. Baaijens & 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 with either annuals or perennials, 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 & Peterson (1998) suggested that *S. junceus* and *S. purpurascens* may be sibling species. This hypothesis is supported in part by our ITS tree, in which the North American samples of *S. purpurascens* and both samples of *S. junceus* are sister taxa, whereas in the plastid tree all samples of *S. purpurascens* and *S. junceus* are part of different, strongly supported subclades.

In our ITS and plastid trees, clade D includes a subclade we call the 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 species 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 and an accession of *S. purpurascens* collected in Ecuador form a strongly supported clade (Figs. 1A, 2A; BS = 99, 97, 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, U.S.A. whereas in the plastid tree all three accessions of *S. purpurascens* form a strongly supported clade (Fig. 2A, BS = 100, PP = 1.00). We see no major morphological differences between these three accessions of *S. purpurascens* other than the North American plants are taller and have longer leaf blades. Several smaller two- to several-taxon clades are present in the nuclear and plastid trees, and in some cases their affinities in sect. *Triachyrum* are incongruent between the trees.

In the plastid tree *S. mildbraedii* Pilg. and *S. dinklagei* Mez appear distinct from the rest of the clade. The placement of the former taxon reflects missing data as we have only the *rpl32-trnL* marker (see Appendix 1; ITS data were not obtained for this taxon). *Sporobolus dinklagei*, for which we obtained plastid data from three of the four regions, is on a long branch in the plastid tree, and is nested deeper in the ITS tree.

**Clade E.** — This lineage is recovered in nuclear and plastid analyses with strong support 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 C<sub>4</sub>



NAD-ME leaf metabolism, Baaijens & 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 2, along with *S. compositus*, *S. spicatus*, and *S. rigens*, which we place in other lineages or incertae sedis based on their positions in our trees. Ortiz-Diaz & 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 in the ITS phylogram, and in the plastid phylogeny these two species align with *S. humilis*, *S. oxylepsis*, and *S. robustus*. In contrast to the ITS tree, the four accessions of *Sporobolus virginicus* are not recovered as monophyletic in the combined plastid phylogeny, which indicates possible incomplete plastid lineage sorting in the speciation process. *Sporobolus oxylepsis* and *S. robustus* are sister taxa in the ITS tree, while *S. humilis* is part of clade C, as noted above. *Sporobolus robustus* is a tall species with individuals up to 1 m in height similar to *S. consimilis* (with which it is closely related in the ITS tree, but not in the plastid tree) with open panicles that bear densely spikeleted primary branches. Each primary branch in *S. robustus* and *S. consimilis* is remarkably similar to the entire inflorescence in *S. humilis*, *S. pungens*, and *S. virginicus*. *Sporobolus oxylepsis* is a small caespitose perennial that does not have stolons, rhizomes, or contracted panicles. Instead, *S. oxylepsis* has open and diffuse panicles with spikelets borne on long pedicels, and has short lower glumes less than 1/3 as long as the floret. The characteristics in *S. oxylepsis* do not support inclusion into *S. sect. Virginicae*, therefore we have placed *S. oxylepsis* in incertae sedis. We also include *S. consimilis* in incertae sedis because in the ITS phylogram it is sister to *Thellungia advena* and in the plastid analysis it is sister to clade C.

**Clade F.** — This strongly supported clade, that 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 in our trees. In the plastid tree, *S. arabicus* joins clade F forming a trichotomy with the other two clades, whereas in the ITS tree *S. arabicus* is placed in clade I. Our data included only the plastid *rps16* marker for *S. arabicus* and it seems best to tentatively place this taxon in clade I. Clayton (1974) placed *S. verdcourtii* and *S. arabicus* as synonyms of *S. kentrophyllus* and Cope (1999) placed *S. arabicus* and *S. kentrophyllus* as synonyms of *S. ioclados* (Trin.) Nees. We retain all four taxa as separate species since the samples are genetically distinct with some morphological variation as well. These African species are characterized in having the perennial habit with caespitose often tussocky culms, often connected by stolons, culms 15–80 cm tall; whorled primary panicle branches that are naked on lower 1/4–1/2; lower glumes 1/3–3/4 as long as the spikelet; upper glumes 2/3 to as long as the spikelet; and ellipsoid caryopses 0.8–2 mm long. We place the species of clade F in *S. sect. Pyramidati* subsect. *Subulati* (see discussion of clade I below).

**Clade G.** — This strongly supported clade, consisting of only African species, has not previously been recovered in molecular studies. Three accessions of the primarily

mat-forming, tufted perennial with pungent leaf blades, *S. spicatus* form a weakly or strongly supported clade (Fig. 1B, BS = 64, PP = 0.61; Fig. 2B, BS = 100, PP = 1.00) that is sister to a strongly supported *S. microprotus* Stapf–*S. scabriflorus* Stapf ex Massey–*S. uniglumis* Stent & J.M.Ratray clade (Fig. 1B, BS = 100, PP = 1.00) consisting of three small, caespitose annuals. However, in our plastid tree, *S. scabriflorus* is not a member of this clade and is placed in the *S. indicus* complex (clade A). There are three missing plastid markers (*ndhA*, *rpl32-trnL*, *rps16-trnK*) in our dataset for *S. scabriflorus* so this might be the underlying reason for the ambiguous results. Clayton (1974) placed *S. scabriflorus* as a synonym of *S. microprotus* but our ITS sequences are not identical and there seems 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. Morphological characteristics that support recognition of clade G include: caespitose annuals or perennials, sometimes stoloniferous; 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 <1/3 as long as the spikelet, the scales often suppressed or lacking; upper glumes 2/3 to as long as the spikelet; and caryopses 0.7–1.1 mm long, elliptic, obovate to spherical or subglobose, usually laterally flattened. We place the species of clade G in *S. sect. Pyramidati* subsect. *Spicati* (see discussion of clade I below).

**Clade H.** — Three endemic species from Australia, *S. actinocladus* (F.Muell.) F.Muell., *S. australasicus* Domin, and *S. caroli* Mez form a moderately supported clade (Fig. 1B, BS = 72, PP = 0.98) and are sister to the southern African, *S. nitens* Stent in the ITS tree. In the plastid tree four endemic Australian species (*S. actinocladus*, *S. australasicus*, *S. caroli*, *S. scabridus*) form a moderately supported clade (Fig. 2B, BS = 76, PP = 0.97) that includes the South American *S. phleoides* Hack., and all of these are sister to *S. nitens*–*S. olivaceus* Napper clade (Fig. 2B, BS = 99, PP = 1.00). Even though *S. phleoides* has an extremely narrow inflorescence and is nearly impossible to determine when the lower panicle branches are whorled, we include it in clade H since it is sister to the three Australian endemics in our combined plastid phylogram. Only a single plastid marker (*rpl32-trnL*) for *S. olivaceus* was included in our dataset and we have no ITS marker. These five species have not been previously recovered as a clade in molecular studies. There are four more 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 1/4–1/2; lower glumes 1/3–2/3 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. We place the species of clade H in *S. sect. Pyramidati* subsect. *Actinocladi* (see discussion of clade I below).

**Clade I.** — We refer to this lineage as the *S. pyramidatus* (Lam.) Hitchc. complex only because this species is the most wide-ranging member of this lineage in the Western Hemisphere. All species in clade I 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 1/5 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 in Africa, North and South America, and Australia; however the deepest split in the nuclear tree, a strongly supported clade (Figs. 1B, 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. In the plastid tree, the American *S. domingensis* (Trin.) Kunth is sister to the remaining species in the *S. pyramidatus* complex. There is strikingly little morphological and genetic variation among the wide ranging *S. pyramidatus* 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 three accessions of *S. cordofanus* and two of *S. marginatus* are found in different, moderate to strongly supported, subclades. This could be the result of multiple gene copies (particularly in ITS), multiple origins of these taxa, or there could have been a mishandling or misidentification of our samples in the laboratory. Another possibility might be missing data since one accession of *S. cordofanus* (Greenway 10191) has only plastid marker (*rpl32-trnL*) and neither accession of *S. marginatus* has a complete set of plastid markers. Baaijens & Veldkamp (1991) had tentatively included *S. coromandelianus* in their *S. sect. Triachyrum* (*S. junceus* complex) but noted it differed by numerous anatomical characters from other members.

In the plastid tree a strongly supported clade containing “F, G, H, and I” lineages (Fig. 2B, BS = 96, PP = 1.00) is found and this clade is also present in the ITS tree but with less support (Fig. 1B, BS < 50, PP = 0.51). Many morphological features that delineate each of these clades separately are of course repeated in the F-G-H-I clade. The most obvious feature of whorled primary panicle branches is seen in the F-G-H-I clade and has arisen independently at least two times within *Sporobolus* since this character state is also found in the *S. junceus* complex (clade D). Therefore, we place all species in the F-G-H-I clade in a new section, *S. sect. Pyramidati* and within this section we recognize four subsections that correspond to the F (*Subulati*), G (*Spicati*), H (*Actinocladi*), and I (*Pyramidati*) clades. Morphological characteristics of *S. sect. Pyramidati* include: annual, biennial or perennial habit, sometimes rhizomatous or

stoloniferous; panicles with whorled primary branches, especially on the lower nodes; lower glumes 1/6–1/2 (–3/4) as long as the spikelet; and upper glumes 2/3 to as long as the spikelet.

**Clade J.** — This clade was first recovered by Ortiz-Diaz & Culham (2000), and is recovered with strong support in the plastid and nuclear trees. 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*) with spiciform (*S. spiciformis*) to pyramidal panicles and ascending or spreading primary branches, short spikelets 1.3–2.8 mm long, and lower glumes about 1/2 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 & al., 2003). The South American *S. rigens* is a member of this clade and is found on a long branch in the combined plastid phylogram. We have included *S. rigens* in incertae sedis (see Table 2) since it aligns outside the *S. airoides* clade in our ITS tree. Ortiz-Diaz & Culham (2000) also found *S. rigens* in a separate clade outside of the *S. airoides* clade (*S. sect. Airoides*). Our plastid tree suggests that *S. rigens* shares a maternal parent that is part of, or perhaps an ancestor of a member of the *S. airoides* complex. Additional study of *S. rigens*, perhaps using low copy nuclear genes, is needed to clarify this result and elucidate its origin.

**Clade K.** — The *Sporobolus cryptandrus* (Torr.) A. Gray lineage (*S. sect. Cryptandri*), 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 in the ITS-derived phylogram (Fig. 1B, BS = 87, PP = 1.00), and forms an unsupported grade basal to *Sporobolus sect. Airoides* (clade J) in the plastid tree, suggesting limited plastid variation among these closely related taxa. Ortiz-Diaz & Culham (2000) recovered this clade in their ITS analysis, which included four of the five species sampled here plus *S. contractus*. In our analyses, *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: the caespitose perennial habit, lower branches of the panicles are usually included in the uppermost culm sheath, lower glumes that are 1/3 to nearly as long as the lemma, upper glumes about as long as 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 & al., 2003). Although the complex is not monophyletic in the plastid data, this morphologically distinct lineage is supported in the ITS tree, thus we formally recognize this as a new section, *S. sect. Cryptandri*. Neither ITS or the plastid markers have sufficient discriminatory power to differentiate among accessions of *S. cryptandrus*, *S. flexuosus*, or *S. giganteus*. Apparently, these three taxa are closely related and they appear in the same clade in the ITS and plastid trees.

**Clade L.** — Pilger (1956) delineated this as group 5 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*, *S. compositus*, *S. neglectus*, and *S. vaginiflorus* (Torr. ex A.Gray) Alph.Wood from a common ancestor. In the ITS tree one individual of *S. clandestinus* (*Waterfall 5881*) does not align with three other samples of *S. clandestinus*; rather, *S. clandestinus* (*Waterfall 5881*) and *S. compositus* form a clade that is the unsupported sister of the rest of the *S. compositus* complex whereas in the plastid tree all members of the complex are part of a strongly supported clade. This could indicate hybridization with a member of the highly variable *S. compositus* complex (Peterson & al., 2003, 2009), multiple origins of this taxon, or simply the occurrence of multiple copies since *S. compositus* (syn. *S. asper* (P.Beauv.) Kunth) is a known hexaploid (Riggins, 1977). Likewise, in the combined plastid tree *S. vaginiflorus* var. *ozarkanus* falls within the *S. airoides* clade and is sister to *S. splendens* whereas in the ITS tree it aligns with three other samples of *S. vaginiflorus* as expected. Acquisition of the *S. airoides* plastid haplotype is probably the result of an ancient hybridization event. *Sporobolus neglectus* also does not align within the combined plastid tree with other members of the *S. compositus* complex but is found as sister to the C plus the J–O clades.

Important characters in the L lineage include panicles included in the uppermost sheath with cleistogamous spikelets and laterally flattened caryopses. In addition, we tentatively place *S. aldabrensis* Renvoise in this lineage since it shares a spiciform inflorescence (0.2–1.6 cm wide) with other members of the lineage, although we have data from only a single plastid (*rpl32-trnL*) marker. Important characters in this lineage are panicles included in the uppermost sheath with cleistogamous spikelets and laterally flattened caryopses. Based on only two plastid markers *S. conrathii* appears as a member of this clade (see Fig. 2B), although we are not convinced it is closely related since it differs morphologically in having diffuse, subdichotomously branched panicles (Gibbs Russell & al., 1991). Ortiz-Diaz & Culham (2000) sampled only *S. compositus* from this complex, which was placed in a clade with *Calamovilfa*, in contrast with our ITS results.

**Clade M.** — This is the strongly supported *Calamovilfa* lineage, congruent with multiple molecular studies that have found *Calamovilfa* to be nested within *Sporobolus* (Ortiz-Diaz & Culham, 2000; Hilu & Alice, 2001; Columbus & al., 2007; Peterson & al., 2010a). No previous study has sampled all of the five *Calamovilfa* species (Thieret, 2003), as we do here. Based on caryopsis, embryo, lodicule, leaf epidermal, and anatomical characteristics, Reeder & 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 & Ellington (1960) concluded, “while such hairs are lacking among species of *Sporobolus* is apparently a matter of relatively minor taxonomic importance.” The occurrence of callus hairs 1/4 to 7/8 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. brevipilis* (Torr.) Hack. ex Scribn. & Southw., *C. curtissii* (Vasey) Scribn., *C. gigantea* (Nutt.) Scribn. & Merr., *C. longifolia*).

Thieret (1966, 2003) recognized two sections: sect. *Calamovilfa*, including *C. arcuata*, *C. curtissii* and *C. brevipilis*, distinguished primarily 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 plastid and nuclear analyses do not support his sectional classification. In the ITS tree, *C. brevipilis*, *C. arcuata* and *C. longifolia* are successive sister groups (all strongly supported) of *C. gigantea* (*C. curtissii* was not sampled for ITS), and in the plastid tree *C. arcuata* and *C. brevipilis* are a clade that is sister to a clade of *C. gigantea*, *C. curtissii* and *C. longifolia*.

**Clade N.** — This clade consists of seven species (Table 2), five of which (*S. curtissii* Small ex Kearney, *S. floridanus*, *S. pinetorum* Weakley & P.M.Peterson, *S. silveanus* Swallen, *S. teretifolius* R.M.Harper) were previously studied and attributed to the *Sporobolus floridanus* complex, a group found in pine savannahs and seeps of the coastal plain in southeastern U.S.A. (Weakley & Peterson, 1998). The plastid and nuclear trees include in this lineage *S. heterolepis*, a species distributed in northcentral U.S.A., which has been considered to be a close relative to members of clade N (Pilger, 1956; Weakley & Peterson, 1998). *Sporobolus heterolepis* was placed in a strongly supported clade with *Calamovilfa* in the *matK* analysis of Hilu & Alice (2001). Weakley & Peterson (1998) hypothesized a close relationship between *S. heterolepis* and *S. silveanus*, which is supported by our plastid data. *Sporobolus interruptus* Vasey, an Arizonian endemic, has also been considered to be close to this lineage, and possibly the sister species of *S. heterolepis* (Weakley & Peterson, 1998). Although we have not sampled *S. interruptus*, we include it in this lineage based on its morphology. Members of the *S. floridanus* complex (including *S. heterolepis* and *S. interruptus*) share the following morphological features: 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 spikelets (3–7(–7.2) mm) that are purplish or plumbeous, spikelets with a glabrous callus and paleas, and caryopses that fall free from the lemma and palea at maturity. We recognize this lineage as *Sporobolus* sect. *Calamovilfa* subsect. *Floridani*. Weakley & Peterson (1998) also considered *S. junceus* and *S. purpurascens* to be closely related to the *S. floridanus* complex and noted the former two species can be distinguished in having distinctly whorled panicle branches in well-marked verticils. Our analyses do not support this, as these species are part of the distantly related clade D (*S.* sect. *Triachyrum*).

In the ITS tree one individual of *S. clandestinus* (*Waterfall 5881*) does not align with three other samples of *S. clandestinus*; rather, *S. clandestinus* (*Waterfall 5881*) and *S. compositus* form a clade that is the unsupported sister of the rest of the *S. compositus* complex whereas in the plastid tree all members of

the complex are part of a strongly supported clade. Clades M and N are depicted as strongly supported sister clades in our trees (Figs. 1B, 2B; BS = 97, 98, PP = 1.00), consistent with earlier results (Hilu & Alice, 2001; Peterson & 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). The morphological similarities between clades M and N include: robust culms usually 1–2.5 m tall with indurated (hardened) basal sheaths, a line of hairs for a ligule, panicles much longer than broad, spikelets with 1-veined glumes and lemmas, and caryopses with free pericarps (Peterson & al., 2003; Thieret, 2003). For this reason we recognize the species of clades M and N in separate subsections, *Calamovilfa* and *Floridani* of *S.* sect. *Calamovilfa*.

**Clade O.** — This is the strongly supported *Spartina* lineage. Hubbard (1947) and Clayton & Renvoize (1986) 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 (Mobberley, 1956). Molecular studies have since firmly placed *Spartina* within the Sporobolinae, nested within *Sporobolus*, as reflected in recent classifications (Hilu & Alice, 2001; Columbus & al., 2007; Peterson & al., 2010a). These earlier analyses, which all had sparse sampling of *Spartina*, *Sporobolus* and relatives, variously placed *Spartina* in a strongly supported clade with *Calamovilfa* plus *Sporobolus heterolepis* (Hilu & Alice, 2001; *matK*), *Calamovilfa* (Columbus & al., 2007; combined ITS and *trnL-F*), and *Calamovilfa longifolia* plus *Sporobolus teretifolius*–*S. pinetorum* (Peterson & al., 2010a; combined ITS and plastid data). Our better-sampled trees are consistent with these earlier results. In our plastid tree *Spartina* is the sister group of a clade comprising *Calamovilfa* (clade M) and the *Sporobolus floridanus* complex (clade N), which includes *S. heterolepis*, *S. teretifolius* and *S. pinetorum* sampled in earlier studies. In the ITS tree *Spartina* is part of a well-supported clade 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 remaining members of the *Sporobolus compositus* complex (clade L). These three lineages (L, M, N) in the ITS tree form an unsupported clade. The affinities of clade L to *Spartina* in the plastid tree are less clear, although the lineage is part of the strongly supported North American clade that includes *Spartina*. Both datasets suggest that *Spartina* and several of the other major North American lineages are derived from a common ancestor.

Within *Spartina*, our nuclear tree identifies three major lineages, one comprising the mostly tetraploid ( $2n = 40$ ) *Spartina gracilis*, *S. cynosuroides*, *S. ×caespitosa*, *S. pectinata*, *S. bakeri*, *S. patens*, *S. ciliata*, and *S. densiflora*; one comprising the hexaploid ( $2n = 60, 62$ ) *S. alterniflora*, *S. foliosa*, and *S. maritima*; and *S. spartinae*. 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 & al., 2002; Fortune & al., 2008), with

the caveat that we did not sample *S. arundinacea* (Thouars) Carmich. The earlier plastid trees did not resolve the monophyly of the tetraploid clade; the increased resolution of this clade here likely reflects our analysis of more nucleotides (four gene regions vs. one). However, inferred relationships between *S. densiflora* and *S. argentinensis* (= *S. spartinae*) differ among studies. For the nuclear data, the trees differ only in the inferred relationships among *S. cynosuroides*, *S. pectinata* and *S. gracilis*. In the earlier ITS trees these form 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). Our sampling includes *S. ×townsendii*, a sterile F1 hybrid of *S. alterniflora* (the female parent) and *S. maritima* (the male parent) and the precursor of the amphidiploid *S. anglica* (reviewed in Saarela, 2012); the parentage of *S. ×townsendii* was confirmed based on variation in plastid regions (*trnT-trnL*, *rpl16*) and molecular fingerprinting (Ferris & al., 1997; Baumel & al., 2002, 2003). Curiously, neither *S. ×townsendii* nor *S. anglica* were sampled in the earlier phylogenetic studies (Baumel & al., 2002; Fortune & al., 2007, 2008). They are included here, and in our phylogenetic trees, the plastid sequences are identical for all individuals of *S. alterniflora*, *S. anglica* and *S. ×townsendii*, consistent with *S. alterniflora* being the female parent of *S. ×townsendii*, and *S. ×townsendii*, in turn, being the progenitor of *S. anglica*. *Spartina foliosa* is the sister group of this latter clade, and *S. maritima* is the sister group of the *S. foliosa* and *S. anglica*–*S. alterniflora*–*S. ×townsendii* clade. Relationships among species in the hexaploid clade in the ITS trees are different. *Spartina maritima* and *S. ×townsendii* comprise a weakly supported clade that is the sister group of *S. anglica*, with ITS sequences different than those of its hybrid progenitor, and this strongly-supported three taxon clade is the sister group of a *S. foliosa*–*S. alterniflora* clade. The minor variation in ITS between *S. anglica* and *S. ×townsendii* may reflect post-origin directional concerted evolution in *S. anglica*.

The plastid *trnT-trnL* region has also been used to identify hybrids between *S. foliosa* and *S. alterniflora*, and *S. foliosa* and *S. densiflora* in California, in combination with complementary data sources (Antilla & al., 2000, Ayres & al., 2008). Some hybrid individuals shared their plastid haplotypes with *S. densiflora*, and others with *S. foliosa*. Our sample of *S. foliosa* (Reeder 6652 & Reeder) was collected in Baja California Sur, Mexico, in 1975, where neither of these taxa is known to be introduced, and is thus highly unlikely to be a hybrid with either *S. alterniflora* (introduced to adjacent California in the 1970s; Spicher & Josselyn, 1985) or *S. densiflora* (introduced to California in the 1800s; Spicher & Josselyn, 1985; Bortolus, 2006). Although none of the samples analyzed here represent either of these hybrids, we expect that, if the hybrids were sampled with the plastid markers used here, the same haplotype patterns in *trnT-trnL* would be prevalent in these other plastid regions.

Baumel & al. (2002) also sampled the nuclear *waxy* (GBSSI) locus, which is incongruent with ITS and plastid data in some respects. In the *waxy* trees the tetraploid species *S. argentinensis* Parodi (= *S. spartinae*) was sister to the hexaploid clade, and the



heptaploid *S. densiflora* ( $2n = 70$ , Ayres & al., 2008, Fortune & 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 & al., 2007) and *S. densiflora* (Fortune & al., 2008). In the former study, two major lineages were identified, neither of which was congruent with the clades identified in ITS and plastid analyses. 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 and plastid data (Fortune & 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 & 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 in our analyses suggests that the gene duplication may have occurred early during, or prior to, the evolution of the Sporobolinae lineage. Broader sampling of *waxy* among taxa of Sporobolinae and other Chloridoideae taxa is needed to discern this. Further study of *waxy* in *S. densiflora* identified three divergent copies of the gene, one in each major *waxy* clade, supporting a polyphyletic origin for this species involving a member of the tetraploid lineage (probably *S. arundinacea*) and a member of the hexaploid lineage (Fortune & al., 2008). An overview of the history of reticulation among *Spartina* species is given in Ainouche & al. (2009).

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 phylograms (Figs. 1B and 2B, clade O). Moberley (1956) described complex 1 (*Spartina arundinacea*, *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* [now considered to be a hybrid between *S. alterniflora* and *S. densiflora*; Bortolus, 2006], *S. maritima*, *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*, *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 3 on the basis of its morphology. Formal names for these *Spartina* lineages, hitherto referred to as the tetraploid and hexaploid lineages or clade I and clade II (e.g., Baumel & al., 2002; Fortune & al., 2007, 2008), should facilitate precise communication about these clades. We thus recognize Moberley's (1956) three complexes (with modification to his complex 1) as subsections within *Sporobolus* sect. *Spartina*: subsect. *Ponceletia* (complex 1), subsect. *Alterniflori* (complex 2), and subsect. *Spartina* (complex 3).

**Cytology.**— Base chromosome numbers for the Zoysieae reported in Goldblatt & Johnson (1979–) are  $x = 6, 8, 9, 10$ , and 12; and the common base chromosome number (plesiomorphy) for the Chloridoideae is  $x = 10$  (Peterson & al., 2007, 2010a). The following counts were reported in Goldblatt & Johnson (1979–), Baaijens & Veldkamp (1991), Simon & Jacobs (1999), Roodt & Spies (2003), and Peterson & al. (2003, 2004):  $x = 10$  for 2 species of *Calamovilfa*;  $x = 8$  for 3 species and  $x = 9$  for 1 species of *Crypsis*;  $x = 10$  for 14 species of *Spartina*;  $x = 6$  for 8 species (sometimes reported as  $x = 12$ ),  $x = 9$  for 29 species, and  $x = 10$  for 13 species of *Sporobolus*; and  $x = 10$  for 2 species of *Zoysia* (see Table 2 for chromosome numbers). There are no known chromosome counts for *Psilolemma* or *Urochondra*. Obviously, cytological work has progressed more rapidly in *Spartina* (13 of the 59 chromosome counts in Table 2) since it is a dominant species of coastal habitats such as intertidal mud flats, estuaries, and salt marshes (Saarela, 2012). Hypothetically within *Sporobolus* s.l., 12 species in six clades have diploid populations, although only six species are known with only diploid chromosome reports, i.e.,  $2n = 12, 18$  or 20 (*Crypsis alopecuroides*, *Sporobolus maderaspatanus*, *S. mollerii* Hack., *S. montanus* (Hook.f.) Engl., *S. sanguineus*, *S. tenuissimus*). The  $x = 6$  base chromosome number is found in clades A, B, and I;  $x = 9$  base number is found in clades A, B, C, E, F, I, J, K, L, N, and X; base number  $x = 10$  is found in clades A, C, D, E, J, K, M, N, and O. Since there are at least 120 species without a known chromosome number (67% listed in Table 2) it is not easy to draw meaningful conclusions. Only clade A (*S. sect. Sporobolus*) contains species with all three base numbers ( $x = 6, 9$ , and 10); clades B (*S. sect. Fimbriatae*) and I (*S. subsect. Pyramidati*) contain species with  $x = 6$  and 9; and clades C (*S. subsect. Helvoli*), E (*S. sect. Virginicae*), J (*S. sect. Airoides*), K (*S. sect. Cryptandri*), and N (*S. subsect. Floridani*) contain species with  $x = 9$  and 10.

**Incongruences between the ITS and combined plastid phylograms.**— The two phylogenetic trees in our study of the Zoysieae based on combined plastid and ITS DNA sequences are incongruent and their topologies are not mutually exclusive (Fig. 3). The 16 major clades (A–O, X) were found in both analyses and have been maintained with high support in 12 clades in the combined plastid tree and 11 clades in the nuclear tree. In the combined plastid and ITS trees the X and A clades are shown to be the first and second diverging lineages, and the unity of the North American clade (J–O) and a group of mostly Austral-African clades (E–I) are also preserved. The placement of *Sporobolus rigens* outside the J clade in the ITS tree could be attributed to high amounts of homoplasy in the



nuclear dataset while the possession of “H” and “F” plastid haplotypes in *S. scabridus* and *S. arabicus*, respectively (both members of the I clade in the ITS tree), suggest possible hybridization events between these two sister lineages. One major structural difference that prevents congruence between the ITS and combined plastid trees is the B-C-D clade.

## ■ TAXONOMY

Because our molecular analysis renders *Sporobolus* paraphyletic, we propose incorporating *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia* within *Sporobolus*. Expansion of the circumscription of *Sporobolus* to include these four genera requires the least amount of nomenclatural changes and still allows us to recognize a strongly supported monophyletic and morphologically cohesive unit. Since *Spartina* is the oldest genus, Peterson & al. (2014c) prepared a proposal supporting the conservation (nomina conservanda) of *Sporobolus*. Below, we list all species previously recognized in *Calamovilfa*, *Crypsis*, *Spartina*, and *Thellungia* and provide their names in *Sporobolus*. Our analysis supports the recognition of 11 sections and 11 subsections (see Table 2) within *Sporobolus*, and for consistency in rank, we propose new sectional and subsectional names below. Species not included in our DNA analysis are preceded by an asterisk (\*).

- Sporobolus*** R.Br., Prodr.: 169. 1810, nom. cons. prop. – Type: *Sporobolus indicus* (L.) R.Br. (≡ *Agrostis indica* L.).
- = *Pallasia* Scop., Intr. Hist. Nat.: 72. 1777, non *Pallasia* Houttuyn 1775 ≡ *Crypsis* Aiton, Hort. Kew. 1: 48. 1789, nom. rej. prop. ≡ *Antitragus* Gaertn., Fruct. Sem. Pl. 2: 7. 1790, nom. illeg. superfl. ≡ *Raddia* Mazziari, Ionios Antologia 2: 448. 1834, non *Raddia* Bertol. 1819 – Type: *Pallasia aculeata* (L.) Kuntze (≡ *Schoenus aculeatus* L.; *Sporobolus aculeatus* (L.) P.M.Peterson).
- = *Spartina* Schreb., Gen. Pl.: 43. 1789, nom. rej. prop. – Type (designated by Moberley in Iowa State Coll. J. Sci. 30: 477. 1956): *Spartina cynosuroides* (L.) Roth. (≡ *Dactylis cynosuroides* L.; *Sporobolus cynosuroides* (L.) P.M.Peterson & Saarela).
- = *Ponceletia* Thouars, Esquisse Fl. Tristan D’Acugna: 36. 1808, nom. rej. prop. – Type: *Ponceletia arundinacea* Thouars (≡ *Sporobolus moberleyanus* P.M.Peterson & Saarela).
- = *Heleochloa* Host ex Roem., Collectanea: 233. 1809, nom. rej. prop. – Type: (designated by Nash in Britton & Brown, Ill. Fl. N. U.S., ed. 2, 1: 190. 1913): *Heleochloa alopecuroides* (Piller & Mitterp.) Host ex Roem. (≡ *Phleum alopecuroides* Piller & Mitterp.; *Sporobolus alopecuroides* (Pillar & Mitterp.) P.M.Peterson).
- = *Agrosticula* Raddi, Agrostogr. Bras.: 33. 1823 – Type: *Agrosticula muralis* Raddi (≡ *Sporobolus muralis* (Raddi) Hitchc. & Chase; = *Sporobolus tenuissimus* (Mart. ex Schrank) Kuntze).
- = *Bennetia* Raf. in Bull. Bot. (Geneva) 1: 220. 1830 – Type: *Bennetia juncea* Raf. ex B.D.Jacks. (≡ *Agrostis juncea* Michx., nom. illeg.; *Sporobolus junceus* (P.Beauv.) Kunth).

- = *Triachyrum* Hochst. ex A.Braun in Flora 24(2): 712. 1841 – Type: *Triachyrum adoense* Hochst. ex A.Braun (= *Sporobolus discosporus* Nees).
- = *Spermachiton* Llanos, Fragm. Pl. Filip.: 25. 1851 – Type: *Spermachiton involutum* Llanos (= *Sporobolus diandrus* (Retz.) P.Beauv.).
- = *Cryptostachys* Steud., Syn. Pl. Glumac. 1: 181. 1854 – Type: *Cryptostachys vaginata* Steud. (≡ *Sporobolus vaginatus* (Steud.) Scribn.; = *S. vaginiflorus* (Torr. ex A.Gray) Alph. Wood).
- = *Diachyrium* Griseb. in Abh. Königl. Ges. Wiss. Göttingen 19: 257–258, t. 2, fig. 8. 1874 – Type: *Diachyrium arundinaceum* Griseb. (= *Sporobolus rigens* (Trin.) E.Desv.).
- = *Bauchea* E.Fourn., Mexic. Pl. 2: 87. 1886 – Type: *Bauchea karwinskyi* E.Fourn. (= *Sporobolus wrightii* Munro ex Scribn.).
- = *Calamovilfa* (A.Gray) Hack. ex Scribn. & Southw., True Grasses: 113. 1890 – Type (designated by Thieret in Castanea 31: 146. 1966): *Calamovilfa brevipilis* (Torr.) Hack. ex Scribn. & Southw. (≡ *Arundo brevipilis* Torr.; *Sporobolus brevipilis* (Torr.) P.M.Peterson).
- = *Torgesia* Bornm. in Mitth. Thüring. Bot. Vereins, n.s., 30: 83. 1913 – Type: (≡ *Torgesia minuartioides* Bornm.; *Sporobolus minuartioides* (Bornm.) P.M.Peterson).
- = *Thellungia* Stapf in Bull. Misc. Inform. Kew 1920(3): 97, fig. 1–11. 1920 – Type: *Thellungia advena* Stapf (≡ *Sporobolus advenus* (Stapf) P.M.Peterson).

***Sporobolus advenus*** (Stapf) P.M.Peterson, **comb. nov.** ≡ *Thellungia advena* Stapf in Bull. Misc. Inform. Kew 1920(3): 98, fig. 1–11. 1920 ≡ *Eragrostis advena* (Stapf) S.M.Phillips in Kew Bull. 37(1): 159. 1982 – Holotype: SWITZERLAND (introduced from Australia). Derendingen Mill, near Solothurn, 10 Aug–1 Sep 1918, *R. Probst s.n.* (K barcode 000643476 [image!]; isotypes: BRI, US No. 2947408!).

***Sporobolus megalospermus*** (F.Muell. ex Benth.) P.M.Peterson, **comb. nov.** ≡ *Eragrostis megalosperma* F.Muell. ex Benth., Fl. Austral. 7: 644–645. 1878 – Lectotype (designated by Lazarides in Austral. Syst. Bot. 10: 133. 1997): AUSTRALIA. Queensland, Port Curtis District, Rockhampton, 23°02’S, 150°03’E, Herb. F. Mueller 1877, *O’Shanesy s.n.* (K barcode 000643530 [image!]; isolectotype: BRI).

= *Sporobolus indicus* var. *intermedius* Bailey in Queensland Agric. J. 30: 316. 1913.

***Sporobolus* sect. *Airoides*** P.M.Peterson, **sect. nov.** – Type: *Agrostis airoides* Torr. in Ann. Lyceum Nat. Hist. New York 1(1): 151–152. 1824 ≡ *Sporobolus airoides* (Torr.) Torr. Caespitose perennials, culms 30–250 cm tall. Panicles spiciform or pyramidal with widely spreading branches. Spikelets 1.3–2.8 mm long; lower glumes about 1/2 as long as the lemma.

Species included: *S. airoides*, *S. spiciformis* Swallen, *S. splendens* Swallen, *S. wrightii* Munro ex Scribn.

*Sporobolus* sect. *Calamovilfa* (A.Gray) P.M.Peterson, **comb. & stat. nov.** ≡ *Calamagrostis* subg. *Calamovilfa* A.Gray, Manual: 582. 1848 ≡ *Calamovilfa* (A.Gray) Hack. ex Scribn. & Southw., True Grasses: 113. 1890 – Type (designated by Thieret in *Castanea* 31: 146. 1966): *Sporobolus brevipilis* (Torr.) P.M.Peterson (≡ *Arundo brevipilis* Torr. ≡ *Calamovilfa brevipilis* (Torr.) Hack. ex Scribn. & Southw.). = *Calamovilfa* sect. *Interior* Thieret in *Castanea* 31(2): 150. 1966 – Type: *Sporobolus curtissianus* (Vasey) P.M.Peterson (≡ *Calamovilfa giganteus* (Nutt.) Scribn. & Merr. ≡ *Calamagrostis gigantea* Nutt.).

As per Art. 11.6, the autonym *Calamovilfa* (A.Gray) Hack. ex Scribn. & Southw. sect. *Calamovilfa* has priority over the name that established it (i.e., *C.* sect. *Interior*).

*Sporobolus* subsect. *Calamovilfa* (A.Gray) P.M.Peterson, **comb. & stat. nov.** ≡ *Calamagrostis* subg. *Calamovilfa* A.Gray, Manual: 582. 1848. [see *Sporobolus* sect. *Calamovilfa* entry above]

Rhizomatous perennials; rhizomes covered with shiny, coriaceous scale-like leaves or with dull, persistent foliage leaves; culms 1–2.5 m tall. Sheaths indurated. Panicles mostly open or contracted at maturity, usually longer than wide. Spikelets 5–10.8 mm long; callus hairy, the hairs 1/4–7/8 as long as the lemma; paleas mostly pubescent. Caryopses falling with the lemma and the palea.

Species included:

1. *Sporobolus arcuatus* (K.E.Rodgers) P.M.Peterson, **comb. nov.** ≡ *Calamovilfa arcuata* K.E.Rodgers in *Rhodora* 72(789): 72–79, fig. 1–2. 1970 – Holotype: U.S.A. Tennessee, Cumberland Co., Along Daddy’s Creek Road from Rockwood to Crab Orchard about 7–8 mi from Crab Orchard at Antioch Bridge, 3 Oct 1968, *K.E. Rogers 42409, A.J. Sharp, C. Delgadillo & W. Meijer* (US No. 281796 [not found]; isotypes: BRIT No. 23386 [image!], ISC barcode 0000509 [image!], LAF, TAES, TENN, US No. 74241!).

2. *Sporobolus arenicola* P.M.Peterson, **nom. nov.** ≡ *Calamagrostis gigantea* Nutt. in *Trans. Amer. Philos. Soc.*, n.s., 5: 143–144. 1835 (“1837”) ≡ *Calamovilfa gigantea* (Nutt.) Scribn. & Merr. in *Circ. Div. Agrostol. U.S.D.A.* 35: 2. 1901, non *Sporobolus giganteus* Nash – Holotype: U.S.A. Arkansas Territory, Habitat on the sandy banks of Great Salt River of the Arkansas, [1819], *T. Nuttall s.n.* (BM barcode BM001042438 [image!]; isotypes: PH barcode 00010144 [image!], US No. 865774A! fragm. ex BM, US No. A865773A! fragm. ex PH).

The epithet refers to the sand dune habitat where the species is commonly found.

3. *Sporobolus brevipilis* (Torr.) P.M.Peterson, **comb. nov.** ≡ *Arundo brevipilis* Torr., *Fl. N. Middle United States* 1: 95. 1823 ≡ *Calamagrostis brevipilis* (Torr.) L.C.Beck, *Bot. North. Middle States*: 401. 1833 ≡ *Ammophila brevipilis* (Torr.) Benth. ex Vasey, *Grass. U.S.*: 29. 1883 ≡ *Calamovilfa*

*brevipilis* (Torr.) Hack. ex Scribn. & Southw., *True Grasses* 113. 1890 – Holotype: U.S.A. New Jersey, 1820, *s.coll. s.n.* (NY barcode 00346013 [image!]; isotypes: NY barcode 00346015 [image!], US No. A865368! fragm. ex Herb. Torrey, US No. 78850! fragm. ex Herb. Torrey).

4. \**Sporobolus vaseyi* P.M.Peterson, **nom. nov.** ≡ *Ammophila curtissii* Vasey in *Bull. Torrey Bot. Club* 11: 7. 1884 ≡ *Calamagrostis curtissii* (Vasey) Vasey in *Bot. Gaz.* 15: 269. 1890 ≡ *Calamovilfa curtissii* (Vasey) Scribn. in *Bull. Div. Agrostol. U.S.D.A.* 17: 199. 1899, non *Sporobolus curtissii* Small ex Kearney – Holotype: U.S.A. Florida, Brevard Co., dry or moist pine barrens on Merritt’s Island, Indian River, Jul 1879, *A.H. Curtiss 3412* (US No. 76420!; isotypes: BR barcode 0000006866068 [image!], GH barcode 00023345 [image!], MO Nos. 992438 & 992439 [images!], NY barcode 00327700 [image!], PH barcode 00002959 [image!]).

The epithet commemorates George S. Vasey (1822–1893), an eminent agrostologist who in 1872 was appointed botanist of the USDA grass herbarium and in 1889 the Smithsonian Institution appointed Vasey honorary curator in the Department of Botany (Pennington, 2004).

5a. *Sporobolus rigidus* (Buckley) P.M.Peterson, **comb. nov.** ≡ *Vilfa rigida* Buckley in *Proc. Acad. Nat. Sci. Philadelphia* 14: 89. 1862 – Holotype: U.S.A. Oregon, [1834–35], *T. Nuttall s.n.* (PH barcode 00029017 [image!]).

= *Calamagrostis longifolia* Hook., *Fl. Bor.-Amer.* 2: 241. 1840 ≡ *Ammophila longifolia* (Hook.) Benth. ex Vasey, *Grass. U.S.*: 29. 1883 ≡ *Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., *True Grasses*: 113. 1890 ≡ *Athernotus longifolius* (Hook.) Lunell in *Amer. Midl. Naturalist* 4: 218. 1915, non *Sporobolus longifolius* (Torr.) Alph.Wood.

5b. \**Sporobolus rigidus* var. *magnus* (Scribn. & Merr.) P.M. Peterson, **comb. nov.** ≡ *Calamovilfa longifolia* var. *magna* Scribn. & Merr. in *Circ. Div. Agrostol. U.S.D.A.* 35: 3. 1901 – Holotype: U.S.A. Michigan, Allegan Co., lake shore at the mouth of the Kalamazoo River, 1894, *W.A. Taylor s.n.* (US No. 201912!).

*Sporobolus* subsect. *Floridani* P.M.Peterson, **subject. nov.** – Type: *Sporobolus floridanus* Chapm., *Fl. South. U.S.*: 550. 1860.

Caespitose perennials; culms (0.2–)0.25–2(–2.5) m tall. Basal sheaths shiny and indurated or dull and fibrous. Panicles open at maturity to somewhat contracted, longer than wide, narrowly pyramidal to ovate; lower nodes with 1–2(–3) branches. Spikelets 3–7(–7.2) mm long, purplish or plumbeous; callus glabrous; paleas glabrous. Caryopses falling free from the lemma and palea.

Species included: \**S. curtissii* Small ex Kearney, *S. floridanus*, *S. heterolepis* (A.Gray) A.Gray, \**S. interruptus* Vasey, *S. pinetorum* Weakley & P.M.Peterson, *S. silveanus* Swallen, *S. teretifolius* R.M.Harper.

*Sporobolus* sect. **Clandestini** P.M.Peterson, **sect. nov.** – Type: *Sporobolus clandestinus* (Biehler) Hitchc. (≡ *Agrostis clandestina* Biehler, Pl. Nov. Herb. Spreng.: 8. 1807).

Caespitose annuals or perennials, sometimes with rhizomes. Panicles 0.2–1.6 cm wide, contracted, spiciform, spike-like, usually included in the uppermost sheath, terminal and axillary. Spikelets 1.3–9(–10) mm long, often cleistogamous. Caryopses laterally flattened.

Species included: *S. aldabrensis* Renvoize, *S. compositus* (Poir.) Merr., *S. clandestinus*, *S. neglectus* Nash, *S. vaginiflorus* (Torr. ex A.Gray) Alph.Wood.

*Sporobolus* sect. **Crypsis** (Aiton) P.M.Peterson, **comb. & stat. nov.** ≡ *Crypsis* Aiton, Hort. Kew. 1: 48. 1789 – Type: *Sporobolus aculeatus* (L.) P.M.Peterson (≡ *Schoenus aculeatus* L.).

Geniculate annuals or perennials with wiry culms. Panicles short, <12 cm long, spike-like to subspiciform (ovate with stiffly spreading branches in *S. ruspolianus*). Spikelets 1-flowered; glumes usually shorter than the lemma; lemmas 1–3-veined.

*Sporobolus* subsect. **Crypsis** (Aiton) P.M.Peterson, **comb. & stat. nov.** ≡ *Crypsis* Aiton, Hort. Kew. 1: 48. 1789. [see *Sporobolus* sect. *Crypsis* entry above]

Erect, geniculate, or prostrate annuals; culms 1–40(–90) cm long. Panicles 0.4–7.5 cm long, 0.2–0.8 cm wide, spiciform or capitate, often embraced or enclosed in the sheath. Spikelets 2–6 mm long, strongly laterally compressed; lemmas 2–5.2 mm long, keeled. Caryopses 1–2.5 mm long.

Species included:

1. *Sporobolus aculeatus* (L.) P.M.Peterson, **comb. nov.** ≡ *Schoenus aculeatus* L., Sp. Pl.: 42. 1753 ≡ *Crypsis aculeata* (L.) Aiton, Hort. Kew 1: 48. 1789 – Lectotype (designated by Meikle, Fl. Cyprus 2: 1848. 1985): *Loefling s.n.* (LINN No. 68.3 [image!]).

2. *Sporobolus alopecuroides* (Piller & Mitterp.) P.M.Peterson, **comb. nov.** ≡ *Phleum alopecuroides* Piller & Mitterp., Iter Poseg. Slavon.: 147, t. 16. 1783 ≡ *Heleochloa alopecuroides* (Piller & Mitterp.) Host, Icon. Descr. Gram. Austriac. 1: 23, t. 29. 1801 ≡ *Crypsis alopecuroides* (Piller & Mitterp.) Schrad., Fl. Germ. 1: 167. 1806 – Holotype: HUNGARY. Iter per Poseganum Slavoniae provinciam.

3a. *\*Sporobolus borszczowii* Regel

3b. *\*Sporobolus borszczowii* subsp. **acuminatus** (Trin.) P.M. Peterson, **comb. & stat. nov.** ≡ *Crypsis acuminata* Trin., Neue Entd. 2: 57. 1821 – Lectotype (designated by Tsvelev in Fedorov, Zlaki SSSR [Grasses of the Soviet Union]: 647. 1976): KAZAKHSTAN. Lower reaches of the Ural River (LE TRIN 1523B1! [Trinius herbarium collection housed at LE, given a microfiche number in Soreng & al., 1995]).

3c. *\*Sporobolus borszczowii* subsp. **ambiguus** (Boiss. & Balansa ex Boiss.) P.M.Peterson, **comb. nov.** ≡ *Heleochloa*

*ambigua* Boiss. & Balansa ex Boiss., Fl. Orient. 5: 477. 1884 ≡ *Crypsis ambigua* (Boiss. & Balansa ex Boiss.) Lorch in Bull. Res. Council Israel, Sect. D, Bot. 11: 97. 1962 ≡ *Crypsis acuminata* subsp. *ambigua* (Boiss. & Balansa ex Boiss) Kit Tan, Fl. Turkey & E. Aegean Isl. 9: 584. 1985 – **Lectotype (designated here)**: TURKEY. İzmir, Station de Boudja, près de Smyrne, 150 m, 31 Aug. 1866, *B. Balansa 1541* (W barcode 0027063 [image!]; isoelectotype: W barcode 0048400 [image!]).

4. *\*Sporobolus factorovskyi* (Eig) P.M.Peterson, **comb. nov.** ≡ *Crypsis factorovskyi* Eig in Leaflet Agric. Exp. Sta. Zionist Organ. Inst. 6: 58. 1927 – **Lectotype (designated here)**: ISRAEL. Ramath-Gan near Tel-Aviv, banks of a rivulet, 21 Aug 1925, *A. Eig Fl. Pal. Exs. nr. 4* (B barcode 10-0278899 [image!]; isoelectotype: S No. G-1739 [image!]).

5. *\*Sporobolus hadjikyriakou* (Raus & H.Scholz) P.M.Peterson, **comb. nov.** ≡ *Crypsis hadjikyriakou* Raus & H.Scholz in Willdenowia 34: 457. 2004 – Holotype: CYPRUS. Central Troodos area, Almyrolivadon, margin of marshy place, 1600 m, 23 Jul 1999, *G.N. Hadjikyriakou 4721* (B barcode 10 0009595 [image!]; isotypes: B, BTU, Herb. Hadjikyriakou).

6. *\*Sporobolus minuartioides* (Bornm.) P.M.Peterson, **comb. nov.** ≡ *Torgesia minuartioides* Bornm. in Mitth. Thüring. Bot. Vereins, n.s., 30: 84. 1913 ≡ *Crypsis minuartioides* (Bornm.) Mez in Repert Spec. Nov. Regni Veg. 17: 293. 1921 ≡ *Heleochloa minuartioides* (Bornm.) Pilg. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 14d: 62. 1956 – **Lectotype (designated here)**: ISRAEL. Sarona, Aujah River, wet places, 15 m, 12 Jul 1912, *J.E. Dinsmore B1515* (B barcode 10 0367373 [image!]; isoelectotypes: B barcode 10 0367372 [image!], W No. 19160035574 [image!]).

7. *\*Sporobolus niliacus* (Fig. & De Not.) P.M.Peterson, **comb. nov.** ≡ *Crypsis niliaca* Fig. & De Not. in Mém. Acad. Roy. Sci. Turin 14: 322. 1854 – Holotype: EGYPT. In insulis niloticis Aegypti inferioris (not located).

= *Phalaris vaginiflora* Forssk., Fl. Aegypt.-Arab.: 18. 1775 ≡ *Crypsis vaginiflora* (Forssk.) Opiz, Naturalientausch 8: 83. 1823, non *Sporobolus vaginiflorus* (Torr. ex A.Gray) Alph.Wood.

8. *Sporobolus schoenoides* (L.) P.M.Peterson, **comb. nov.** ≡ *Phleum schoenoides* L., Sp. Pl.: 60. 1753 ≡ *Crypsis schoenoides* (L.) Lam., Tabl. Encycl. 1: 166, pl. 42, fig. 1. 1791 ≡ *Heleochloa schoenoides* (L.) Host, Icon. Descr. Gram. Austriac. 1: 23, pl. 30. 1801 – Lectotype (designated by Clayton in Polhill, Fl. Trop. E. Africa, Gramineae 2: 353. 1974): SPAIN. *Löfning s.n.* (LINN No. 81.7 [image!]; isoelectotype: S No. 09-36889 [image!]).

9. *\*Sporobolus turkestanicus* (Eig) P.M.Peterson, **comb. nov.** ≡ *Crypsis turkestanica* Eig in Agric. Rec. Agric. Exp. Sta., Tel Aviv. 2: 206. 1929 – Lectotype (designated by Tsvelev in Fedorov, Zlaki SSSR [Grasses of the Soviet Union]: 648.



1976): Perovskii post, Syr Darya district, Katan-Kamys demarcated area, 20 Jun 1914, *M. Spiridonov s.n.* (LE; isolectotype: LE).

***Sporobolus* subsect. *Helvoli*** P.M.Peterson, **subsect. nov.** – Type: *Sporobolus helvolus* (Trin.) T.Durand & Schinz. (≡ *Vilfa helvola* Trin.).

Decumbent, prostrate or erect perennials with rhizomes or stolons; culms 8–60 cm long. Panicles 1–12.5 cm long, 0.4–2 cm wide, contracted, spiciform to open. Spikelets 1.4–2 mm long, subterete; lemmas 1.4–2 mm long, rounded on back without a keel. Caryopses 0.5–1 mm long.

Species included: *S. helvolus*, *S. mitchellii* (Trin.) C.E.Hubb. ex S.T.Blake, and *S. ruspolianus* Chiov.

***Sporobolus* sect. *Cryptandri*** P.M.Peterson, **sect. nov.** – Type: *Sporobolus cryptandrus* (Torr.) A.Gray, Manual: 576. 1848 (≡ *Agrostis cryptandra* Torr.).

Caespitose perennials; culms 10–200 cm tall. Panicles with the lower branches usually included in the uppermost culm sheath. Spikelets 1.4–3.5(–4) mm long; lower glumes 0.5–2 mm long, 1/3 to nearly as long as the lemma; upper glumes 1.3–3.5(–4) mm long, about as long as the lemma. Caryopses ellipsoid to obovoid.

Species included: *S. cryptandrus*, *S. flexuosus* (Thurb. ex Vasey) Rydb., *S. giganteus* Nash, *S. nealleyi* Vasey, *S. texanus* Vasey

***Sporobolus* sect. *Pyramidati*** P.M.Peterson, **sect. nov.** – Type: *Sporobolus pyramidatus* (Lam.) Hitchc., Man. Grasses W. Ind.: 84. 1936 (≡ *Agrostis pyramidata* Lam.).

Caespitose annuals, biennials or perennials, sometimes rhizomatous or stoloniferous. Panicles with whorled primary branches, especially on the lower nodes. Lower glumes 1/6–1/2 (–3/4) as long as the spikelet; upper glumes 2/3 to as long as the spikelet.

***Sporobolus* subsect. *Actinocladi*** P.M.Peterson, **subsect. nov.** – Type: *Sporobolus actinocladus* (F.Muell.) F.Muell., Fragm. 8: 140. 1873 (≡ *Vilfa actinoclada* F.Muell.).

Caespitose annuals, occasionally biennial or perennial, sometimes 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 1/4–1/2. Lower glumes 1/3–2/3 as long as the spikelet; upper glumes as long as the spikelet. Caryopses 0.6–1.5 mm long, elliptic to oblong, often subterete, sometimes quadrangular or trigonous.

Species included: *S. actinocladus*, *S. australasicus* Domin, *S. caroli* Mez, \**S. contiguus* S.T.Blake, \**S. lenticularis* S.T. Blake, *S. olivaceus* Napper, *S. nitens* Stent, \**S. partimpatens* R.Mills ex B.K.Simon, *S. phleoides* Hack., \**S. pulchellus* R.Br.

***Sporobolus* subsect. *Pyramidati*** (P.M.Peterson) P.M.Peterson, **stat. nov.** Basionym: *Sporobolus* sect. *Pyramidati* P.M. Peterson in Taxon 63: 1235. 2014. [see *Sporobolus* sect. *Pyramidati* entry above]

Caespitose annuals or rhizomatous perennials; culms 7–100(–120) cm tall. 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 1/5 to nearly as long as the spikelet; upper glumes about as long as the spikelet, rarely longer. Caryopses 0.6–1.2 mm long, ellipsoid to obovoid.

Species included: *S. centrifugus* (Trin.) Nees, *S. coahuilensis* Valdés-Reyna, *S. contractus* Hitchc., *S. cordofanus* (Hochst. ex Steud.) Coss., *S. coromandelianus* (Retz.) Kunth, *S. dominicensis* (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.

***Sporobolus* subsect. *Spicati*** P.M.Peterson, **subsect. nov.** – Type: *Sporobolus spicatus* (Vahl) Kunth, Révis. Gramin. 1: 67. 1829 (≡ *Agrostis spicata* Vahl, Symb. Bot. 1: 9. 1790).

Caespitose annuals or perennials, sometimes stoloniferous. Leaf blades with pectinate-ciliate margins near the base. Panicles with whorled primary branches, especially on the lower nodes; primary branches bare below. Lower glumes <1/3 as long as the spikelet, often suppressed or lacking, the scales ovate to oblong, tiny. Caryopses 0.7–1.1 mm long, elliptic, obovate to spherical or subglobose, usually laterally flattened.

Species included: *S. microprotus* Stapf, *S. scabriflorus* Stapf ex Massey, *S. spicatus*, *S. uniglumis* Stent & J.M.Ratray.

***Sporobolus* subsect. *Subulati*** P.M.Peterson, **subsect. nov.** – Type: *Sporobolus subulatus* Hack. in J. Linn. Soc., Bot. 29: 65. 1891.

Caespitose perennials, often with stolons; culms 15–80 cm tall, sometimes tussocky. Panicles with whorled primary branches; primary branches bare on lower 1/4–1/2. Lower glumes 1/3–3/4 as long as the spikelet; upper glumes 2/3 to as long as the spikelet. Caryopses 0.8–2 mm long, ellipsoid.

Species included: *S. arabicus* Boiss., *S. kentrophyllus* (K.Schum. ex Engl.) Clayton, *S. subulatus*, *S. verdcourtii* Napper.

***Sporobolus* sect. *Spartina*** (Schreb.) P.M.Peterson & Saarela, **comb. & stat. nov.** ≡ *Spartina* Schreb., Gen. Pl.: 43. 1789 [see *Spartina* entry above in synonymy of *Sporobolus*] – Type: *Sporobolus cynosuroides* (L.) P.M.Peterson & Saarela (≡ *Dactylis cynosuroides* L.).

Panicles with “spikes” or multiple branches that bear two rows on two sides of a somewhat flattened, triangular rachis, superficially appearing to be one-sided.

***Sporobolus* subsect. *Alterniflori*** P.M.Peterson & Saarela, **subsect. nov.** – Type: *Sporobolus alterniflorus* (Loisel.) P.M.Peterson & Saarela (≡ *Spartina alterniflora* Loisel.).

Culms thick, fleshy and succulent, becoming brownish in age with a distinctly disagreeable odor when fresh; leaf blades smooth and glabrous. Panicles with subremote to moderately imbricate spikes. Spikelets closely imbricate; upper glumes with glabrous or pilose, sometimes hispid keels.

Species included:

1. *Sporobolus alterniflorus* (Loisel.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina alterniflora* Loisel., Fl. Gall.: 719. 1807 ≡ *Trachynotia alterniflora* (Loisel.) DC., Fl. Franç., ed. 3, 5: 279. 1815 ≡ *Spartina stricta* var. *alterniflora* (Loisel.) A.Gray, Manual, ed. 2: 552. 1856 ≡ *Spartina glabra* var. *alterniflora* (Loisel.) Merr. in Bull. Bur. Pl. Industr. U.S.D.A. 9: 9. 1902 ≡ *Spartina maritima* var. *alterniflora* (Loisel.) St.-Yves in Candollea 5: 25, 53, pl. 2, fig. 1–4. 1932 – Holotype: FRANCE. Sur les bord de l’Odo(...?), à Bayonne, dans une prairie au bout des allées marines, 20 Jun 1803, *s. coll. s.n.* (AV!).
2. *Sporobolus anglicus* (C.E.Hubb.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina anglica* C.E.Hubb. in Bot. J. Linn. Soc. 76: 364. 1978 ≡ *Spartina townsendii* var. *anglica* (C.E.Hubb.) Lambinon & Maquet, Nouv. Fl. Belgique, Luxembourg, N. France, ed. 3: 923: 1983 – Lectotype (designated by Saarela in PhytoKeys 10: 15. 2012): UNITED KINGDOM. West Sussex, Bosham, fruiging shore on mud-flats and muddy shingle, extending into water of Chichester Harbour, forming extensive masses, 17 Aug 1968, *C.E. Hubbard S.17868A, sheet II* (K barcode 000710270 [image!]; isolectotypes: K barcode 000710269 [image!], L No. 100190 [image!], S No. G-5726 [image!], US No. 2907471!).
3. *Sporobolus foliosus* (Trin.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina foliosa* Trin. in Mém. Acad. Imp. Sci. Saint-Petersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(1–2): 114. 1840 ≡ *Spartina stricta* var. *foliosa* (Trin.) Thurb. in Wilkes, U.S. Expl. Exped. 17(2): 487. 1874 – Holotype: U.S.A. California, 1831, *D. Peters s.n.* (LE; isotypes: US No. 610993! fragm. ex LE, US No. 92016! fragm.).
4. *\*Sporobolus ×longispicus* (Hauman & Parodi ex St.-Yves) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina longispica* Hauman & Parodi ex St.-Yves in Candollea 5: 27, 92. 1932 – Lectotype (designated by Parodi in a letter to A. Chase in Index to Grass Species 3: 336. 1962): ARGENTINA. Buenas Aires, Pipinas, 24 Mar 1923, *L.R. Parodi 5030* (SI; isolectotype: US No. 0092012!).
5. *Sporobolus maritimus* (Curtis) P.M.Peterson & Saarela, **comb. nov.** ≡ *Dactylis maritima* Curtis, Pract. Observ. Brit. Grasses: 51. 1787 ≡ *Spartina maritima* (Curtis) Fernald in Rhodora 18: 180. 1916 ≡ *Dactylis cynosuroides* Loefl., Iter. Hispan.: 115. 1758 ≡ *Dactylis stricta* Ait., Hort. Kew. 1: 104. 1789 ≡ *Spartina stricta* (Ait.) Roth, Neue Beytr. Bot.: 101. 1802 – Type: Unknown.
6. *Sporobolus ×townsendii* (H.Groves & J.Groves) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina ×townsendii* H.Groves & J.Groves in Rep. Bot. Exch. Club Brit Isles 1880: 37. 1881 – Holotype: ENGLAND. Mud flats, near Hythe, South Hants, 1 Sep 1879, *H.Groves s.n.* (BM barcode 001003965 [image!]; isotypes: C, K barcode 000710272 [image!], W No. 19160030795 [image!], W No. 19160030798 ex Herb.

Groves [image!], US No. 1127161! fragm. ex W, US No. 878793! fragm. ex Herb. Groves).

*Sporobolus* subsect. *Ponceletia* (Thouars) P.M.Peterson & Saarela, **comb. & stat. nov.** ≡ *Ponceletia* Thouars, Esquisse Fl. Tristan D’Acugna: 36: 1808 – Type: *Sporobolus mobberleyanus* P.M.Peterson & Saarela (≡ *Ponceletia arundinacea* Thouars).

Culms hard and slender without or with short and thick rhizomes <1.5 cm long. Panicles spike-like with closely imbricate spikes. Spikelets lanceolate and closely imbricate; upper glumes with hispid keels.

Species included:

1. *\*Sporobolus mobberleyanus* P.M.Peterson & Saarela, **nom. nov.** ≡ *Ponceletia arundinacea* Thouars, Esquisse Fl. Tristan D’Acugna: 36. 1808 ≡ *Spartina arundinacea* (Thouars) Carmich. in Trans. Linn. Soc. London 12: 504. 1819, non *Sporobolus arundinaceus* (Trin.) Kunth – Holotype: SAINT HELENA. *L.M.A. Du Petit-Thouars s.n.* (P barcode 00439484 [image!]).

The epithet commemorates David George Mobberley (1921–2007), who authored an influential monograph of *Spartina*.

2. *Sporobolus spartinus* (Trin.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Vilfa spartinae* Trin. in Mém. Acad. Imp. Sci. Saint-Petersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(1–2): 82. 1840 ≡ *Spartina spartinae* (Trin.) Merr. ex Hitchc. in Contr. U.S. Natl. Herb. 17(3): 329. 1913 – Holotype: U.S.A. Texas, *Hooker s.n.* (LE TRIN 1742.01!).

*Sporobolus* subsect. *Spartina* (Schreb.) P.M.Peterson & Saarela, **comb. & stat. nov.** ≡ *Spartina* Schreb., Gen. Pl.: 43. 1789 [see *Sporobolus* sect. *Spartina* entry above]

Culms hard, often tinged or streaked with purple; leaf blades scabrous. Panicle spikes more or less spreading, often tinged or streaked with purple. Spikelets closely imbricate; upper glumes usually with hispid keels.

Species included:

1. *Sporobolus bakeri* (Merr.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina bakeri* Merr. in Bull. Bur. Pl. Industr. U.S.D.A. 9: 14. 1902 ≡ *Spartina juncea* var. *bakeri* (Merr.) St.-Yves in Candollea 5: 27, 91, t. 9, fig. c. 1932 – Holotype: U.S.A. Florida, east shores of Lake Ola, Near Tangerene, 19 Apr 1898, *C.H. Baker 14* (US No. 81737!).
2. *Sporobolus coarctatus* (Trin.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina coarctata* Trin. in Mém. Acad. Imp. Sci. Saint-Petersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(1–2): 110. 1840 – Holotype: URUGUAY. Montivideo (LE TRIN 2056.01!) = *Spartina ciliata* Brongn. in Duperrey, Voy. Monde, Phan.: 15, t. 2. 1829, non *Sporobolus ciliatus* J.Presl.
3. *Sporobolus cynosuroides* (L.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Dactylis cynosuroides* L., Sp. Pl.: 71. 1753 ≡ *Tra-*

*chynotia cynosuroides* (L.) Michx., Fl. Bor.-Amer. 1: 64. 1803 ≡ *Paspalum cynosuroides* (L.) Brot., Fl. Lusit. 1: 83. 1804 ≡ *Limnetis cynosuroides* (L.) Rich., Syn. Pl. 1: 72. 1805 ≡ *Spartina cynosuroides* (L.) Roth, Catal. Bot. 3: 10. 1806 ≡ *Cynodon cynosuroides* (L.) Raspail in Ann. Sci. Nat., Bot. 5: 303. 1825 ≡ *Spartina polystachya* var. *cynosuroides* (L.) Kuntze, Revis. Gen. Pl.: 793. 1891 – Lectotype (designated by Hitchcock in Contr. U.S. Natl. Herb. 12: 121. 1908): U.S.A. Virginia, *D. Clayton 577* (LINN No. 90.1 [image!]; isolectotypes: BM barcode 000051633 [image!], US No. A865636! fragm.).

4. *Sporobolus densiflorus* (Brongn.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina densiflora* Brongn. in Duperrey, Voy. Monde, Phan.: 14. 1829 – Holotype: CHILE. Concepcion, *D'Urville s.n.* (P No. 02243277!; isotype: US No. 2018! fragm. ex P & photo).

= *Spartina montevidensis* Arechav. in Anales Mus. Nac. Montevideo 1: 378, t. 43. 1896.

5. *Sporobolus ×eatonianus* P.M.Peterson & Saarela, **nom. nov.** ≡ *Spartina ×caespitosa* A.A.Eaton in Bull. Torrey Bot. Club 25: 338. 1898 ≡ *Spartina patens* var. *caespitosa* (A.A.Eaton) Hitchc. in Rhodora 8(95): 210. 1906, non *Sporobolus caespitosus* Kunth – Lectotype (designated by McDonnell & Crow in Rhodora 81: 125. 1979): U.S.A. New Hampshire, Hampton Falls, 26 Aug 1896, *A.A. Eaton 501* (NEBC barcode 00104543 [image!]).

The epithet commemorates Alvah Augustus Eaton (1865–1908), who originally described the species.

6. *Sporobolus hookerianus* P.M.Peterson & Saarela, **nom. nov.** ≡ *Spartina gracilis* Trin. in Mém. Acad. Imp. Sci. Saint-Petersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 6,4(1–2): 110. 1840, non *Sporobolus gracilis* (Trin.) Merr. – Holotype: CANADA. North America, *Hooker s.n.* (LE TRIN 2058.01!; isotype: US No. 0092014! fragm. ex LE). The epithet commemorates Sir William Jackson Hooker (1785–1865), who collected the type.

7. *Sporobolus michauxianus* (Hitchc.) P.M.Peterson & Saarela, **comb. nov.** ≡ *Trachynotia cynosuroides* Michx., Fl. Bor.-Amer. 1: 64. 1803 ≡ *Spartina michauxiana* Hitchc. in Contr. U.S. Natl. Herb. 12: 153. 1908 – Holotype: U.S.A. Illinois, hauteurs des terres, *Michaux s.n.* (P-MICH). = *Spartina pectinata* Link, Jahrb. Gewächsk. 1(3): 92–93. 1820, non *Sporobolus pectinatus* Hack.

8. *Sporobolus pumilus* (Roth) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina pumila* Roth, Catal. Bot. 3: 10. 1806 – Holotype: U.S.A. New York, habitat prope, 1794, *J.C.D. Schreber s.n.* (B barcode 10 0367393 [image!] ex Herb. Roth).

= *Spartina patens* (Aiton) Muhl., Descr. Gram.: 55. 1817 ≡ *Dactylis patens* Aiton, Hort. Kew. 1: 104. 1789, non *Sporobolus patens* Swallen.

9. \**Sporobolus versicolor* (Fabre) P.M.Peterson & Saarela, **comb. nov.** ≡ *Spartina versicolor* Fabre in Ann. Sci. Nat., Bot., ser. 3, 13: 183, pl. 3. 1849 – Holotype: Unknown.

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#### Appendix 1. List of specimens sampled.

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

**OUTGROUP:** *Aristida gypsophila* Beetle, Peterson 15839 & Valdés-Reyna (US), Mexico, GU359977, GU359386, GU360286, GU360570, GU359267; *Chasmanthium latifolium* (Michx.) H.O.Yates, Peterson 22463 (US), U.S.A., GU359891, GU359379, GU360438, GU360517, GU359319; *Danthonia compressa* Austin, Peterson 21986 & Levine (US), U.S.A., GU359865, GU359370, GU360483, GU360521, GU359345; *Capeochloa cincta* subsp. *sericea* (N.P.Barker) N.P.Barker & H.P.Linder, Barker 1545 (GRA), South Africa, JF729173, JF729163, JF729181, JF729074, –, *Rytidosperma pallidum* (R.Br.) A.M.Humphreys & H.P.Linder, Peterson 19685, Saarela & Sears (US), U.S.A., GU359984, GU359518, GU360291, GU360671, GU359183; **CENTROPODIEAE:** \**Ellisochloa rangei* (Pilg.) P.M.Peterson & N.P.Barker, Barker 960 (BOL), Namibia, –, JF729166, JF729184, JF729079, JQ345167; **TRIRAPHIDEAE:** *Neyraudia reynaudiana* (Kunth) Keng ex Hitchcock, Soreng 5318 & Peterson (US), China, GU360003, GU359397, GU360272, –, GU359124; \**Triraphis mollis* R.Br., Peterson 14344, Soreng & Rosenberg (US), Australia, GU359933, GU359539, GU360336, GU360669, GU359187; **ERAGROSTIDEAE:** \**Cottea pappophoroides* Kunth, Peterson 21463, Soreng, LaTorre & Rojas Fox (US), Peru, GU359842, GU359363, GU360456, GU360600, GU359237; *Ectrosia scabrata* C.E.Hubb., Lazarides 4772 (US), Australia, GU359799, GU359476, GU360459, GU360497, GU359317; *Enneapogon desvauxii* P.Beauv., Peterson 21999 & Saarela (US), Mexico, GU359796, GU359474, GU360486, GU360495, GU359339; *Entoplocamia aristulata* (Hack. & Rendle) Stapf, Seydel 187 (US), South Africa, GU359793, GU359469, GU360468, GU360492, GU359342; *Eragrostis desertorum* Domin, Peterson 14358, Soreng & Rosenberg (US), Australia, GU359787, GU359471, GU360462, GU360545, GU359289; *Harpachne harpachnoides* (Hack.) B.S.Sun & S.Wang, Soreng 5288, Peterson & Sun Hang (US), China, GU359815, GU359435, GU360382, GU360611, GU359113; *Pogonarthria squarrosa* (Roem. & Schult.) Pilg., Mawi 180, Majengo, Salum & Samwe (MO), Tanzania, **KM010693**, **KM010534**, **KM010918**, **KM011121**, **KM010325**; \**Psammagrostis wiseana* C.A.Gardner & C.E.Hubb., Peterson 14345, Soreng & Rosenberg (US), Australia, GU359986, GU359533, GU360288, GU360703, GU359137; *Schmidtia pappophoroides* Steud. ex J.A.Schmidt, Smook 10558 (MO), South Africa, **KM010697**, **KM010537**, **KM010921**, **KM011124**, **KM010328**; *Tetrachne dregei* Nees, Jarman 120 (US), South Africa, GU359904, GU359513, GU360365, GU360622, GU359218; *Uniola condensata* Hitchc., Peterson 9342 & Judziewicz (US), Ecuador, GU359927, GU359534, GU360340, GU360649, GU359191; **CYNODONTEAE:** *Pogononeura biflora* Napper, Greenway 10091 (US), Tanzania, **KM010694**, –, –, –, **Triopogoninae:** *Eragrostiella leioptera* (Stapf) Bor, Chand 7961 (US), India, GU359827, GU359486, JQ345280, GU360529, GU359305; *Melanococcyris abyssinica* (R.Br. ex Fresen.) Hochst., DeWilde 6912 (MO), Ethiopia, JQ345355, JQ345228, JQ345310, JQ345268, JQ345198; *Oropetium capense* Stapf, Venter 9939 & Venter (MO), South Africa, **KM010692**, **KM010533**, **KM010917**, **KM011120**, **KM010324**; *Triopogon multiflorus* Miré & H.Gillet, Spellenberg 7441 (MO), Yemen, JQ345360, JQ345232, JQ345315, JQ345274, JQ345204; **Eleusininae:** *Chloris barbata* Sw., Peterson 22255 & Saarela (US), Mexico, GU359873, GU359377, GU360435, GU360514, GU359320; *Cynodon plectostachyus* (K.Schum.) Pilg., Troupin 11610 (US), Rwanda, GU359890, GU359356, GU360449, GU360592, GU359247; *Eleusine indica* (L.) Gaertn., Peterson 21362, Saarela & Flores Villegas (US), Mexico, GU359797, GU359473, GU360472, GU360496, GU359338; **Gymnopogoninae:** *Gymnopogon grandiflorus* Roseng., B.R.Arill. & Izag., Peterson 16642 & Refugio-Rodriguez (US), Peru, GU359816, GU359436, GU360383, GU360581, GU359200; \**Lepitotrium rigidum* Kunth, Davids 3281 (MO), Jamaica, KF827662, KF827596, KF827727, KF827794, KF827541; **ZOYSIEAE, Sporobolinae:** *Calamovilfa arcuata* K.E.Rogers, Rogers 42409, Sharp & Delgadillo (US), U.S.A., **KM010683**, **KM010528**, **KM010912**, **KM011110**, **KM010315**; *Calamovilfa brevipilis* (Torr.) Hack. ex Scribn. & Southw., Strong 848, Kelloff, Schuyler, Wurdack & Churchill (US), U.S.A., **KM010684**, –, –, **KM011111**, **KM010316**; *Calamovilfa curtisii* (Vasey) Scribn., Curtis 5729 (US), U.S.A., –, –, –, **KM011112**, –, *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., Gates 17021 (US), U.S.A., **KM010685**, **KM010529**, **KM010913**, **KM011113**, **KM010317**; *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., Long 1124 (BRY), U.S.A., **KM010686**, **KM010530**, **KM010914**, **KM011114**, **KM010318**; *Calamovilfa gigantea* (Nutt.) Scribn. & Merr., Ungor 1018 (US), U.S.A., **KM010687**, **KM010531**, **KM010915**, **KM011115**, **KM010319**; *Calamovilfa longifolia* (Hook.) Hack. ex Scribn. & Southw., Hatch 5738 & Bearden (US), U.S.A., GU359880, GU359357, GU360441, GU360548, GU359300; \**Crypsis aculeata* (L.) Aiton, Soreng 5469 & Peterson (US), China, GU359841, GU359362, GU360402, GU360599, GU359238; \**Crypsis aculeata* (L.) Aiton, Soreng 7940, Johnson, Johnson, Dzyubenko, Dzyubenko & Schilnikov (US), Russia, JQ345316, JQ345205, JQ345275, JQ345163; *Crypsis alopecuroides* (Piller & Mitterp.) Schrad., Soreng 7941, Johnson, Johnson, Dzyubenko & Schilnikov (US), Russia, **KM010688**, **KM010532**, **KM010916**, **KM011116**, **KM010320**; *Crypsis schoenoides* (L.) Lam., Peterson 19814, Saarela & Sears (US), U.S.A., GU359840, GU359361, GU360455, GU360598, GU359239; *Eragrostis megalosperma* F.Muell. ex Benth., Blake 6966 (US), Australia, **KM010689**, –, –, **KM011117**, **KM010321**; *Eragrostis megalosperma* F.Muell. ex Benth., Lazarides 4215 (US), Australia, **KM010690**, –, –, **KM011118**, **KM010322**; *Eragrostis megalosperma* F.Muell. ex Benth., Lazarides 5647 (US), Australia, **KM010691**, –, –, **KM011119**, **KM010323**; *Psilolemma jaegeri* (Pilg.) S.M.Phillips, Peterson 24247, Soreng & Romaschenko (US), Tanzania, **KM010695**, **KM010535**, **KM010919**, **KM011122**, **KM010326**; *Psilolemma jaegeri* (Pilg.) S.M.Phillips, Peterson 24249, Soreng & Romaschenko (US), Tanzania, **KM010696**, **KM010536**, **KM010920**, **KM011123**, **KM010327**; *Spartina ×townsendii* H.Groves & J.Groves, Hubbard 12 (US), United Kingdom, **KM010698**, –, –, **KM011125**, –, *Spartina ×townsendii* H.Groves & J.Groves, Saarela 791 & Percy (UBC), Canada, **KM010699**, **KM010538**, **KM010922**, **KM011126**, **KM010329**; *Spartina alterniflora* Loisel., Lakela 26573 (US), U.S.A., **KM010700**, **KM010539**, **KM010923**, **KM011127**, **KM010330**; *Spartina alterniflora* Loisel., Naylov 236 (US), U.S.A., **KM010701**, **KM010540**, **KM010924**, **KM011128**, **KM010331**; *Spartina anglica* C.E.Hubb., Matthews s.n. (CAN), United Kingdom, **KM010702**, **KM010541**, **KM010925**, **KM011129**, **KM010332**; *Spartina anglica* C.E.Hubb., Williams 2004-1 (UBC), Canada, **KM010703**, **KM010542**, **KM010926**, **KM011130**, **KM010333**; *Spartina anglica* C.E.Hubb., Williams 2004-2 (UBC), Canada, **KM010704**, **KM010543**, **KM010927**, **KM011131**, **KM010334**; *Spartina bakeri* Merr., Killip 44361 (US), U.S.A., **KM010705**, **KM010544**, **KM010928**, **KM011132**, **KM010335**; *Spartina ×caespitosa* A.A.Eaton, Eaton 587 (US), U.S.A., **KM010706**, –, –, **KM011133**, **KM010336**; *Spartina ciliata* Brongn., Rambo 56450 (US), Brazil, **KM010707**, –, **KM010929**, **KM011134**, **KM010337**; \**Spartina cynosuroides* (L.) Roth, Fisher 33123 (US), U.S.A., **KM010708**, **KM010545**, **KM010930**, **KM011135**, **KM010338**; \**Spartina cynosuroides* (L.) Roth, Hill 15630 (US), U.S.A., **KM010709**, **KM010546**, **KM010931**, **KM011136**, **KM010339**; *Spartina densiflora* Brongn., Lomer 5723 (UBC), Canada, **KM010710**, **KM010547**, **KM010932**, **KM011137**, **KM010340**; *Spartina densiflora* Brongn., Peterson 19154, Soreng, Salarido & Panizza (US), Argentina, GU359916, GU359510, GU360352, JQ345271, GU359206; *Spartina foliosa* Trin., Reeder 6652 & Reeder (US), Mexico, **KM010711**, **KM010548**, **KM010933**, **KM011138**, **KM010341**; *Spartina gracilis* Trin., Hendrickson 41 (USZ), U.S.A., **KM010712**, **KM010549**, **KM010934**, **KM011139**, **KM010342**;



## Appendix 1. Continued.

*Spartina gracilis* Trin., *Lewis 78-1013* (CAN), Canada, **KM010713, KM010550, KM010935, KM011140, KM010343**; *Spartina gracilis* Trin., *Scoggan 15626* (CAN), Canada, **KM010714, KM010551, KM010936, KM011141, KM010344**; *Spartina maritima* (Curtis) Fernald, *Fernández Casas 5537, Castroviejo, Muñoz Garmendia & Susanna* (US), Morocco, **KM010715, KM010552, KM010937, KM011142, KM010345**; *Spartina maritima* (Curtis) Fernald, *Marchant s.n.* (UBC), United Kingdom, **KM010716, –, KM010938, KM011143, –**; *Spartina montevidensis* Arechav., *Clayton 4723 & Eiten* (US), Brazil, **KM010717, KM010553, KM010939, KM011144, KM010346**; *Spartina montevidensis* Arechav., *Rosengurt 10853* (US), Uruguay, **KM010718, –, –, KM011145, –**; *Spartina patens* (Aiton) Muhl., *Dutton 2536* (CAN), U.S.A., **KM010719, KM010554, KM010940, KM011146, KM010347**; *Spartina patens* (Aiton) Muhl., *Peterson 24435, Romaschenko & Knapp* (US), U.S.A., **KM010720, –, KM010941, KM011147, KM010348**; *Spartina patens* (Aiton) Muhl., *Shchepanek 6426 & Dugal* (CAN), Canada, **KM010721, KM010555, KM010942, KM011148, KM010349**; *Spartina pectinata* Link, *Cooperrider s.n.* (US), U.S.A., **KM010722, KM010556, KM010943, KM011149, KM010350**; *Spartina pectinata* Link, *Dirig 2812* (US), U.S.A., **KM010723, KM010557, KM010944, KM011150, KM010351**; *Spartina spartinae* (Trin.) Merr. ex Hitchc., *Reeder 4568 & C. Reeder* (US), Mexico, **KM010724, KM010558, KM010945, KM011151, KM010352**; *Spartina spartinae* (Trin.) Merr. ex Hitchc., *Villarreal 3201* (US), Mexico, **KM010725, KM010559, KM010946, KM011152, KM010353**; *Sporobolus acinifolius* Stapf, *Smook 10167* (US), South Africa, **KM010726, –, –, –**; *Sporobolus acinifolius* Stapf, *Smook 3530* (US), South Africa, **KM010727, KM010560, KM010947, KM011153, KM010354**; *Sporobolus actinocladius* (F.Muell.) F.Muell., *Batjanoff 0411164* (MEL), Australia, **KM010728, KM010561, KM010948, KM011154, KM010355**; *Sporobolus actinocladius* (F.Muell.) F.Muell., *Saarela 1625, Peterson & Soreng* (US), Australia, **KM010729, KM010562, KM010949, –, KM010356**; *Sporobolus actinocladius* (F.Muell.) F.Muell., *Saarela 1670, Peterson & Soreng* (US), Australia, **KM010730, KM010563, KM010950, KM011155, KM010357**; *Sporobolus actinocladius* (F.Muell.) F.Muell., *Senaratne E6082-5* (US), Australia, **KM010731, KM010564, KM010951, KM011156, KM010358**; *Sporobolus acuminatus* (Trin.) Hack., *Guala 1372 & Filgueiras* (US), Brazil, **KM010732, KM010565, KM010952, KM011157, KM010359**; *Sporobolus acuminatus* (Trin.) Hack., *Irwin 11586, Souza & Reis dos Santos* (US), Brazil, **KM010733, KM010566, KM010953, KM011158, KM010360**; *Sporobolus aeneus* (Trin.) Kunth, *Irwin 25327, Onishi, da Fonseca, Souza, Reis dos Santos & Ramos* (US), Brazil, **KM010734, –, KM010954, KM011159, KM010361**; *Sporobolus africanus* (Poir.) Robyns & Tournay, *Peterson 24024, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010735, KM010567, KM010955, KM011160, KM010362**; *Sporobolus africanus* (Poir.) Robyns & Tournay, *Peterson 24121, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010736, KM010568, KM010956, KM011161, KM010363**; *Sporobolus agrostoides* Chiov., *Semsei 2806* (US), Tanzania, **KM010792, –, –, –**; *Sporobolus airoides* (Torr.) Torr., *Peterson 10002, Annable & Valdés-Reyna* (US), Mexico, **KM010737, KM010569, KM010957, KM011162, KM010364**; *Sporobolus airoides* subsp. *airoides*, *Peterson 24587 & Romaschenko* (US), Mexico, **KM010738, KM010570, KM010958, KM011163, KM010365**; *Sporobolus airoides* subsp. *airoides*, *Peterson 24853 & Romaschenko* (US), Mexico, **KM010739, KM010571, KM010959, KM011164, KM010366**; *Sporobolus airoides* (Torr.) Torr., *Peterson 24895 & Romaschenko* (US), Mexico, **KM010740, KM010572, KM010960, KM011165, KM010367**; *Sporobolus airoides* (Torr.) Torr., *Peterson 24956 & Romaschenko* (US), Mexico, **KM010741, KM010573, KM010961, KM011166, KM010368**; *Sporobolus albicans* Nees, *Smook 2459 & Russell* (US), South Africa, **KM010742, –, –, –, KM010369**; *Sporobolus albicans* Nees, *Smook 6270* (US), South Africa, **KM010743, –, –, –**; *Sporobolus aldbarensis* Renvoize, *Fosberg 48867* (US), Seychelles, **KM010744, –, –, –**; *Sporobolus apiculatus* Boechat & Longhi-Wagner, *Irwin 8041, Souza & Reis dos Santos* (US), Brazil, **–, –, KM010962, KM011167, KM010370**; *Sporobolus arabicus* Boiss., *Rawi 10781, Jalili & Armer* (US), Kuwait, **–, –, KM010963, –, KM010371**; *Sporobolus atrovirens* (Kunth) Kunth, *Peterson 22342 & Saarela* (US), Mexico, **GU359915, GU359508, GU360315, GU360632, GU359207**; *Sporobolus atrovirens* (Kunth) Kunth, *Peterson 24661 & Romaschenko* (US), Mexico, **KM010746, KM010575, KM010964, KM011169, KM010373**; *Sporobolus atrovirens* (Kunth) Kunth, *Peterson 24729 & Romaschenko* (US), Mexico, **KM010747, KM010576, KM010965, KM011170, KM010374**; *Sporobolus atrovirens* (Kunth) Kunth, *Rosalen 3381 & Herrera* (CIIDIR), Mexico, **KM010748, KM010577, KM010966, KM011171, KM010375**; *Sporobolus australasicus* Domin, *Peterson 14404, Soreng & Rosenberg* (US), Australia, **KM010749, KM010578, KM010967, KM011172, KM010376**; *Sporobolus australasicus* Domin, *Walsh 4237* (MEL), Australia, **KM010750, KM010579, KM010968, KM011173, KM010377**; *Sporobolus berterianus* (Trin.) Hitchc. & Chase, *Peterson 8753, Annable & Poston* (US), Ecuador, **KM010751, –, –, KM011174, KM010378**; *Sporobolus blakei* De Nardi ex B.K.Simon, *Latz 10662* (MEL), Australia, **KM010752, KM010580, KM010969, KM011175, KM010379**; *Sporobolus bogotensis* Swallen & Garcia-Barr., *Peterson 14970 & Refulio Rodriguez* (US), Peru, **KM010753, –, KM010970, KM011176, KM010380**; *Sporobolus brockmanii* Stapf, *Gillet 4016* (US), Somalia, **KM010754, KM010581, KM010971, KM011177, KM010381**; *Sporobolus buckleyi* Vasey, *Lira 546, Martinez, Alvarez, Ramirez, Medrod & Gamboa* (CIIDIR), Mexico, **KM010755, KM010582, KM010972, KM011178, KM010382**; *Sporobolus buckleyi* Vasey, *Piedra s.n.* (CIIDIR), Mexico, **KM010756, –, KM010973, KM011179, KM010383**; *Sporobolus buckleyi* Vasey, *Rodriguez 94 & Villareal* (CIIDIR), Mexico, **KM010757, KM010583, KM010974, KM011180, KM010384**; *Sporobolus caroli* Mez, *Saarela 1626, Peterson & Soreng* (US), Australia, **KM010759, KM010584, KM010976, KM011182, KM010386**; *Sporobolus caroli* Mez, *Speak 1915* (US), Australia, **KM010760, KM010585, KM010977, KM011183, KM010980, KM010982, KM011188, KM010391**; *Sporobolus centrifugus* (Trin.) Nees, *Hoener 2133* (US), South Africa, **KM010761, KM010586, KM010978, KM011184, KM010388**; *Sporobolus clandestinus* (Biehler) Hitchc., *Freeman 6687* (US), U.S.A., **KM010762, KM010587, KM010979, KM011185, KM010389**; *Sporobolus clandestinus* (Biehler) Hitchc., *Peterson 24422, Romaschenko & Knapp* (US), U.S.A., **KM010763, –, KM010980, KM011186, –**; *Sporobolus clandestinus* (Biehler) Hitchc., *Schuster 197* (US), U.S.A., **KM010764, KM010588, KM010981, KM011187, KM010390**; *Sporobolus clandestinus* (Biehler) Hitchc., *Waterfall 12309* (US), U.S.A., **KM010765, KM010589, KM010982, KM011188, KM010391**; *Sporobolus clandestinus* (Biehler) Hitchc., *Waterfall 5881* (US), U.S.A., **KM010758, –, KM010975, KM011181, KM010385**; *Sporobolus coahuilensis* Valdés-Reyna, *Gonzales 3600* (CIIDIR), Mexico, **KM010766, KM010590, KM010983, KM011189, KM010392**; *Sporobolus coahuilensis* Valdés-Reyna, *Peterson 10000 & Annable* (US), Mexico, **KM010767, KM010591, KM010984, KM011190, KM010393**; *Sporobolus compositus* (Poir.) Merr., *Brodowicz 1305* (US), U.S.A., **KM010745, KM010574, –, KM011168, KM010372**; *Sporobolus confinis* (Steud.) Chiov., *Peterson 24303, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010768, KM010592, KM010985, KM011191, KM010394**; *Sporobolus conrathii* (Conrath & Hack.) Chiov., *Smook 1444* (US), South Africa, **KM010769, KM010593, –, –, –**; *Sporobolus consimilis* Fresen., *Collenette 17* (US), Somalia, **KM010770, KM010594, KM010986, KM011192, KM010395**; *Sporobolus consimilis* Fresen., *Peterson 24252, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010771, KM010595, KM010987, KM011193, KM010396**; *Sporobolus contractus* Hitchc., *Perez 196* (US), Mexico, **KM010772, –, KM010988, KM011194, KM010397**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Greenway 10191* (US), Tanzania, **KM010773, –, –, –, KM010398**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Laegaard 15973* (US), Zimbabwe, **KM010774, KM010596, KM010989, KM011195, KM010399**; *Sporobolus cordofanus* (Hochst. ex Steud.) Coss., *Peterson 24232, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010775, KM010597, KM010990, KM011196, KM010400**; *Sporobolus coromandelianus* (Retz.) Kunth, *Fosberg 51193, Mueller-Dombois, Wirawan, Cooray & Balakrishnan* (US), Sri Lanka, **KM010776, –, KM010991, KM011197, KM010401**; *Sporobolus coromandelianus* (Retz.) Kunth, *Peterson 24269, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010777, KM010598, KM010992, KM011198, KM010402**; *Sporobolus coromandelianus* (Retz.) Kunth, *Schweinfurth 896 & Nil* (US), Ethiopia, **KM010778, KM010599, KM010993, KM011199, KM010403**; *Sporobolus creber* De Nardi, *Brown 498* (MEL), Australia, **KM010779, KM010600, KM010994, KM011200, KM010404**; *Sporobolus cryptandrus* (Torr.) A.Gray, *Peterson 24454, Romaschenko & Valdés-Reyna* (US), Mexico, **KM010780, KM010601, KM010995, KM011201, KM010405**; *Sporobolus cryptandrus* (Torr.) A.Gray, *Peterson 24485 & Romaschenko* (US), Mexico, **KM010781, KM010602, KM010996, KM011202, KM010406**; *Sporobolus diandrus* (Retz.) P.Beauv., *Peterson 14389, Soreng & Rosenberg* (US), Australia, **KM010782, KM010603, KM010997, KM011203, KM010407**; *Sporobolus diffusus* Clayton, *Lovett 2179, Handy & Bygott* (DSM), Tanzania, **KM010783, –, –, KM011204, KM010408**; *Sporobolus dinklagei* Mez, *Hale II* (US), Liberia, **KM010784, KM010604, KM010998, –, KM010409**; *Sporobolus domingensis* (Trin.) Kunth, *Swallen 10669* (US), U.S.A., **KM010785, KM010605, KM010999, KM011205, KM010410**; *Sporobolus elongatus* R.Br., *Balansa 896* (US), New Caledonia, **KM010786, –, –, –, –**; *Sporobolus eylesii* Stent & J.M.Rattray, *Wiche 717* (US), Malawi, **KM010787, –, KM011000, –, KM010411**; *Sporobolus farinosus* Hosok., *Wood 3275 & Perlman* (US), Guam, **KM010788, KM010606, KM011001, KM011206, KM010412**; *Sporobolus fertilis* (Steud.) Clayton, *Gould 13535* (US), Sri Lanka, **KM010789, KM010607, KM011002, KM011207, KM010413**; *Sporobolus fertilis* (Steud.) Clayton, *Raulerson 775* (US), Guam, **KM010790, –, KM011003, KM011208, KM010414**; *Sporobolus festivus* Hochst. ex A.Rich., *Peterson 23853, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010791, –, –, –, –**

## Appendix 1. Continued.

**KM010608, KM011004, KM011209, KM010415;** *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24206, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010793, KM010609, KM011005, KM011210, KM010416;** *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24241, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010794, KM010610, KM011006, KM011211, KM010417;** *Sporobolus fimbriatus* (Trin.) Nees, *Peterson 24280, Soreng, Romaschenko & Mbago* (US), Tanzania, –, **KM010611, KM011007, KM011212, KM010418;** *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb., *Reeder 5477 & Reeder* (US), U.S.A., **KM010795, –, KM011008, KM011213, KM010419;** *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb., *Valdés-Reyna 2014 & Peterson* (CIIDIR), Mexico, **KM010796, KM010612, KM011009, KM011214, KM010420;** *Sporobolus floridanus* Chapm., *Curtiss s.n.* (US), U.S.A., **KM010797, –, –, –, –;** *Sporobolus floridanus* Chapm., *Harper s.n.* (US), U.S.A., **KM010798, –, –, –, –;** *Sporobolus giganteus* Nash, *Page 2628* (US), U.S.A., **KM010800, –, KM011011, KM011216, KM010422;** *Sporobolus greenwayi* Napper, *Greenway 12526* (US), Tanzania, **KM010801, KM010614, KM011012, –, KM010423;** *Sporobolus helvolus* (Trin.) T.Durand & Schinz, *Laegaard 17063 & Traore* (US), Senegal, **KM010802, –, KM011013, KM011217, KM010424;** *Sporobolus helvolus* (Trin.) T.Durand & Schinz, *Peterson 24217, Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010803, KM010615, KM011014, KM011218, KM010425;** *Sporobolus heterolepis* (A.Gray) A.Gray, *Davidse 19101* (US), U.S.A., **KM010804, –, KM011015, KM011219, KM010426;** *Sporobolus humilis* subsp. *humilis* Veldkamp, *Clayton 5879* (US), Sri Lanka, **KM010805, KM010616, KM011016, KM011220, KM010427;** \**Sporobolus indicus* (L.) R.Br., *Peterson 22025 & Saarela* (US), Mexico, GU359913, GU359504, GU360355, GU360630, GU359209; \**Sporobolus indicus* (L.) R.Br., *Peterson 7337 & Annable* (US), Panama, **KM010806, KM010617, KM011017, KM011221, KM010428;** *Sporobolus infirmus* Mez, *Haines 332* (US), Nigeria, **KM010807, KM010618, KM011018, KM011222, KM010429;** *Sporobolus ioclados* (Nees ex Trin.) Nees, *Smook 5920* (US), South Africa, **KM010808, KM010619, KM011019, KM011223, KM010430;** *Sporobolus jacquemontii* Kunth, *Estrada 18964* (CIIDIR), Mexico, **KM010809, KM010620, KM011020, KM011224, KM010431;** *Sporobolus jacquemontii* Kunth, *Peterson 15902 & Valdés-Reyna* (US), Mexico, **KM010810, KM010621, KM011021, KM011225, KM010432;** *Sporobolus junceus* (P.Beauv.) Kunth, *Strong 2332* (US), U.S.A., **KM010811, KM010622, KM011022, KM011226, KM010433;** *Sporobolus junceus* (P.Beauv.) Kunth, *Thieret 25181* (US), U.S.A., **KM010812, KM010623, KM011023, KM011227, KM010434;** *Sporobolus kentrophyllus* (K.Schum. ex Engl.) Clayton, *Bogdan 3306* (US), Kenya, **KM010813, KM010624, KM011024, KM011228, KM010435;** *Sporobolus kentrophyllus* (K.Schum. ex Engl.) Clayton, *Mwasumbi 13049* (DSM), Tanzania, **KM010814, –, KM011025, KM011229, KM010436;** *Sporobolus lasiophyllus* Pilg., *Peterson 21820 & Soreng* (US), Peru, **KM010815, KM010625, KM011026, KM011230, KM010437;** *Sporobolus lasiophyllus* Pilg., *Peterson 21870 & Soreng* (US), Peru, **KM010816, –, KM011027, KM011231, –;** *Sporobolus lasiophyllus* Pilg., *Peterson 21879, Soreng & Sanchez Vega* (US), Peru, GU359912, GU359505, GU360356, GU360629, GU359210; *Sporobolus laxus* B.K.Simon, *Simon 4166* (MEL), Australia, **KM010817, KM010626, KM011028, KM011232, KM010438;** *Sporobolus linearifolius* Nicora, *Reitz 5292* (US), Brazil, **KM010818, –, KM011029, –, KM010439;** *Sporobolus ludwigii* Hochst., *Smook 2857* (US), South Africa, **KM010819, KM010627, KM011030, KM011233, KM010440;** *Sporobolus macrospermus* Scribn. ex Beal, *Peterson 9857 & Annable* (US), Mexico, **KM010820, –, KM011031, KM011234, –;** *Sporobolus maderaspatanus* Bor., *Davidse 8220 & Sumithraarachi* (US), Sri Lanka, **KM010821, –, –, –, –;** *Sporobolus marginatus* Hochst. ex A.Rich., *Leippert 5101* (US), Uganda, **KM010822, –, KM011032, –, KM010441;** *Sporobolus marginatus* Hochst. ex A.Rich., *Rattray 664* (US), Zimbabwe, **KM010823, KM010628, KM011033, –, KM010442;** *Sporobolus micranthus* (Steud.) T.Durand & Schinz, *Brain 3370* (US), Zimbabwe, –, –, **KM011034, –, –;** *Sporobolus microprotus* Stapf, *Laegaard 17894 & Traore* (US), Senegal, **KM010824, KM010629, KM011035, KM011235, KM010443;** *Sporobolus mildbraedii* Pilg., *Milne-Redhead 8570 & Taylor* (US), Tanzania, **KM010825, –, –, –, –;** *Sporobolus mitchellii* (Trin.) C.E.Hubb. ex S.T.Blake, *Forster 22301* (MEL), Australia, **KM010826, –, –, KM011236, KM010444;** *Sporobolus molleri* Hack., *Gereau 5790, Mbago & Kayombo* (DSM), Tanzania, **KM010827, –, –, KM011237, KM010445;** *Sporobolus molleri* Hack., *Rwaburindore 2183* (US), Uganda, **KM010828, –, –, KM011238, KM010446;** *Sporobolus montanus* (Hook.f.) Engl., *Dusen 420* (US), Cameroon, **KM010829, KM010630, KM011036, –, KM010447;** *Sporobolus myrianthus* Benth., *Gereau 3491, Lovett & Kayombo* (DSM), Tanzania, **KM010830, –, –, KM011239, KM010448;** *Sporobolus natalensis* (Steud.) T.Durand & Schinz, *Eddie 1141* (MEL), Australia, **KM010831, KM010631, KM011037, KM011240, KM010449;** *Sporobolus nealleyi* Vasey, *Correll 18548 & Johnston* (US), U.S.A., **KM010832, –, KM011038, KM011241, –;** *Sporobolus nealleyi* Vasey, *Peterson 17839, Valdés-Reyna & Hinton* (US), Mexico, **KM010833, KM010632, KM011039, KM011242, KM010450;** *Sporobolus nealleyi* Vasey, *Villarreal 1991, Carranza & Valdez* (CIIDIR), Mexico, **KM010834, –, KM011040, KM011243, KM010451;** *Sporobolus neglectus* Nash, *Theodore 5890 & Cochrane* (US), U.S.A., **KM010835, –, KM011041, KM011244, KM010452;** *Sporobolus nervosus* Hochst., *Wood 2021* (US), Yemen, **KM010836, KM010633, KM010642, KM011042, KM011245, KM010453;** *Sporobolus nitens* Stent, *Laegaard 15893* (US), Zimbabwe, **KM010837, KM010634, KM011043, KM011246, KM010454;** *Sporobolus olivaceus* Napper, *Ash 2921* (US), Ethiopia, **KM010838, –, –, –, –;** *Sporobolus oxylepsis* Mez, *Schlieben 6158* (US), Tanzania, **KM010839, –, KM011044, –, KM010455;** *Sporobolus palmeri* Scribn., *Peterson 24862 & Romaschenko* (US), Mexico, **KM010841, KM010636, KM011046, KM011248, KM010457;** *Sporobolus palmeri* Scribn., *Peterson 24918 & Romaschenko* (US), Mexico, **KM010842, KM010637, KM011047, KM011249, KM010458;** *Sporobolus palmeri* Scribn., *Peterson 24955a & Romaschenko* (USZ), Mexico, **KM010843, KM010638, KM011048, KM011250, KM010459;** *Sporobolus palmeri* Scribn., *Peterson 24955b & Romaschenko* (US), Mexico, **KM010844, KM010639, KM011049, KM011251, KM010460;** *Sporobolus panicoides* A.Rich., *Biggood 1005, Mwasumbi & Vollesen* (DSM), Tanzania, **KM010845, –, –, –, –;** *Sporobolus panicoides* A.Rich., *Smook 9865* (US), South Africa, **KM010846, KM010640, KM011050, –, KM010461;** *Sporobolus pectinellus* Mez, *Fay 7131* (US), Central African Republic, **KM010847, –, KM011051, –, KM010462;** *Sporobolus pectinellus* Mez, *Peterson 23978, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010848, KM010641, KM011052, KM011252, KM010463;** *Sporobolus pellucidus* Hochst., *Fitzgerald 5226* (US), Tanzania, **KM010849, –, KM011053, –, KM010464;** *Sporobolus phleoides* Hack., *Venturi 2039* (US), Argentina, **KM010850, –, KM011054, KM011253, KM010465;** *Sporobolus phyllotrichus* Hochst., *Greenway 11844 & Kanuri* (US), Tanzania, **KM010851, –, KM011055, –, KM010466;** *Sporobolus piliferus* (Trin.) Kunth, *Peterson 24012, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010852, KM010642, KM011056, KM011254, KM010467;** *Sporobolus pinetorum* Weakley & P.M.Peterson, *Peterson 14233, Weakley & LeBlond* (US), U.S.A., GU359911, GU359506, GU360358, **KM011255, GU359211;** *Sporobolus pseudairoides* Parodi, *Wasum 2670* (US), Brazil, **KM010853, –, KM011057, KM011256, KM010468;** *Sporobolus pungens* (Schreb.) Kunth, *Durandi s.n.* (US), Spain, –, –, –, **KM010469;** *Sporobolus pungens* (Schreb.) Kunth, *Zohary 489 & Amdursky* (US), Israel, **KM010854, KM010643, KM011058, KM011257, KM010470;** *Sporobolus purpurascens* (Sw.) Ham., *Peterson 9453 & Judziewicz* (US), Ecuador, **KM010855, KM010644, KM011059, KM011258, KM010471;** *Sporobolus purpurascens* (Sw.) Ham., *Swallen 10179* (US), U.S.A., **KM010856, KM010645, KM011060, KM011259, KM010472;** *Sporobolus purpurascens* (Sw.) Ham., *Trouart 25* (US), U.S.A., **KM010857, –, KM011061, KM011260, KM010473;** *Sporobolus pyramidalis* P.Beauv., *Peterson 24150, Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010858, KM010646, KM011062, KM011261, KM010474;** *Sporobolus pyramidalis* P.Beauv., *Senaratne E6082-11* (US), Australia, **KM010859, KM010647, KM011063, KM011262, KM010475;** *Sporobolus pyramidalis* (Lam.) Hitchc., *Garcia 3757* (CIIDIR), Mexico, **KM010860, –, KM011064, KM011263, KM010476;** *Sporobolus pyramidalis* (Lam.) Hitchc., *Gooding 191-45* (US), U.S.A., –, –, **KM011264, KM010477;** *Sporobolus pyramidalis* (Lam.) Hitchc., *Peterson 18994, González-Elizondo, Carter, Rosen, Guaglianone & Torres Soto* (US), Mexico, **KM010861, KM010648, KM011065, KM011265, KM010478;** *Sporobolus pyramidalis* (Lam.) Hitchc., *Peterson 21163, Saarela, Rosen & Reid* (US), Mexico, GU359910, GU359507, GU360359, GU360628, GU359228; *Sporobolus pyramidalis* (Lam.) Hitchc., *Peterson 24868 & Romaschenko* (US), Mexico, **KM010862, KM010649, KM011066, KM011266, KM010479;** *Sporobolus pyramidalis* (Lam.) Hitchc., *Peterson 8920, Annable & Poston* (US), Ecuador, **KM010863, –, KM011067, KM011267, KM010480;** *Sporobolus rigens* (Trin.) Desv., *Peterson 19224, Soreng, Salariado & Panizza* (US), Argentina, GU359909, GU359517, GU360360, GU360627, GU359213; *Sporobolus robustus* Kunth, *Laegaard 17398, Goudiaby, Madesn, Samba & Traore* (US), Senegal, **KM010864, KM010650, KM011068, KM011268, KM010481;** *Sporobolus ruspolianus* Chiov., *Bally 15581 & Melville* (DSM), Somalia, **KM010865, –, KM011069, KM011269, KM010482;** *Sporobolus ruspolianus* Chiov., *Flemming 2136* (US), Somalia, **KM010866, KM010651, KM011070, KM011270, KM010483;** *Sporobolus ruspolianus* Chiov., *McKinnon s.n.* (US), Somalia, **KM010799, KM010613, KM011010, KM011215, KM010421;** *Sporobolus sanguineus* Rendle, *Biggood 2397, Mbago & Vollesen* (DSM), Tanzania, **KM010867, –, –, KM011271, KM010484;** *Sporobolus sanguineus* Rendle, *Gereau 6014, Mbago, Kayombo & Lyanga* (DSM), Tanzania, **KM010868, –, –, KM011272, KM010485;** *Sporobolus scabridus* S.T.Blake, *Forster 20462* (MEL), Australia, **KM010869, KM010652, KM011071, KM011273, KM010486;** *Sporobolus scabriflorus* Stapf



## Appendix 1. Continued.

ex Massey, *Troupin 1319* (US), Congo (Kinshasa) Dem. Rep., **KM010870**, –, **KM011072**, –, **KM010487**; *Sporobolus sessilis* B.K.Simon, *Senaratne E6095-1* (US), Australia, **KM010871**, **KM010653**, **KM011073**, **KM011274**, **KM010488**; *Sporobolus silveanus* Swallen, *Waller 3128 & Bauml* (US), U.S.A., **KM010872**, –, **KM011074**, **KM011275**, **KM010489**; *Sporobolus smutsii* Stent, *Oakes 1454* (US), South Africa, –, –, –, **KM010490**; *Sporobolus somalensis* Chiov., *Boalev 317* (US), Somalia, **KM010873**, **KM010654**, **KM011075**, –, **KM010491**; *Sporobolus somalensis* Chiov., *Herruming 2022* (US), Somalia, **KM010874**, **KM010655**, **KM011076**, –, **KM010492**; *Sporobolus spicatus* (Vahl) Kunth, *Baldini s.n.* (US), Oman, **KM010875**, **KM010656**, **KM011077**, **KM011276**, **KM010493**; *Sporobolus spicatus* (Vahl) Kunth, *Laegaard 17790 & Traore* (US), Senegal, **KM010876**, **KM010657**, **KM011078**, **KM011277**, **KM010494**; *Sporobolus spicatus* (Vahl) Kunth, *Peterson 24055*, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010877**, **KM010658**, **KM011079**, **KM011278**, **KM010495**; *Sporobolus spicatus* (Vahl) Kunth, *Peterson 24230*, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010878**, **KM010659**, **KM011080**, **KM011279**, **KM010496**; *Sporobolus spiciformis* Swallen, *Garcia 2638* (CHDIR), Mexico, **KM010879**, **KM010660**, **KM011081**, **KM011280**, **KM010497**; *Sporobolus spiciformis* Swallen, *Garcia 2814* (CHDIR), Mexico, **KM010880**, **KM010661**, **KM011082**, **KM011281**, **KM010498**; *Sporobolus splendens* Swallen, *King 1687* (US), Mexico, **KM010881**, **KM010662**, **KM011083**, **KM011282**, **KM010499**; *Sporobolus stapfianus* Gand., *Laegaard 15939* (US), Zimbabwe, **KM010882**, –, **KM011084**, **KM011283**, **KM010500**; *Sporobolus stolzii* Mez, *Peterson 23946*, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010883**, **KM010663**, **KM011085**, **KM011284**, **KM010501**; *Sporobolus stolzii* Mez, *Peterson 24133*, *Soreng, Romaschenko & Abeid* (US), Tanzania, –, **KM010664**, **KM011086**, **KM011285**, **KM010502**; *Sporobolus stolzii* Mez, *Richards 21377* (US), Zambia, **KM010884**, **KM010665**, **KM011087**, **KM011286**, **KM010503**; *Sporobolus subglobosus* Stapf ex C.E.Hubb., *Gambaga 581* (US), Ghana, **KM010885**, –, **KM011088**, –, **KM010504**; *Sporobolus subulatus* Hack., *Peterson 24317*, *Soreng, Romaschenko & Mbago* (US), Tanzania, **KM010886**, **KM010666**, **KM011089**, **KM011287**, **KM010505**; *Sporobolus tenacissimus* (L.f.) P.Beauv., *Rusby 55* (US), Bolivia, –, –, –, **KM010506**; *Sporobolus tenellus* (Spreng.) Kunth, *Smook 2874* (US), South Africa, **KM010887**, **KM010667**, **KM011090**, –, **KM010507**; *Sporobolus tenuissimus* (Mart. ex Schrank) Kuntze, *Greenway 1745* (US), Tanzania, **KM010888**, **KM010668**, –, **KM011288**, –, *Sporobolus tenuissimus* (Mart. ex Schrank) Kuntze, *Peterson 9523 & Judziewicz* (US), Ecuador, **KM010889**, **KM010669**, **KM011091**, **KM011289**, **KM010508**; *Sporobolus teretifolius* R.M.Harper, *McDonald 9988* (US), U.S.A., **KM010890**, **KM010670**, **KM011092**, **KM011290**, **KM010509**; *Sporobolus teretifolius* R.M.Harper, *Peterson 14232*, *Weakley & LeBlond* (US), U.S.A., GU359908, GU359509, GU360376, GU360626, GU359199; *Sporobolus texanus* Vasey, *Churchill 2645 & Kaul* (US), U.S.A., **KM010891**, **KM010671**, **KM011093**, **KM011291**, **KM010510**; *Sporobolus tourneuxii* Coss., *Adam 19416* (US), Mauritania, **KM010892**, **KM010672**, **KM011094**, **KM011292**, **KM010511**; *Sporobolus trichodes* Hitchc., *Rzedowski 39901* (CHDIR), Mexico, **KM010893**, **KM010673**, **KM011095**, **KM011293**, **KM010512**; *Sporobolus uniglumis* Stent & J.M.Rattray, *Robinson 48* (US), Zambia, **KM010894**, –, **KM011096**, –, **KM010513**; *Sporobolus vaginiflorus* (Torr. ex A.Gray) Alph.Wood, *Peterson 24441*, *Romaschenko & Knapp* (US), U.S.A., **KM010895**, –, **KM011097**, **KM011294**, –, *Sporobolus vaginiflorus* (Torr. ex A.Gray) Alph.Wood, *Rogers 40059* (US), U.S.A., **KM010896**, –, **KM011098**, **KM011295**, **KM010514**; *Sporobolus vaginiflorus* (Torr. ex A.Gray) Alph.Wood, *Wherry s.n.* (US), U.S.A., **KM010897**, –, **KM011099**, **KM011296**, **KM010515**; *Sporobolus vaginiflorus* var. *ozarkanus* Fernald, *Riggins 481* (US), U.S.A., **KM010840**, **KM010635**, **KM011045**, **KM011247**, **KM010456**; *Sporobolus verdcourtii* Napper, *Vesey-Fitzgerald 5336* (US), Kenya, **KM010898**, **KM010674**, **KM011100**, **KM011297**, **KM010516**; *Sporobolus virginicus* (L.) Kunth, *Peterson 14311*, *Soreng, Rosenberg & Macfarlane* (US), Australia, **KM010899**, **KM010675**, **KM011101**, **KM011298**, **KM010517**; *Sporobolus virginicus* (L.) Kunth, *Peterson 15683 & Soreng* (US), Chile, GU359892, GU359502, GU360362, GU360610, GU359215; *Sporobolus virginicus* (L.) Kunth, *Peterson 23820*, *Soreng, Romaschenko & Abeid* (US), Tanzania, **KM010900**, –, **KM011102**, **KM011299**, **KM010518**; *Sporobolus virginicus* (L.) Kunth, *Whistler 6132* (US), Polynesia, **KM010901**, **KM010676**, **KM011103**, **KM011300**, **KM010519**; *Sporobolus wrightii* Munro ex Scribn., *Peterson 10638 & Annable* (US), Mexico, **KM010902**, **KM010677**, **KM011104**, **KM011301**, **KM010520**; *Sporobolus wrightii* Munro ex Scribn., *Peterson 19841 & Lara-Contreras* (US), Mexico, GU359906, GU359511, GU360348, GU360624, GU359216; *Sporobolus wrightii* Munro ex Scribn., *Peterson 24841 & Romaschenko* (US), Mexico, **KM010903**, **KM010678**, **KM011105**, **KM011302**, **KM010521**; *Thellungia advena* Stapf, *Belson 1930* (US), Australia, **KM010904**, –, –, **KM011303**, **KM010522**; *Thellungia advena* Stapf, *Lazarides 4185* (US), Australia, **KM010905**, –, –, **KM011304**, **KM010523**; *Zoysiinae: Urochondra setulosa* (Trin.) C.E.Hubb., *Bailey 10868* (US), Somalia, **KM010906**, **KM010679**, **KM011106**, **KM011305**, **KM010524**; *Urochondra setulosa* (Trin.) C.E.Hubb., *Baldini s.n.* (US), Oman, **KM010907**, **KM010680**, **KM011107**, **KM011306**, **KM010525**; *Urochondra setulosa* (Trin.) C.E.Hubb., *Inckennon 181* (US), Somalia, **KM010908**, **KM010681**, **KM011108**, **KM011307**, **KM010526**; *Urochondra setulosa* (Trin.) C.E.Hubb., *Rechinger 27496* (US), Pakistan, **KM010909**, **KM010682**, **KM011109**, **KM011308**, **KM010527**; *Zoysia japonica* Steud., *Kuragadake s.n.* (US), Japan, GU359923, GU359547, –, GU360643, GU359196; *Zoysia macrantha* subsp. *walshii* M.E.Nightingale, *Loch 435* (US), Australia, GU359922, GU359548, GU360345, GU360642, GU359197; *Zoysia macrantha* Desv., *Soreng 5913 & Peterson* (US), Australia, GU360017, GU359558, GU360346, GU360641, GU359142; *Zoysia pacifica* (Goudswaard) M.Hotta & Kuroki, *Lorence 7651* (US), U.S.A.Hawaii, **KM010910**, –, –, –, *Zoysia pacifica* (Goudswaard) M.Hotta & Kuroki, *Lorence 9432 & Flynn* (US), Kiribati, **KM010911**, –, –, –,